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Research Article

Trends and Carrying Capacity of Sea Otters in Southeast Alaska

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ABSTRACT Sea otter populations in Southeast Alaska, USA, have increased dramatically from just over 400 translocated animals in the late 1960s to >8,000 by 2003. The recovery of sea otters to ecosystems from which they had been absent has affected coastal food webs, including commercially important fisheries, and thus information on expected growth and equilibrium abundances can help inform resource management. We compile available survey data for Southeast Alaska and fit a Bayesian state-space model to estimate past trends and current abundance. Our model improves upon previous analyses by partitioning and quantifying sources of estimation error, accounting for over-dispersion of aerial count data, and providing realistic measurements of uncertainty around point estimates of abundance at multiple spatial scales. We also provide estimates of carrying capacity (K) for Southeast Alaska, at regional and sub-regional scales, and analyze growth rates, current population status and expected future trends. At the regional scale, the population increased from 13,221 otters in 2003 to 25,584 otters in 2011. The average annual growth rate in southern Southeast Alaska (7.8%) was higher than northern Southeast Alaska (2.7%); however, growth varied at the sub-regional scale and there was a negative relationship between growth rates and the number of years sea otters were present in an area. Local populations vary in terms of current densities and expected future growth; the mean estimated density at K was 4.2 ± 1.58 sea otters/km^2 of habitat (i.e., the sub-tidal benthos between 0 m and 40 m depth) and current densities correspond on average to 50% of projected equilibrium values (range = 1–97%) with the earliest-colonized sub-regions tending to be closer to K. Assuming a similar range of equilibrium densities for currently un-occupied habitats, the projected value of K for all of Southeast Alaska is 74,650 sea otters. Future analyses can improve upon the precision of K estimates by employing more frequent surveys at index sites and incorporating environmental covariates into the process model to generate more accurate, location-specific estimates of equilibrium density. © 2019 The Authors. *The Journal of Wildlife Management* Published by Wiley Periodicals, Inc.

KEY WORDS aerial survey, Bayesian model, density dependence, *Enhydra lutris*, population abundance, sea otter, state space model.

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Large carnivore species have historically been threatened by human activities (Ripple et al. 2014); however, after decades of concerted management efforts aimed at protecting and restoring endangered carnivore populations, some species are recovering (Roman et al. 2015). As depleted carnivore populations have recovered, it has become evident that they can have

disproportionately large effects on the ecosystems they return to. For example, recovering wolf (*Canis lupus*) populations in western North America indirectly affect riparian vegetation regimes via their influence on elk (*Cervus elaphus*) abundance and habitat use (Beschta and Ripple 2009), and recovered alligator (*Alligator mississippiensis*) populations in southeastern North America exert top-down regulation of salt-marsh food webs (Nifong and Silliman 2013). To properly understand the scope and magnitude of ecological effects of recovering carnivore populations, it is important to obtain accurate and precise information on their abundance and distribution. Moreover, managers often wish to anticipate population trends and predict carnivore densities at equilibrium (i.e., environmental carrying capacity [*K*]). Estimates of equilibrium abundances are especially important when they influence management actions (e.g., populations may no longer require legal protection as they approach *K*), and when they are used to predict future effects on natural resources or conflicts over commercially valuable species that the recovering carnivore may consume.

Sea otters (*Enhydra lutris*) are apex carnivores in nearshore marine ecosystems of the North Pacific that declined to near-extinction during the fur trade but have gradually recovered since the mid-1900s (Kenyon 1969, Bodkin 2015). Recovery over much of their historical range in North America resulted from successful management actions, such as translocations of sea otters in the 1960s and 1970s (Burris and McKnight 1973). In Southeast Alaska, USA, sea otter populations increased from fewer than 500 animals translocated from Amchitka Island and Prince William Sound in the late 1960s (Jameson et al. 1982) to an estimated >8,000 animals by 2003 (Esslinger and Bodkin 2009). The recovery of sea otters to ecosystems and locales from which they had been absent for almost a century has had profound effects on food web structure and dynamics in rocky and soft-sediment areas (Kvitek et al. 1992, Estes et al. 2004). Some of these changes are considered beneficial, such as increased productivity in kelp (e.g., *Macrocystis pyrifera*, *Nereocystis leutkeana*, *Alaria fistulosa*; Duggins et al. 1989), the associated restoration of ecosystem function (Estes et al. 2010, Estes 2015), and restoration of subsistence uses of sea otters by indigenous communities (Salomon et al. 2015). The recovery of sea otters, however, also leads to conflict with humans over particular marine resources, most notably large marine invertebrates (Wild and Ames 1974, Garshelis and Garshelis 1984, Carswell et al. 2015). In Southeast Alaska, sea otter recovery has resulted in conflicts with several commercial shell-fisheries (Larson et al. 2013, Hoyt 2015). Reliable information on current sea otter distribution and abundance and projections of future population dynamics and range spread, will help resource managers anticipate potential conflicts and tailor management strategies to benefit sea otters and human communities in Southeast Alaska.

Monitoring population abundance and trends of widely distributed carnivores often poses logistical and funding hurdles; in the case of sea otters in Southeast Alaska, the vast area and limited access (Fig. 1) have created substantial challenges to population assessment. A number of different methods have been employed at different times and over different areas, including skiff- and aerial-based surveys (Esslinger and Bodkin 2009). A standardized aerial survey method allows for bias-corrected estimates of abundance

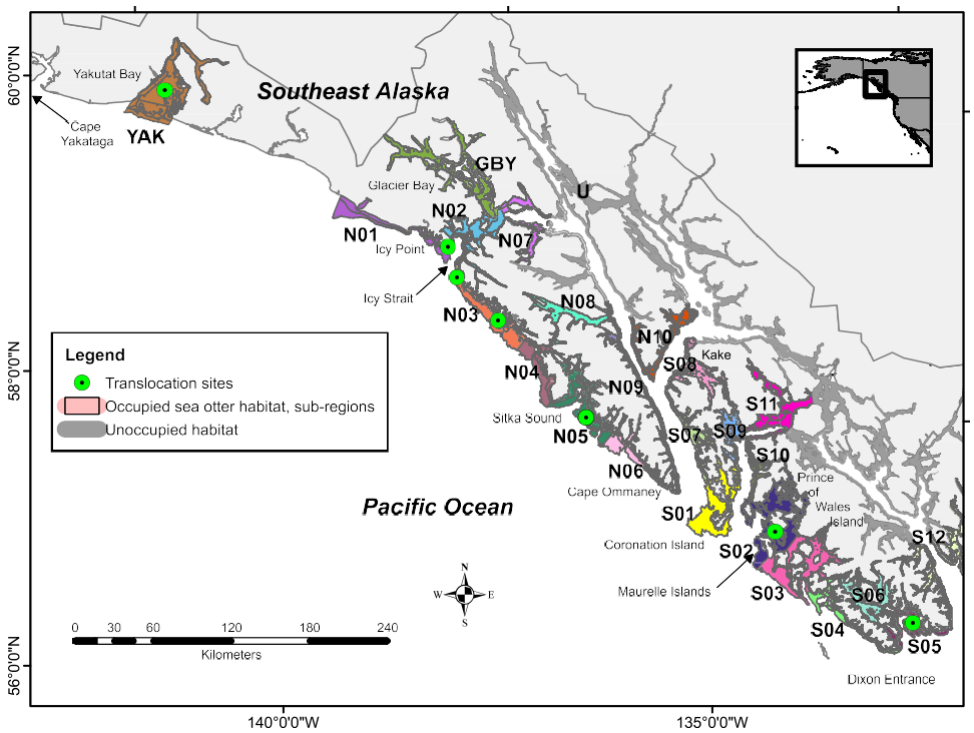

Figure 1. Southeast Alaska, USA, showing existing or potential sea otter habitat as-of 2012, defined as the nearshore zone <100 m in depth. Habitat is divided into currently un-occupied areas (dark gray shaded areas) and occupied areas (colored polygons), with the latter divided into smaller sub-regions for the purpose of analysis and labeled with sub-region identifiers. Also shown are the 7 sea otter translocation sites (green circles).

(Bodkin and Udevitz 1999); however, because of the associated cost and time commitments, large-scale surveys using this method are conducted infrequently. The disparate methods, piecemeal spatial coverage, and infrequent timing of past surveys has hampered assessment of population abundance and dynamics over all of Southeast Alaska (Esslinger and Bodkin 2009), though analyses of abundance and trends have been completed for some smaller areas such as Glacier Bay (Fig. 1; Esslinger et al. 2015, Williams et al. 2017). Moreover, because the population is apparently still recovering and expanding its range, with large areas of unoccupied habitat remaining (Fig. 1), no quantitative estimates of carrying capacity have been made, leaving uncertainty about how long the population will keep growing and what densities will look like at equilibrium. Obtaining a full picture of past sea otter trends, and potential growth into the future, demands a flexible analytical approach that can make use of multiple data types and sparse or incomplete time series.

In recent years, state-space models have been employed as powerful tools in the analysis of population abundance and trends (Berliner 1996, Royle and Dorazio 2008). These models have a number of distinct advantages over traditional analyses of survey data (Cressie et al. 2009). By explicitly separating the state process (the fixed and random effects that cause variation in population abundance) from the observation process (the functional relationship between true abundance and survey data), they allow for partitioning of variance into process error and observer error components, and provide clearer insights into trends and ecological mechanisms (Berliner 1996). State-space models are well suited to analysis using Bayesian methods, which can easily incorporate multiple data types with different error structures (often collected at different temporal or spatial scales), enable the use of prior information to improve parameter estimates, and allow random effects in both state and observer processes to be treated as hierarchical stochastic variables (Congdon 2010). Previous researchers have used Bayesian state-space models to analyze line transect survey data and make probabilistic inferences about abundance, trends, and population parameters (Gerrodette et al. 2011, Moore and Barlow 2011). We used Bayesian methods to analyze and integrate the various survey data sets available, including a previously unreported dataset collected in 2010–2012, for sea otters in Southeast Alaska. Our goals were to provide a comprehensive picture of population trends and abundance estimates at different spatial scales and to estimate equilibrium densities of sea otter populations in Southeast Alaska, and how they vary over space, as a tool to help resource managers anticipate ecological effects of sea otters and plan future monitoring activities.

STUDY AREA

Southeast Alaska is defined as the region of Alaska east of 144°W longitude, consisting of the large group of islands called the Alexander Archipelago and a narrow strip of mainland separated from the remainder of North America by the vast Coastal Mountain Range (Fig. 1). The region is roughly 900 km long, averages 230 km in width, and encompasses approximately 25,000 km of shoreline. The coastal landscape of Southeast Alaska is characterized by rugged topography, varying in elevation from sea level to 5,489 m, and the coastline consists of a complex shoreline of inlets, bays, glacial fjords, and over 2,000 islands. The terrestrial landscape is dominated by temperate rainforest, some of which has been altered by commercial timber harvest, intermixed with mountainous terrain, wetlands, and various fine-scale disturbances (e.g., wind-throw). Dominant flora and fauna are typical of Pacific northwest temperate rain forests (O'Clair et al. 1997). Most of the land is managed by the United States Forest Service as the Tongass National Forest (~80%) and the National Park Service as Glacier Bay National Park and Preserve (~12%). Southeast Alaska has a cool, wet maritime climate with 75–500 cm of precipitation distributed evenly through the year.

The Southeast Alaska stock of sea otters is one of 3 recognized sea otter stocks in Alaska and is bounded by Cape Yakataga in the north and the Dixon Entrance in the south (Fig. 1). Unlike the Southwest Alaska stock, the Southeast Alaska stock is not listed under the United States Endangered Species Act (ESA), though it is protected under the United States Marine Mammal Protection Act (MMPA; U.S. Fish and Wildlife Service [USFWS] 2014). The United States Geological Survey (USGS) and USFWS conducted standardized aerial surveys of sea otters in Southeast Alaska in 2002–2003 and 2010–2011, respectively (Bodkin and Udevitz 1999, Esslinger and Bodkin 2009, USFWS, unpublished data). The northern half of the region (northern Southeast Alaska), from Icy Point to Cape Ommaney, was surveyed in 2002 and 2011, and the southern half of the region (southern Southeast Alaska), from Kake to Dixon Entrance, was surveyed in 2003 and 2010. Surveys of Glacier Bay National Park (in northern Southeast Alaska) were conducted using similar methods (but using randomized replicate surveys) between 1999 and 2012 (Esslinger et al. 2015) and replicate aerial surveys of Yakutat Bay also were completed in 1995 and 2005 (Doroff and Gorbics 1997, Gill and Burn 2007).

Sea otters inhabit coastal waters, with their offshore range limited by bottom depth and their capability to dive for food (Estes and Riedman 1990, Bodkin et al. 2004). For the purpose of standardized surveys, otter habitat typically is divided into high-density and low-density strata based on the likelihood of an animal occurring in that strata given the bathymetry (Bodkin and Udevitz 1999). The high-density stratum extends over water <40 m in depth or up to 400 m from shore where water depth exceeds 40 m, and also includes embayments with narrow entrances (Bodkin and Udevitz 1999). The low-density stratum is bounded by the offshore boundary of the high-density stratum out to the 100-m-depth contour or 2 km from shore, whichever is greater.

To facilitate the incorporation of demographic structure within our analyses, we further divided sea otter habitat into 24 sub-regions, contiguous spatial polygons that encompass

the coastal areas of Southeast Alaska occupied by sea otters at the time of the most recent survey (Fig. 1), though aerial survey data are available for only 21 of these. We defined sub-regions in such a way as to be large enough so that intrinsic demographic processes (births and deaths) would have far greater influence on trends than movement between sub-regions over limited time frames (the period between adjacent surveys), but small enough so that otters within a sub-region can be viewed as a mixed population experiencing similar environmental and density-dependent conditions. The average area of high-density habitat within delineated sub-regions was 461 km^2 (SD = 283), approximately 100 times the area of a typical sea otter annual home range (Tarjan and Tinker 2016), though males moving between frontal zones and established female areas may routinely travel ≥100 km between areas (Garshelis and Garshelis 1984). We defined boundaries between sub-regions arbitrarily, although we used natural geographic boundaries wherever possible to minimize the potential influence of immigration and emigration.

METHODS

Survey Methods

Skiff-based surveys and aerial surveys have been used to estimate abundance and distribution of sea otters in Southeast Alaska (Esslinger and Bodkin 2009), although only the aerial survey methods analyzed for this paper provide data necessary to estimate abundance with corrections for imperfect detection and associated uncertainty. Skiff surveys were the primary method of population monitoring in Southeast Alaska prior to 1995 (Pitcher 1989), when numbers and occupied habitats were small. Skiff surveys consist of paired observers (observer and skiff operator, observer and recorder) in a small skiff (5–7 m long) moving parallel to the shoreline and counting all observed animals in high-density habitat (nearshore or in water depths <40 m). Offshore transects also are conducted when groups are sighted farther from shore or when habitat features indicate a likelihood of offshore animals. These skiff surveys were an attempt to provide a census of the population in occupied habitats but did not account for availability and sightability biases (Pitcher 1989). From 1993 to 1998, aerial surveys were flown to document the distribution and relative abundance of sea otters in portions of northern Southeast Alaska (Esslinger and Bodkin 2009). Beginning in 1999, a new aerial survey method (Bodkin and Udevitz 1999) was adopted to estimate sea otter abundance. This method consisted of strip transects flown at regularly spaced intervals generally perpendicular to the main coastline axis (spaced so as to sample a pre-determined proportion of available habitat), and with intensive search units (ISUs) flown periodically to determine numbers of otters not detected during transects and thus used to estimate a correction factor (Fig. S1, available online in Supporting Information).

Strip transect surveys (Caughley 1977) are a widely used method for estimating animal abundance, tracking population changes, and documenting habitat use. They are a special case of strip or line transect surveys, in which the distance from the animal to the observer is not recorded (Fewster et al. 2005) and one assumes that all individuals present along a strip transect of a pre-determined width are detected with a constant probability of detection. Any individuals detected at a distance farther than the strip transect width are excluded from the sighting probability model. Bodkin and Udevitz (1999) conducted a study to determine the ideal altitude and corresponding strip transect width (400 m) during aerial surveys for sea otters and a method for conducting ISUs to measure survey-specific detection probability. Selected systematically with the goal of conducting a pre-determined number of ISUs, an ISU is initiated after a group of ≥1 otters is detected on transect. The ISU is positioned tangentially and perpendicular to the direction of the aircraft (Fig. S1) and consists of 5 concentric circles flown within the 400-m strip transect. To avoid affecting sea otters in other ISUs, ≥60 seconds of flight time must pass after finishing one ISU before another ISU can be initiated. The observer records all otters (both adults and pups) sighted during the ISU: these include otters observed on transect and otters not detected (e.g., because they had been diving during the initial transect). The analysis assumes all otters are detected by the time the ISU is terminated, and the detection probability of sea otters by observers during these ISUs has been estimated at ≥0.96 (Bodkin and Udevitz 1999). The probability of detection on survey transects (p) is then calculated as the ratio of the number of otters counted on transects (within the bounds of ISUs) to the number of otters counted during ISUs, after first subtracting initiating groups from both tallies to avoid the bias that would result from including otters that are already known to have been detected (Bodkin and Udevitz 1999). Large groups (>20 individuals) are circled repeatedly until a photograph and a consistent count is obtained (complete counts), and thus these large groups are excluded from the estimate of detection probability and from detection probability correction in the final abundance estimate (i.e., detection is assumed to be 1.0 for large groups). All surveys were conducted under permits issued by the USFWS, as required by the United States Marine Mammal Protection Act (MMPA). Most aerial surveys were conducted under MMPA permit number MA067925 issued to USGS; the remainder (2005, 2010, 2011) were conducted under MMPA permit number MA041309 issued to USFWS.

Harvest Data

The United States Marine Mammal Protection Act prohibits direct harvest of sea otters and other marine mammals; however, exemptions are provided to coastal Alaska Native people provided that the harvest is done for the purposes of subsistence, or for creating and selling authentic native handicrafts and clothing, and that the harvest is not done in a wasteful manner (https://www.fws.gov/alaska/fisheries/mmm/hunting_seaotter.htm, accessed 30 Jan 2018; Marine Mammal Protection Act 16 U.S.C. 1361–1423 and the implementing regulations 50 C.F.R Part 18). Since 1988, the USFWS has recorded the

subsistence harvest of sea otters in Southeast Alaska as part of their marking, tagging, and reporting program (MTRP). When a sea otter is harvested, the hunter is required to report that harvest to a designated USFWS tagger, who records location and time of the harvest, age, and sex of the animal. These data are entered into the MTRP database. We extracted data on the reported numbers of animals harvested annually by sub-region because we suspected that accounting for harvest mortality could improve estimates of carrying capacity (see below).

Spatially Structured State Space Model

Our objective was to estimate the abundance of sea otters (N) across years (t) within designated sub-regions (i), using a process model that incorporates density-dependent population dynamics (in which carrying capacity is assumed to occur at the scale of sub-regions), range expansion and dispersal between sub-regions, harvest mortality, and environmental stochasticity. As part of model fitting, we derived local and regional estimates of K and characterized spatial variation in the density at K. The process model is explicitly related to a data model, consisting of the observed survey counts (C) and harvest records (H) for each sub-region at various points in time. To relate the process model to the data model, we built on previous analyses of aerial survey data (Esslinger and Bodkin 2009) in terms of our assumptions about corrections for otter detection probability and survey effort, and sources of uncertainty in each. The Bayesian approach allowed us to formally incorporate and estimate the variance associated with over-dispersed sea otter count data (reflecting non-random, clumped distribution of groups), accommodate missing or incomplete data (e.g., the absence of ISU data for the 2011 survey), make use of the replicated surveys available for some years and sub-regions to estimate observer-specific variation in detection probabilities among surveys, and characterize spatial variation in sea otter trends and equilibrium densities at varying scales.

Process model.—To describe sea otter population dynamics in Southeast Alaska, we built on previous studies showing that sea otter populations across the North Pacific demonstrate a consistent pattern of density-dependent growth (Estes 1990, Estes et al. 1996). Specifically, for populations not experiencing strong density-independent mortality such as predation or oil spill effects (Estes et al. 1998; Monson et al. 2000*a*, 2011; Bodkin et al. 2012), a simple logistic model describes sea otter population dynamics at local scales (Lafferty and Tinker 2014, Bodkin 2015, Tinker 2015). Populations increase predictably at a rate near the theoretical r_{max} (0.25) at low densities or in recently colonized habitats, but growth rate slows as density increases and populations approach K (Estes 1990). The density at which populations reach equilibrium (K', in units of otters/km^2 of habitat) varies depending on local habitat characteristics and prey productivity (Laidre et al. 2001, 2002; Burn et al. 2003; Gregr et al. 2008). In addition to density-dependent variation in growth, trends in abundance are affected by dispersal between areas, influences of non-density-dependent mortality factors such as predation (Estes et al. 1998), fishing entanglement (Hatfield et al. 2011), or harvest mortality (Bodkin and Ballachey 2010), and stochastic variation in annual mortality caused by factors such as infectious disease (Goldstein et al. 2011). Our process model incorporates all these features.

The variable of primary interest is $N_{i,t}$, the estimated abundance of otters in sub-region i at time t. At time $t = 1$ (which corresponds to 1975 in our model), sea otters had spread from the 7 translocation sites (Fig. 1) to become established in the 9 surrounding sub-regions (Fig. S2, available online in Supporting Information). We therefore initialize $N_{i,1}$ using the earliest reliable post-translocation estimates for these sub-regions (Schneider 1975), and to allow for uncertainty we use a gamma prior for $N_{i,1}$ with mean of $N_{init,i}$ (the 1975 point estimates; Table S1, available online in Supporting Information) and variance corresponding to a coefficient of variation of 0.2. We set $N_{i,1}$ to zero for all remaining sub-regions. For years $t = 2$ to $t = T$ (where T corresponds to 2012), we calculated population dynamics using the recursive equation:

$$N_{i,t} = N_{i,t-1}(\lambda_{i,t} - v \cdot \psi_{i,t}) + \sum_j D_{j,i,t} - \sum_j D_{i,j,t}, \quad (1)$$

where $\lambda_{i,t}$ represents the finite annual growth rate (reflecting both density dependence and stochasticity), the term $v \cdot \psi_{i,t}$ adjusts for the effect of annual harvest mortality (Liz and Hilker 2014), and the summation terms $\Sigma D_{j,i,t}$ and $\Sigma D_{i,j,t}$ adjust for dispersal of animals into sub-region i (immigration) and out of sub-region i (emigration).

The finite annual growth rate $\lambda_{i,t}$ combines discrete logistic population growth with environmental stochasticity. Specifically, the log-transformed growth rate in sub-region i at year t is assumed to be drawn from a random normal distribution:

$$log\,(\lambda_{i,t}) \sim Normal\,(\bar{x} = r_{max}(1 - N_{i,t-1}/K_i), \text{SD} = \sigma_e), \quad (2)$$

where r_{max} is the maximum intrinsic rate of growth, K_i is the estimated carrying capacity for sub-region i, and the standard error term σ_e (representing environmental stochasticity) is itself a fitted parameter (Table 1). We fixed r_{max} at a value of 0.25, based on previous studies demonstrating that r_{max} is essentially invariant across sea otter populations and has consistently been estimated as approximately 0.25 in both empirical studies and life-history theoretical models (Jameson et al. 1982, Estes 1990, Monson et al. 2000*b*, Gerber et al. 2004, Lafferty and Tinker 2014). We use a hierarchical approach for estimating K_i: specifically, we assume there is a median equilibrium density, $\bar{K}'$, which we treat as a hyper-parameter drawn from a uniform distribution. Log-transformed equilibrium densities for sub-regions are drawn from a normal distribution with mean equal to log ($\bar{K}'$):

$$\log(K'_i) \sim Normal\,(\bar{x} = \log(\hat{K}'), \text{SD} = \sigma_k), \quad (3)$$

where the standard error term σ_k is a fitted hyper-parameter (Table 1). We convert K'_i from density units (otters/km^2) to the

Table 1. Summary of Bayesian state-space model used to estimate population dynamics for sea otters in Southeast Alaska, USA. Equations are organized according to the hierarchical structure of the model: a data model (consisting of observed data sets), a process model (describing dynamics of the population and estimation of key population parameters), a set of equations relating the data model to the process model, and the prior model (probability distributions representing our prior knowledge of the model parameters).

Model component	Description
Data model	
$C_{i,t,d,g=sm,s} \sim Negative\ Binomial\ (\bar{x} = N_{i,t,d,g=sm} \cdot F_{i,t,d,s} \cdot p_s,\ \delta_{sm})$	Survey counts (C) for sub-region i, time t, strata d, and survey s, in small groups. Dispersion parameter (δ) determines degree of over-dispersion in counts. Mean expected value depends on true population abundance (N), fraction of area surveyed (F), and detection probability (p).
$C_{i,t,d,g=lg,s} \sim Negative\ Binomial\ (\bar{x} = N_{i,t,d,g=sm} \cdot F_{i,t,d,s},\ \delta_{lg})$	Survey counts for sub-region I, time t, strata d, and survey s, in large groups (assumed to be complete counts)
$C_{isu,s} \sim Binomial\ (probability = p_s,\ n = U_s)$	Survey counts on transects within intensive survey unit (ISU) boundaries during survey s (for comparison with corresponding ISU counts, U_s)
$Q_{i,t} \sim Negative\ Binomial\ (\bar{x} = N_{i,t},\ \delta_q)$	Survey counts in skiff surveys (Q), assumed to be complete counts
$H_{i,t} \sim Poisson\ (\bar{x} = N_{i,t-1} \cdot \psi_{i,t})$	Reported harvest numbers (H) for sub-region i at time t. Mean expected value depends on true abundance and annual harvest rate (ψ)
Process model	
$N_{i,t} = N_{i,t-1}\ (\lambda_{i,t} - \nu \cdot \psi_{i,t}) + \Sigma_j D_{j,i,t} - \Sigma_j D_{i,j,t}$	Population abundance dynamics for sub-region i at year t, including intrinsic demographic processes (λ, the finite annual growth rate), harvest mortality (ψ adjusted by compensatory mortality parameter, ν), immigration and emigration (D)
$log\ (\lambda_{i,t}) \sim Normal\ (\bar{x} = r_{max}\ (1 - N_{i,t-1}/K_i),\ SD = \sigma_e)$	Finite annual growth rate (λ), incorporating density dependence and environmental stochasticity
$logit\ (\psi_{i,t}) \sim Normal\ (\bar{x} = 2 \cdot logit\ (\psi_{i,t-1}) - logit\ (\psi_{i,t-2}),\ SD = \sigma_\psi)$	Temporal variation in annual harvest rate, as estimated using conditional autoregressive (CAR) methods
$log\ (K_i') \sim Normal\ (\bar{x} = log\ (\hat{K}'),\ SD = \sigma_K),\quad K_i = K_i' \cdot A_{H,i}$	Density at K and abundance at K for sub-region i
Equations relating data model to process model	
$logit\ (p_s) = \beta_0 + \beta_1 \cdot log\ (E_s + 0.5) + \beta_2 \cdot (log\ (E_s + 0.5))^2 + \varepsilon_o + \varepsilon_{s\|o}$	Survey-specific detection probability for small groups, calculated as a logit function of observed otter encounter rate during survey (E_s)
$\varepsilon_o \sim Normal\ (\bar{x} = 0,\ SD = \sigma_o)$	Variation in detection probability, random effect of observer o
$\varepsilon_{s\|o} \sim Normal\ (\bar{x} = 0,\ SD = \sigma_s)$	Variation in detection probability, random effect of survey s for observer o
$N_{i,t,d=H,g=sm} = N_{i,t} \cdot \alpha_{i,t} \cdot \theta_{i,t,d=H}$	Number of animals in small groups in high-density strata, in sub-region i at time t
$N_{i,t,d=H,g=lg} = N_{i,t} \cdot \alpha_{i,t} \cdot (1 - \theta_{i,t,d=H})$	Number of animals in large groups in high-density strata, in sub-region i at time t
$N_{i,t,d=L,g=sm} = (N_{i,t} - (N_{i,t} \cdot \alpha_{i,t})) \cdot \theta_{i,t,d=L}$	Number of animals in small groups in low-density strata, sub-region i at time t
$N_{i,t,d=L,g=lg} = (N_{i,t} - (N_{i,t} \cdot \alpha_{i,t})) \cdot (1 - \theta_{i,t,d=L})$	Number of animals in large groups in low-density strata, sub-region i at time t
$logit\ (\alpha_{i,t}) \sim Normal\ (\bar{x} = logit\ (\bar{\alpha}),\ SD = \sigma_\alpha)$	Proportion of otters in high-density strata (α), in sub-region i at time t
$logit\ (\theta_{i,t,d}) \sim Normal\ (\bar{x} = logit\ (\bar{\theta}_d),\ SD = \sigma_\theta)$	Proportion of otters in small groups (θ) in strata d, in sub-region i at time t
Prior model	
$N_{i,1} \sim Gamma\ (\bar{x} = N_{init,i},\ CV = 0.5)$	Initial abundance in sub-region i at time $t = 1$ for 9 sub-regions proximal to translocation sites: mean corresponds to 1975 abundance estimate from Schneider (1975; refer to Table S1). For all other sub-regions, $N_{i,t} = 0$.
$D_{i,j,t} \sim Gamma\ (\bar{x} = 10^*,\ CV = 0.5)$	Number of animals emigrating (D) to region j from sub-region i at time t as part of a colonization event. Prior mean arbitrarily set to 10, except for colonization of Glacier Bay from sub-region N02, where prior mean was set to 500 based on previous reports
$logit\ (\psi_{i,1}) \sim Uniform\ (min = -10,\ max = 0)$	Logit of harvest rate in year 1 (1975)
$\hat{K}' \sim Uniform\ (min = 0.01,\ max = 15)$	Median equilibrium density at K (hyper-parameter for K'_i)
$\beta_x \sim Cauchy\ (location = 0,\ scale = 2.5)$	Parameter for logit function estimating p_s
$logit\ (\bar{\alpha}) \sim Cauchy\ (location = 0,\ scale = 2.5)$	Logit of mean proportion of animals in high-density strata
$logit\ (\bar{\theta}_d) \sim Cauchy\ (location = 0,\ scale = 2.5)$	Logit of mean proportion of animals in small groups, for strata d
$\sigma_K \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in density at K among sub-regions
$\sigma_e \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in annual rate of increase (environmental stochasticity)
$\sigma_\psi \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in harvest rate across years
$\sigma_\alpha \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in proportion of otters in high-density strata
$\sigma_\theta \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in proportion of otters in small groups
$\sigma_o \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in otter detection probability among observers
$\sigma_s \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Variance in otter detection probability among surveys, within observers
$\delta_{sm} \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Dispersion parameter, counts of otters in small groups
$\delta_{lg} \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Dispersion parameter, counts of otters in large groups
$\delta_q \sim Half\ Cauchy\ (location = 0,\ scale = 2.5)$	Dispersion parameter, counts of otters in skiff surveys

absolute number of otters expected at equilibrium (K_i) by taking the product of K'_i and $A_{H,i}$ (the area of high-density strata in sub-region i). We restrict consideration to high-density strata for this calculation because 98% of all foraging by female sea otters in Southeast Alaska occurs at depths <40 m (Bodkin et al. 2004) and thus the area of high-density strata is the primary determinant of carrying capacity (i.e., although males do forage more at depths >40 m, their survival and reproductive success is not limiting to population growth).

To account for the density-independent effects of harvest mortality, we define $\psi_{i,t}$ as the annual *per capita* harvest rate for sub-region i at year t. Anecdotal evidence suggests that harvest mortality varies substantially over time and space in Southeast Alaska, so we use a conditional auto-regressive approach (Carlin and Banerjee 2003) to estimate variation in ψ because this non-parametric method is flexible and readily incorporated into Bayesian analyses. In year 1 of the time series for each sub-region, we assume that the logit of $\psi_{i,1}$ is drawn from a uniform distribution (Table 1). The logit of $\psi_{i,2}$ is drawn from a normal distribution with mean of logit($\psi_{i,1}$) and standard error of σ_ψ (itself a fitted parameter drawn with vague prior), and for $t > 2$ we estimate $\psi_{i,t}$ as:

$$logit\,(\psi_{i,t}) \sim Normal\,(\bar{x} = 2 \cdot logit\,(\psi_{i,t-1}) - logit\,(\psi_{i,t-2}),\ SD = \sigma_\psi). \quad (4)$$

Equation (4) results in a temporally smoothed estimate of time-specific harvest rate for each sub-region, with the degree of smoothing influenced by the data (see next section). To model the effects of harvest mortality on population growth (eq. 1), we first multiply $\psi_{i,t}$ by parameter v to adjust for the compensatory nature of harvest mortality (i.e., some fraction of harvested animals would have died of other causes had they not been harvested). We conservatively set $v = 0.8$, corresponding to a typical survival rate for sub-adults and non-territorial males (Monson et al. 2000*b*), which comprised a large proportion of harvested animals (USFWS 2014).

Although intrinsic demographic processes are expected to be the primary determinants of population growth within a given sub-region, our model must account for some dispersal between sub-regions, specifically the colonization events that occur when an un-occupied subregion is colonized by a neighboring occupied sub-region. The precise timing of these colonization events was difficult to determine based solely on survey data because of the infrequency of surveys; however, we were able to determine the timing of these events more precisely from annual harvest records. Specifically, for a sub-region that was un-occupied at the time of one survey and occupied at the next survey, we inferred the year of colonization as the year prior to the first records in the harvest database for that sub-region. For each colonization event, we assigned the source population as the nearest neighboring occupied sub-region (in most cases this assignment was unambiguous given the spatial distribution of survey observations). We define $D_{j,i,t}$ as the number of dispersing otters moving from source population j to recipient population i at time t, the inferred year of colonization. We treated the value of $D_{j,i,t}$ as an unknown parameter to be fit, with a weakly informed gamma prior; we arbitrarily assigned a mean of 10 and large coefficient of variation of 0.5. In the case of the colonization of Glacier Bay, previous reports suggest that colonization occurred when an unusually large number of animals immigrated from nearby Icy Straits (Esslinger et al. 2015), so in this case we assigned a gamma prior with mean of 500 and coefficient of variation of 0.5. For each colonization event, we enforced equality of $D_{j,i,t}$ (immigration to the recipient population) and $D_{i,j,t}$ (emigration from the source population), such that solving equation (1) for all sub-regions resulted in a net balance of immigration and emigration. With the exception of colonization events, we set $D_{j,i,t}$ and $D_{i,j,t}$ to zero; this was not because we expected no dispersal between established sub-regions but rather because the limited movements that do occur largely cancel each other out, and in any case are indistinguishable (based on survey data) from the environmental stochasticity that affects growth from year to year within each sub-region (eq. 2).

Data model.—Consistent with earlier analyses of aerial survey data (Bodkin and Udevitz 1999), our data model assumes that $N_{i,t}$ is partitioned in 2 separate ways: animals are distributed between high-density strata ($d = H$) and low-density strata ($d = L$) and animals are distributed between small groups ($g = sm$, defined as <20 animals) and large groups ($g = lg$, defined as ≥20 animals). Animals in small groups are assumed to be counted incompletely (i.e., a correction for un-detected animals is required), whereas large groups are assumed to be counted completely and thus no correction for missed animals is needed. We define parameter α as the proportion of animals occurring in high-density strata and parameter θ as the proportion of animals occurring in small groups. Logit-transformed values of the global means of both parameters ($\bar{\alpha}$ and $\bar{\theta}$) are drawn from Cauchy distributions with vague priors (Table 1), and $\bar{\theta}$ is estimated separately for high and low strata. The logit-transformed values of α and θ for sub-region i at time t are treated as hierarchical parameters, normally distributed around the global mean values:

$$logit\,(\alpha_{i,t}) \sim Normal\ (\bar{x} = logit\,(\bar{\alpha}),\ SD = \sigma_\alpha) \quad (5)$$

$$logit\,(\theta_{i,t,d}) \sim Normal\,(\bar{x} = logit\,(\bar{\theta}_d),\ SD = \sigma_\theta). \quad (6)$$

The standard error terms σ_α and σ_θ in equations (5) and (6) are themselves fitted hyper-parameters. We use these estimated parameters to calculate the number of animals in high and low strata, and in small and large groups, for sub-region i at time t:

$$N_{i,t,d=H,g=sm} = N_{i,t} \cdot \alpha_{i,t} \cdot \theta_{i,t,d=H}, \quad (7)$$

$$N_{i,t,d=H,g=lg} = N_{i,t} \cdot \alpha_{i,t} \cdot (1 - \theta_{i,t,d=H}), \quad (8)$$

$$N_{i,t,d=L,g=sm} = (N_{i,t} - (N_{i,t} \cdot \alpha_{i,t})) \cdot (\theta_{i,t,d=L}), \quad (9)$$

$$N_{i,t,d=L,g=lg} = (N_{i,t} - (N_{i,t} \cdot \alpha_{i,t})) \cdot (1 - \theta_{i,t,d=L}). \quad (10)$$

The 4 compartments of the population described by equations (7)–(10) must sum to $N_{i,t}$, and are probabilistically related to observed variables C, the number of otters in each compartment counted on transects during aerial survey s. We note that the survey count data are described by negative binomial distributions, as the clumped distribution of otters leads to over-dispersion of counts relative to a Poisson distribution. In the case of animals observed in small groups, the expected value of C is the product of the true abundance (N), the fraction of habitat surveyed (F), and the survey-specific detection probabilities (p_s)

$$C_{i,t,d,g=sm,s} \sim Negative\ Binomial(\bar{x} = N_{i,t,d,g=sm} \cdot F_{i,t,d,s} \cdot p_s, \quad \delta_{sm}), \quad (11)$$

where the fitted parameter δ_{sm} represents the dispersion parameter of the negative binomial distribution, which determines the variance. In the case of animals observed in large groups, p_s is assumed to equal 1 and thus the expected value of C is the product of the true abundance (N) and the fraction of habitat surveyed (F):

$$C_{i,t,d,g=lg,s} \sim Negative\ Binomial(\bar{x} = N_{i,t,d,g=sm} \cdot F_{i,t,d,s}, \delta_{lg}). \quad (12)$$

A separate dispersion parameter is fit for large groups (δ_{lg}) because previous analyses suggested that the distribution of large groups was particularly clumped.

We measured the fraction of habitat surveyed in a given region, year, strata, and survey replicate ($F_{i,t,d,s}$) by dividing the total area encompassed within transects (assuming a 400-m observation band) by the total area of available habitat as determined using a geographic information system (GIS). We excluded from analyses any otters observed outside the survey transect strip. We assumed the survey-specific detection probability (p_s) differed among observers (o), and also as a function of the relative density of sea otters on a survey based on anecdotal information from previous analyses suggesting that sighting probability decreases when otters are encountered very infrequently, or when they are so abundant that some groups are missed while others are being counted. To allow for a potential non-linear effect of density on sightability, we calculated the mean otter encounter rate for each survey (E_s, in units of otters observed/km of transect), and incorporated it within a quadratic equation to estimate p_s

$$logit(p_s) = \beta_0 + \beta_1 \cdot log(E_s + 0.5) + \beta_2 \cdot (\log(E_s + 0.5))^2 + \varepsilon_o + \varepsilon_{s|o}, \quad (13)$$

where the fitted β parameters determine the effect of encounter rate on detection probability. Note that we omit subscript o from the left side of equation (13) for simplicity, because each survey has only 1 observer, and we re-scale encounter rate by adding 0.5 in recognition of the fact that the average value of $log(E + 0.5)$ across all surveys was approximately zero and thus the overall average value for p_s is simply the inverse logit of β_0. The 2 random effects in equation (13) account for variation in sighting probability among observers (ε_o) and variation among surveys flown by an observer ($\varepsilon_{s|o}$), and we drew both from normal distributions

$$\varepsilon_o \sim Normal(\bar{x} = 0, SD = \sigma_o), \quad (14)$$

$$\varepsilon_{s|o} \sim Normal(\bar{x} = 0, SD = \sigma_s). \quad (15)$$

The standard error terms σ_o and σ_s in equations (14) and (15) are fitted parameters. Because we had replicate surveys for some sub-regions and years (Table 2), it was possible to disentangle among-observer variance from within-observer variance in detection. Partitioning error this way allowed us to obtain appropriate estimates of p_s (and associated uncertainty) for surveys in which an observer did not conduct ISUs; $\varepsilon_{s|o}$ in such cases is simply drawn from the posterior predictive distribution for that parameter. Finally, we treated the observed number of otters counted on transects within ISU boundaries on a given survey ($C_{isu,s}$) as a random variable drawn from a binomial distribution

$$C_{isu,s} \sim Binomial(probability = p_s, n = U_s), \quad (16)$$

where U_s is the total number of otters counted during ISUs on survey s. We excluded initiating groups from both $C_{isu,s}$ and U_s.

We fit count data from skiff-based surveys (Pitcher 1989) in an analogous way to aerial survey data, except that there was no correction for un-detected otters (and thus no ISU counts) because we assumed data represented complete counts of all available animals. As with aerial survey data, we treated skiff counts ($Q_{i,t}$) as a random variable drawn from a negative binomial distribution with a fitted dispersion parameter δ_q

$$Q_{i,t} \sim Negative\ Binomial(\bar{x} = N_{i,t}, \quad \delta_q). \quad (17)$$

In addition to aerial and skiff-based survey data, we used harvest records as an observed data source for model fitting. We treated the reported number of harvested otters in sub-region i at year t ($H_{i,t}$) as a random variable drawn from a Poisson distribution with mean equal to the product of the previous year's abundance ($N_{i,t-1}$) and estimated harvest rate, $\psi_{i,t}$

$$H_{i,t} \sim Poisson(\bar{x} = N_{i,t-1} \cdot \psi_{i,t}). \quad (18)$$

To summarize, the observed data variables (C, C_{isu}, U, Q, H) allow us to estimate posterior distributions for model parameters

Table 2. Summary of effort (total length of transects and proportion of habitat area covered), number of replicate surveys, uncorrected counts in intensive survey unit (ISU) areas and corresponding ISU counts, for all aerial surveys of sea otters conducted in Southeast Alaska between 1995 and 2012. Data are shown for 4 regions within Southeast Alaska: Glacier Bay, Yakutat, northern Southeast Alaska excluding Glacier Bay (N SEAK) and southern Southeast Alaska (S SEAK).

			High-density strata			Low-density strata				
Survey region	Year	Replicates	Transect length (km)	Habitat area (km²)	Proportion surveyed	Transect length (km)	Habitat area (km²)	Proportion surveyed	Transect counts in ISU areas	ISU counts
Glacier Bay	1999	5	225.40	309.73	0.29	106.95	239.72	0.18	17	36
Glacier Bay	2000	4	227.21	309.73	0.29	110.52	239.72	0.18	51	98
Glacier Bay	2001	5	223.46	309.73	0.29	100.92	239.72	0.17	60	88
Glacier Bay	2002	5	219.85	309.73	0.28	110.18	239.72	0.18	56	83
Glacier Bay	2003	5	166.33	309.73	0.21	86.34	239.72	0.14	96	140
Glacier Bay	2004	4	151.97	309.73	0.20	77.13	239.72	0.13	143	210
Glacier Bay	2006	4	135.32	309.73	0.17	70.04	239.72	0.12	163	241
Glacier Bay	2012	3	163.00	390.23	0.17	129.98	329.57	0.16	83	207
N SEAK	2002	1	1,779.52	2,593.96	0.27	350.81	2,095.13	0.06	49	57
N SEAK	2011	1	1,251.10	2,605.15	0.19	274.61	2,342.36	0.04		
S SEAK	2003	1	2,233.69	4,459.60	0.20	431.58	2,404.41	0.08	86	149
S SEAK	2010	1	2,146.25	4,487.63	0.19	180.35	2,454.58	0.03	69	205
Yakutat	1995	4	248.49	321.15	0.31	34.73	277.84	0.05	39	88
Yakutat	2005	4	176.54	260.20	0.27	41.66	523.70	0.04	48	153

(N, K, D, α, θ, β, δ, σ) using standard Markov chain Monte Carlo (MCMC) methods. We used vague prior distributions for all parameters (weakly informed based on biological feasibility but having no information specific to the analysis; Table 1), including Cauchy priors for logit-transformed parameters and half-Cauchy priors for variance and dispersion parameters (Gelman 2006, Gelman et al. 2008). We used R (R Foundation for Statistical Computing, Vienna, Austria) and JAGS software (Plummer 2003) to code and fit the model, saving 20,000 samples after a burn-in of 5,000 samples. We report all statistics as the mean and 95% credible interval (CI) of the posterior distributions. We evaluated model convergence by graphical examination of trace plots from 20 independent chains, and by ensuring that Gelman-Rubin convergence diagnostic (psrf) was ≤1.1 for all fitted model parameters. We also conducted posterior predictive checking (PPC) to evaluate model goodness of fit, using the summed deviance (sum of squared Pearson residuals of survey counts vs. expected abundance) as a test statistic for comparison between observed and new data generated from the same distributions (Gelman et al. 2000). We examined scatter plots of the posterior distribution of summed deviance scores for new versus observed data (in the case of well-fitting models, points in such a plot should be distributed around a line with slope 1) and we computed the associated Bayesian-P value (the proportion of new observations more extreme than existing observations; Gelman 2005, Ghosh et al. 2007), which should fall within the range 0.3–0.7 for a well-fit model.

Model derived estimates.—For sub-regions having ≥2 aerial surveys, we estimated mean annual growth rates over each inter-survey interval. Assuming that 1 survey is conducted at $t = yr1$ and a second survey is conducted at $t = yr2$, we drew from posterior samples of $N_{i,t=yr1}$ and $N_{i,t=yr2}$ to calculate a posterior distribution for mean annual growth as

$$\lambda_{i,yr1\rightarrow yr2} = \left(N_{i,t=yr2}/N_{i,t=yr1}\right)^{\frac{1}{yr2-yr1}}. \quad (19)$$

We evaluated support for the hypothesis that growth rates of established populations will decrease over time as carrying capacity is approached (i.e., when mean growth rate = 0); specifically, we fit a linear model to $log(\lambda_{i,yr1\rightarrow yr2})$ versus the number of years since colonization (as measured midway between yr1 and yr2), iteratively fitting the linear model to posterior samples to calculate the 95% CI for the slope and intercept. We considered a negative slope as supportive of the expected hypothesis and estimated the average time from colonization to carrying capacity as the point at which the fitted model = 0.

In addition to sub-regional abundance estimates, we also derived estimates of abundance for larger geographic areas (i.e., northern Southeast Alaska, southern Southeast Alaska, all of Southeast Alaska) by summing across posterior distributions for the relevant N_i. We report means and 95% CI for these derived abundance estimates and calculated associated growth rates as described in equation (19).

Finally, we computed an estimated value of K for all of Southeast Alaska, summed across both occupied and un-occupied habitats. This calculation requires an assumption about the relative quality (and thus eventual equilibrium densities) of currently un-occupied habitats; given that there is little information available on important habitat features for sea otters in Southeast Alaska, and that equilibrium densities vary widely among outer coastal and inside habitats (Coletti et al. 2016), we made the simplifying assumption that eventual equilibrium densities would be similar in currently un-occupied areas. Under this assumption, the total projected K is obtained by multiplying the average density of occupied areas at K by the total area of high-density habitat for all of Southeast Alaska. To obtain a representative and robust estimate of average density at K (K'), we restricted consideration to those sub-regions that had been occupied for ≥30 years ($n = 12$), reasoning that these would provide the most reliable estimates of long-term K. We averaged across posterior samples of K'_i for these

long-occupied sub-regions to obtain a posterior distribution of K', then multiplied posterior samples of $\overline{K}'$ by total area to obtain a mean and 95% CI for regional K.

RESULTS

Between 1995 and 2012, >20,000 km of transects were flown as part of 14 aerial surveys in Southeast Alaska (Table 2). On average, 24% of high-density strata and 11% of the low-density strata were surveyed. Over all surveys, 934 useable ISUs (i.e., ISUs containing more than just the initiating group) were flown with 1,755 sea otters counted within ISUs, as compared to 961 counted in the initial strip count of the same areas. The Bayesian state-space model fit to these data converged well, with well-mixed chains providing robust posterior estimates for all model parameters. The maximum psrf statistic for any fitted parameter was 1.11 (for σ_ε), and all other psrf statistics were <1.05 (Table S2, available online in Supporting Information). The posterior predictive check indicated a good fit of the model to the data (Fig. S3, available online in Supporting Information) with an associated Bayesian P value of 0.61.

Almost all sea otters were located within high-density strata ($\overline{\pi}$ = 0.95, CI = 0.92–0.97), and most otters occurred either singly or in small groups (<20 animals) both in the high-density strata ($\theta_{d=H}$ = 0.65, CI = 0.51–0.79) and low-density strata ($\theta_{d=L}$ = 0.90, CI = 0.81–0.97; Table S2). Survey-specific detection probability (p_s) varied by observer, with among-observer variance in logit-transformed p_s (σ_o = 0.67 ± 0.30) approximately 60% greater than variance among surveys conducted by the same observer (σ_s = 0.42 ± 0.09); p_s also varied as a function of sea otter density, with an increasing but asymptotic functional relationship between encounter rate and sighting probability (Fig. 2).

Spatiotemporal Variation in Abundance, Trends, and Carrying Capacity

Model results indicated that the sea otter population of Southeast Alaska increased from 13,221 otters in 2003 (CI = 9,990–16,828) to 25,584 otters in 2011 (CI = 18,739–33,163). This represents a regional annual growth rate of approximately 8.6% over an 8-year period. Based on the most recent surveys (Table 3), southern Southeast Alaska supports a greater number of sea otters (13,178) than northern Southeast Alaska (11,635); however, over half the sea otters in northern Southeast Alaska (7,955) occur in a single sub-region, Glacier Bay. Because Glacier Bay was anomalous from the rest of northern Southeast Alaska in terms of its rapid population growth and high densities, and its non-harvest management status as a national park, we henceforth report statistics for this sub-region separately and report statistics for northern Southeast Alaska without Glacier Bay. The density of sea otters in Glacier Bay as of 2012 (9.0 otters/km^2) is 3 times the most recent estimated average for southern Southeast Alaska (2.9 otters/km^2); however, the average density for the rest of northern Southeast Alaska (1.1 otters/km^2) is considerably lower than that of southern Southeast Alaska (Fig. 3; Table S1).

Trends in abundance were not constant across Southeast Alaska, but rather varied at a sub-regional scale (Table 3). Population growth in Glacier Bay was higher than the rest of the northern half of the region, with 20.6% annual growth rate between 2002 and 2012, whereas Yakutat exhibited only a third that rate (7.6%). The average annual growth rate in southern Southeast Alaska (7.8%) was almost 3 times higher than northern Southeast Alaska (2.7%),

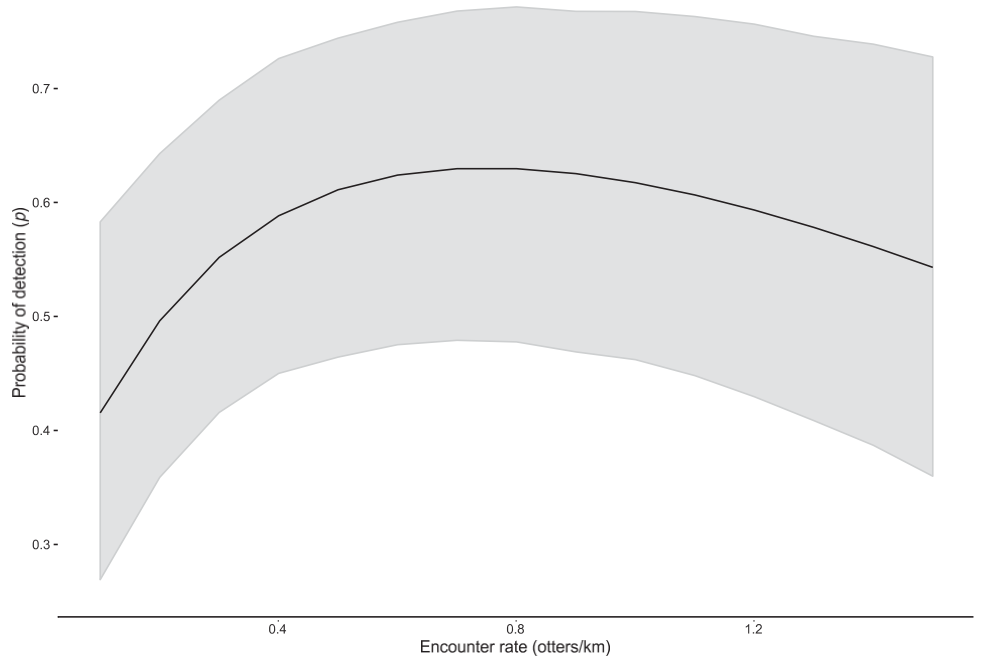

Figure 2. Estimated detection probability function, describing the probability that a group of sea otters is detected by observers during an aerial survey as a function of the mean encounter rate (the frequency with which sea otters are counted along transects, in units of otters/km) in Southeast Alaska, USA, 1995–2012. The solid line shows the mean estimated function, and the grey-shaded bars show the 95% credible interval for the fitted function.

Table 3. Summary of abundance estimates and population growth rate estimates for sea otters in Southeast Alaska, USA, between 1995 and 2012. Statistics shown include mean ($\bar{x}$), standard deviation (SD), and 95% credible intervals ($CI_{95\text{-low}}$ and $CI_{95\text{-high}}$). Estimates are shown for the years of the 2 most recent sets of surveys for all Southeast Alaska (SEAK) and 4 regions within Southeast Alaska: Glacier Bay, Yakutat, northern Southeast Alaska excluding Glacier Bay (N SEAK) and southern Southeast Alaska (S SEAK). In the case of all SEAK, model estimates correspond to 2003 and 2011, the mid-points of survey years for contained sub-regions. For the second set of surveys in each area, we also provide the number of years between subsequent surveys and the estimated mean annual growth rates (and 95% CI).

		Abundance					Growth rate		
Geographic area	Year	$\bar{x}$	SD	$CI_{95\text{-low}}$	$CI_{95\text{-high}}$	Years between surveys	$\bar{x}$(%)	$CI_{95\text{-low}}$ (%)	$CI_{95\text{-high}}$ (%)
All SEAK	2003	13,221	1,842	9,990	16,828				
	2011	25,584	3,828	18,739	33,163	8	8.59	5.39	12.10
Yakutat	1995	445	126	225	690				
	2005	919	274	483	1,474	10	7.55	1.00	15.26
Glacier Bay	2002	1,209	187	892	1,598				
	2012	7,955	1,973	4,788	12,154	10	20.56	14.64	26.91
N SEAK	2002	2,888	621	1,820	4,078				
	2011	3,680	883	2,226	5,482	9	2.69	−0.93	7.50
S SEAK	2003	7,814	1,417	5,371	10,667				
	2010	13,178	2,355	8,977	17,769	7	7.78	3.32	12.34

although there was considerable variation in the growth rate among sub-regions in the north and the south (Table S3, available online in Supporting Information). In general, the highest growth rates occurred in more recently occupied sub-regions, whereas long-occupied sub-regions (those adjacent to translocation sites) exhibited low growth rates. There was a significant negative relationship between annual growth rate and the number of years occupied, with the average growth rate approaching 0 after 35 years of occupation (Fig. 4).

State-space model results suggested a smooth growth curve at the scale of Southeast Alaska (Fig. 5A); however, trends at this regional scale represent the sum of more variable growth trajectories at the sub-regional scale (Fig. 5B–C and E–H). The geographic distribution of sea otters in Southeast Alaska has increased considerably since 1975 (Fig. S2); thus, a combination of range expansion and density-dependent population growth both contribute to variation in trends. Areas with established populations often exhibited short-term declines when otters emigrated (Fig. 5E,G), whereas the neighboring areas colonized by these emigration events experienced rapid exponential growth following colonization (Fig. 5F,H). Growth rates also tended to slow in long-established sub-regions as these

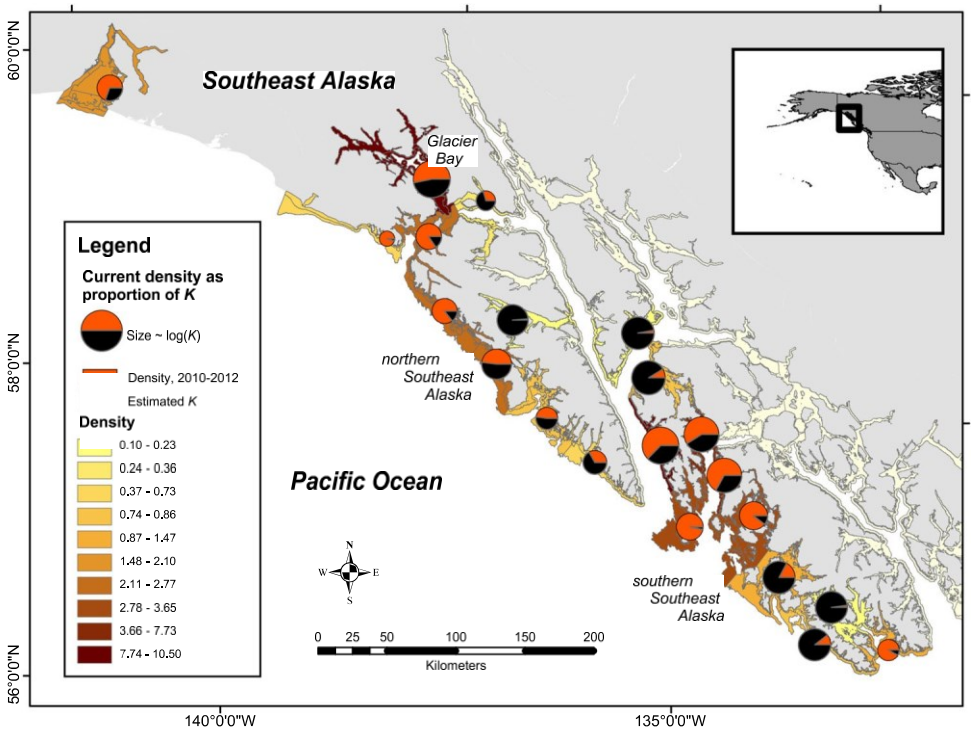

Figure 3. Southeast Alaska, USA, illustrating spatial variation in current sea otter densities (color-varying nearshore habitat zone; local density estimates are based on most recent survey) and status with respect to carrying capacity (K) as pie charts. The proportion of each pie chart shaded orange indicates the ratio of current density (2010–2012) to estimated K for different sub-regions.

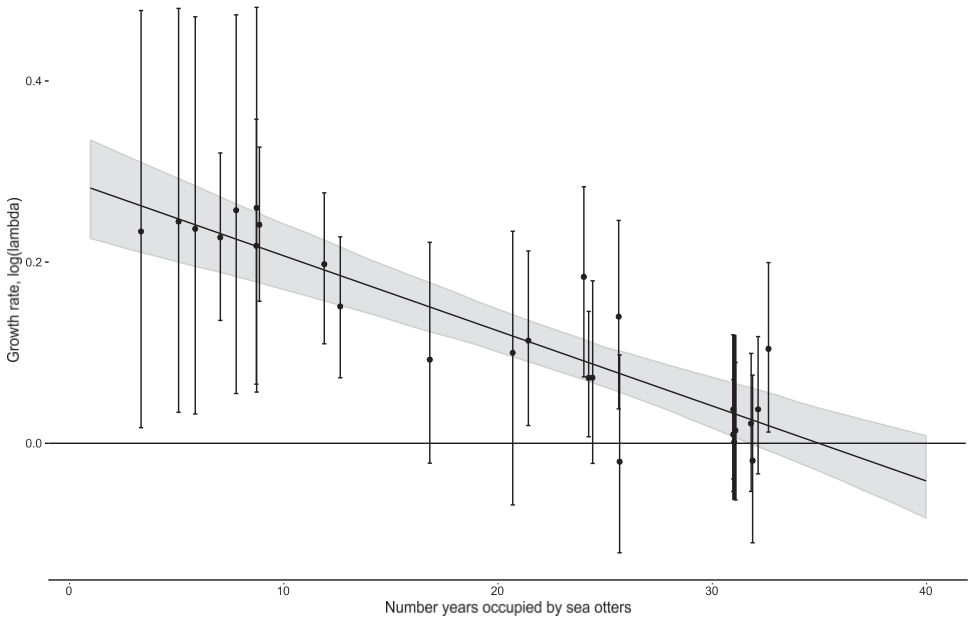

Figure 4. The functional relationship between the number of years that an area or sub-region of Southeast Alaska, USA, has been occupied by sea otters and the log-transformed annual growth rate of the local population (1995–2012). The mean fitted linear function is plotted as a solid line, and the grey-shaded bars show the 95% credible interval for the fitted function. Error bars around points indicate 95% credible intervals around each estimated growth rate. The function suggests that the average growth rate approaches zero (equilibrium abundance) after 35 years of occupation.

areas approached local carrying capacity (Fig. 5B,C,E,G). Another factor that may play a role in the growth trajectories of some sub-regions is harvest mortality. Estimated mean harvest rates varied considerably over space and time (Table S4, available online in Supporting Information), and for some sub-regions periods of slow or negative growth (Fig. 5B,C) appear to coincide with periods of higher than average harvest rates (Fig. 5D). A weaker signal of slower growth coinciding with elevated harvest was also evident at the regional scale (Fig. 5A).

Estimates of carrying capacity converged well for all sub-regions (Table S1), although we obtained the most precise estimates for those sub-regions occupied for the longest (>30 yr). The average density at equilibrium for these long-occupied sub-regions (K') was 4.2 otters/km^2 (±1.58, CI = 2.06–7.66). As with abundance estimates, however, there was considerable variation in K' among sub-regions (Fig. 6), ranging from 0.7 to 16.6 otters/km^2 (Table S1). Estimated equilibrium densities were generally higher in southern Southeast Alaska ($\bar{x}$ = 8.3) than in northern Southeast Alaska ($\bar{x}$ = 3.6, or 4.9 if Glacier Bay is included). For the most recent surveys (2010–2012), densities corresponded (on average) to 50% of projected carrying capacity, although this fraction varied among sub-regions from 1% to 97%, with the earliest-colonized sub-regions tending to be closer to K (Table S1). The projected estimate of carrying capacity for all of Southeast Alaska was 74,650 sea otters (CI = 36,778–136,506).

DISCUSSION

The sea otter population in Southeast Alaska has grown extensively since the translocation of just over 400 sea otters to 6 locations in the late 1960s. Our results suggest that the population now exceeds 25,000 sea otters and could eventually grow to 3 times that number, if the current patterns of range expansion and density-dependent growth continue. The geographic distribution of the population also has increased greatly, now encompassing over 9,000 km^2 of habitat (Fig. 1). Spatiotemporal trends in abundance and distribution are explained by intrinsic demographic processes (as described by a logistic growth model) and by range expansion, which occurs as sea otters disperse from occupied habitats to neighboring un-occupied habitats (Lafferty and Tinker 2014, Williams et al. 2017). In some cases, dispersal events involved large numbers of animals, leading to a noticeable drop in numbers from the source population combined with a very rapid increase in the recipient population that often exceeds theoretical r_{max}. Such a colonization event occurred in the late 1990s in Glacier Bay (Esslinger et al. 2015), fueled by immigration from the neighboring Icy Strait habitat (sub-region N02; Fig. 5E–F).

Our results show that sub-regional growth rates are often high in the first years following colonization but then decrease over time as the population approaches K of the local habitat. Our model incorporated density-dependent processes at the sub-regional scale, which is increasingly recognized to be the scale at which sea otter populations are regulated (Bodkin 2015, Tinker 2015, Tinker et al. 2017). Thus, even as some long-occupied sub-regions approach carrying capacity, more recently colonized sub-regions near the range periphery continue to grow rapidly (Figs. 3 and 4). Aside from differences in growth explained by duration of occupation, we also found a large range of equilibrium densities, from <1

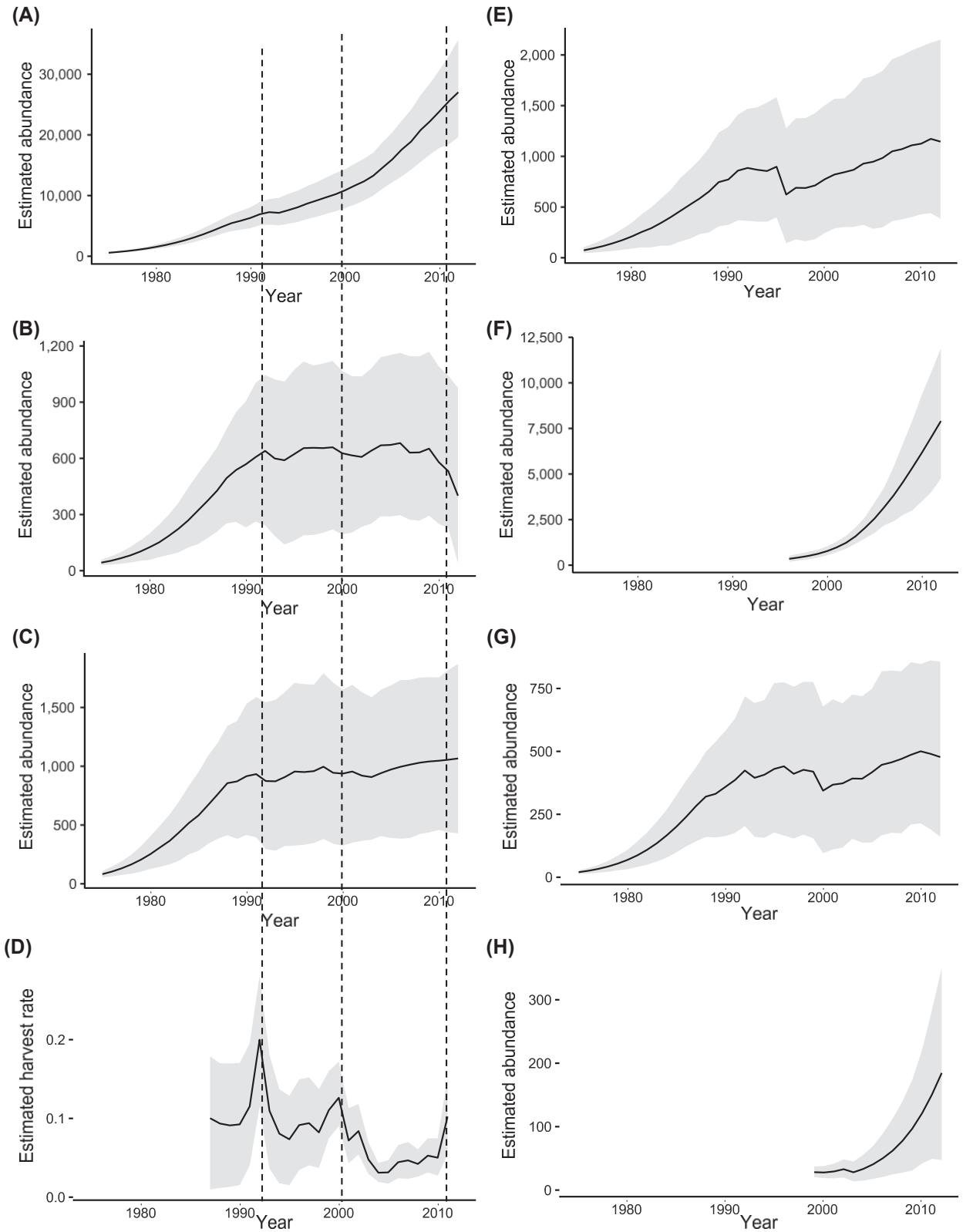

Figure 5. Estimated trends in abundance and harvest mortality for sea otters in Southeast Alaska, USA (1975–2012). Panels on left illustrate abundance trends for all of Southeast Alaska (A) and for sub-regions N05 (B) and S01 (C). The estimated harvest rate averaged across sub-sections (ψ_t) is shown in panel (D), with vertical dashed lines indicating periods of higher than average harvest rates and their potential effects on trends in panels (A)–(C). Panels on right illustrate trends for representative sub-regions from northern and southern Southeast Alaska, with vertical lines linking colonization events for source-recipient pairs: sub-region N02 (E) colonized sub-region GBY (F) and sub-region S05 (G) colonized sub-region S06 (H). In each panel the solid trend line shows the mean estimated value and the grey-shaded bars show the 95% credible intervals.

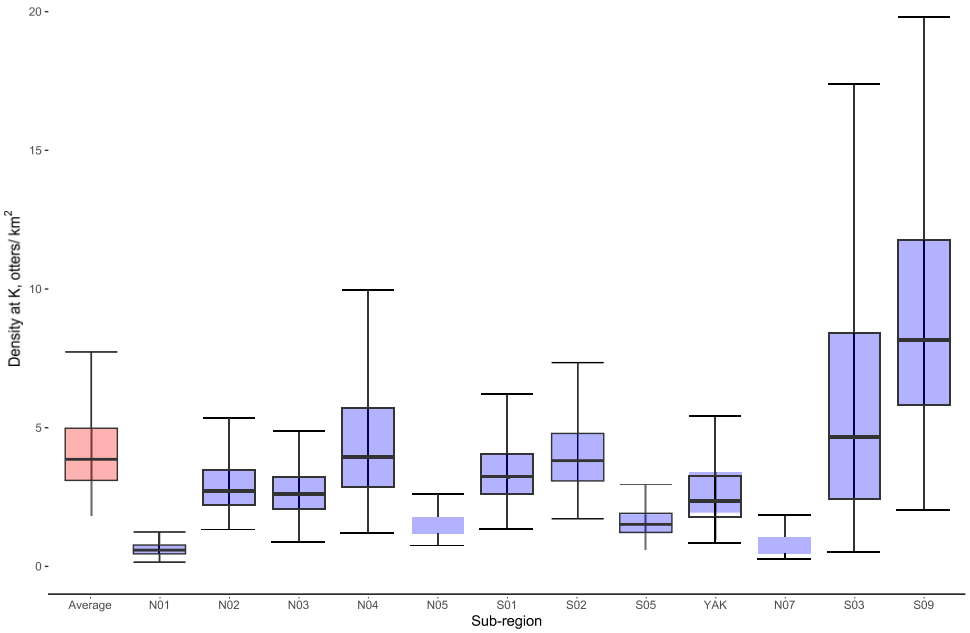

Figure 6. Boxplot showing posterior distributions for average estimated density of sea otters at carrying capacity (*K*) over all Southeast Alaska, USA (red bar) and estimated density at *K* for 12 sub-regions (blue bars), based on analysis of survey data from 1975 to 2012. Box depth indicates inter-quartile range, upper limit of error bars represents the third quartile plus 1.5 times the inter-quartile range, lower limit of error bars represents the first quartile minus 1.5 times the inter-quartile range.

to >15 otters/km^2. The most precise and reliable estimates of *K* are those for the longest-established sub-regions (Fig. 6), for which the mean estimated density at *K* (4.2 otters/km^2) is similar to equivalent estimates of *K* for California, USA, and British Columbia, Canada (Laidre et al. 2001, Gregr et al. 2008). Generally, equilibrium densities appear to be higher in the southern half of the region (Fig. 3), although both low and high values of *K* occur in northern Southeast Alaska and southern Southeast Alaska. The density of Glacier Bay is unusually high, possibly reflecting high productivity of bivalve populations fueled by glacial run-off and high tidal flux (Esslinger et al. 2015), but at this time, the geospatial data needed to examine environmental factors that explain variation in *K* are not available. Previous studies of other populations have reported that differences in habitat complexity and invertebrate productivity explain differences in *K* (Laidre et al. 2001, 2002; Gregr et al. 2008; Tinker et al. 2017) and we would expect similar ecological influences in Southeast Alaska. Future studies should use environmental and habitat data for Southeast Alaska as they become available, to develop more refined, predictive models of carrying capacity.

In addition to density-dependent population regulation, density-independent factors can play significant roles in driving sea otter population trends. Density-independent factors can include environmental stressors (e.g., red tides or other harmful algal bloom events; Kvitek and Bretz 2004, Lefebvre et al. 2016), certain infectious disease outbreaks (Johnson et al. 2009, Goldstein et al. 2011), inter-specific interactions (e.g., predation mortality from killer whales [*Orcinus orca*] or white sharks [*Carcharodon carcharias*]; Estes et al. 1998, Tinker et al. 2016), and anthropogenic factors, including oil spills (Monson et al. 2000*a*, 2011; Bodkin et al. 2012) and direct human harvest. Our results suggest that human harvest may be affecting trends in some sub-regions of Southeast Alaska, particularly long-established areas where mean annual harvest rates exceed 10% of population size (with some years as high as 20%; Table S4). The consistency of timing between peaks in harvest and measurable decreases in population trends in the same areas (Fig. 5) are strongly suggestive of harvest impacts on local populations and warrant further investigation.

Our hierarchical model allows for appropriate partitioning of error, unbiased estimation of abundance even in cases with missing data (e.g., when ISUs were not conducted), improved insights into the survey process (e.g., sources of variation in detection probability; Fig. 2), and appropriate statistical treatment of over-dispersed large groups. Williams et al. (2017) used another approach, a 2-dimensional diffusion approximation, to analyze spatiotemporal dynamics of sea otters at fine spatial scales within Glacier Bay. A diffusion-based approach has some advantages, including more accurate characterization of population distribution as a continuous variable, and allowing for habitat-based covariates of movement and demographic parameters. At present, however, a high-resolution diffusion model similar to that used by Williams et al. (2017) is computationally intractable at the scale of Southeast Alaska and also limited by availability of fine-scale GIS data on bathymetry and habitat for areas outside of Glacier Bay. Future region-wide analyses might incorporate aspects of a diffusion model, most likely at a courser resolution, and also incorporate effects of habitat characteristics, weather variables, and other co-covariates into the detection function. Another improvement would be the explicit incorporation

of group size into the process model: specifically, group-size in sea otters is largely predictable as a function of density, habitat characteristics, and demographic composition of the local population, with larger groups often occurring in male-dominated areas and smaller groups in female-dominated areas (Jameson 1989, Lafferty and Tinker 2014). These functional relationships predicting group size could be formally incorporated into model design to improve precision of estimates.

The fitting of Bayesian models to survey time series to estimate density-dependent growth parameters (especially K) has been conducted with a variety of other taxa (Millar and Meyer 2000, Chaloupka and Balazs 2007, Wang 2007, Iijima et al. 2013), though not previously with sea otters. A notable difference is our estimation of K is based on a relatively small number of standardized survey estimates, a fact that was possible because the survey design provided survey-specific estimates of detection probability and observer error (via the ISU data), the auxiliary data on harvest mortality allowed us to estimate density-independent mortality and narrow down the time of population establishment at the sub-regional scale, and the intrinsic growth parameter for sea otters (r_{max}) is highly consistent across all populations, allowing us in effect to solve the growth rate function (eq. 2) for a single unknown parameter (K). However, this method resulted in wide credible intervals for K, especially for those sub-regions with shorter occupation histories and thus lower densities relative to K. More precise estimates of K will be possible with more extensive time series of abundance estimates (Wang 2007), and models can be further improved by using habitat characteristics and environmental variables as covariates (Laidre et al. 2001).

MANAGEMENT IMPLICATIONS

Our model results show considerable variation in trends and equilibrium densities of sea otters throughout Southeast Alaska, highlighting the fact that the effective scale at which sea otter populations are regulated is much smaller than the regional scale at which they are managed. Because the factors that influence trends occur at the scale of tens of kilometers, rather than hundreds of kilometers, effective management strategies are likely to benefit from explicitly incorporating this fine-scale population structure. For example, calculation of fisheries effects and harvest quotas will be more accurate and precise if monitored and managed at the sub-regional scale. Failure to recognize fine-scale demographic structure could lead to erroneous assumptions about potential risk factors and ineffective strategies for mitigating sea otter–fishery interactions.

The current approach to monitoring sea otter populations in Southeast Alaska, using aerial abundance surveys with ISU-based corrections for detectability, is at present the best approach for obtaining a comprehensive, unbiased estimate of regional abundance. Regional abundance estimates are required for management purposes, including estimation of sea otter impacts on fisheries, assessment of sustainable harvest levels of sea otters, and for stock assessment requirements under the MMPA. Our analytical approach allows the resulting data to be used to estimate trends and derive estimates of K at regional and sub-regional scales. The region-wide aerial surveys, however, are expensive and logistically difficult, and thus are completed infrequently, so that the resulting time series is sparse and not well-suited to detailed trend analyses. Conducting smaller-scale but more frequent surveys of multiple index sites, spread out geographically and stratified according to habitat features such as bathymetry and benthic substrate, could be a more cost-effective means of acquiring the data needed to estimate trends and K at sub-regional scales. Index surveys could include analysis of high-definition photographic images from un-manned aerial systems (Williams et al. 2017). Paired with GIS layers of habitat characteristics and environmental parameters, such data could be used to derive a mechanistic understanding of variation in K for sea otters in Southeast Alaska.

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SUPPORTING INFORMATION

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