esa ECOSPHERE

Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska

Wendel W. Raymond,[1,]† M. Tim Tinker,[2] Michelle L. Kissling,[3] Brad Benter,[4]
Verena A. Gill,[5] and Ginny L. Eckert[1]

[1]*College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801 USA*
[2]*Department of Ecology & Evolutionary Biology, University of California Santa Cruz, 1156 High Street, Santa Cruz, California 95064 USA*
[3]*Marine Mammal Management, United States Fish and Wildlife Service, 3000 Vintage Boulevard, Suite 201, Juneau, Alaska 99801 USA*
[4]*Marking, Tagging & Reporting Program, United States Fish and Wildlife Service, 1011 East Tudor Road # 200, Anchorage, Alaska 99503 USA*
[5]*National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 222 West 7th Avenue, Rm 552, Anchorage, Alaska 99513 USA*

Citation: Raymond, W. W., M. T. Tinker, M. L. Kissling, B. Benter, V. A. Gill, and G. L. Eckert. 2019. Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. Ecosphere 10(9):e02874. 10.1002/ecs2.2874

Abstract. To better understand the spatial context of population dynamics of sea otters (*Enhydra lutris*) in Southeast Alaska (SEAK), we investigated the spatial and temporal patterns of subsistence sea otter harvest and assessed the effect of harvest on population growth. U.S. federal law permits subsistence harvest of sea otters and sale of clothing and handicrafts made by coastal Alaska Natives. Hunters are required to self-report these harvests along with information on date, location, age class, and sex. Using harvest data collected from 1988 to 2015, we developed a spatially explicit, age-structured, density-dependent population simulation model to explore the potential impacts of harvest on sea otter population dynamics. We examined patterns of harvest and simulation model results at two spatial scales: the SEAK stock and three smaller subregions that vary in sea otter occupation time and carrying capacity: Sitka Sound, Keku Strait, and the Maurelle Islands. Annual sea otter harvest in SEAK increased from 55 animals in 1988 to a reported maximum of 1449 animals in 2013. Estimated mean annual harvest rate was 2.8% at the SEAK stock scale, but ranged from 0% to 39.3% across the three focal subregions described above. Across all subregions (n = 55), annual sea otter harvest rate was strongly influenced by time since recolonization, sea otter population density, and proximity to communities with sea otter hunters. The simulation model predicted population trends and per capita harvest rates similar to those estimated from aerial survey data, providing a reasonable approximation of population dynamics. Results of the simulation model suggested that current harvest levels can reduce population size at both the SEAK and subregional scales. Variation in harvest impacts was a function of subregion-specific factors, including time since recolonization and population status with respect to carrying capacity. We found that subsistence harvest and its population effects were scale- and location-dependent, indicating that higher spatial and temporal resolution of sea otter population and hunting data could help address emerging sea otter management and conservation concerns in this region.

Key words: apex predator; harvest; population simulation; spatial dependence; subsistence.

Received 18 April 2019; revised 1 August 2019; accepted 2 August 2019. Corresponding Editor: Hunter S. Lenihan.

† **E-mail:** wraymond2@alaska.edu

INTRODUCTION

Variation in ecological and demographic processes across different scales can lead to spatial structure in populations (Turner 1989, Dunning et al. 1992). Therefore, effective management of populations requires information about population status and dynamics at spatial scales relevant to the species in question. For populations that are hunted for subsistence, harvest data can provide local-scale information that can be used to evaluate population status, management actions, and harvest sustainability (Shaffer et al. 2017, Mahoney et al. 2018). Furthermore, subsistence harvest data can inform our understanding of population dynamics and highlight spatially dependent factors that may influence the population and hunting itself (van Vliet et al. 2010). For example, bowhead whale (*Balaena mysticetus*) populations declined significantly as a result of commercial whaling in the 1800s. After commercial whaling ceased, populations recovered slowly (George et al. 2004, Minerals Management Service 2009, Phillips et al. 2013, North Slope Borough 2018). Thus, the use of subsistence harvest data has great potential to improve population management of particular species, in part because of the investment of local hunters in maintaining a viable population for future harvest, provided that competing interests do not exist. Here, we examine the spatial and temporal patterns of sea otter subsistence harvest and test for effects of harvest on population abundance and trends, to better understand the factors affecting population trends of sea otters in Southeast Alaska (SEAK).

Sea otters are apex predators that once inhabited much of the coastal North Pacific Ocean from Baja California to the northeastern coast of Asia including the Kamchatka Peninsula and northern Japan. Indigenous peoples have hunted sea otters primarily for their fur as an integral part of their culture for thousands of years (Fedje et al. 2001, Erlandson et al. 2005, Szpak et al. 2012). However, commercialization of sea otter harvest for fur beginning in the mid-1700s drove populations to near extinction (Kenyon 1969, Riedman and Estes 1990). Through legal protections, reintroductions, and other conservation efforts, sea otters have recovered to a global population of approximately 125,000 (Doroff and Burdin 2015). One area of notable recovery is SEAK, where sea otters were extirpated around the turn of the 20th century and then reintroduced to seven sites in the late 1960s (Burris and McKnight 1973; Fig. 1). From the 1970s through 1990s, the initial population of 413 sea otters grew rapidly in areas near reintroduction sites on the outer coast. By the 2000s, the distribution and numbers of sea otters increased greatly, and from 2003 to 2011, the population grew at an average rate of approximately 8.6% per year (Tinker et al. 2019*a*). The most recent abundance estimate (2011) for the SEAK stock was 25,584 individuals (Tinker et al. 2019*a*), which represents approximately one quarter of the sea otters in the United States and one fifth of the global population (Doroff and Burdin 2015). The SEAK population now extends across much of the outer coast of SEAK, from Icy Bay in the north to Dixon Entrance in the south, and into the inside waters of SEAK including Glacier Bay, Icy Strait, Kuiu Island, and Sumner Strait (Fig. 1).

While commercial harvest of sea otters is illegal, the U.S. Marine Mammal Protection Act (MMPA) permits coastal Alaskan Natives to harvest sea otters, as long as the harvest is done for subsistence and "is done for purposes of creating and selling authentic native articles of handicrafts and clothing" (50 CFR 18.23). Anecdotal reports indicate that sea otters are eaten very rarely, and the primary motivation for harvest is to obtain pelts. The U.S. Fish and Wildlife Service (USFWS) is responsible for the management and conservation of sea otters in the United States and collects data on subsistence sea otter harvest in Alaska (no harvest is permitted outside of Alaska). Harvest data are collected by USFWS designees, usually Alaska Natives who are sea otter hunters or artisans. These designees, called taggers, record information on the harvest and other basic demographic information and physically tag the pelt, as required under the MMPA. Previous analyses of the SEAK sea otter population have postulated that subsistence harvest of sea otters may affect sea otter population growth (Esslinger and Bodkin 2009), especially at local scales (Bodkin and Ballachey 2010, Tinker et al. 2019*a*). USFWS conducts aerial surveys to estimate population size and trend, but owing to budget and logistical constraints, surveys occur

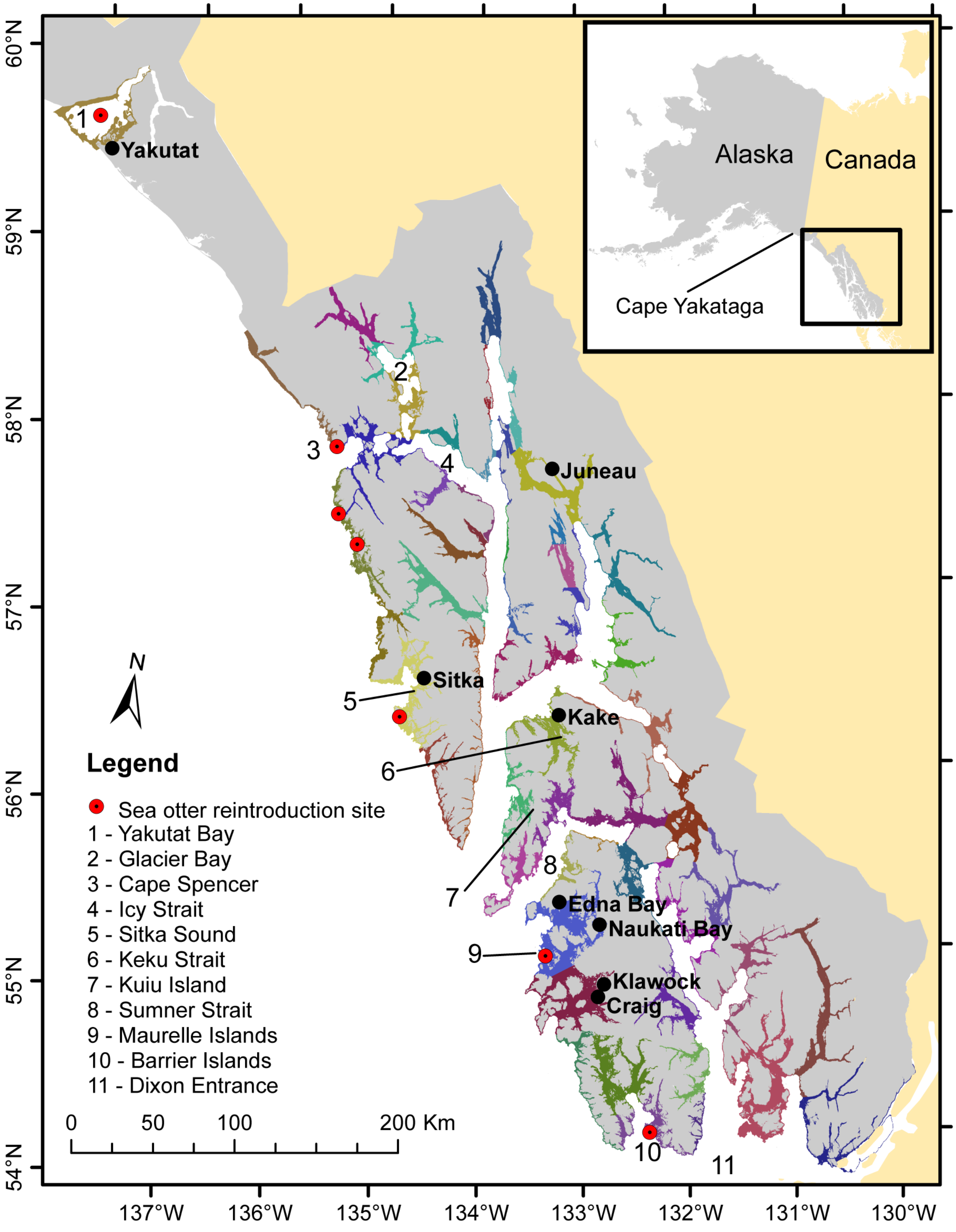

Fig. 1. Map of Southeast Alaska with sea otter reintroduction sites and sea otter population subregions (colors denote different subregions).

infrequently (7–10 yr). Tinker et al. (2019*a*) recently estimated population trends and carrying capacity at multiple spatial scales, but to date, SEAK sea otter harvest data have not been analyzed for spatial and temporal trends or for potential effects to the sea otter population.

While hailed as a conservation success story, the return of sea otters exemplifies the challenge of a predator returning to its native range, which raises ecological, conservation, and management questions (Roman et al. 2015, Silliman et al. 2018). In particular, the recovery of sea otter populations resulted in conflicts with human interests for shellfish resources (Carswell et al. 2015). In SEAK from 2009 to 2012, commercially important marine species represented 46% of sea otter diets, and sea otter expansion contributed to declines in shellfish available for commercial harvest (Larson et al. 2013, Hoyt 2015). In response, legislation was introduced to the Alaska State Senate in 2013 that proposed a bounty for sea otters that would be given to Alaskan Native harvesters (Carswell et al. 2015). However, its passage would have put the State of Alaska in direct conflict with the federal government who has the legal authority to implement the MMPA and manage sea otter harvest. More recently, a resolution was introduced in the Alaska State Senate urging the federal government to amend the MMPA to allow for comanagement of sea otters between Alaska Native organizations and the Alaska Department of Fish and Game (which has no management authority over sea otters), arguing that local organizations may be better able to manage the population (Stedman et al. 2018). Furthermore, recent summaries of sea otter harvest in SEAK indicate a marked increase since 2010 (USFWS 2014*a*). These legislative actions and recent harvest increases have caught the attention of conservation organizations that want to prevent changes to current law (Friends of the Sea Otter 2018). This situation highlights the need for information surrounding the patterns of sea otter harvest and the impacts of harvesting on the SEAK population.

A recent analysis of population trends and estimation of carrying capacity for sea otters in SEAK (Tinker et al. 2019*a*), together with the existence of hunter-reported data on harvest numbers, provide a unique opportunity to evaluate harvest impacts for this species and assess the spatial structure of the population. To assess population effects, we developed a spatially explicit, age-structured, density-dependent population simulation model for sea otters in SEAK using empirical demographic data and recently derived carrying capacity values from Tinker et al. (2019*a*). We hypothesized that sea otter harvest and any effect of harvest on the population would vary as a function of geographic location. Sea otters have small home ranges compared with most marine mammals, ranging from 1.0 to 11.0 km^2 (Garshelis and Garshelis 1984, Tarjan and Tinker 2016), aggregate in social groups (Jameson 1989, Laidre et al. 2009), and show spatial variability in carrying capacity (Tinker et al. 2019*a*) and variability in the history of sea otter recolonization and expansion in SEAK (Burris and McKnight 1973, USFWS 2008, 2014*b*). These factors all suggest that sea otter population dynamics and therefore patterns of harvest and harvest effects are likely to vary at scales smaller than the current scale of management, which is all of SEAK. Our analysis provides a structure for quantifying and testing the relationship between subsistence harvest and sea otter population dynamics and resilience in SEAK and the rest of Alaska where this species is harvested for subsistence. Our analysis provides a structure for quantifying and testing the relationship between subsistence harvest and sea otter population dynamics and resilience in SEAK and serves as a framework for further analysis of the sea otter population in SEAK and other regions in Alaska where this species is harvested for subsistence purposes.

METHODS

Study area

The SEAK stock of sea otters is spatially defined as all sea otters from Dixon Entrance to Cape Yakataga on the southeastern coast of Alaska, which stretches over 850 km in length and encompasses 17,790 km^2 of suitable sea otter habitat (Bodkin and Udevitz 1999; Fig. 1). The region is comprised of large and small islands, fjords, exposed and protected shorelines, and a wide array of nearshore habitats including kelp forests, seagrass beds, rocky reefs, and mudflats. Harvest occurs throughout most of this region with the exception of Glacier Bay National Park, where U.S. National Park Service regulations prohibit it. While the USFWS manages sea otters at the stock level, a number of recent studies and reviews have highlighted that demographically important processes in sea otter populations, including density-dependent resource limitation, occur at much smaller scales because of the low mobility and high site fidelity of mature sea otters (Bodkin 2015, Tinker 2015, Tinker et al. 2017, Gagne et al. 2018). Therefore, we examined harvest patterns and potential impacts of harvest at both the stock and subregional scales.

We adopted the same subregions used by Tinker et al. (2019*a*) to estimate carrying capacity of sea otters in SEAK. The authors delineated these subregions in order to track population trends in SEAK at an appropriate spatial scale based on sea otter life history and ecology and on recent findings of fine-scale demographic structuring of sea otter populations (Bodkin 2015, Tinker 2015, Gagne et al. 2018, Johnson et al. 2019, Tinker et al. 2019*b*). Specifically, each subregion encompassed an area of sea otter habitat approximately 100 times the size of a typical adult home range, which ranges from 1.0 to 11.0 km^2 (Garshelis and Garshelis 1984, Tarjan and Tinker 2016), bounded by the low tide line inshore and the 40 m depth contour offshore (Fig. 1). Subregion size was chosen to be small enough so that individuals within a subregion could be considered a well-mixed population experiencing similar environmental and density-dependent conditions, but large enough so that demographic processes (births and deaths) would have a greater influence on population trends than movement between subregions (Tinker et al. 2019*a*). Thus, the mean swimmable distance (calculations below) from the centroid of a given subregion to its nearest neighbor was 50 km (±28 km standard deviation [SD]), twice the mean annual net displacement distance for female sea otters (Tinker et al. 2008), and boundaries between subregions corresponded, whenever possible, to natural geographic features (e.g., prominent headlands) that were assumed to discourage movements. In our analysis, we used 21 subregions identified by Tinker et al. (2019*a*; N01–N10, S01–S12, and YAK). To ensure size consistency, we further subdivided Glacier Bay (GBY) into three subregions (GBYA, GBYB, and GBYC) and subdivided the coastal area of SEAK not occupied by sea otters at the time of the most recent survey (referred to in Tinker et al. 2019*a*, as "un-surveyed") into 29 additional subregions (N11–N27 and S13–S24; Fig. 1). Thus, in our analysis we used 55 subregions across SEAK.

We summarized spatial and temporal patterns of sea otter harvest and population effects at two spatial scales, the SEAK stock and at three focal subregions that represented a range of sea otter occupation time, estimated carrying capacity, proximity to human communities, and harvest history and trends: Sitka Sound, Keku Strait, and the Maurelle Islands (Table 1). The Sitka Sound subregion includes a sea otter introduction site, is adjacent to the community of Sitka with a human population of 8881 (U. S. Census Bureau 2010), and has a long history of sea otter harvests (USFWS 2014*a*). Keku Strait was recently colonized by sea otters and is adjacent to the community of Kake with a human population of 557 (U. S. Census Bureau 2010, USFWS 2014*a*, Hoyt 2015) and has reported variable sea otter harvest since sea otters colonized this subregion (USFWS 2014*a*). The Maurelle Islands includes another reintroduction site, is directly adjacent to the small communities of Edna Bay and Naukati Bay, with a combined population of 155, and is reasonably accessible from the communities of Craig and Klawock with a combined human population of 1956 (U. S. Census Bureau 2010). The Maurelle Islands subregion has had on average relatively high numbers of sea otter harvests but high year-to-year variability (USFWS 2014*a*).

Subsistence sea otter harvest data

We analyzed sea otter harvest data for SEAK from the start of records in 1988 through 2015. These data were collected by USFWS taggers who record information provided by hunters for each harvested sea otter and tag each pelt with a unique identifying physical tag. Data include date of tagging, date of harvest, location of tagging (community), location of harvest (latitude and longitude and description), age class (adult, subadult, or pup), and sex of the harvested sea otter. The tagger also records if tissue specimens

Table 1. Subregion data and reported sea otter harvest statistics from the Southeast Alaska population, Sitka Sound, Keku Strait, and the Maurelle Islands.

Region	Area (km^2)	Carrying capacity (±SD)†	Percent Alaska Native‡	Mean annual hunters reporting (±SD)	Min annual harvest	Max annual harvest	Cumulative harvest (%)	Mean annual contribution to total harvest % (±SD)
Southeast Alaska	17,790	4.20 (1.58)	16.6§	53.5 (28.6)	55	1449	12,546	
Sitka Sound (N05)	615	1.76 (1.35)	24.6	18.9 (10.4)	4	498	2744 (21.9)	18.6 (10.1)
Keku Strait (S08)	472	9.89 (9.61)	80.6	2.4 (1.4)	0	195	641 (5.1)	2.7 (4.4)
Maurelle Is. (S02)	976	4.09 (1.58)	4.5, 42.1¶	12.2 (7.6)	4	167	1880 (15.0)	19.0 (15.0)

Notes: Includes subregion area, estimated carrying capacity, percent Alaska Native population minimum and maximum annual harvest, cumulative harvest, and mean annual contribution to total harvest. SD, standard deviation.

†Tinker et al. (2019*a*).

‡U.S. Census Bureau (2010).

§Robinson et al. (2017).

¶Percent Alaskan Native population of the communities of Craig and Klawock AK, which are not directly adjacent to the Maurelle Islands subregion but are reasonably close to permit harvest.

were taken and any other relevant information. The physical tag remains with the pelt, as only tagged pelts can be tanned by commercial tanning operators.

Before analysis, we reviewed data for consistency and spatial ambiguity. After removing duplicate harvests and addressing typographic errors, 13,151 harvest records remained. Of those, 12,546 (95%) included acceptable geographic information and were used for spatial and temporal analyses and simulation models. We used the latitude and longitude of harvest to assign a geographic subregion. If the geographic coordinates of a harvest location resulted in a land-based location, we used the reported geographic description to generate coordinates in the adjacent marine-based subregion. If the geographic description was not specific enough to assign new coordinates, and the harvest location was less than 1-km inland, we adjusted the harvest latitude and longitude to the nearest subregion. In all other instances of spatial ambiguity, we removed records from analysis. All analyses were conducted at the subregion scale; thus, the specific coordinates were not used after this assignment.

For parameterization of the population simulation model, we converted hunter-reported age and sex into four age/sex classes: adult male, adult female, juvenile male, and juvenile female. If age and/or sex were missing, we assigned the age/sex as unreported for purposes of harvest summaries. For the population simulation model, we assigned harvest records with unreported age and sex data were assigned age/sex classes corresponding to the proportion of reported age/sex classes for the appropriate subregion and year.

Patterns of sea otter harvest

For SEAK as a whole and the three focal subregions, we summarized annual reported number of harvested sea otters, the age/sex class of harvested sea otters, and the annual harvest rate using the estimated preharvest population abundance for that year from Tinker et al. (2019*a*, *b*; Eq. 1).

$$\text{Harvest rate}_{y,i} = \frac{\text{harvest}_{y,i}}{\text{population}'_{y,i}} \tag{1}$$

where $\text{harvest}_{y,i}$ is the number of sea otters harvest in subregion, i in year y, and $\text{population}'_{y,i}$ is the estimated preharvest sea otter population from Tinker et al. (2019*a*). We also calculated the mean annual percent contribution to total harvest for each subregion (Eq. 2).

$$\text{Mean annual percent contribution}_i = \frac{\sum\left(\frac{\text{harvest}_{y,i}}{\sum_i \text{harvest}_y} \times 100\right)}{N\,\text{years of reported harvest}_i}. \tag{2}$$

To identify factors that may be driving variation in sea otter harvest rate at the subregional scale, we constructed a linear mixed-effects model to test for effects of time since sea otter recolonization (TimeOcc), sea otter population density (SODens), proximity to human communities (PopProx), and proximity to sea otter hunters (HunterProx):

$$\begin{aligned}\mathrm{HR}_{y,i} = {} & \mathrm{TimeOcc}_{y,i} + \mathrm{TimeOcc}^2_{y,i} + \mathrm{SODens}'_{y,i} \\ & + \mathrm{PopProx}_{y,i} + \mathrm{HunterProx}_{y,i} + \mathrm{SRerr}_i\end{aligned} \tag{3}$$

where $\mathrm{HR}_{y,i}$ is the harvest rate for subregion i in year y, measured as the number of sea otters harvested divided by the estimated preharvest population abundance. Time since occupation for each subregion and year ($\mathrm{TimeOcc}_{y,i}$) was measured as the interval (in years) between a harvest record and the year in which sea otters were known to have first recolonized a given subregion (or year of translocation in the case of subregions containing translocation sites). We allowed for both linear and quadratic effects of $\mathrm{TimeOcc}_{y,i}$, based on the a priori hypothesis that duration of sea otter occupation could have a nonlinear relationship with harvest rate. Sea otter population density for each subregion and year was calculated as estimated abundance divided by habitat area (km^2). To account for collinearity between years of occupation and sea otter density (Tinker et al. 2019*a*), we first fit a separate linear model of sea otter population density as a function of years of sea otter occupation (Appendix S1: Table S1) and extracted the residuals from this model, thereby creating a de-trended metric of relative sea otter population density ($\mathrm{SODens}'_{y,i}$). We used inverse distance weighting (IWD) to interpolate the cumulative effects of human population centers ($\mathrm{PopProx}_{y,i}$) and sea otter hunters ($\mathrm{HunterProx}_{y,i}$) at each subregion and year (Shepard 1968). This was calculated as the sum of the inverse Euclidean (straight-line) distances from each community to the center of each subregion, multiplied by the natural log of that community's population size (human population proximity) or the reported number of unique sea otter hunters that tagged a sea otter pelt (sea otter hunter proximity). Finally, to account for unexplained spatial variation in harvest rate we also included a random effect of subregion (SRerr_i). In the absence of reliable survey data, we assumed that sea otters colonized a subregion one year prior to the first reported harvest. While the true time from recolonization to first harvest is unknown in many subregions, our exploration of harvest trends indicated that in many subregions where the year of colonization is well-documented through aerial surveys, reported harvest appears immediately. We restricted the linear mixed-effects analysis to the period of 1990–2010 and to subregions with reported harvest to avoid biases associated with limited data availability. We performed a simultaneous forward and backward selection procedure with delta Akaike's information criterion (AIC) discrimination to identify the best model from our initial full model. For the purpose of model fitting, sea otter harvest rate was arcsine-square root-transformed, human population proximity was natural log-transformed, and sea otter hunter proximity was square root-transformed to reduce the effect of extreme values. Human population data were obtained from the U.S. Census Bureau (U. S. Census Bureau 2010). Anonymized sea otter hunter data were obtained from USFWS.

Population simulation model

We developed a spatially structured matrix projection model (Caswel 2001) to simulate population dynamics of SEAK sea otters both with and without harvest mortality. Assuming that the model accurately captures the key processes underlying sea otter population dynamics through the subregions defined above, we aimed to use the difference between projected abundance under the two scenarios, at both subregional and stock scales, as a quantitative measure of harvest impacts. While other population models have assessed the effects of sea otter harvest mortality generally (Samuel and Foin 1983, Bodkin and Ballachey 2010), our model differs in key ways. (1) Our model incorporates spatial structure at a scale that is meaningful for tracking demographic processes in sea otter populations (Bodkin 2015, Tinker 2015, Tinker et al. 2019*a*). (2) The model allows for density dependence, demographic stochasticity, and environmental stochasticity in age- and sex-specific vital rates. (3) The model incorporates annually reported sea otter harvest data, including the spatial distribution, age, and sex structure of harvest. (4) The model allows for realistic spatial dynamics, including range expansion and dispersal/movement among subregions. (5) The model uses empirically derived and spatially explicit carrying capacity estimates. (6) The model is initiated in 1970 using the known location and abundance of translocated populations, and then iteratively run forward in time, allowing validation of model performance by comparison of predicted dynamics with observed dynamics between 1970 and 2015 based on a recent analysis of survey data in Tinker et al. (2019*a*).

The simulation model is constructed on a stage-based projection model, where life stages correspond to easily recognized and demographically relevant age/sex classes (Caswel 2001). Adult male sea otters become sexually mature at age 4–8 and adult females at age 2, and have an annual reproductive cycle (Jameson and Johnson 1993, Riedman et al. 1994). After a gestation period of six months, females give birth to a single pup that enters the juvenile age class (if weaned successfully) after a dependency period of approximately six months (Jameson and Johnson 1993). Our matrix model therefore tracks demographic transitions for two age classes of each sex, prereproductive juveniles and subadults (weaning—2.5 yr of age) and reproductive adults (>2.5 yr of age). This division corresponds to the female age of first reproduction, because population dynamics are determined primarily by female survival and reproduction. We used an annual time step to track dynamics, and for each stage i, we defined the following vital rates: annual survival rate (s_i), growth transition probability for juveniles (g), birth rates (b), and weaning success rates (w) for adult females. These demographic transitions were combined mathematically into a population projection matrix for subregion j at time t:

$$M_{j,t} = \begin{bmatrix} s_1(1-g) & \frac{b}{2}\cdot w\cdot s_2 & 0 & 0 \\ s_1\cdot g & s_2 & 0 & 0 \\ 0 & \frac{b}{2}\cdot w\cdot s_2 & s_3(1-g) & 0 \\ 0 & 0 & s_3\cdot g & s_4 \end{bmatrix}. \quad (4)$$

The reproductive contributions to the juvenile stage depend on birth rate (halved to reflect a 50:50 sex ratio at birth) and weaning success rate and are conditional upon the mother's survival (s_2). The growth transition probability parameter (g) was calculated for each new parameterization of Eq. 5 using the standard equation for fixed-duration age classes (Caswel 2001):

$$g = \left(\frac{(s_1/\lambda)^T - (s_1/\lambda)^{T-1}}{(s_1/\lambda)^T - 1}\right) \quad (5)$$

where T represents the time from recruitment to maturity (2 yr) and λ is the annual growth rate associated with a particular matrix parameterization. Eq. 5 is solved iteratively, whereby λ is initially set to 1, Eq. 5 and then Eq. 4 are solved, λ is recomputed as the dominant eigenvalue of $M_{j,t}$, and then calculations repeated until the value of λ stabilizes to two decimal places.

The primary goal of our simulation model was to approximate realistically demographic processes within a sea otter population while avoiding over. We parameterized vital rates based on estimates from previously published studies of sea otter populations. Adult female birth rates for sea otters remain almost invariant at approximately one pup per year (Monson et al. 2000, Tinker et al. 2006, Riedman et al. 2019), while all other vital rates exhibit both stochasticity and density-dependent variation (Siniff and Ralls 1991, Eberhardt 1995, Monnett and Rotterman 2000, Monson et al. 2000, Gerber et al. 2004, Tinker et al. 2017). To account for this variation, we first generated a large number (A = 1000) of random but biologically feasible sets of vital rates, $\mathrm{VR}_a = \{b, w, s_1, s_2, s_3, s_4\}$. Each random array VR_a was consistent with published sea otter life-history schedules and implied an associated annual rate of growth (λ_a) that was calculated algebraically as the dominant eigenvalue of $M_{j,t}$. We first created two extreme VR arrays corresponding to published vital rates for a population growing rapidly near the theoretical $r_{\max}$ (λ_a = 1.22 for $\mathrm{VR}_{\mathrm{high}}$) and a declining population (λ_a = 0.95 for $\mathrm{VR}_{\mathrm{low}}$; Monson et al. 2000). We then generated random adjustment factors to interpolate between the extreme values for each vital rate:

$$\mathrm{VR}_a = \mathrm{adj}_a \cdot \mathrm{VR}_{\mathrm{low}} + (1 - \mathrm{adj}_a) \cdot \mathrm{VR}_{\mathrm{high}} \quad (6)$$

where 0 < adj < 1. To allow flexibility in stage-specific vital rates (representing the effects of demographic stochasticity), while maintaining appropriate life-history schedules (e.g., $s_2 > s_1 > w$), we used Cholesky decomposition to ensure that the random adjustment factors were correlated across vital rates (assuming a correlation coefficient of 0.95). Solving Eq. 6 resulted in 1000 unique sets of correlated vital rates, each with an associated value of λ_a. These random vital rate arrays were then selected during population simulations so as to account for density dependence and stochastic variation (Appendix S1: Fig. S1). At each year and for each subregion within a given simulation, an expected growth rate ($\hat{\lambda}_{j,t}$) was calculated to reflect environmental stochasticity and density dependence. Specifically, if $N_{j,t-1}$ represents the abundance for subregion j at time $t-1$, K_j is the estimated carrying capacity for subregion j, and σ_e is the standard error of log(λ) across years (estimates of K_j and σ_e were based on Tinker et al. 2019*a*), we calculate $\hat{\lambda}_{j,t}$ as

$$\hat{\lambda}_{j,t} = \exp\left(r_{\max}\left(1 - \frac{N_{j,t-1}}{K_j}\right) + \varepsilon_{j,t}\right), \quad (7)$$

where $\varepsilon_{j,t} \sim \mathrm{Normal}(0, \sigma_e)$. An appropriate set of vital rates (VR$_a$) was then selected randomly after filtering by $\lambda_a = \hat{\lambda}_{j,t}$, and used to parametrize $M_{j,t}$. We then calculated demographic transitions for subregion j at year t using standard matrix multiplication:

$$n'_{i,j,t} = M_{j,t} \times n_{i,j,t-1} \quad (8)$$

where $n'_{i,j,t}$ represents the expected number of individuals of stage i in subregion j at year t, prior to the effects of harvest and redistribution (dispersal) among subregions.

We next adjusted $n'_{i,j,t}$ to reflect harvest mortality (for simulation runs including harvest) and dispersal:

$$n_{i,j,t} = n'_{i,j,t} - H_{i,j,t} + I_{i,j,t} - E_{i,j,t} \quad (9)$$

where $H_{i,j,t}$ is the total recorded harvest mortality for a given year, subregion, and age/sex class, $I_{i,j,t}$ represents immigration to subregion j from other occupied subregions, and $E_{i,j,t}$ represents emigration of animals out of subregion j to other occupied subregions. Immigration and emigration were treated as stochastic Poisson processes, with stage-specific dispersal probabilities computed from dispersal kernels fit to empirical data on tagged sea otter movements (Tinker et al. 2008). Specifically, following previous analyses (Tinker et al. 2008, 2019*b*) we used maximum-likelihood methods to fit Weibull probability distributions to stage-specific data on annual net linear displacement (NLD) measurements from radio-tagged sea otters (Hoyt 2015). We calculated NLD as the most direct, swimmable distance between an individual's recorded position at the start and end of one year. We used minimum cost path (MCP) analysis to prevent overland movements when calculating distances between an otters' starting and ending locations. We also used MCP to compute pairwise swimmable distances between the geographic centroids of all subregions, resulting in a distance matrix D giving the pairwise movement distances between any two subregions. The probability that a sea otter of stage i does not disperse from subregion j is computed by evaluating the fitted Weibull cumulative density function at critical distance δ_j, defined as the average distance between the centroid of subregion j and the centroids of adjacent subregions that share a common boundary. The probability of emigration (P_E) is then calculated as one minus this value, and the actual number of animals of stage i emigrating from subregion j in year t is calculated as a stochastic variable:

$$E_{i,j,t} \sim \mathrm{Poisson}(n_{i,j,t} \cdot P_{E,i}). \quad (10)$$

For those sea otters that emigrate from subregion j, we also must specify the recipient subregion. We did this by first restricting consideration to those subregions known to be colonized at time t (as explained in the next paragraph): For this subset of potential recipient subregions (z = 1, 2 . . . z), the relative probability of dispersal from j to z was computed by evaluating the Weibull density function at the pairwise distances in column j of matrix D (excluding the diagonal), and then rescaling these probabilities to sum to 1 over all z. We distributed the emigrating otters stochastically among occupied subregions by drawing from a multinomial probability distribution with parameters $\alpha_{j,z}$ equal to these rescaled movement probabilities. The number of otters immigrating to subregion j ($I_{i,j,t}$) was computed as the sum of emigrants from all other occupied subregions for which j was randomly selected as the recipient subregion:

$$I_{i,j,t} = \sum_{z \neq j} E_{i,z,t} \to j. \quad (11)$$

We augmented the stochastic movements between subregions with published data on two specific dispersal events: the colonization of

Coronation Island by approximately 50 sea otters from the Maurelle Islands around 1975 (Pitcher 1989) and the colonization of Glacier Bay by approximately 500 sea otters from Icy Strait in 1995 (Esslinger and Bodkin 2009). The inclusion of these two well-documented dispersal events in the simulation model greatly improved overall performance; however, except for these two events, all modeled other dispersal between subregions was stochastic and determined by the simple probabilistic functions described above. Finally, after accounting for the dynamics of immigration, emigration, and harvest mortality (Eq. 9), we computed the expected population abundance for subregion j at time t as:

$$N_{j,t} = \sum_{i} n_{i,j,t}. \tag{12}$$

The simulation model was initiated at $t_0 = 1970$, with the 413 sea otters reintroduced in the late 1960s distributed among seven subregions (Appendix S1: Table S2; Burris and McKnight 1973). The year at which additional subregions became colonized (and thus eligible for receiving dispersers from other subregions) was set according to data from aerial and skiff surveys (Pitcher 1989, Esslinger and Bodkin 2009, Tinker et al. 2019*a*), and/or based on harvest records. As in our regression analysis of factors influencing harvest rate, in the absence of precise survey-based estimates of colonization year for a given subregion, we assumed colonization occurred the year before the first harvest records were recorded for that area. We ran simulations for each of two scenarios: (1) including known sea otter harvest and (2) without harvest (i.e., $H_{i,j,t}$ forced to 0). Each model was run for 46 yr (1970–2015) with 10,000 iterations. Mean projected abundance was calculated for all of SEAK and for the three focal subregions. We generated 95% confidence intervals (CIs) for annual expected abundance using a bootstrapping procedure with 10,000 samples. We calculated the simulation-based harvest rate as the ratio of harvested sea otters to the prehunted simulated population. Our simulation ran from 1970 through 2015, however scenarios with and without harvest did not differ from 1970 through 1987, before sea otter harvest data collection began, so we therefore present model results from 1988 through 2015. All simulation model parameters are summarized in Table 2.

Table 2. Key to symbology used to denote model parameters.

Symbol	Description
s_i	Annual survival of life stage *i*
g	Juvenile growth transition probability
b	Birth rate
w	Adult female weaning success rate
$M_{j,t}$	Projection matrix for subregion *j* and time *t*
T	Time from recruitment to maternity
λ	Annual growth rate associated with a particular $M_{j,t}$ parameterization
$\hat{\lambda}_{j,t}$	Expected growth rate for subregion *j* and time *t*
$N_{j,t-1}$	Sea otter abundance subregion *j* and time *t*
K_j	Estimated carrying capacity for subregion *j*
σ_e	Standard error of log(λ)
$n'_{i,j,t}$	Expected number of individuals of stage *i* in subregion *j* at year *t*, prior to the effects of harvest and dispersal among subregions
$H_{i,j,t}$	Total recorded harvest mortality of life stage *i*, subregion *j*, and year *t*
$I_{i,j,t}$	Immigration to subregion *j* of life stage *i* in year *t* from other occupied subregions
$E_{i,j,t}$	Emigration of animals out of subregion *j* of life stage *i* in year to other occupied subregions
$P_{E,i}$	Probability of emigration of life stage *i*
δ_j	Average distance between the centroid of subregion *j* and the centroids of adjacent subregions that share a common boundary
D	Distance matrix

Assessing model performance

To evaluate the ability of the simulation model to produce realistic dynamics, we compared model projections to observed abundance trends estimated from aerial survey data (Tinker et al. 2019*a*). Because the model consists of forward projections from the initial translocated population in 1970 and is not fit in any way to the survey data (although certain parameters such as local carrying capacity and environmental stochasticity are based on previous analysis of survey data), agreement between the simulations and observed trends would suggest that the model successfully captures the key factors driving sea otter population growth and range expansion. We visually compared the expected abundance from simulations to the most recent survey results (2010–2012) for the 21 subregions for which survey data were available.

Harvest effects on population

We measured the effect of harvest on sea otter population dynamics by comparing the projected trends with and without sea otter harvest mortality, using paired simulations. This meant that for a given random sequence of environmental stochastic effects, we ran a simulation with observed harvest numbers and a matching simulation with harvest mortality set to zero. We calculated the relative effect of harvest as the proportional difference in abundance at year t between paired simulations using all i bootstrap samples described above: $(N_{i,t,\text{harvest}} - N_{i,t,\text{no harvest}})/\text{mean}(N_{,t,\text{no harvest}})$. Thus, a negative value would indicate decreased abundance due to harvest. As with abundance estimates, we used bootstrap resampling with 10,000 replicate samples to calculate the mean difference and 95% CI for each year and area of interest. We considered years where the 95% CI did not include zero to be instances of significant differences between the two scenarios. We evaluated harvest effects by visually comparing temporal variation in the instantaneous growth rate of simulations with per capita harvest rates.

All statistical analyses and population simulation runs and calculations were performed using R version 3.5.1 (R Core Team 2018). Data and analysis code can be viewed at https://doi.org/10.5281/zenodo.3378051. Sea otter harvest data are available from the USFWS Marking, Tagging, and Reporting Program.

RESULTS

Patterns of sea otter harvest and population effects generally differed between the SEAK stock and the smaller subregions, and among subregions. Harvest records indicated an increase in harvested sea otters over time with stable harvest rates at the SEAK scale but variable harvest rates at the subregional scale. Furthermore, analysis indicated that harvest rate appears to be driven by factors that operate at the subregion scale. Sea otter population simulation results suggested that harvest can lead to reduced populations and in some cases population declines. Overall, our results indicate that variation in harvest itself and its effects on the sea otter population was dependent on the spatial location of interest and that small-scale patterns did not necessarily appear at the SEAK scale.

Reported sea otter harvest

Reported sea otter harvest in the SEAK stock increased from 55 in 1988 to a maximum harvest of 1449 animals in 2013 (Appendix S1: Table S3; Fig. 2e; see Fig. 2a–d for sea otter population estimates from Tinker et al. 2019*a*, *b*). Annual total harvest was low (range = 55–147) relative to the total sea otter population size in the late 1980s, but increased in the early 1990s from 313 to 833. Total annual harvest was low and stable (range = 120–432), from the mid-1990s through the late 2000s. From 2009 to 2013, total annual harvest increased from 597 to 1449. Sea otter harvest remained greater than 1000 per year through 2015. These fluctuations in harvest over time were largely mirrored in Sitka Sound, but at a lower magnitude (Appendix S1: Table S3; Fig. 2f). Harvest patterns differed in the other two focal subregions. Harvest in Keku Strait began in 2000, a few years after sea otter colonization of this area in 1995. From 2000 to 2011, harvest was low, but then increased from 2012 to 2014 (Appendix S1: Table S3; Fig. 2g). The Maurelle Islands experienced periodic pulsed harvest events that were consistently around 100–150 animals (Appendix S1: Table S3; Fig. 2h). Sitka Sound and Maurelle Islands accounted for a similar and high contribution to average annual sea otter harvest in SEAK (18.6% ± 10.10 SD and 19.0% ± 15.0 SD, respectively). Keku Strait accounted for only 2.7% (±4.40 SD) of annual harvest in SEAK (Table 3).

Annual reported sea otter harvest rate varied among the different geographic areas and spatial scales investigated (Table 3, Figs. 2i–l). Annual harvest rate over the whole region was low and stable through time (mean 2.9% ± 1.9 SD), with the exception of the early 1990s, when a maximum harvest rate of 10.6% in 1993 was estimated (Table 3, Fig. 2i). Sitka Sound consistently showed a high annual harvest rate (mean 9.8% ± 9.4 SD) that peaked in 1993 at 39.3% (Table 3, Fig. 2j). In contrast, Keku Strait had low harvest rates when sea otters first colonized the area in 1995. After 2000, the harvest rate increased and became more variable, fluctuating between 0% and 23%, with a mean annual harvest rate of 5.0% (±6.4 SD; Table 3, Fig. 2k). The

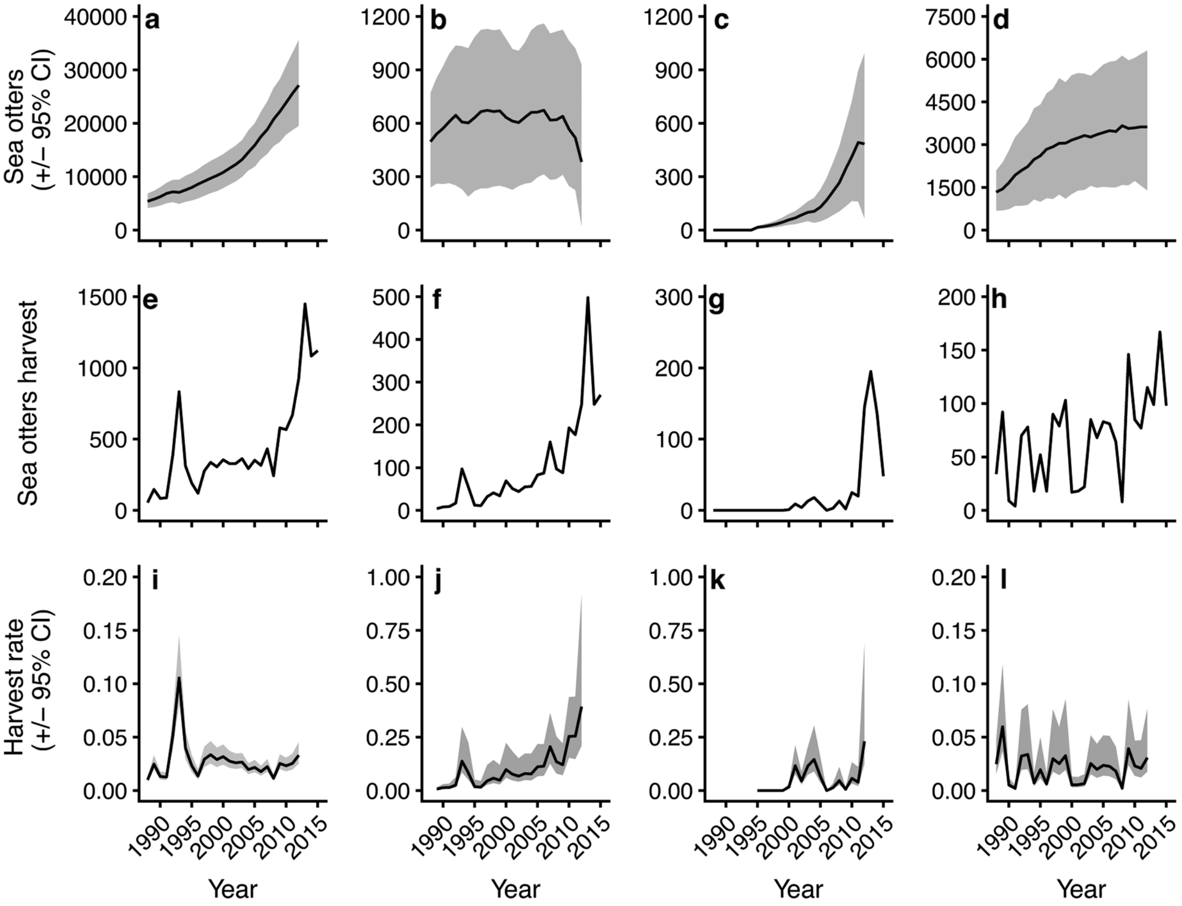

Fig. 2. (a–d) Sea otter population estimates from Tinker et al. (2019*a*), (e–h) annual sea otter harvest, and (i–l) annual sea otter harvest rate from 1988 to 2015 for (a, e, i) Southeast Alaska, (b, f, j) Sitka Sound, (c, g, k) Keku Strait, and (d, h, l) the Maurelle Islands. Annual harvest rate was calculated as the proportion of harvested sea otters to the estimated preharvested sea otter abundance in a given year and location. Note the different *y*-axis scale on (a–d) sea otter population estimates, (e–h) annual sea otter harvest, and (i–l) annual harvest rate.

Table 3. Minimum, maximum, and mean sea otter harvest rate calculated from survey data/population simulation data.

Region	Min	Max	Mean (±SD)
Southeast Alaska	1.0/1.2	10.6/12.6	2.9 (1.9)/3.2 (2.2)
Sitka Sound (N05)	0.7/0.7	39.3/53.4	9.8 (9.4)/12.4 (14.1)
Keku Strait (S08)	0.0/0.0	23.0/78.7	5.0 (6.4)/35.0 (27.9)
Maurelle Is. (S02)	0.2/0.3	6.0/11.4	2.1 (1.4)/3.3 (2.3)

Note: SD, standard deviation.

Maurelle Islands showed periodic sharp increases in harvest rate (0.2–6.0%) followed by little to no harvest, with a mean harvest rate of 2.0% (±1.4 SD; Table 3, Fig. 2l).

Adult sea otters accounted for 82%, juveniles for 14%, and unidentified as 4% of all reported harvests (Appendix S1: Table S4, Fig. S3). The male:female sex ratio of harvested animals was 70:30 for adults and 60:40 for juveniles. Age and sex ratios of harvested otters varied little across years and focal subregions (Appendix S1: Table S4, Fig. S3), regardless of total number of animals harvested (Appendix S1: Table S3).

Our examination of factors potentially explaining variation in annual sea otter harvest rates found that inclusion of the random effect of subregion improved model performance (ΔAIC = 20.25). The best-supported mixed-effects model included linear and quadratic effects of years of sea otter occupation, a negative effect of sea otter population density (de-trended for occupation time), and a positive effect of proximity to sea otter hunters (Table 4). These results indicate that, on average, harvest rate increases after initial colonization, then stabilizes, and eventually decreases. Furthermore, our results on the temporal patterns of sea otter harvest (above) indicate that even after sea otters colonize a subregion, like Keku Strait, hunting may not immediately increase. After controlling for years of sea otter occupation, subregions with higher sea otter densities had lower harvest rates. Finally, subregions with greater proximity to more hunters experienced higher harvest rates.

The spatial extent of sea otter harvest increased from 1988 to 2015, following the range expansion of sea otters. By 2015, harvest had occurred in nearly all subregions that sea otters occupied. Only the Glacier Bay subregions GBYB and GBYC and N01, and N10 had no reported sea otter harvest (Appendix S1: Table S3).

Simulation model: estimating harvest effects on sea otter population dynamics

The simulation model produced estimated trends at both the SEAK stock and subregion scales that were consistent with observed trends based on survey data (compare Fig. 2a–d to Fig. 3a–d). Visual comparison between survey-based estimates of abundance and simulation-based estimates suggested good agreement for subregions all but GBY, where the simulation-based estimates were lower than survey-based estimates (Appendix S1: Fig. S2).

Comparison of simulations between harvest and no-harvest scenarios indicated that harvest of sea otters reduced sea otter growth for the SEAK stock and for the three focal subregions. However, the relative magnitude of this reduction varied among subregions (Fig. 3a–d). For the SEAK stock, the difference between harvest and no-harvest scenarios was evident in the early 1990s. Simulations including harvest showed 15–20% lower abundances relative to simulations without harvest in all years after 1990 (Fig. 3a, e). In the Sitka Sound subregion, the effect of harvest was more striking. From 1994 to 2010, simulations including harvest showed abundances that were approximately 20% lower relative to simulations without harvest. This difference increased sharply after 2010, when the simulations including harvest indicated population declines (Fig. 3b). By 2015, simulations including harvest predicted 50–70% lower sea otter abundance than simulations without harvest (Fig. 3f). In Keku Strait, the impacts of harvest did not precipitate a population decline, but harvest mortality was associated with a reduction in the rate of population increase after the area was colonized in the mid-2000s (Fig. 3c). Simulations including harvest showed a reduction in abundance of approximately 75% relative to simulations without harvest between 2011 and 2015 (Fig. 3g). Model results from the Maurelle Islands indicated a more limited effect of harvest than in Sitka Sound or Keku Strait subregions, with a slight reduction in the rate of growth associated with harvest mortality (Fig. 3d). Simulations including harvest showed a significant reduction in abundance relative to no-harvest

Table 4. Regression output of the best fit model testing the effects of years of sea otter occupation, sea otter population density, human population effect, and sea otter hunter effect on square root-transformed annual harvest rates.

Effect	Estimate	Lower	Upper	SE	*t*	*P*
Random effect of subregion						
Intercept	0.1166	0.0798	0.1703			
Residual	0.2018	0.1883	0.2164			
Fixed effect						
Intercept	0.0376			0.0430	0.8747	0.3823
Years of sea otter occupation	0.0087			0.0038	2.3016	0.0219
Years of sea otter occupation^2	−0.0002			0.0001	−2.1340	0.0212
Sea otter population density	−0.1565			0.0422	−3.7064	0.0002
Sea otter hunter	2.6655			1.2439	2.1429	0.0327

Note: SE, standard error.

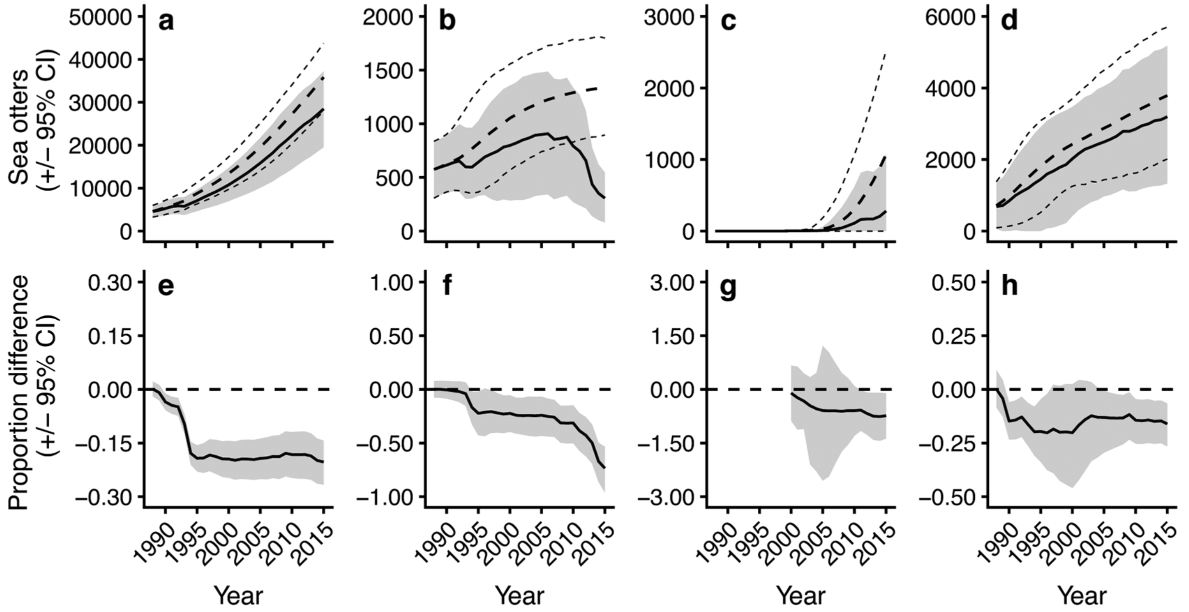

Fig. 3. (a–d) Results from sea otter population simulation models (±95% confidence intervals [CIs]) without reported harvest (dashed lines) and with reported harvest (solid lines and shading). (e–h) Proportional difference (±95% CIs) between simulation model runs with and without reported sea otter harvest calculated from 10,000 bootstrap samples from 1988 to 2015 from (a, e) SEAK, (b, f) Sitka Sound, (c, g) Keku Strait, and (d, h) the Maurelle Islands. Simulation model harvest rate was calculated as the proportion of reported harvest to modeled sea otter population preharvest. Note difference in *y*-axis scale of (a–d) annual sea otter abundance plots, and (e–h) proportional difference plots.

simulations between 1990 and 1996 and between 2005 and 2015. Simulations including harvest predicted a population size approximately 15–20% lower than no-harvest simulations (Fig. 3h).

In summary, simulation models including sea otter harvest predicted a lower abundance of sea otters as compared to models without harvest. However, harvest was not necessarily associated with population declines at the SEAK or subregional level. The exception to this pattern was Sitka Sound, where the simulation estimated that the sea otter population declined from 575 (309–838, 95% CI) in 1988 to 307 (81–546, 95% CI) in 1998, presumably in response to high harvest rates (Fig. 3b).

DISCUSSION

Our analysis of 27 yr of sea otter harvest data, combined with the results of a spatially structured population simulation model built around these data, demonstrates that harvest mortality has strongly influenced population trends in SEAK. However, our results also highlight the importance of considering spatial scale and demographic context when evaluating harvest trends and effects on population dynamics. Patterns of harvest at the entire SEAK stock scale were comparatively muted to the patterns seen at the subregional scale, which showed much more year-to-year variability. The effects of harvest were most apparent at subregional scales and less evident at the scale of the entire SEAK stock, consistent with other recent findings indicating that demographic processes in sea otter populations are structured at relatively small scales (Garshelis and Garshelis 1984, Tarjan and Tinker 2016, Tinker et al. 2019*a*). Thus, concentrated local harvest mortality can have substantial impacts on trends at these scales, even causing local declines. However, sea otter population status with respect to carrying capacity appeared to mediate these effects. Moreover, the magnitude of harvest rate in a given area depended on both the social context (proximity to communities with hunters) and the number of years since that area was first colonized by sea otters.

A key insight gained from our simulation model was that the effects of harvest on population status were most relevant at spatial scales smaller than the SEAK stock scale at which management currently operates. At the SEAK stock scale, sea otter populations may be resilient to periods of high harvest, especially if they are followed by periods of low harvest. This resilience may be explained in part by the heterogeneity of sea otter population dynamics and carrying capacity across SEAK. For example, our analyses and other modeling efforts (Tinker et al. 2019*a*) showed that while some subregions may experience decline or reduced growth rate, they were usually compensated by other subregions experiencing high growth. Synchronous elevated mortality across the entire region, such as occurred in the early 1990s, resulted in a brief cessation of population recovery at the stock scale, but this was the exception rather than the rule. In contrast, year-to-year patterns of population growth or decline at the subregional scale were more closely coupled to variation in harvest rate. The difference between stock and subregional patterns of harvest and population effects highlights the challenge of detecting impacts of localized perturbations at larger spatial scales. As seen in the range of environmental gradients across Hawaiian monk seal (*Monachus schauinslandi*) populations (Schmelzer 2000, Baker et al. 2007) and predatory control of coyotes (*Canis latrans*; Mahoney et al. 2018), a clear understanding of the demographic impacts and context of a given perturbation is best achieved by monitoring dynamics at the appropriate spatial scale. For species which have high site fidelity and small home ranges, localized disturbances can have outsized effects possibly leading to genetic bottlenecking, as seen in sea otters (Larson et al. 2002, 2012) and wolves (Moura et al. 2014).

Considering harvest in terms of a population's carrying capacity can be essential for evaluating critical population thresholds or tipping points (Lande et al. 1995). Samuel and Foin (1983) suggested that a sea otter harvest rate between 2% and 4% of an established population at or near carrying capacity may lead to a stable, albeit lower, sea otter population in approximately 25 yr. Furthermore, Samuel and Foin (1983) and Tinker et al. (2019*a*) suggested that harvest rates greater than 8–10% may lead to population instability and decline. While these results do provide some guidelines for managers, they apply only to established populations at or near carrying capacity, and indeed, they assume availability of reliable estimates of carrying capacity at appropriate scales. Equilibrium densities for sea otters in SEAK are estimated to range from 0.65 to 16.89 sea otters/km^2 with a mean of 4.20 sea otters/km^2 (±1.58 SD; Tinker et al. 2019*a*; Appendix S1: Table S2). Variability across space in equilibrium densities, combined with differences in occupation time and current densities, implies that sustainable harvest levels also could vary widely. For example, Sitka Sound, a long-established subregion thought to be near carrying capacity by the mid-1990s (Tinker et al. 2019*a*), has declined in recent years, likely in response to high levels of harvest (annual average harvest rate of 9.8%; Fig. 2j). In contrast, Keku Strait is a recently established and rapidly growing population, still well-below carrying capacity, where similar harvest rates (above 10% or more) slowed but did not stop growth. Thus, to predict and manage harvest levels sustainably, it is important to consider the subregional population history and status with respect to carrying capacity in addition to the ecology of the species.

Our analysis also provided important insights into some of the factors that determine the magnitude of sea otter harvest rates, including sea otter population status and proximity to human communities, both of which vary across subregions in SEAK (van Vliet et al. 2010). On average, sea otter harvests were greater in subregions that were in close proximity to sea otter hunters. However, the realized per capita harvest rate also depended on how long sea otters had been in a subregion and the current density of the otter population in that location. The nonlinear relationship between harvest rate and years of sea otter occupation suggests that when sea otters first occupy an area, there were several years of increased harvest effort, perhaps in part as communities respond to depletion of local subsistence shellfish resources (Carswell et al. 2015). Therefore, harvest rate increased initially, but then tended to decrease over time as the sea otter population continued to grow and as individual otters responded by moving away from higher-risk areas near communities (Hoyt 2015). Thus, some combination of avoidance behavior by sea otters and numerical saturation (i.e., a type II functional response) ultimately led to a reduced per capita harvest rate. Furthermore, demand for sea otter pelts may not be as high as hunters anticipated, leading to oversupply of pelts, reducing the need to harvest more sea otters.

In addition to considering subregional scale processes in management, it has been suggested that viewing sea otter population and the human communities that harvest them as a coupled social–ecological system may improve management overall (van Vliet et al. 2015). In SEAK, the intensity of sea otter harvest has varied over time and space, with periods of elevated harvest associated with periods of increased information and outreach about sea otter hunting. The increase in hunting in the early 1990s may have been a result of increased awareness of the laws surrounding sea otter harvest. During that period, the USFWS led a series of meetings in SEAK communities to clarify the laws involving harvest of sea otters and other marine mammals under the MMPA (A. R. DeGange, *personal communication*). The number of unique sea otter hunters in SEAK increased from 8 in 1992 before these meetings to 55 in 1994 after these meetings. Similarly, in the early 2000s, regional and local Alaska Native organizations supported classes focused on fur sewing (Sealaska 2013, Eddy 2015, Baxter 2018). Furthermore, increased discussion of commercial and subsistence fishery impacts and proposed sea otter legislation likely contributed to greater awareness (Stedman et al. 2018, Carswell et al. 2015). Collectively, these events likely increased awareness of sea otter hunting in the regions and the number of unique hunters in SEAK has continued to increase, from 60 in 2009 to an overall high of 103 in 2014 (B. Benter, *personal communication*). Furthermore, our analyses found that increased hunter participation was linked to increased reported harvest rate (Table 4). A comprehensive and effective management strategy should therefore recognize and incorporate these social factors.

Our simulation model predicted spatial and temporal trends in sea otter populations consistent with those estimated from aerial survey data, indicating that our model successfully captured the key processes influencing population dynamics in sea otters. However, data availability and quality likely influenced model prediction accuracy at both subregional and stock scales. For example, harvest mortality estimates in our analyses were based only on reported sea otter harvest numbers, even though unreported sources of hunting mortality undoubtedly exist. As seen in the subsistence harvest of beluga whales in Cook Inlet, Alaska, inaccuracies in reported harvest numbers may occur when hunters shoot an animal but are unable to recover the body, a phenomenon called "struck and loss" (Mahoney and Shelden 2000). Estimates of struck and loss from subsistence harvest marine mammals can be high. For example, struck and loss estimates of walrus (*Odobenus rosmarus*) in Alaska average 42% (Fay et al. 1994) and of harp seals (*Pagophilus groenlandicus*) in the northeastern Atlantic range from 0% to 50% (Sjare and Stenson 2002). Currently, USFWS does not have empirical estimates of struck and loss for sea otter harvests in SEAK. Inaccuracies in the sex composition of reported harvests also could have affected estimates of hunting impacts on the population. Following general population dynamic theory, removal of females reduces the reproductive capacity of the population while removal of males does not, except in extreme cases (Bodkin and Ballachey 2010). The sex of a harvested sea otter is hunter-reported and is not necessarily confirmed by the tagger or USWFS, potentially introducing further unaccounted noise to the data. Finally, our data filtering procedure removed 605 harvest records from the analyses. While this is a small proportion of the dataset (5%), it could have had a disproportionate effect on results. Low harvest numbers can result in high harvest rates for newly established populations and have a large effect on growth, as observed for Keku Strait.

Another limitation of our simulation model is that it did not explicitly account for variation in extrinsic mortality factors that are known to influence sea otter population growth (although we did indirectly account for such factors via inclusion of environmental stochasticity in the model). Extrinsic mortality can occur due to variation in food availability or habitat quality (Laidre et al. 2001, 2002, Gregr et al. 2008, Tinker et al. 2017), predation mortality from sharks (Estes and Hatfield 2003, Tinker et al. 2016), killer whale (*Orcinus orca*; Estes et al. 1998), and bald eagles (*Haliaeetus leucocephalus*; Sherrod et al. 1975), disease-associated mortality (DeGange and Vacca 1989, Kreuder et al. 2003), and mortality associated with fisheries, including gillnet and crab pot fisheries that have the potential to entangle sea otters (Wendell et al. 1986, Hatfield et al. 2011), though reports of entanglement of sea otters in Alaska are rare (Worton et al. 2016). Inclusion of any or all of these factors (data permitting) could improve precision and accuracy of future models.

As predator populations continue to recover worldwide, ecologists, conservation biologists, managers, and other stakeholders are likely to face new questions regarding the management of these species (Silliman et al. 2018). In preparation for, or in response to, recovering predator populations, it will be important to re-examine the spatial context of current management frameworks and their ability to effectively manage spatially heterogeneous populations (Mahoney et al. 2018). Our analyses showed that spatial scale, proximity to human settlements, and status and trends of the local population are all important considerations when evaluating the effects of harvest on SEAK sea otter populations. Historically, observer-based aerial surveys have been the primary tool to monitor sea otter populations. While these surveys provide comprehensive data on abundance, they are expensive and time-consuming and therefore have occurred infrequently, at intervals of 7–10 yr (USFWS 2008, 2014*b*). In light of the growing conflicts between humans and recovering sea otter populations and the spatial heterogeneity of status, trends, and equilibrium densities (Tinker et al. 2019*a*), a new approach may be necessary to help resolve some of these issues. To improve current management of sea otters in SEAK, we recommend (1) collecting sea otter population data at the subregional scale and at more regular intervals, perhaps through repeatedly sampling index sites; and (2) expanding harvest data collection to include information on struck and loss, hunter effort, and improve consistency of hunting location accuracy. These goals may be achieved, in part, by changing the management paradigm to one of a social–ecological system rather than considering harvest, population dynamics, and human interests in isolation (van Vliet et al. 2015). If the spreading sea otter population in SEAK and other predator populations around the world are to coexist with human interests, more contemporary approaches to management and conservation are needed to ensure future sustainability of those populations.

ACKNOWLEDGMENTS

This research was supported by Alaska Sea Grant, University of Alaska Fairbanks (project R/111-03), with funds from the National Oceanic and Atmospheric Administration (grant NA14OAR4170079), and from the University of Alaska with funds appropriated by the state of Alaska, and a National Science Foundation Graduate Research Fellowship awarded to Wendel Raymond. This study was completed in partial fulfillment of the requirements for Wendel Raymond's PhD at the University of Alaska Fairbanks. We kindly thank the sea otter hunters and taggers for providing data, without which, this study would not have been possible. We also thank the U.S. Fish and Wildlife Service (USFWS) for funding and running the Marking, Tagging, and Reporting Program and their employees who diligently maintained the subsistence harvest database. We thank Franz Mueter, Anne Beaudreau, and Aaron Galloway and two anonymous reviewers whose comments greatly improved the manuscript. The findings and conclusions in this manuscript are those of the authors and do not necessarily represent the views of the USFWS. Wendel Raymond led analyses and wrote the manuscript, M. Tim Tinker developed the population simulation model with Wendel Raymond and provided comments analyses and the manuscript, Michelle Kissling provided comments on analysis and reviewed the manuscript, Brad Benter manages the subsistence harvest database at USFWS and reviewed the manuscript, and Verena Gill and Ginny Eckert conceived the original project and provided comments on analyses and the manuscript.

LITERATURE CITED

Baker, J. D., J. J. Polovina, and E. A. Howell. 2007. Effect of variable oceanic productivity on the survival of an upper trophic predator, the Hawaiian monk seal *Monachus schauinslandi*. Marine Ecology Progress Series 346:277–283.

Baxter, A. 2018. Otter skin-sewing workshops promote 'sustainable cottage industry' in coastal Alaska. https://www.ktoo.org/2018/11/23/otterskin-sewing-workshops-promote-sustainable-cottage-industry-in-coastal-alaska/

Bodkin, J. L. 2015. Historic and contemporary status of sea otters in the North Pacific. Pages 43–61 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. Sea otter conservation. Academic Press, Boston, Massachusetts, USA.

Bodkin, J. L., and B. E. Ballachey. 2010. Modeling the effects of mortality on sea otter populations. Scientific Investigations Report 2010-5096. U.S. Geological Survey, Reston, Virginia, USA.

Bodkin, J. L., and M. S. Udevitz. 1999. An aerial survey method to estimate sea otter abundance. Pages 13–26 *in* G. W. Garner, S. C. Amstrup, J. L. Laake, B. F. J. Manly, L. L. McDonals, and D. C. Robertson, editors. Marine mammal survey and assessment methods. A.A. Balkema, Rotterdam, The Netherlands.

Burris, O., and D. McKnight. 1973. Game transplants in Alaska. Wildlife Technical Bulletin No. 4. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Carswell, L. P., S. G. Speckman, and V. A. Gill. 2015. Shellfish fishery conflicts and perceptions of sea otters in California and Alaska. Pages 333–368 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaircom, editors. Sea otter conservation. Academic Press, Boston, Massachusetts, USA.

Caswel, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

DeGange, A. R., and M. M. Vacca. 1989. Sea otter mortality at Kodiak Island, Alaska, during summer 1987. Journal of Mammalogy 70:836–838.

Doroff, A., and A. Burdin. 2015. *Enhydra lutris*, sea otter. *In* IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Dunning, J. B., B. J. Danielson, H. R. Pulliam, and I. Ecology. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.

Eberhardt, L. 1995. Using the Lotka-Leslie model for sea otters author. Journal of Wildlife Management 59:222–227.

Eddy, R. 2015. Sea otter sewing class offered in Hydaburg. https://www.krbd.org/2015/09/04/sea-otter-sewing-class-in-hydaburg/

Erlandson, J. M., T. C. Rick, J. A. Estes, M. H. Graham, T. J. Braje, and R. L. Vellanoweth. 2005. Sea otters, shellfish, and humans: a 10,000 year record from San Miguel Island, California. Pages 58–69 *in* D. K. Garcelon and C. A. Schwemm. Proceedings of the Sixth California Island Symposium. Institute for Wildlife Studies, Eureka, California, USA.

Esslinger, G., and J. L. Bodkin. 2009. Status and trends of sea otter populations in southeast Alaska, 1969–2003. Pages 1–18 *in* Scientific Investigations Report 2009-5045. U.S. Geological Survey, Reston, Virginia, USA.

Estes, J. A., and B. B. Hatfield. 2003. Causes of mortality in California sea otters during periods of population growth and decline. Marine Mammal Science 19:198–216.

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

Fay, F. H., J. J. Burns, S. W. Stoker, and J. S. Grundy. 1994. The struck-and-lost factor in Alaskan walrus harvests, 1952–1972. Arctic 47:368–373.

Fedje, D. W., R. J. Wigen, Q. Mackie, C. R. Lake, D. Ian, D. W. Fedje, R. J. Wigen, Q. Mackie, R. Cynthia, and I. D. Sumpter. 2001. Preliminary results from investigations at Kilgii Gwaay: an early holocene archaeological site on Ellen Island, Haida Gwaii, British Columbia. Canadian Journal of Archaeology 25:98–120.

Friends of the Sea Otter. 2018. Alaska program. http://www.seaotters.org/alaska-program/

Gagne, R. B., M. T. Tinker, K. D. Gustafson, K. Ralls, S. Larson, L. M. Tarjan, M. A. Miller, and H. B. Ernest. 2018. Measures of effective population size in sea otters reveal special considerations for wide-ranging species. Evolutionary Applications 11:1779–1790.

Garshelis, D. L., and J. A. Garshelis. 1984. Movements and management of sea otters in Alaska. Journal of Wildlife Management 48:665.

George, J. C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20:755–773.

Gerber, L. R., M. T. Tinker, D. F. Doak, J. A. Estes, and D. A. Jessup. 2004. Mortality sensitivity in life-stage simulation analysis: a case study of southern sea otters. Ecological Applications 14:1554–1565.

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

Hatfield, B. B., J. A. Ames, J. A. Estes, M. T. Tinker, A. B. Johnson, M. M. Staedler, and M. D. Harris. 2011. Sea otter mortality in fish and shellfish traps: estimating potential impacts and exploring possible solutions. Endangered Species Research 13:219–229.

Hoyt, Z. N. 2015. Resource competition, space use and forage ecology of sea otters, *Enhydra lutris*, in southern southeast Alaska. University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Jameson, R. J. 1989. Movements, home range, and territories of male sea otter off central California. Marine Mammal Science 5:159–172.

Jameson, J., and A. Johnson. 1993. Reproductive characteristics of female sea otters. Marine Mammal Science 9:156–167.

Johnson, A. C., J. Noel, D. P. Gregovich, L. E. Kruger, and B. Buma. 2019. Impacts of submerging and emerging shorelines on various biota and indigenous Alaskan harvesting patterns. Journal of Coastal Research 35:765.

Kenyon, K. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna 68:1–352.

Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad, and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998–2001. Journal of Wildlife Diseases 39:495–509.

Laidre, K. L., R. C. Hobbs, G. R. VanBlaricom, R. J. Jameson, S. J. Jeffries, and C. E. Bowlby. 2002. Estimates of carrying capacity for sea otters in Washington State. Wildlife Society Bulletin 30:1172–1181.

Laidre, K. L., R. J. Jameson, and D. P. Demaster. 2001. An estimation of carrying capacity for sea otters long the California coast. Marine Mammal Science 17:294–309.

Laidre, K. L., R. J. Jameson, E. Gurarie, S. J. Jeffries, and H. Allen. 2009. Spatial habitat use patterns of sea otters in coastal Washington. Journal of Mammalogy 90:906–917.

Lande, R., S. Engen, and B.-E. Saether. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. American Naturalist 145:728–745.

Larson, S. D., Z. N. Hoyt, G. L. Eckert, and V. A. Gill. 2013. Impacts of sea otter (*Enhydra lutris*) predation on commercially important sea cucumbers (*Parastichopus californicus*) in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 70:1498–1507.

Larson, S., R. Jameson, M. Etnier, M. Fleming, and P. Bentzen. 2002. Loss of genetic diversity in sea otters (*Enhydra lutris*) associated with the fur trade of the 18th and 19th centuries. Molecular Ecology 11:1899–1903.

Larson, S., R. Jameson, M. Etnier, T. Jones, and R. Hall. 2012. Genetic diversity and population parameters of sea otters, *Enhydra lutris*, before fur trade extirpation from 1741–1911. PLOS ONE 7:e32205.

Mahoney, B. A., and K. E. W. Shelden. 2000. Harvest history of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. Marine Fisheries Review 62:124–133.

Mahoney, P. J., J. K. Young, K. R. Hersey, R. T. Larsen, B. R. McMillan, and D. C. Stoner. 2018. Spatial processes decouple management from objectives in a heterogeneous landscape: predator control as a case study. Ecological Applications 28:786–797.

Minerals Management Service. 2009. Alaska native hunters and whalers: actively engage in satellite tracking studies. Ocean Science 6:7–9.

Monnett, C., and L. Rotterman. 2000. Survival rates of sea otter pups in Alaska and California. Marine Mammal Science 16:794–810.

Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. Oikos 90:457–468.

Moura, A. E., E. Tsingarska, M. J. Dabrowski, S. D. Czarnomska, B. Jedrzejewska, and M. Pilot. 2014. Unregulated hunting and genetic recovery from a severe population decline: the cautionary case of Bulgarian wolves. Conservation Genetics 15:405–417.

North Slope Borough. 2018. Bowhead whales. http://www.north-slope.org/departments/wildlife-management/studies-and-research-projects/bowhead-whales

Phillips, C. D., J. I. Hoffman, J. C. George, R. S. Suydam, R. M. Huebinger, J. C. Patton, and J. W. Bickham. 2013. Molecular insights into the historic demography of bowhead whales: understanding the evolutionary basis of contemporary management practices. Ecology and Evolution 3:18–37.

Pitcher, K. 1989. Studies of southeastern Alaska sea otter populations: distribution, abundance population growth, range expansion and population productivity. U. S. Fish and Wildlife Service, Anchorage, Alaska, USA.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riedman, M. L., and J. A. Estes. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. Pages 1–136 *in* Biological Report 90. U. S. Department of Interior Fish and Wildlife Service, Washington, D. C., USA.

Riedman, M. L., J. A. Estes, M. M. Staedler, A. A. Giles, and D. R. Carlson. 1994. Breeding patterns and reproductive success of California sea otters Journal of Wildlife Management 58:391–399.

Riedman, M. L., J. A. Estes, M. M. Staedler, A. A. Giles, and D. R. Carlson. 2019. Breeding patterns and reproductive success of California sea otters. Journal of Wildlife Management 58:391–399.

Robinson, D., E. Hunsinger, E. Sandber, and L. Brooks. 2017. Alaska Boroughs and Census Areas. *In* Alaska population overview: 2016 estimates. Alaska Department of Labor and Workforce Development, Juneau, Alaska, USA.

Roman, J., M. M. Dunphy-Daly, D. W. Johnston, and A. J. Read. 2015. Lifting baselines to address the consequences of conservation success. Trends in Ecology and Evolution 30:299–302.

Samuel, M. D., and T. C. Foin. 1983. Exploiting sea otter populations: a simulation analysis. Ecological Modelling 20:297–309.

Schmelzer, I. 2000. Seals and seascapes: covariation in Hawaiian monk seal subpopulations and the oceanic landscape of the Hawaiian Archipelago. Journal of Biogeography 27:901–914.

Sealaska, H. 2013, March 7. SHI to sponsor skin-sewing workshops. Juneau Empire, Juneau, Alaska, USA.

Shaffer, C. A., M. S. Milstein, C. Yukuma, E. Marawanaru, and P. Suse. 2017. Sustainability and comanagement of subsistence hunting in an indigenous reserve in Guyana. Conservation Biology 31:1119–1131.

Shepard, D. 1968. A two-dimensional interpolation function for irregularly-spaced data. Pages 517–524 *in* Proceedings of the 1968 23rd ACM National Conference. ACM Press, New York, New York, USA.

Sherrod, S. K., J. A. Estes, and C. M. White. 1975. Depredation of sea otter pups by bald eagles at Amchitka Island, Alaska. Journal of Mammalogy 56:701.

Silliman, B. R., B. B. Hughes, L. C. Gaskins, Q. He, M. T. Tinker, A. Read, J. Nifong, and R. Stepp. 2018. Are the ghosts of nature's past haunting ecology today? Current Biology 28:R532–R537.

Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. Marine Mammal Science 7:211–299.

Sjare, B., and G. B. Stenson. 2002. Estimating struck and loss rates for harp seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. Marine Mammal Science 18:710–720.

Stedman, B., et al. 2018. Urging co-management plan for sea otters. Pages 1–5. Alaska State Senate, Juneau, Alaska, USA.

Szpak, P., T. J. Orchard, I. McKechnie, and D. R. Gröcke. 2012. Historical ecology of late Holocene sea otters (*Enhydra lutris*) from northern British Columbia: isotopic and zooarchaeological perspectives. Journal of Archaeological Science 39:1553–1571.

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

Tinker, M. T. 2015. The use of quantitative models in sea otter conservation. Pages 257–300 *in* S. Larson, J. L. Bodkin, and G. R. Vanblaircom, editors. Sea otter conservation. Elsevier, Amsterdam, The Netherlands.

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

Tinker, M. T., D. F. Doak, J. A. Estes, B. B. Hatfield, M. M. Staedler, and J. L. Bodkin. 2006. Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. Ecological Applications 16:2293–2312.

Tinker, M. T., V. A. Gill, G. G. Esslinger, J. Bodkin, M. Monk, M. Mangel, D. H. Monson, W. W. Raymond, and M. L. Kissling. 2019*a*. Trends and carrying capacity of sea otters in southeast Alaska. Journal of Wildlife Management 83:1073–1089.

Tinker, M. T., et al. 2019*b*. 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. U. S. Geological Survey, Reston, Virginia, USA.

Tinker, M. T., B. B. Hatfield, M. D. Harris, and J. A. Ames. 2016. Dramatic increase in sea otter mortality from white sharks in California. Marine Mammal Science 32:309–326.

Tinker, M. T., J. Tomoleoni, N. LaRoche, L. Bowen, A. K. Miles, M. Murray, M. Staedler, and Z. Randell. 2017. Page 76 *in* Southern sea otter range expansion and habitat use in the Santa Barbara Channel, California. U.S. Geological Survey, Reston, Virginia, USA.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171–197.

U. S. Census Bureau. 2010. United States census. U. S. Census Bureau, Suitland, Maryland, USA.

USFWS. 2008. Northern sea otter (*Enhydra lutris kenyoni*): Pages 1–6 *in* Southeast Alaska Stock 2000. U. S. Fish and Wildlife Service, Anchorage, Alaska, USA.

USFWS. 2014*a*. Sea otter tagging statistics by hunt origin. USFWS, Anchorage, Alaska, USA.

USFWS. 2014*b*. USFWS Stock Assessment Reports – Northern Sea Otter (*Enhydra lutris kenyoni*): Southeast Alaska Stock. USFWS, Anchorage, Alaska, USA.

van Vliet, N., J. Fa, and R. Nasi. 2015. Managing hunting under uncertainty: from one-off ecological indicators to esilience approaches in assessing the sustainability of bushmeat hunting. Ecology and Society 20:7.

van Vliet, N., E. J. Milner-Gulland, F. Bousquet, M. Saqalli, and R. Nasi. 2010. Effect of small-scale heterogeneity of prey and hunter distributions on the sustainability of bushmeat hunting. Conservation Biology 24:1327–1337.

Wendell, F. E., R. A. Hardy, and J. A. Ames. 1986. An assessment of the accidental take of sea otters, *Enhydra lutris*, in gill and trammel nets. Marine Resources Technical Report No. 54. California Department of Fish and Game, Sacramento, California, USA.

Worton, C., K. Nesvacil, P. Tschersich, R. Baer, and V. Gill. 2016. Dungeness crab pot survey and spatial monitoring of sea otter bycatch in Ugak Bay, the Trinity Islands, and Alitak Bay in the Kodiak area, 2014. Alaska Department of Fish and Game, Division of Sport Fish, Research and Technical Services, Anchorage, Alaska, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2874/full