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NOTE

Sea otter (*Enhydra lutris*) abundance assessment for the Kuril Island population in Far Eastern Russia

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The distribution and habitat use by a species can be influenced by a number of factors, including availability of resources, ecological space (shelter, individual range, etc.), the presence of other species (predators and/or competitors), human disturbance, and cultural preferences (Friedlaender et al., 2006; Hauser, Logsdon, Holmes, VanBlaricom & Osborne, 2007; Sergio, Marchesi & Pedrini, 2004; Willems & Hill, 2009). In cases where a species has been driven to near extinction through anthropogenic interference, recolonization of the former range can happen unevenly. Some areas may not be recolonized, even though they provide suitable habitat (Kenyon, 1969). Understanding which factors influence the distribution of a species allows us to assess the species' ecological potential (its capacity to utilize available habitat under current environmental conditions) in certain environments and to evaluate the level of change that it can tolerate.

Sea otters (*Enhydra lutris* L.) are a keystone species of temperate coastal ecosystems (Estes, Heithaus, McCauley, Rasher & Worm, 2016). The species abundance was substantially depleted as a result of devastating hunting pressure during the fur trade of the 18th and 19th centuries (Bodkin, 2015; Kenyon, 1969). Some populations have recovered successfully, others have not recovered, and some recovered but have subsequently declined again (Bodkin, 2015; Doroff, Estes, Tinker, Burn & Evans, 2003; Esslinger & Bodkin, 2009). Sea otters in Russian waters belong to the Asian subspecies (*E. lutris lutris* L.) and include two recognized populations, one around the Commander Islands and another around the Kuril Islands and Kamchatka (Wilson, Bogan, Brownell, Burdin & Maminov, 1991). It is likely that there is little, if any, mixing between the populations because the Commander Islands are separated from the Kamchatka mainland by 200 km of open sea (Barabash-Nikiforov, 1947; Wilson et al., 1991).

After a century of unregulated commercial hunting in the 18th and 19th centuries (Bodkin, 2015; Kenyon, 1969), by 1913 Kuril Island population numbers were estimated to have been reduced to about 200–7,750 sea otters (Barabash-Nikiforov, 1947). The Kamchatka portion of this population, due to its proximity to humans, was depleted even earlier, soon after its discovery, and by the end of the 19th century sea otters were no longer observed there (Barabash-Nikiforov, 1947).

Russian sea otter populations currently comprise about 13% of the total species abundance globally and are considered to have recovered from the detrimental effects of fur-trade-era hunting (Bodkin, 2015; Kornev, 2010a). Both the Commander Islands and Kuril-Kamchatka populations appeared to have reached the point of maximum abundance in the first decade of the 2000s and then seemingly started to decline (Kornev, 2010a; Mamaev, 2016; Zagrebelniy, 2014). Around the Commander Islands, sea otters reached what was believed to be carrying capacity by the late 1980s and generally have remained at these levels since, reaching maximum numbers in 2007 (Zagrebelniy, 2010, 2014). Occasional monitoring efforts and an analysis of mortality indicated that the number of sea otters in the Commander Islands population fluctuated between 4,000 and 6,500 for at least couple of decades (Zagrebelniy, 2014). However, a more recent study has reported that numbers at the Commander Islands might be declining. The 2015 survey found fewer than 3,300 animals (including pups) around both islands (Mamaev, 2016).

By 1963, the Kuril-Kamchatka population was estimated at

3,000–3,500 animals. In 1970, Shitikov (1971) reported it to be about 5,000 animals, with a comment that it was likely to be at equilibrium density. However, other authors suggested that the islands were likely to be able to sustain up to 10,000 animals or more (Klumov, 1968 as cited in Shitikov, 1971). Shitikov (1971) also mentioned that the highest concentrations were observed around Urup and Paramushir Islands. A 2003 study reported an unusually high number of sea otters around Paramushir and Shumshu Islands (15,447 animals), bringing total abundance around the Kuril Islands to a posthunting maximum of 20,768 sea otters (Kornev & Korneva, 2006). According to the authors, density near Shumshu Island was 2.6 times higher than the proposed “optimal” level based on data from the Commander Islands (Kornev & Korneva, 2006). Subsequent surveys did not cover the entire Kuril chain but indicated a sharp decline, with numbers at Paramushir and Shumshu Islands dropping 64%, from 15,447 in 2003 to 5,534 in 2008–2009 (Kornev, 2010a). The extremely high estimates of Kornev & Korneva (2006) from 2003 have been questioned by some researchers, and their methodology was not clearly explained in their paper. However, the same authors produced the 2008–2009 abundance estimate, presumably using the same methods, so even if their numbers are not a reliable indicator of absolute abundance, they are likely sufficient to indicate a trend. Accounts from local residents and other anecdotal evidence also suggest that a decline in the Northern Kurils is occurring (Sakhalin.Info, 2017). Considering that the Northern Kurils have historically been known to contain the greatest portion of the Kuril-Kamchatka population, this reduction in numbers, if substantiated, is of concern for the population and the subspecies as a whole (Kornev 2010a; Shitikov, 1971). However, because of its remoteness, the Kuril-Kamchatka population, especially south of Paramushir Island, has not been systematically monitored.

In this study, we provide additional data to assess the population trend of the Kuril population of sea otters based on results of our 2012 survey of sea otters around the Kuril Islands.

In May 2012, we conducted a survey along the Kuril Islands chain south of the Second Kuril Strait. A separate expedition to the Northern Kurils occurred in September 2012. We conducted small boat surveys along randomly chosen portions of the coastline of the Kuril Islands in each geographical region (Northern, Middle, and Southern Kurils; see Figure 1). Counts were conducted both on the Pacific and the Sea of Okhotsk sides using two 6-m inflatable boats with at least two experienced observers (who have had previous experience in sea otter observations) and 2–4 volunteers for better coverage. Boats travelled simultaneously parallel to the shore and to each other. The first boat followed the coastline about 100 m offshore (depending on the extent of the kelp forest), and observers counted only those sea otters between the boat and the shore, including those hauled out on reefs. The second boat followed a parallel course about 200 m further offshore, counting offshore and between the two boats. Although skiff surveys are typically conducted using only one boat (Burn, 1994, Doroff et al., 2003), using two boats provided more coverage and increased our capacity to spot animals further offshore in areas with extensive shallow waters, which are common in the Kuril Islands. To ensure that the same sea otters were not counted by both boats in cases where there was a group of animals on the border of the counting areas, we coordinated by VHF radio which boat team would record the sighting. It has been reported that boat counts can underestimate the number of sea otters by up to 30% due to animals fleeing upon approach of the boat (Udevitz, Bodkin & Costa, 1995). Aerial surveys have been used to provide a correction coefficient for boat-based counts (Doroff et al., 2003), but the expense and practical difficulties of conducting aerial surveys in the Kuril Islands prevented us from using this method. Udevitz et al. (1995) suggested conducting ground-based counts from a high vantage point simultaneously with boat counts to account for possible bias. We attempted to develop a correction coefficient using simultaneous ground-based and boat-based counts, but due to weather and logistical challenges arising from local topography and the inaccessibility of appropriate vantage points, we were able to conduct only three simultaneous counts. These counts were an insufficient basis for the development of a correction coefficient, so we used uncorrected boat counts as the basis for our analysis. The high level of uncertainty in the data is reflected in the broad confidence interval of our resulting estimate.

For the purposes of data analysis, we divided the Kuril Island chain into four geographic regions based on biologically meaningful locations in relation to sea otter distribution: Southern Kurils, Urup Island, Central Kurils, and Northern Kurils (Figure 1). Southern Kurils included the Lesser Kuril Chain, Kunashir, and Iturup Islands. Central Kurils included all islands between Urup and Paramushir. Northern Kurils included Paramushir, Shumshu, and nearby outlying islands. As our survey did not cover any areas further north than Shumshu Island, we do not have direct count data for the First Kuril Strait (between Kamchatka Peninsula and Shumshu Island) and Southern Kamchatka.

Sea otters depend heavily on coastal benthic invertebrates and have been shown to feed within depths typically not exceeding 50 m (Bodkin, Esslinger & Monson, 2004; Esslinger, Esler, Howlin & Starcevich, 2015; Kenyon, 1969). Within this depth range, females tend to use shallower average depths, whereas males, which are unconstrained by the diving abilities of pups, use deeper average depths (Laidre, Jameson, Gurarie, Jeffries & Allen, 2009; Rechsteiner et al. 2019; Thometz et al., 2016). Because dives deeper than 50 m are relatively rare, we estimated sea otter presence only within the potentially productive shallow water area inshore of the 50-m isobath.

We used a general additive linear model framework to evaluate the relationship between sea otter presence, sea otter number, and explanatory variables in order to generate estimated numbers and distribution of sea otters for unsurveyed sections based on the parameters these areas shared with the surveyed sections. Since our survey covered areas with high numbers of sea otters, as well as unoccupied territories that appeared to provide suitable habitat, we used our data to model sea otter distribution over the entire unsurveyed area of the Kuril chain. We created polygons by connecting the 50-m isobath with the coastline for the length of the survey sectors. Each of the surveyed sectors was approximately 20 km in length. The 50-m isobath was defined using a high-resolution chart, “The General Bathymetric Chart of the Oceans” (GEBCO, 2014). We then incorporated the parameters of habitat assigned to these polygons into a generalized additive model.

In this study, we mainly focused on physical parameters of the habitat to assess its suitability for sea otters. While prey availability is likely the most important determinant of sea otter distribution, abiotic factors also play an important role (Stewart, Konar & Doroff, 2014; Tarjan & Tinker, 2016). As is often the case for large or remote areas inhabited by sea otters, prey survey data are not available for the Kuril chain. In the absence of such data, physical qualities of the coastline, bottom profile, and benthic substrate have been used to predict the abundance and distribution of sea otters (Gregr, Nichol, Watson, Ford & Ellis, 2008; Laidre, Jameson & DeMaster, 2001). Sea otters prefer areas with complex, long coastlines with reefs, rocky outcrops, sheltered bays, and kelp forests (Barabash-Nikiforov, 1947; Gregr et al., 2008; Kenyon, 1969; Shitikov, 1971). We evaluated the influence of coastline complexity on sea otter abundance by calculating a fractal dimension index (FDI) (Burrough, 1986) for each polygon, where FDI = 2*log(Perimeter)/log(Area). FDI approaches 1 for shapes with very simple perimeters such as rectangles and approaches 2 for shapes with highly complex, plane-filling perimeters (e.g., habitat sections with tortuous coastlines, complex bathymetry and many offshore islets) (U.S. Fish and Wildlife Service Alaska

Region, 2015). To quantify the extent of the shallow area, we calculated the average shortest distance from the shore to the 50-m isobath for each of the sections. The geographic position of each section was assigned using the latitude and longitude of the polygon center. We used the total area of the sector as a covariate, as well as exposure to either the Pacific Ocean or the Sea of Okhotsk side.

Model fitting was performed in R statistical computing environment (R Core Team, 2017) using the “mgcv” package (Wood, 2017). Generalized additive model fits were performed using the quadratically penalized likelihood approach with Tweedie exponential distribution. For model specifications and parameters, see Figures S1a,b and S2.

The spatial distribution of sea otters was uneven. High numbers of sea otters were present in the Northern Kurils and fewer in the Central Kurils. Urup Island also had a large number of sea otters, which dropped again in the Southern Kurils (Figure 2).

The largest concentration of sea otters (66.6% of the total, Table 1) was found around northern Paramushir and Shumshu

Islands (Figure 2). The next most populated area was around Urup Island (13.23% of the total, Table 1). Sea otter numbers were consistently high around the entire island, which made it the second most important area for sea otters in the Kuril Island archipelago after the Second Kuril Strait and the main stronghold for the southern part of the population. The distribution of sea otter numbers was very different between different regions, as seen in Table 1.

The total abundance for the Kuril chain was estimated at 6,010 (4,492–11,314 CI 95%, Table 1). As noted, Southern Kamchatka was not included in our analysis, so to arrive at a total estimate for the entire Kuril-Kamchatka population, we added an estimate for that area based on existing literature. Over the past decade, approximately 1,500 otters have been surveyed there relatively consistently, so for comparison with historical data, this number was added to the total estimate (Kornev, 2010a; Zavadskaya, Nikolaeva, Sazhina, Shpilenok & Shuvalova, 2017). The comparison of our estimates of abundance with historical data is shown in Table 2.

Data from our survey show that sea otters are most abundant in only a few locations in the Kuril Islands, such as in the Second Kuril Strait (between Paramushir and Shumshu Islands) and around Urup Island (Table 1). These findings align with historical data, which indicate these areas were the most abundant in sea otters (Barabash-Nikiforov, 1947; Kornev, 2010b; Shitikov, 1971). Our analysis presents a new estimate of the numbers and distribution of the Kuril-Kamchatka sea otter population based on parameters that are available for remote and data-deficient locations in the Russian Far East.

Despite differences in methodology, our surveys revealed similar sea otter distribution patterns around the islands as have previous studies. The uneven distribution of sea otters along the Kuril chain that we detected is similar to what is described in post fur trade literature (Barabash-Nikiforov, 1947; Kornev, 2010b; Shitikov, 1971). Our data are consistent with a possible decline in the Kuril Islands and indicate that the Northern Kurils and Urup Island continue to be critically important areas for this sea otter population. Large areas of seemingly suitable habitat remain scarcely inhabited by this population. However, it remains unclear whether this pattern is the result of biological constraints on recolonization after years of unsustainable harvesting or other factors. Preharvesting records are scarce and lacking in detail, and it is difficult to evaluate what the distribution was before intense hunting took place in the region (Barabash-Nikiforov, 1947; Kenyon, 1969). Sea otters are known to have relatively small and well-defined home ranges, on the order of tens of kilometers, which may limit the ability of a recovering population to expand into new areas. This is particularly the case for adult females, the drivers of intrinsic population growth, which are known to have smaller average home range sizes than males and to make long-distance movements only very rarely (Garshelis & Garshelis, 1984; Ralls, Eagle & Siniff, 1996; Tinker, Doak & Estes, 2008; Tinker et al., 2017, 2019). Kenyon (1969) noted that sea otters are so conservative in their fidelity to their home range that they choose to remain in overpopulated areas for some time, even when areas of suitable habitat are available nearby. In light of these behavioral characteristics of sea otters, it is possible that areas of optimal habitat (the Northern Kurils and Urup Island) were not densely populated long enough for the excess population to fully expand into the adjacent territory before the population stopped increasing.

The Middle Kuril Islands may present a natural obstacle for north-to-south movement of sea otters because they are a chain of small islands with relatively little shallow-water foraging area that also provide poor protection from the elements. These factors might impede exchange between the northern and southern parts of the population, but they are unlikely to prevent animals from moving across altogether. Average distances between small groups of islands in this area are 20–30 km, and the distance between Urup and Iturup Islands is 40 km. These crossing distances are feasible for sea otters, not only males, but also potentially for juvenile/subadult females and adult females (Barabash-Nikiforov, 1947, Kenyon, 1969, Ralls et al., 1996). It is likely that if the population of Urup Island remained stable for a sufficiently long time, numbers in the Southern Kurils would also increase.

Given the possibility of a population decline, we recommend additional surveys. Several factors that could potentially influence abundance should also be evaluated. Sea otters may have exceeded carrying capacity in some areas, but no significant increases have been observed in the areas adjacent to the areas of maximum abundance (Zavadskaya et al., 2017), as would be expected under this scenario. Killer whale predation has been reported for other populations (Doroff et al., 2003; Estes, Tinker, Williams & Doak, 1998), but the presence of the mammal-eating ecotype of killer whales along the Kuril Island chain is very limited (Filatova et al., 2019). Anthropogenic activities and habitat changes driven by environmental and climatic conditions are more likely influences. There are currently fishing and marine traffic exclusion zones to protect marine mammals in various parts of the Kuril Islands, including Paramushir, Shumshu and Urup Islands, which prohibit fishing using any type of gear except set seine nets within 2–22 nautical miles (3.7-22 km) off the coast (Kornev, Antonov, & Buslov, 2007). However, the enforcement of these rules is lacking in remote areas. Another possible factor is poaching, which is likely to be present in Russian waters according to anecdotal reports, but no statistics on its extent are available. Finally, changing climatic conditions may be altering the availability of prey for sea otters. Additional research is needed to confirm whether a decline is occurring and, if so, to evaluate its potential causes.

The Northern Kurils and Urup Island remain critical population centers from which sea otter range expansion could occur, and these areas should be strictly protected. However, neither the Northern Kurils nor Urup Island have any protection measures besides the marine exclusion zones indicated above. Despite proposed plans by the Russian government to make Urup Island a Federal Protected Area, this decision was not finalized. Instead, a gold mining operation using liquid cyanides was established on the island, creating high levels of industrial activity that could lead to significant damage to this important habitat.

The current status of sea otters in the Kuril Islands is uncertain. A better understanding of sea otter population dynamics in the Kuril Islands is necessary to protect the population from threats. At a minimum, future research should include regular monitoring of the population and its prey base and an assessment of possible anthropogenic impacts on sea otters in the region. Foraging studies and the retrieval/necropsy of stranded carcasses would help to clarify the factors driving population trends. We recommend implementing measures for sea otter protection, such as designating and enforcing protected areas and issuing regulations to restrict the activities of extractive operations that may harm marine life in the region.

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REFERENCES

Barabash-Nikiforov, N. I. (1947). *Sea otter* (Enhydra lutris L.), *its biology and management issues*. Moscow, Russia: Moskva.

Bodkin, J. L. (2015). Historic and contemporary status of sea otters. In Shawn E. Larson, James L. Bodkin, Glenn R. VanBlaricom (Eds.), *Sea otter conservation* (pp. 43–61). Boston, MA: Academic Press.

Bodkin, J. L., Esslinger, G. G., & Monson, D. H. (2004). Foraging depths of sea otters and implications to coastal marine communities. *Marine Mammal Science*, *20*, 305–321.

Burn, D. M. (1994). Boat-based population surveys of sea otters in Prince William Sound. In T. R. Loughlin (Ed.), *Marine mammals and the* Exxon Valdez (pp. 61–80). San Diego, CA: Academic Press.

Burrough, P. A. (1986). *Principles of geographical information systems for land resources assessment*. Monographs on Soil and Resources Survey No. 12. Oxford, UK: Clarendon Press.

Doroff, A. M., Estes, J. A., Tinker, M. T., Burn, D. M., & Evans, T. J. (2003). Sea otter population declines in the Aleutian archipelago. *Journal of Mammalogy*, *84*, 55–64.

Esslinger, G. G. and Bodkin, J. L. (2009). *Status and trends of sea otter populations in Southeast Alaska, 1969–2003* (Scientific Investigations Report 2009–5045). Reston, VA: U.S. Geological Survey.

Esslinger, G. G., Esler, D., Howlin, S., & Starcevich, L. A. (2015). *Monitoring population status of sea otters* (Enhydra lutris) *in Glacier Bay National Park and Preserve, Alaska—Options and considerations* (Open-File Report 2015-1119). Reston, VA, U.S. Geological Survey.

Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., &

Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, *41*, 83–116.

Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, *282*(5388), 473–476.

Filatova, O. A., Shpak, O. V., Ivkovich, T. V., Volkova, E. V., Fedutin, I. D., Ovsyanikova, E. N., … Hoyt, E. (2019). Large-scale habitat segregation of fish-eating and mammal-eating killer whales (*Orcinus orca*) in the western North Pacific. *Polar Biology*, *42*, 931–941.

Friedlaender, A. S., Halpin, P. N., Qian, S. S., Lawson, G. L., Wiebe, P. H., Thiele, D., & Read, A. J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series*, *317*, 297–310.

Garshelis, D. L., & Garshelis, J. A. (1984). Movements and management of sea otters in Alaska. *Journal of Wildlife*

Management, *48*, 665–678.

GEBCO. (2014). *GEBCO 30 arc-second global grid of elevations*. Retrieved from http://www.gebco.net

Gregr, E. J., Nichol, L. M., Watson, J. C., Ford, J. K. B., & Ellis, G. M. (2008). Estimating carrying capacity for sea otters in British Columbia. *Journal of Wildlife Management 72*, 382–388.

Hauser, D., Logsdon, M., Holmes, E., Vanblaricom, G., & Osborne, R. (2007). Summer distribution patterns of southern resident killer whales (*Orcinus orca*): Core areas and spatial segregation of social groups. *Marine Ecology Progress Series 351*, 301–310.

Kenyon, K. W. (1969). The sea otter in the Eastern Pacific Ocean. *North American Fauna*, *68*, 1–352.

Kornev, S. I. (2010a). The present status of sea otter (*Enhydra lutris*) population in Russian part of areal. *Research of Aquatic Biological Resources of Kamchatka and Northwest of Pacific Ocean*, *19*, 6–24.

Kornev, S. I. (2010b). *Present status of sea otter (*Enhydra lutris) *populations in north Kurile and Commander Islands* *basing on factor of density per habitat.* Paper presented at the Sixth International Conference Marine Mammals of the Holarctic, Kaliningrad, Russia.

Kornev, S. I., Antonov, N. P. and Buslov, A. V. (2007). To a problem of relationships of a coastal fishery and preservation sea otter, other marine mammalian for Northern Kuril Islands. *Problems of Fisheries*, *8*(3(31)), 407–417.

Kornev, S. I. and Korneva, S. M. (2004). *Population dynamics and present status of sea otters* (Enhydra lutris) *of the Kuril Islands and Southern Kamchatka.* Paper presented at the Third International Conference Marine Mammals of the Holarctic, Koktebel, Ukraine.

Kornev, S. I., & Korneva, S. M. (2006). Some criteria of asessment of condition and dynamics of population of sea otters (*Enhydra lutris*) in the Russian part of the range. *Ecologiya*, *3*, 190–198.

Laidre, K. L., Jameson, R. J., & Demaster, D. P. (2001). An estimation of carrying capacity for sea otters along the California coast. *Marine Mammal Science*, *17*, 294–309.

Laidre, K. L., Jameson, R. J., Gurarie, E., Jeffries, S. J., &

Allen, H. (2009). Spatial habitat use patterns of sea otters in coastal Washington. *Journal of Mammalogy*, *90*, 906–917.

Mamaev, E. G. 2016. *Present status of the sea otter (Enhydra lutris L.) population on the Commander Islands*. Paper presented at the Marine Mammals of the Holarctic International Conference, Astrakhan, Russia.

R Core Team (2017). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Ralls, K., Eagle, T. C., & Siniff, D. B. (1996). Movement and spatial use patterns of California sea otters. *Canadian Journal of Zoology*, *74*, 1841–1849.

Rechsteiner, E. U., Watson, J. C., Tinker, M. T., Nichol, L. M., Morgan Henderson, M. J., Mcmillan, C. J., … Darimont, C. T. (2019). Sex and occupation time influence niche space of a recovering keystone predator. *Ecology and Evolution*, *9*, 3321–3334.

Sakhalin.Info. (2017). *Population of sea otters in the Northern Kuril Islands has declined by 73% in the last five years* [in Russian]. Retrieved from https://sakhalin.info/news/134879.

Sergio, F., Marchesi, L. and Pedrini, P. (2004). Integrating individual habitat choices and regional distribution of a biodiversity indicator and top predator. *Journal of Biogeography*, *31*, 619–628.

Shitikov, A. M. (1971). Influence of the trophic factor on the distribution of sea otters on the middle and northern Kuril Islands. *Works of VNIRO-TINRO "Marine Mammals"*, *80*, 227–239.

Stewart, N., Konar, B., & Doroff, A. (2014). Sea otter (*Enhydra lutris*) foraging habitat use in a heterogeneous environment in Kachemak Bay off Alaska. *Bulletin of Marine Science*, *90*, 921–939.

Tarjan, L. M., & Tinker, M. T. (2016). Permissible home range estimation (PHRE) in restricted habitats: A new algorithm and an evaluation for sea otters. *PLoS ONE*, *11*(3), 1–20.

Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. B., & Tinker, M. T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology*, *27*, 1552–1566.

Tinker, M. T., Doak, D. F., & Estes, J. A. (2008). Using demography and movement behavior to predict range expansion of the southern sea otter. *Ecological Applications*, *18*, 1781–1794.

Tinker, M. T., Tomoleoni, J., Laroche, N., Bowen, L., Miles, A. K., Murray, M., … Randell, Z. (2017). *Southern sea otter range expansion and habitat use in the Santa Barbara Channel, California* (Open-File Report2017–1001). Reston, VA: U.S. Geological Survey.

Tinker, M. T., Tomoleoni, J. A., Weitzman, B. P., Staedler, M., Jessup, D., Murray, M. J., … Conrad, P. (2019). *Southern sea otter* (Enhydra lutris nereis) *population biology at Big Sur and Monterey, California—Investigating the consequences of resource abundance and anthropogenic stressors for sea otter recovery* (Open-File Report 2019–1022). Reston, VA: U.S. Geological Survey.

U.S. Fish and Wildlife Service Alaska Region. (2015). *Marine Mammal Survey Project: Northern sea otter* (Enhydra lutris kenyoni)—*southwest Alaska distinct population segment.* Report prepared for the US Air Force, 611th Air Support Group-Alaska Operations.

Udevitz, M. S., Bodkin, J. L. and Costa, D. P. (1995). Detection of sea otters in boat-based surveys of Prince William Sound, Alaska. *Marine Mammal Science*, *11*, 59–71.

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology*, *90*, 546–555.

Wilson, D., E., Bogan, M. A., Brownell, R. L., Jr., Burdin, A. M., & Maminov, M. K. (1991). Geographic variation in sea otters, *Enhydra lutris*. *Journal of Mammalogy*, *72*, 22–36.

Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd. ed.). Boca Raton, FL: CRC Press/Taylor & Francis Group.

Zagrebelniy, S. V. 2010. *Parameters of demography and modern status of social structure of sea otter (*Enhydra lutris*) population of the Bering Island (Commander archipelago)*. Paper presented at the Marine Mammals of the Holarctic International Conference, Kaliningrad, Russia.

Zagrebelnyi, S. V. 2014. *Short history of exploitation and restoration and assessment of current state of the Commander group of sea otters* (Enhydra lutris L.). Paper presented at the Marine Mammals of the Holarctic International Conference, St. Petersburg, Russia.

Zavadskaya, A., Nikolaeva, E., Sazhina, V., Shpilenok, T. and Shuvalova, O. (2017). *Values and Ecosystem Services of Kronockiy Reserve and Yuzhno-Kamchatskiy Sanctuary.* In S. Bobylev (ed.). Petropavlovsk-Kamchatskiy, Russia: Publishing House “Kamchatpress”.

TABLE 1 Estimated numbers and densities of sea otters for each geographic region.

Geographic region	Abundance estimates			Average density estimate		
	Number	95% Confidence interval		Density	95% Confidence interval	
		lower	upper		lower	upper
Southern Kuril Islands	459	170	1,916	0.11	0.04	0.43
Urup Island	795	323	2,110	1.36	0.55	3.55
Central Kuril Islands	753	328	3,015	0.67	0.29	2.61
North Kuril Islands	4,003	2,370	7,754	1.57	0.91	3.03
Total	6,010	4,492	11,314	0.71	0.53	1.33

TABLE 2 Comparison of abundance of sea otters for different parts of the range compared to available historical estimates since the 1960s. All studies other than ours do not have a detailed description of their methodology, so it can only be presumed that they used a direct one-skiff count and attempted total coverage for their evaluations.

	1960s–1970s (Shitikov, 1971)	**1980s–1990s (Kornev & Korneva, 2004)**	**Early 2000s (Kornev & Korneva, 2006)**	**2008 (Kornev 2010a; Kornev, Antonov, & Buslov 2007)**	**2012 (our data)**
Kamchatka	800	2,500–3,000	About 2,500	About 1,200	Adopted from literature as about 1,500 (Zavadskaya et al., 2017)
Northern Kurils	1,700 (Paramushir)	1,791–2,686 (Paramushir)	16,417	5,367	4,003
Central Kurils	About 600	About 500	About 400	400-600	753

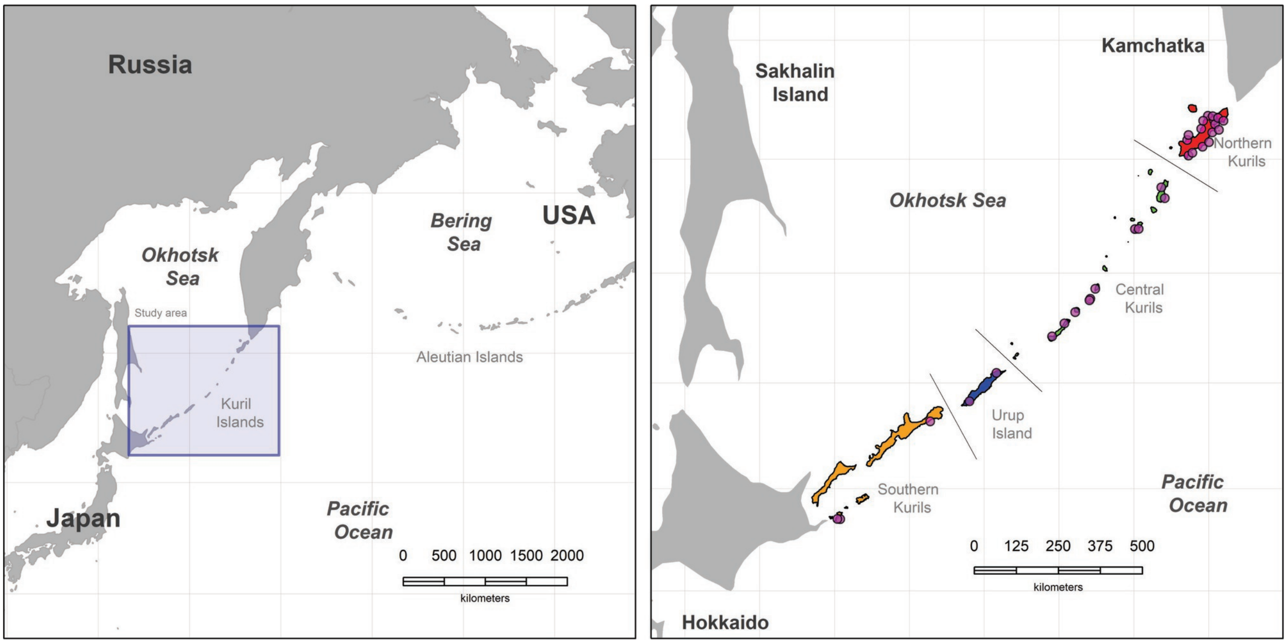
Urup	2,300	2,500	—		795
Southern Kurils	238-365	1,052	1,054	3,500 (including Urup)	459
Small Kurils	Occasional solitary sightings	—	31–44	—	
Total	4,100+	About 9,500	About 22,000	About 10,600	6,010 (4,492–11,314 CI 95%), and around 1,500 for Kamchatka

FIGURE 1 Area of the survey and geographic designations of the Kuril Islands adopted in this paper. Circles show islands along which transect surveys were conducted.

FIGURE 2 Spatial distribution of estimated sea otter numbers for each section. The coastline of each island was divided into segments (polygons), for which the sea otter abundance was calculated.

FIGURE S1 (a) Residual diagnostic plot shows no sign of heteroskedasticity. (b) Estimates of the autocorrelation function for residuals of the model.

FIGURE S2 The fractal dimension index (FDI) component smooth functions on the scale of the linear predictor.



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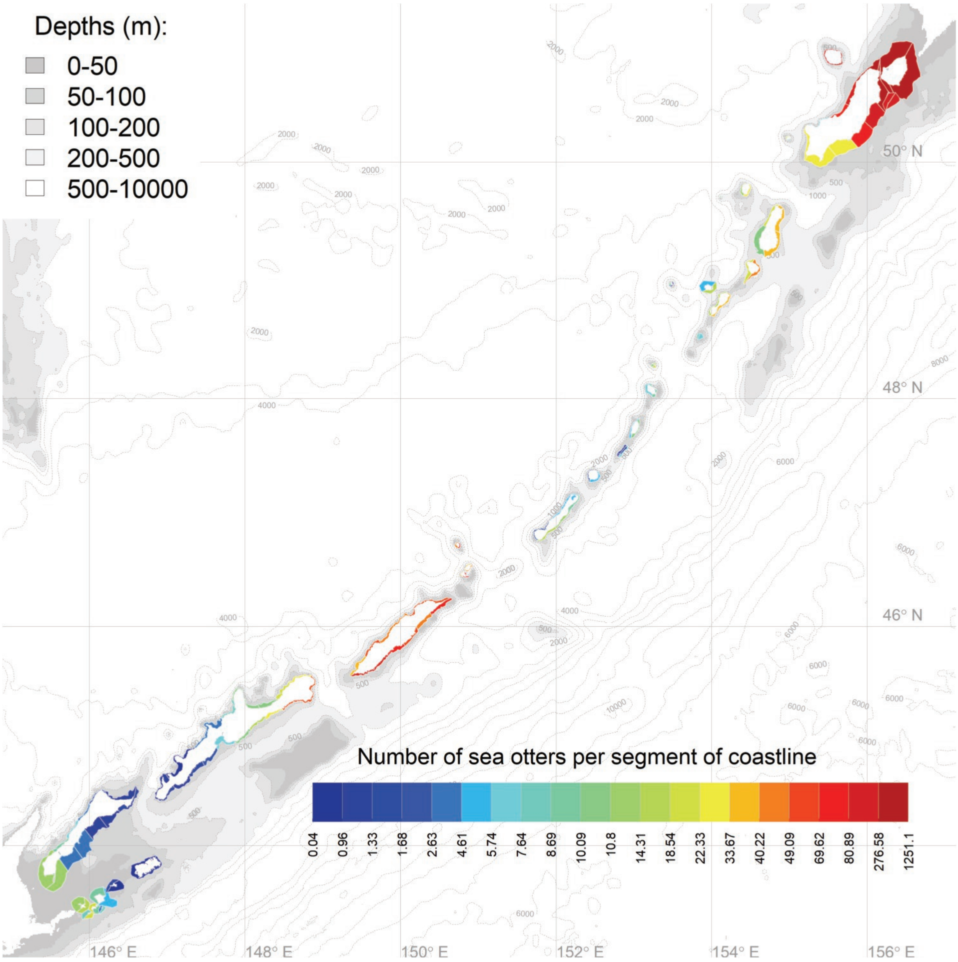

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