

Modeling the Pacific Flyway Population of Caspian Terns to Investigate Current Population Dynamics and Evaluate Future Management Options

Phase 3: Model Results

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EXECUTIVE SUMMARY

In order to evaluate the effects of potential management options on future trends in the Pacific Flyway population of Caspian terns (*Hydroprogne caspia*), we developed a demographic population model in HexSim, a spatially explicit population simulator software package where individual terns are simulated to move through key life history events (e.g., recruiting into the adult breeding population, natal and breeding dispersal, producing young). Demographic parameters included in the model, such as survival rates and inter-regional movement rates, were estimated in a capture-recapture framework using data collected from 5,239 individuals marked with field-readable leg bands. This model was designed to forecast sub-population trajectories in five regions that encompass the entire breeding range of the Pacific Flyway population, which currently consists of about 12,000 breeding pairs. Empirically-based carrying capacity in each region was used to constrain the size of the breeding population.

We used this population model to project the Pacific Flyway population of Caspian terns under 16 different scenarios of management and environmental conditions for breeding. First, we ran the model under a “baseline” or status quo management scenario to assess the current (as of 2017) population trajectory, under the assumption of no change in management or environmental conditions for breeding. The other 15 scenarios used for population simulation were based on various prospective or hypothetical management actions that might be implemented in the future (e.g., changes in available nesting habitat, reduced adult survival due to a cull) and environmental conditions for breeding (e.g., changes in predator disturbance rates) that the current population may have transitioned to or could experience in the future. Many other possible management scenarios or changes in environmental conditions could be assessed using

this population modeling framework, either individually or in combination, if new management proposals or alternative environmental conditions emerge in the future.

Using current demographic parameter estimates, model simulations assuming status quo management in the Columbia River basin (baseline) projected a larger Flyway-wide population of Caspian terns, with a 41% increase over a 30-year simulation period. The breeding portion of the population increased by about 25%, with a much more pronounced increase in the non-breeding portion of the population (261%) during the simulation period; stability occurred in both portions of the population at about 33 years. The proportion of the adult population that was non-breeders increased from 7% to 18% over the course of the 30-year simulation period. Current rates of survival and fledgling production, and adequate carrying capacity throughout the Flyway, if sustained, appear sufficient to allow population persistence at or somewhat above the current level, even with recent managed reductions in available tern nesting habitat in the Columbia River estuary and the Columbia Plateau region. Nevertheless, the presence of at least a small colony (ca. 1,000 breeding pairs) at East Sand Island in the Columbia River estuary, with the high adult survival and peaks in fecundity associated with that site, appears to be critical to the long-term persistence of a significant Caspian tern population in the Pacific Flyway under current conditions. A hypothetical scenario to simulate complete elimination of the large Caspian tern colony at East Sand Island projects a long-term decreasing trend in the Pacific Flyway population, well beyond the 30-year simulation period.

The Pacific Flyway population of Caspian terns was also simulated under eight different management scenarios to evaluate the potential effects of prospective or hypothetical tern habitat management actions, singly and in combination, on the trajectory of the Flyway-wide population. These management scenarios all reduced the available nesting habitat in one or more regions

(Columbia River estuary, Columbia Plateau, and/or southern Oregon and northeastern California [SONEC]) to limit the number of breeding pairs that could nest. These three regions were selected for simulating the population-level effects of various management options because they are areas where some management has already been conducted and where additional management has been proposed. Additionally, the most complete empirical datasets allowing estimation of vital rates and movement rates were available for these regions. Habitat reductions were modeled as reductions in the estimated maximum carrying capacity of a given region.

Prospective management scenarios that reduced tern nesting habitat in only a single region at a time produced increases in the overall Pacific Flyway-wide population, albeit at a lower rate than in the baseline management scenario. Potential management scenarios involving the simultaneous reduction of carrying capacity in two of the three regions revealed an additive effect of reduction in nesting habitat, and a management scenario involving the simultaneous reduction in tern nesting habitat in all three regions eliminated all projected growth in the Flyway-wide population.

A potential management scenario to simulate the creation of new Caspian tern nesting habitat on the Washington coast, by increasing carrying capacity in the Salish Sea region to commensurately compensate for reduced carrying capacity in the Columbia River estuary, produced a steady increase in the total Flyway-wide population, but at a lower rate than in the baseline scenario. The population trajectory under this scenario stabilized at a level similar to that under the baseline scenario, but not until about 50 years.

Scenarios where survival rates of breeding adults in the Columbia River estuary were temporarily reduced to simulate lethal control (a hypothetical 4-year cull of breeding adults) produced a decline in the Flyway-wide population during years when the cull was conducted. No

long-term impact on underlying demographic rates was presumed as part of these scenarios; thus, the population increased once the culling of breeding adults ceased. Because only the direct effects of a cull on adult survival were incorporated in the model under these culling scenarios, the potential indirect effects frequently associated with culls at breeding colonies (e.g., reduced fecundity, colony abandonment) were not considered. The decline of breeding adults in the Columbia River estuary during the cull was less than the number of adults lethally removed, due to recruitment and immigration from other regions replacing culled individuals, indicating that the benefits to salmonid populations per tern culled would be less than predicted by analyses that do not incorporate recruitment and movement patterns.

Environmental conditions for breeding in the Columbia River estuary were quite favorable for Caspian terns in the early 2000s. When these early, productive years were excluded from model inputs and breeding conditions (categorized based on fledging success rates) were based on just those observed during the last decade, the model still projected an increasing Pacific Flyway population, but a smaller increase (30%) than in the baseline management scenario (41%). In a scenario that simulated even poorer environmental conditions for breeding in the Columbia River estuary than the average observed over the last decade (representing a possible permanent shift in the impacts of predators such as bald eagles, or the degradation of habitat quality on the East Sand Island colony due to vegetation encroachment and island erosion), the Flyway-wide population was projected to remain stable after about a 14% increase. This level of constrained growth was similar to the prospective management scenario where reduced carrying capacity was only applied to the Columbia River estuary. We did not examine a scenario where both habitat at East Sand Island was reduced due to management *and* breeding conditions degraded due to predators, vegetation encroachment, or island erosion, but if

management were entirely additive to degraded breeding conditions then both effects combined would result in a 13% decline in the Pacific Flyway population over the 30-year simulation period.

Under a scenario that simulated better environmental conditions for breeding in the SONEC region (due to ameliorating drought conditions) than were observed during the last decade, the Flyway-wide population was projected to increase to a slightly higher level than under the baseline management scenario (45% vs. 41%).

The model developed herein to examine the Pacific Flyway population of Caspian terns is among the most sophisticated population models available for colonial waterbirds. It incorporates both life history complexity (e.g., delayed maturity, age structured survival and breeding propensity) and spatial specificity (e.g., natal and breeding dispersal, region-specific demographic rates across five distinct regions of the breeding range), and is based on empirical data collected throughout the Flyway over more than a decade.

Model simulations indicate resiliency of the Pacific Flyway population of Caspian terns under some prospective management scenarios. Caution should be exercised, however, because the model population trajectories under the baseline management scenario and under other prospective or hypothetical management scenarios depend on the quantity and quality of nesting habitat available for Caspian terns in the Pacific Flyway, the predominant limiting factor for this population. Also, certain combinations of management actions coupled with realistic changes in breeding conditions that follow recent trends (e.g., simultaneous reductions in nesting habitat in the Columbia River estuary and the Columbia Plateau region due to management, coupled with recent environmental conditions for breeding in the Columbia River estuary persisting into the future) would likely result in long-term declines in the Pacific Flyway population, even when

assumptions are made for the continued availability of nesting habitat outside of the Columbia River basin at the maximum levels observed to date. In particular, circumstances that substantially reduce the unique capacity for fledgling production at the East Sand Island colony in the Columbia River estuary, if not compensated for by a similar high capacity for fledgling production elsewhere in the Pacific Flyway, are likely to result in a population of substantially reduced size, or potentially even a long-term downward trend that could put the Pacific Flyway population of Caspian terns at risk of greatly reduced resiliency.

INTRODUCTION

Based on the most recent survey of the Caspian tern (*Hydroprogne caspia*) population in the Pacific Flyway, there is evidence of a recent decline in the numbers of breeding pairs in the population, from approximately 18,872 breeding pairs in 2009 to about 12,407 breeding pairs in 2015 (Peterson et al. 2017). Concurrently, two management plans have been implemented to reduce the size of breeding colonies of Caspian terns in the Columbia River estuary and in the Columbia Plateau region, with the goal of reducing mortality of smolts belonging to several populations of anadromous salmonids (*Oncorhynchus* spp.) listed under the U.S. Endangered Species Act. The Caspian tern colony at East Sand Island in the Columbia River estuary, one of the colonies subjected to management under the plans, represents approximately 50% of the Pacific Flyway breeding population by itself (Peterson et al. 2017). Thus, these management actions, plus prospective additional management of Caspian terns in the Columbia River basin to benefit salmonid population recovery, would affect the majority of breeding adult Caspian terns in the Pacific Flyway population. Consequently, understanding the demography, current population status, and likely future population trends of this Caspian tern population are necessary for implementing science-based adaptive management.

Developing reliable population models that are based on empirical data is a key component in structured decision-making and adaptive management plans for a wide variety of wildlife populations and other natural resources (Lahoz-Monfort et al. 2014). One example is the demographic population model developed by the U.S. Fish and Wildlife Service (USFWS) as part of the management plan for double-crested cormorants (*Phalacrocorax auritus*) nesting on East Sand Island in the Columbia River estuary (U.S. Army Corps of Engineers 2015), where about 40% of the Pacific Flyway population formerly nested. This model incorporates estimates

of breeding colony size and productivity for double-crested cormorants from throughout the range of the Pacific Flyway population, plus empirical vital rates (demographic variables such as survival and reproduction) measured for other populations of the species, as a basis for predicting the growth trajectory of the population under a variety of management scenarios. Population models such as this are valuable tools for managers seeking to adaptively manage the population as new data on breeding colony size and distribution are obtained through monitoring efforts. A comparable population model does not exist for the Pacific Flyway population of Caspian terns, however, and the model described in this report seeks to fill that gap.

The first population model for Pacific Flyway Caspian terns that was developed by Bird Research Northwest (BRNW) was a simple deterministic model to assess population status and trends during 1981-2000 (Suryan et al. 2004). The model included demographic parameters derived using metal leg-band returns from dead individuals. Results of this population model were used by management agencies to help guide the management of a large breeding colony of Caspian terns at Rice Island in the upper Columbia River estuary, and later to guide management of an even larger colony at East Sand Island, located in the lower Columbia River estuary (USFWS 2005). Part of the motivation for developing this population model was the recognition that about two-thirds of all the Caspian terns breeding in the Pacific Flyway were nesting at these two colonies in the Columbia River estuary.

Since the early population modeling efforts of Suryan et al. (2004), 974 adult and 4,265 fledgling Caspian terns in the Pacific Flyway population have been banded with field-readable alpha-numeric leg bands. Resightings of these marked individuals over the last 12 years have provided sufficient data on which to base reliable estimates of the vital rates and inter-colony movement rates of Caspian terns in this population. Resighting data collected in more recent

years, after implementation of the Caspian Tern Management Plan for the Columbia River Estuary (USFWS 2005) and the Inland Avian Predation Management Plan (USACE 2014), have provided information on changes in movement rates and vital rates within the Pacific Flyway population during and post-management (Suzuki 2012, BRNW 2017a, 2017b).

The large dataset of banded tern resightings, together with the reliable vital and movement rates it supports, allows development of a far more comprehensive and data-rich second-generation demographic population model for Pacific Flyway Caspian terns as compared to previous population modeling efforts (Gill and Mewaldt 1983, Suryan et al. 2004). Unlike previous models, this model can also incorporate metapopulation dynamics (i.e. differences in vital rates among regions within the Flyway, movements among regions) and environmental stochasticity (e.g., severe drought, failure of the food supply, predation events that affect breeding success). Metapopulation dynamics and environmental stochasticity are particularly influential for the demography of highly vagile species, such as the Caspian tern, living in a highly variable landscape of nesting opportunities.

The first version of the second-generation population model was developed in 2016; however, the model was limited to the Columbia River basin and the southern Oregon/northeastern California (SONEC) region, where frequent monitoring of breeding colonies of Caspian terns has been conducted by BRNW (see description below for the full breeding range of the Pacific Flyway population of Caspian terns). In addition, the model lacked a robust treatment of transitions between life stages (i.e. juvenile to pre-breeder, pre-breeder to adult), and was implemented in simulation software using a pre-defined life history template that could not incorporate the full complexity of Caspian tern metapopulation dynamics. This modeling effort represented a significant improvement in complexity and realism, and allowed

us to prioritize areas where greater model complexity was needed; thus, we were better able to refine our current objectives.

Since that effort, we have added more geographic complexity by including two more regions of the breeding range of the Pacific Flyway population (Salish Sea, Remainder of the Pacific Flyway) so as to encompass the entire breeding range of this population of Caspian terns (Figure 1). We also added more demographic complexity by including details about how individuals progress through various life stages. For example, the population model described here includes Caspian terns unlikely to be associated with any particular breeding colony due to delayed maturity or skipped breeding (e.g., due to poor foraging conditions or limited availability of nesting habitat). This non-breeding portion of the population is especially difficult to census because population size estimates generally rely on counting breeding individuals at nesting colonies, where non-breeders are only transients. The non-breeder life stage is one of the most important components of the life cycle to consider when projecting possible long-term population trends of a long-lived species such as the Caspian tern, but it is often excluded from population status assessments because survey data for non-breeders are lacking.

The primary objective of developing the second-generation population model for Pacific Flyway Caspian terns is to provide resource managers with an informative tool to make science-based adaptive management decisions. The model allows the evaluation of population trajectories based on different potential future management scenarios and changing environmental conditions for breeding. In this report, we describe the structure of the second-generation population model, the input parameters to the model that are based on the best available empirical data on movement rates and vital rates for the Pacific Flyway population of Caspian terns, and the population trajectories produced by the population model.

METHODS

Pacific Flyway

In this model, the breeding range of the Pacific Flyway population of Caspian terns consists of five distinct groupings of breeding colonies, or “regions” in western North America: (1) Columbia River estuary, (2) Columbia Plateau, (3) SONEC (southern Oregon/northeastern California, including artificial islands constructed by the U.S. Army Corps of Engineers [Corps] to restore and enhance nesting habitat as part of the Caspian Tern Management Plan for the Columbia River Estuary), (4) Salish Sea (including Grays Harbor and Willapa Bay for the purpose of this study), and (5) the Remainder of the Pacific Flyway (remaining portions of the Pacific Flyway where Caspian terns breed, including Corps-constructed tern islands in San Francisco Bay). The breeding range of Caspian terns in the Pacific Flyway population for the purposes of this population model includes Alaska, British Columbia, Washington, Oregon, California, southern Idaho, Montana, Wyoming, western Nevada, northern Utah, and Baja California, Mexico; this area is defined by the USFWS (2015) as the breeding range of the Pacific Flyway population of Caspian terns (Figure 1). A wintering/staging area for young Caspian terns (juveniles and non-migratory pre-breeders) is also included in the model, separate from the five regions delineated for the breeding population. The Pacific Flyway population of Caspian terns is considered, for the purposes of this model, a closed population; dispersal of banded and tagged terns from the Pacific Flyway to other flyways (e.g., Central Flyway) has been observed to be minimal during the last two decades, consistent with the findings from other studies of the species (Boutilier et al. 2013, Craig and Larson 2017)

Model Design

Progression through Life Stages

This model is an individual-based, stage structured population model with age-specific estimates used for vital rate parameters (i.e. demographic variables such as survival, age at first reproduction) that are inputs to the model. It is a female-only model and, for interpretation, it can be assumed that the sex ratio of Caspian terns in the Pacific Flyway is 1:1. Including only females in the model simplifies the calculations, and is a common practice in population modeling because only females produce offspring, a vital component of the life cycle that influences subsequent population dynamics. To estimate population size based on the number of breeding pairs, the model output, which is in numbers of females, can be used without conversion. To estimate population size based on the number of individuals, however, the model output must be doubled so that it includes males.

Observations of known-age Caspian terns, which were previously marked with field-readable leg bands when they were fledglings, allow us to estimate age-specific parameters of the population. For purposes of modeling demographic processes, the life cycle of Caspian terns can be divided into five life stages: juveniles, non-migratory pre-breeders, migratory pre-breeders, breeding adults, and non-breeding adults (Figure 2). The timing of each individual's transition from one life stage to the next is based on the resighting of banded, known-age individuals on the breeding grounds. Figure 3 is a detailed schematic that illustrates how individual terns progress through the various life stages in the model.

The juvenile life stage consists of females that have left their natal colony for the wintering range, and are not yet old enough to return to the breeding range where they can be resighted and detected. In the model, all young terns up to 2 years post-fledging belong to the

juvenile life stage, because young Caspian terns very rarely return to the breeding range at one-year post-fledging, but instead remain on the wintering range. The non-migratory pre-breeder life stage consists of females that are older than 2 years post-fledging, but have not yet returned to the breeding range; consequently, this life stage remains undetectable as marked individuals on the breeding range and has no immediate prospects for becoming breeders. The migratory pre-breeder life stage consists of females that are old enough to return to the breeding range (at least 2 years post-fledging), but not old enough to recruit into the breeding population and potentially produce offspring.

Once an individual attains the age at first reproduction, it transitions into one of two adult life stages: breeding adults or non-breeding adults. In the population model, we use colony attendance to distinguish breeders from non-breeders, for reasons described below. The adult life stage is separated into breeding and non-breeding categories because some mature adult Caspian terns in the Pacific Flyway population have been documented to skip breeding seasons and not attempt to nest in some years when breeding conditions are unfavorable. This behavior is consistent with the intermittent breeding observed in other tern species (Nisbet and Ratcliffe 2008).

To parameterize the most realistic population model for Caspian terns, it would be ideal if breeding adults (hereafter “breeders”) could be readily distinguished from non-breeding adults (hereafter “non-breeders”) in the field. But the detection probability of breeding status (i.e. confirming that an adult bird is attending either eggs or chicks) in Caspian terns and other colonial waterbirds is generally less than 1.0. This is the case for many breeding colonies of Caspian terns in the Pacific Flyway because observers must monitor individually marked terns from a distance to avoid disturbing nesting pairs and causing nest failure. Caspian terns do not

tolerate frequent, repeated forays into the breeding colony by researchers to monitor breeding status of marked individuals. Human disturbance often causes breeding adult terns to flush from their nests, exposing nest contents to predation by communally nesting gulls (*Larus* spp.) or other avian nest predators (BRNW 2009). In extreme cases, human disturbance can cause complete colony abandonment (Penland 1982). Consequently, nesting status of marked adult terns is most often assessed from a distance, making it difficult to determine with certainty the nesting status of adults that reside on the colony.

An alternative approach, which can serve as a substitute for being able to distinguish with certainty between breeder and non-breeder life stages, is to classify adults into different stages based on colony attendance. This approach also relies on separating marked adults into two categories: colony attender and non-colony attender. Colony attenders, marked individuals that are repeatedly detected at a particular colony site during the nesting season, are very likely to be nesting or at least attempting to nest at that colony; marked individuals that do not meet these criteria are likely to be transients at a colony site and not actively breeding there. Details for how marked individuals in the adult life stage were assigned to either the colony attender or non-colony attender category are described below (*Colony Attendance Status* section).

In the population model, adult terns transition between two life stages, colony attender and non-colony attender, depending on availability of nesting habitat in their region of the breeding range of the Pacific Flyway population. When the number of breeding pairs in a region of the breeding range reaches carrying capacity (set by the maximum number of pairs that have nested in the available suitable habitat, not on the estimated acreage of suitable nesting habitat or an average nesting density), some adults remain as colony attenders while others become non-colony attenders. There is no density-dependent mortality in adult terns associated with a

regional sub-population reaching carrying capacity in the model; we assumed that adult terns that failed to secure a spot in the available nesting habitat simply skipped breeding that year (non-colony attenders). We assumed that those individuals classified as colony attenders nested (or attempted to nest), while non-colony attenders did not nest. The life stages of colony attender and non-colony attender parallel the classification of terns during colony size estimates in the field, when determination of the breeding status of an individual present on the colony with certainty is also not possible in many cases.

Only colony attenders can produce fledglings in this model. Once female Caspian tern fledglings leave their natal colony, they migrate south with adults during their first fall and stay in the wintering range in southern California, Mexico, and Central America during their first winter (Cuthbert and Wires 1999). The model then holds the young terns (“juvenile” life stage) in the wintering range until they become old enough to potentially return to the breeding range for the first time. The age at which young terns first return to the breeding range varies considerably, as described in detail below (see *Parameter Estimates* section), necessitating the next life stage “non-migratory pre-breeders.” Non-migratory pre-breeders are individuals that are older than the juvenile life stage (> 2 years post-fledging), but have not yet returned to the breeding range for the first time, where they could be detected.

Once non-migratory pre-breeders return to the breeding range, they are assigned to a different life stage, depending on whether they are old enough to nest (breeding capability) and whether there is space available for nesting on a breeding colony in their region of the breeding range (colony attendance status). When an individual that has returned to the breeding range is not old enough to breed, based on the parameter “age at first reproduction,” the model assigns it to the life stage “migratory pre-breeder.” When an individual is old enough to nest, it becomes an

adult, and the model assigns it to either the “colony attender” life stage or the “non-colony attender” life stage, depending on availability of nesting habitat in its region of the breeding range (Figure 3).

Colony Attendance Status of Banded Terns

Demographic parameters (e.g., age at first return to the breeding range, age at first reproduction, survival rates) and movement rates in this population model are based on analyses of data collected from individual terns that were marked with field readable leg bands. Colony attenders were distinguished from non-colony attenders using two criteria: (1) a time window during the breeding season when resighting of banded individuals was considered evidence of nesting and (2) a minimum number of observations of each banded individual (detection threshold) at a given colony in a given year as further evidence of nesting at that colony. The data used for making this distinction were collected at breeding colonies that were monitored at least once a week.

The first step in defining colony attenders was to identify a range of dates (time window) during the nesting season when most adults attending a particular colony are actively nesting. We chose to use a date range that encompassed the period when colony size (number of active breeding pairs) was at or near a peak because other parameters in the model, such as initial population size and colony carrying capacity, were measured during this period. The date range when peak colony size was estimated each year during 2006-2016 was averaged for each region to obtain one date range per region. A 90-day time window was set around the average date when peak colony sizes were detected in each region, 45 days before the peak to 45 days after the peak. The duration of the time window (90 days) was selected to provide a time period of

sufficient duration to accurately identify colony attenders that were likely nesting, including the average duration of the incubation period plus the chick-rearing period. A 90-day time window also allowed breeding adults that initiated nesting earlier or later than the average to be classified as colony attenders, while excluding those marked individuals that were only visiting the colony at the beginning or end of the nesting season.

For the second step, an optimal threshold number of resightings was identified. Four thresholds (3, 5, 8, and 10) of number of resightings of a banded individual within the 90-day peak nesting period that would classify individuals as colony attenders were evaluated for each colony during the study period. We compared the number of banded individuals classified as colony attenders using each resighting threshold to the number of banded individuals that were confirmed to be breeding at that colony in that year. Because the number of banded individuals that were confirmed as breeders (i.e. banded individuals observed with eggs and/or chicks) was always less than the true number (due to detection probabilities < 1.0), a resighting threshold that resulted in a smaller number of colony attenders than the number of confirmed breeders was considered too restrictive a criterion. The resighting threshold where the number of marked individuals classified as colony attenders exceeded the number of marked individuals confirmed as breeders varied among years at each colony. In order to identify a resighting threshold consistent across years within a region, the lowest threshold among all years and all colonies within each region that met the criterion of colony attenders $>$ confirmed breeders was selected and used to determine which marked individuals were considered colony attenders. A minimum of 5 resightings of a marked individual within the 90-day peak nesting period was used as the criterion for classifying an individual as a colony attender in the Columbia River estuary, and a minimum of 3 resightings of a marked individual within the 90-day peak nesting period was used

as the criterion in the Columbia Plateau region or at the Corps-constructed colony sites in the SONEC (southern Oregon/northeastern California) region.

Small colonies in the Columbia Plateau region, some colonies at the Corps-constructed colony sites in the SONEC region in some years, and all colonies in the Salish Sea region were visited only infrequently. Thus, the time window and resighting threshold criteria for designating colony attenders described above was not applicable to those colonies/years. For those colonies/years, all banded terns seen attending nests with eggs and/or chicks were considered colony attenders first. Then the proportion of colony attenders was derived from the ratio of the total number of adults attending active nests at that colony to the total number of adults present at that colony during the peak of the nesting period. This ratio of colony attenders to total adults present was then applied to the total number of banded adults observed at the colony in the same year to obtain an unbiased estimate of the number of banded colony attenders. After taking into account those banded adults seen attending active nests, the remaining number of banded terns designated as colony attenders was randomly assigned to banded adults resighted at the colony, but without confirmation of nesting.

In the analyses using data collected from banded individuals, terns in the migratory pre-breeder life stage remained in that life stage until becoming colony attenders for the first time. Non-colony attender status was assigned only to individuals that had already experienced at least one year of colony attender status. Terns in the migratory pre-breeder life stage were distinguished from colony attenders based on the same resighting criteria (time window and detection threshold) as described above.

Parameter Estimates

Initial Population Size and Carrying Capacity

The best available data on the size of each breeding colony of Caspian terns in the Pacific Flyway, collected during 2015-2017, were used to set the initial number of female colony attenders in each of the five regions within the breeding range (Table 1). Non-colony attenders were assumed to be present in the regions where the initial number of female colony attenders was at or close to carrying capacity (e.g., Columbia River estuary and Columbia Plateau). In the model, 10% of colony attenders was used as the initial number of female non-colony attenders in these regions. Data on the initial number of juvenile and non-migratory pre-breeder females in the wintering range and the number of migratory pre-breeder females in each region of the breeding range were not available. To identify a stable composition of these life stages, we ran a 40-year initialization model using the initial numbers of colony attenders and non-colony attenders to build pools of juveniles, non-migratory pre-breeders, and migratory pre-breeders. The characteristics of these three life stages (abundance, distribution, individual age and natal region) were captured at year 10, when the number of females in these life stages stabilized, and were used as the starting conditions for the full population model.

Baseline carrying capacity for breeding Caspian terns was set in each region based on the highest breeding population recorded in each region in recent years when colony sizes were measured (i.e. 2007–2017), or based on recent colony sizes after management actions had been implemented at colonies in the Columbia River basin (i.e. 2014-2017; Table 1). For the Columbia River estuary region, colony size in 2016, when the highest nesting density was observed on East Sand Island was observed, was used as baseline carrying capacity. These empirically-derived estimates of carrying capacity are considered more accurate than the

alternative approach of trying to measure the area of potentially suitable nesting habitat and multiplying by an arbitrary nesting density.

First Return to the Breeding Range and First Reproductive Attempt

We used resighting data collected from known-age individuals marked with field-readable leg bands as fledglings during the 2006-2017 breeding seasons ($n = 4,265$ banded terns; Tables 2 and 3) to (1) estimate the age-specific distribution of first returns of juvenile or non-migratory pre-breeder females from the wintering range to the breeding range and (2) to estimate the age-specific distribution of first reproductive attempts by migratory pre-breeding females. Data collected from four regions (exclusive of the Remainder of the Pacific Flyway region) were pooled for this analysis in order to maximize robustness. Multi-state analysis (Hestbeck et al. 1991, Brownie et al. 1993) in program MARK (White and Burnham 1999) was used to estimate age-specific transition probabilities between life stages, survival probabilities, and resighting probabilities (Spendelov et al. 2002, Jones et al. 2011). For this analysis, four states were established in a multi-state model in program MARK to reflect the four life stages (juvenile and non-migratory pre-breeder life stages were combined into one life stage). Two assumptions of the multi-state model that are susceptible to violation are (1) that resighting probabilities at a given time are the same among marked animals and (2) that survival probabilities from one occasion (t) to the next ($t + 1$) are the same among marked animals. In this analysis, we stratified data by life stage to minimize the possibility of violating these assumptions. We believe that other assumptions of the multi-state model (e.g., no band loss) were met. Resighting events outside the four-region study area were considered as “no resighting” for the input data (encounter history) matrix in the analysis in program MARK, while those individuals resighted

outside the study area were retained in the analysis. Thus, temporary emigration from the study area was reflected in resighting probabilities within the study area. Individuals with known mortality were excluded from the encounter history matrix.

Based on field observations, virtually all juvenile Caspian terns in the Pacific Flyway population remain in the wintering range during their first breeding season post-fledging, and some non-migratory pre-breeders do not return to the breeding range until their third or fourth breeding season, or even later (Lebreton et al. 2003, Crespin et al. 2006). Thus, we incorporated delayed maturation in our analysis. Following other demographic studies on marked seabirds (Lebreton et al. 2003, Nevoux et al. 2010), the youngest observed age at first return for Caspian terns in the Pacific Flyway population (2 years post-fledging) was selected as the cut-off age between two age groups (juveniles and all later life stages) with distinctly different survival rates. Annual survivorship of juveniles in long-lived bird species is generally lower, sometimes much lower, than annual survivorship of older individuals (Jenouvrier et al. 2008, Nevoux et al. 2010). Annual survival from age 0 (fledging) to age 1 (one year post-fledging), and from age 1 to age 2 (two years post-fledging) were not estimated separately because marked terns were not observable while they remained in the wintering range. Thus, survival probabilities that covered from age 0 to age 2 (the entire juvenile life stage) were used in the population model.

Using the median c -hat approach in program MARK, a goodness-of-fit test was performed on the most general model within the set of candidate models in the four-state analysis, which indicated over dispersion of data (median c -hat = 1.210). Thus, model results were adjusted using the median c -hat value. Life stage and time effects on resighting and survival probabilities, plus age effects on transition probabilities between life stages, were evaluated in our analysis. Akaike's Information Criterion adjusted for small sample size and over

dispersion (QAICc) was used to select the best model (Burnham and Anderson 2002) among 23 *a priori* models for estimating transition probabilities. The best model and the two competitive models within two delta QAICc units indicated a cohort effect (a cohort consists of fledglings grouped by the year and region where banded) on survival rates of juvenile terns (0-2 years post-hatch) and life stage and time effects on annual survival of older terns (Table 4). These competitive models also suggested an age effect on life stage transitions from juveniles and non-migratory pre-breeders in the wintering ground to migratory pre-breeders, and migratory pre-breeders to colony attender. The best model indicated that the maximum age when the transition from non-migratory pre-breeder to migratory pre-breeder occurred was 9 years post-hatch.

Following the method by Hadley et al. (2006), survival rates and age-specific transition probabilities between life stages estimated from the best model were used to estimate both the cumulative proportions of age at first return to the breeding range and the cumulative proportions of age at first reproduction for the Pacific Flyway population (Table 5). These cumulative proportions were then used to determine when individuals in the wintering range (juveniles or non-migratory pre-breeders) return to the breeding range for the first time and become migratory pre-breeders, and when individual migratory pre-breeders recruit into the breeding population to become colony attenders in the population model. Median age at first return from the wintering range to the breeding range was 4 years post-fledging and median age at first reproduction was 5 years post-fledging. Parameter estimates from the four-state analysis in program MARK are included in Appendix A.

We also estimated region-specific proportions of first returns to the breeding range so that the model can assign a destination region to each individual returning to the breeding range for the first time (Table 6). For this analysis, 12 states were established in a multi-state model in

program MARK, based on the four previously described life stages (juvenile and non-migratory pre-breeder life stages were combined in program MARK) and the three data-rich regions in the model (Columbia River estuary, Columbia Plateau, and SONEC regions); Caspian terns nesting in these three regions represent approximately 65% of the breeding adults in the Pacific Flyway population (Peterson et al. 2017). Details of this analysis are described below (see the *Survival Rates* section).

Transition probabilities among the 12 states from the best model (Table 9) were used to estimate region-specific proportions of first returns, which reflect empirical rates of natal philopatry (returning to a natal region during the first visit to the breeding range) and natal dispersal (dispersing to a non-natal region during the first visit to the breeding range). Natal philopatry was more prominent for terns fledged from the SONEC region than terns fledged from the Columbia River estuary or the Columbia Plateau region. Natal dispersal of terns fledged from the SONEC region to the two other regions were below detectible level. Some terns that fledged from the Columbia River estuary and the Columbia Plateau region dispersed to the SONEC region for their first return to the breeding range. Natal dispersal to the SONEC region was greater than natal philopatry for terns fledged from the Columbia Plateau region. The sample size of banded tern resightings from the Salish Sea region was too small for the 12-state analysis in program MARK, and few resighting data were available from the Remainder of the Pacific Flyway region. To calculate natal philopatry and dispersal from/to the Salish Sea region and the Remainder of Pacific Flyway region, we made similar assumptions to those used to calculate inter-regional movements for these two regions based on field observations (see Table 11 and the section on *Inter-regional Movement Rates* below for details).

Regional Environmental Stochasticity

Environmental conditions for breeding have major effects on fledging success of Caspian terns, and vary widely both temporally and regionally within the Pacific Flyway. Major predation events at nesting colonies, low food availability, and extreme weather conditions (e.g., severe drought, heavy rain storms) are examples of adverse environmental conditions that can have major negative effects on fledging success throughout the breeding range of the Pacific Flyway population. To account for this in the population model, we constructed a historical time series of breeding conditions for each region. Each time series was based on fledging success observed within the four regions of the breeding range that were regularly monitored (exclusive of the Remainder of the Pacific Flyway region), with the most extensive data sets covering the last 18 years (2000-2017). For those regions where less than 17 years of data on breeding conditions were available (e.g., the SONEC region, where only data during 2008-2015 were available), the period when data were available was cycled more than once to obtain a frequency of breeding conditions over an 18-year period.

We classified breeding conditions as one of five possible levels: two levels of favorable conditions (“exceptionally favorable” and “favorable”), “typical” conditions, and two levels of unfavorable conditions (“unfavorable” and “exceptionally unfavorable”), based on the observed range of fledging success rates (Table 7). Details of the fledging success rates used in the model are described below (*Fledging Success* section). We used these categories to describe breeding conditions in each region during each year of the model run. Because breeding conditions are solely based on fledging success, breeding condition levels are comparable across regions.

Region-wide data on breeding conditions were not available for the Remainder of the Pacific Flyway region. Thus, we calculated an average frequency of breeding conditions based

on the four other regions of the Pacific Flyway during 2008-2015 (years when data from all four regions were available), and we randomly assigned breeding conditions in these frequencies to the 18-year time series for the Remainder of the Pacific Flyway region. Because of the substantially higher number of individual breeding colonies grouped into the Remainder of the Pacific Flyway region, and because those colonies are distributed widely across the entire Flyway, “exceptionally unfavorable” conditions (i.e. all colonies in the region nearly or completely failed to fledge young) would not be expected. Similarly, the limited data on fledging success available from the Remainder of Pacific Flyway region indicated that above average fledging success has not occurred in recent years. Thus, we limited the range of possible breeding conditions in that region to just two of the three categories observed in all four of the other regions, “typical” and “unfavorable.”

We then randomized the time series of breeding conditions for fledging success such that in every year of the model run when population size was forecast, a new breeding condition was assigned from the randomized time series. We did not know to what degree breeding conditions might be correlated across regions, so to allow for that possibility in the model, the regimes of breeding conditions in each region were designed to mimic the condition regimes across regions for a particular year. For example, the randomly assigned breeding condition regime for a particular year in the model’s population projection might be based on the regime of breeding conditions observed in the five regions of the Pacific Flyway during 2010. We adjusted fledging success in the model based on the level of breeding conditions assigned to a given region in each year. By using this approach, we maintained the observed inter-regional synchrony in the magnitude and frequency of favorable or unfavorable conditions for fledging success, while the pattern of variation in breeding conditions across years remained random. Thus, the model does

not include any increase in the frequency or intensity of adverse environmental conditions for breeding (e.g., drought, severe weather events) that might be associated with prospective directional climate change. Although not evaluated in this report, simulation of various climate change scenarios by altering environmental conditions for breeding, reducing suitable nesting habitat (carrying capacity), or some combination of prospective input data is possible using this population model structure here.

Fledging Success Rates

We estimated annual fledging success (average number of female offspring fledged per female parent) in each region of the breeding range as 0.5 times the average number of young fledged per breeding pair; this assumes a sex ratio at fledging of 1:1 in the Pacific Flyway population. Measurements of annual fledging success at active breeding colonies monitored during 2000-2017 were used to generate fledging success rates in the model (Table 8). The model assumed that only colony attenders produce fledglings; thus, fledging success is associated with only the colony attender life stage in the model.

Fledging success is one vital rate parameter that is strongly influenced by regional breeding conditions. In the model, mean fledging success rates were estimated for each region in each year based on the assigned level of breeding conditions in that region. Fledging success rates for active colonies in the Remainder of the Pacific Flyway region were based on the average fledging success rate in the other four regions in the model, because a region-wide dataset on fledging success was not available for that region. Standard deviations associated with mean fledging success rates for each level of breeding conditions were also estimated so that stochasticity in fledging success rates could be incorporated in the model.

Survival Rates

Region-specific survival probabilities for juvenile Caspian terns are key vital rate parameters for the population model. We estimated life stage-specific survival rates of terns in a multi-state analysis of band resighting data in program MARK, using resighting data collected from known-age terns ($n = 4,050$ terns marked as fledglings during the 2006-2016 breeding seasons) and unknown-age terns ($n = 974$ terns marked as adults during the 2005-2015 breeding seasons) combined in one analysis. The 12-state analysis in program MARK, with four life stages in each of three data-rich regions (Columbia River estuary, Columbia Plateau, and SONEC regions) was used to estimate survival rates. Two assumptions of the multi-state model are susceptible to violation: (1) resighting probabilities at a given time are the same among marked animals and (2) survival probabilities from one occasion (t) to the next ($t + 1$) are the same among marked animals. Stratification of data by life stage and region in this analysis, however, minimized the possibility of violating these assumptions. Other assumptions of the multi-state model (e.g., no band loss) were believed to have been met. Resighting events outside of the three-region study area and known mortalities were dealt with in the same manner as in the four-state analysis. A portion of the encounter history matrix table is shown in Appendix A.

As was the case in the four-state analysis using program MARK, age 2 was selected as the cut-off age between the juvenile and the non-migratory pre-breeder life stages in the 12-state model to estimate survival rates. The sample size of banded tern resightings from the Salish Sea region was too small for estimation of survival rates using multi-state models in program MARK, and few resighting data were available from the Remainder of the Pacific Flyway region. Therefore, the mean of the survival rates from the three data-rich regions was used as the survival rate for both the Salish Sea region and the Remainder of the Pacific Flyway region in

the population model. A goodness-of-fit test was performed on the most general model within the set of candidate models of the 12-state analysis using median $c\text{-hat}$, which indicated over dispersion of data (median $c\text{-hat}$ = 1.396). Thus, model results were adjusted using the median $c\text{-hat}$ value. Life stage, region, and time (year) effects on resighting and survival probabilities were evaluated in the analysis. Life stage effects on transition probabilities for bi-directional inter-regional movements were also evaluated; however, time effects on movement probabilities were not included in order to maintain the robustness of the analysis. Akaike's Information Criterion adjusted for small sample size and over dispersion (QAICc) was used to select the best model from among 25 *a priori* models, given the data.

The best model in the multi-state analysis for estimating survival rate of juveniles (from 0 to 2 years post-fledging) included the effect of natal region and cohort (Table 9), which suggested carry-over effects of breeding conditions on post-fledging survival. Such carry-over effects are consistent with findings in other colonial waterbird species (e.g., Van De Pol et al. 2006). Mean survival rate over the first 2 years post-fledging in the three data-rich regions was 0.53 (Table 10), greater than 2-year juvenile survival reported in other tern species: 0.38 in roseate terns (*Sterna dougallii*; Lebreton et al. 2003); 0.35 in Damara terns (*Sternula balaenarum*; Braby et al. 2011).

The best model included life stage, region, and year effects on annual survival of individuals older than 2 years post-fledging (Table 9). While annual survival of non-migratory pre-breeders (older than 2 years post-fledging and remaining in the wintering range) was estimable in the four-state model used to estimate age at first return to the breeding grounds and age at first reproduction, it was not estimable in models evaluated in the 12-state model. Thus, an estimate from the four-state model for annual survival of non-migratory pre-breeders was used in

the population model. Average annual survival rate of colony attenders in the three data-rich regions was 0.96, similar to or greater than annual survival rates of adults reported in other tern species: 0.96 in arctic terns (*Sterna paradisaea*; Devlin et al. 2008); 0.95 in royal terns (*Thalasseus maximus*; Collins and Doherty 2006); 0.91 in common terns (*Sterna hirundo*; Nisbet and Cam 2002); 0.84 in roseate terns (Spendelov et al. 1995). Annual survival rates of migratory pre-breeders and non-colony attenders were considerably lower than those of colony attenders in all regions (Table 10). Studies of other seabird species indicate that lower survival rates in non-breeders compared to breeders are due to low-quality individuals tending to remain as non-breeders (Harris and Wanless 1995, Cam et al. 1998). Other possible causes for lower survival rates in non-breeders, especially in highly vagile species like Caspian terns (Suzuki 2012), are high energetic demand and risks associated with prospecting for foraging and nesting opportunities in unfamiliar locations. Finally, permanent emigration from the study area (4-region study area in the 4-state model; 3-region study area in the 12-state model) would cause apparent survival rates to underestimate true survival rates to an unknown extent. Based on the survival rates in the three data-rich regions estimated in this analysis, some individuals are expected to live longer than 26 years, the maximum life span recorded for Caspian terns in North America (Cuthbert and Wires 1999). Survival probability estimates from the analysis in program MARK are included in Appendix A.

In order to estimate region-based means and variances in survival rates for juveniles (0-2 years post-fledging) and annual survival of terns older than 2 years post-fledging, we averaged survival rates across years (see Appendix A, Tables A-4, A-5, and A-6) and calculated a standard deviation of the mean value for each region. To estimate survival rates in the Salish Sea region

and the Remainder of the Pacific Flyway region, we used the average of the mean survival rates and standard deviations from the three data-rich regions.

Inter-regional Movement Rates

We estimated life stage-specific inter-annual movement probabilities of Caspian terns among regions within the breeding range of the Pacific Flyway population using the best model in the 12-state analysis in program MARK for estimating survival rates (see description of the 12-state analysis in the previous subsection; the best model is presented in Table 9). In the analysis, inter-regional movements were assumed to differ among life stages because non-breeders in other seabird species exhibit a greater tendency to prospect at multiple breeding colonies than do breeders (Danchin and Cam 2002, Dittman and Becker 2003). Inter-regional movement probabilities among the three data-rich regions estimated in the best model were generally greater in migratory pre-breeders and non-colony attenders than colony attenders (Table 11). Movement probabilities of colony attenders in the Columbia River estuary were lower than those in either the Columbia Plateau region or the SONEC region. In all life stages, movement probabilities from the SONEC region to the Columbia Plateau region were greater than any other directional regional movements within the three-region study area.

We made assumptions about inter-regional movements to and from the Salish Sea region and the Remainder of the Pacific Flyway region because data from these two regions were insufficient for analysis using program MARK. Because of a relatively large number of banded terns observed in the field that dispersed from the Columbia River estuary to the Salish Sea region, compared to the number of banded terns that dispersed from the Columbia Plateau region or the SONEC region, movement rates from the Columbia River estuary to the Salish Sea region

were assumed to be higher than those from the other two data-rich regions to the Salish Sea region. Movement rates from the Salish Sea region to the Columbia River estuary were assumed to be equal to the opposite directional movement rates between the two regions. Movement rates from the Salish Sea to the Columbia Plateau region or to the SONEC region were assumed to be lower than those from the Columbia River estuary to the Salish Sea region. We used the average movement rate from one region to the other three regions as the movement rate to the Remainder of the Pacific Flyway region. Because movement rates from the Remainder of the Pacific Flyway region to the other four regions were unknown, movement rates were estimated based on the assumption that there was no net movement of terns to or from the Remainder of the Pacific Flyway region and the other four regions. The available data on colony sizes in the Remainder of the Pacific Flyway region from the last decade suggest this is a valid assumption.

Because inter-annual variation was not considered in estimating inter-regional movement rates, the movement rates included in the population model were mean estimates of transition rates for each directional inter-regional movement over time. Each estimated mean movement rate included rates from years when high movement rates were observed, presumably due to management actions or adverse environmental conditions for breeding, as well as from years with low-moderate movement rates. Thus, those average movement rates were retained in the model under the various prospective management scenarios, rather than switching to arbitrarily higher movement rates based on the assumption that management yields higher movement rates out of the region where management is implemented. Adjusting inter-regional movement rates higher in response to management that reduces tern nesting habitat, and applying these higher movement rates for an arbitrary period (e.g., 5-10 years after the onset of management) in the model would influence how quickly the model population responds to management, but is

unlikely to have an effect on the longer-term population trajectory. Estimates of inter-regional movement probabilities based on analysis in program MARK are presented in Appendix A.

Population Simulations under Different Scenarios

A total of 16 different scenarios were simulated in the population model in order to assess the effects of different management options and different environmental conditions for breeding on projected population dynamics of the Pacific Flyway population of Caspian terns. The 16 scenarios used for population projections from the model were labeled scenario A through N (Table 12). To evaluate projected population dynamics under current conditions, a baseline or status quo management scenario (scenario A) was simulated. Under this scenario, no additional management of Caspian terns or changes in conditions for breeding were incorporated in model parameters, and regional carrying capacities for numbers of breeding terns were unchanged (Table 1).

A second simulation of the population model (scenario B) was conducted under similar conditions as scenario A, the only difference being the removal of the Caspian tern colony at East Sand Island in the Columbia River estuary. Thus, the carrying capacity for breeding Caspian terns in the Columbia River Estuary region was set at zero, a reduction in carrying capacity of 5,200 breeding females, while all other parameter values from scenario A were retained. The purpose for running the model under scenario B was to demonstrate how model projections of population dynamics respond to changes in conditions relative to baseline population projections (scenario A). Scenario B also illustrates how the elimination of the East Sand Island colony, the largest for the species in the Pacific Flyway, influences the trajectory of the Pacific Flyway population.

The population model was then run under eight additional scenarios (scenarios C-J) that simulated different management options intended to alter available nesting habitat, and therefore carrying capacity, in four different regions of the breeding range of the Pacific Flyway population of Caspian terns (Tables 1 and 12). Model projections under these management actions, either singly or in combination, were evaluated in order to assess the impact of various management options that have been proposed by resource managers for the Pacific Flyway population of Caspian terns. These management actions include (1) further reduction in Caspian tern nesting habitat in the Columbia River estuary in order to limit colony size to 3,125 breeding pairs (scenarios C, F, G, I, and J), a reduction in carrying capacity by 2,075 breeding females; (2) further efforts to prevent Caspian tern colonies larger than 40 breeding pairs from forming in the Columbia Plateau region, thereby limiting the regional breeding population to about 200 breeding pairs (scenarios D, F, H, and I) and reducing carrying capacity by 600 breeding females; (3) cessation of maintenance of Corps-constructed islands in the SONEC region as nesting habitat for Caspian terns, thereby limiting the regional breeding population to about 200 breeding pairs (scenarios E, G, H, and I) and reducing carrying capacity by 1,300 breeding females; and (4) providing alternative nesting habitat along the coast of Washington to accommodate terns dispersed from the Columbia River estuary under management scenario C (scenario J), thereby leaving carrying capacity unchanged from the baseline scenario A. The impacts of managed reductions in regional availability of nesting habitat on the Pacific Flyway population of Caspian terns were evaluated by reducing carrying capacity in only one of the regions in the Flyway (scenarios C-E), in two of the regions simultaneously (scenarios F-H), or in three regions simultaneously (scenario I). The effect on the Flyway-wide population of a

simultaneous reduction of nesting habitat in one region and a compensatory increase in nesting habitat in another region was evaluated in one scenario (scenario J).

The reduction in carrying capacity of the Columbia River estuary for breeding Caspian terns to 3,125 pairs was based on a target colony size for the East Sand Island colony that was identified in the Biological Opinion for operation of the Federal Columbia River Power System, issued by the National Oceanic and Atmospheric Administration (NOAA 2008). This includes management to prevent Caspian terns from nesting at any location in the Columbia River estuary other than on East Sand Island.

The reduction in carrying capacity of the Columbia Plateau region for breeding Caspian terns to 200 pairs was based on a maximum colony size of 40 breeding pairs at five different colonies (the current number of extant Caspian tern colonies in the Columbia Plateau region; BRNW 2017b). The objective of the management plan to prevent the formation of new Caspian tern colonies in excess of 40 breeding pairs is intended to limit predation on ESA-listed juvenile salmonids in the Columbia Plateau region (U.S. Army Corps of Engineers 2014). One Caspian tern colony in the region far exceeds 40 breeding pairs, and is located where it could pose a risk of significant predation rates on some listed Evolutionarily Significant Units (ESUs) of anadromous salmonids in the Columbia River.

The reduction in carrying capacity of Caspian tern nesting habitat in the SONEC region would occur if all active maintenance of Corps-constructed islands as tern nesting habitat would cease and thereby render the sites unsuitable for tern nesting. Current maintenance activities at these islands include removal of invasive plants and nest predators, control of predators on adult terns and their young, and preventing other colonial nesting species (i.e. gulls) from partially or entirely displacing nesting Caspian terns from the islands. If these activities were to cease, we

estimated that the SONEC region would support about 200 breeding pairs of Caspian terns, on average, based on regional estimates of breeding population size in the SONEC region prior to the construction of tern islands by the Corps of Engineers starting in 2008.

Providing alternative nesting habitat for Caspian terns along the coast of Washington has been considered recently by management agencies as a potential approach to accommodate Caspian terns that would disperse from the East Sand Island colony if nesting habitat there was reduced to accommodate no more than 3,125 breeding pairs. In order to simulate population dynamics under this management scenario, we made an assumption that breeding conditions at the prospective alternative colony site in coastal Washington would be similar to those in the Salish Sea region. Thus, the prospective new colony site on the Washington coast was included in the Salish Sea region under that management scenario (scenario J), and the carrying capacity in the Salish Sea region was thereby increased by 2,075 pairs, the same number of pairs that would disperse from the East Sand Island colony should the carrying capacity of the Columbia River estuary be reduced to 3,125 breeding pairs.

Although lethal control of Caspian terns in the Columbia River estuary has not been openly proposed by any natural resource management agency as a means to enhance survival of juvenile salmonids, some NGOs have advocated for such a cull. Consequently, we simulated population dynamics of the Pacific Flyway population of Caspian terns under three management scenarios representing different levels of lethal take and the resultant reduction in annual survival rates for colony attenders at the East Sand Island colony. These simulations were used to evaluate the potential impact on the Flyway-wide population of such lethal management approaches (scenarios K(5), K(15), and K(25); Table 12). The reductions in annual survival rate of colony attenders in each of these scenarios (5%, 15%, and 25%) were implemented during the

first four years in the model, and were intended to simulate the effects of lethal control implemented at three different intensities. Four years is the same duration as the lethal control plan for double-crested cormorants nesting on East Sand Island. Egg and chick losses associated with mortality of colony attenders were not included in these scenarios.

In addition to population modeling under the various management scenarios described above, we evaluated three additional scenarios (L-N) where environmental conditions for breeding were altered to assess how these changes, in the absence of new management actions, would affect population dynamics in the Pacific Flyway. We simulated the population dynamics under two different scenarios where breeding conditions and fledging success (hereafter “breeding conditions” because these two factors are not independent) for Caspian terns in the Columbia River estuary were reduced; the first scenario (scenario L) used average breeding conditions from East Sand Island during 2008-2017, data that reflect more recent and less favorable environmental conditions for breeding than during the early 2000s. The second scenario (scenario M) assumed even poorer environmental conditions for breeding (only unfavorable and exceptionally unfavorable breeding conditions and associated low fledging success) at the East Sand Island colony to simulate breeding conditions that reflect conditions during most recent years. These two scenarios help evaluate the current population dynamics under conditions for breeding that the sub-population in the Columbia River estuary may already have transitioned to.

We also simulated the dynamics of the Flyway-wide population under a scenario where the SONEC region experienced relief from the severe drought of the last five years, causing improved environmental conditions for breeding (scenario N). For this scenario, tern survival

rates in all life stages and breeding conditions in the SONEC region were assumed equal to those of the Columbia Plateau region.

The prospective management actions and changes in breeding conditions for Caspian terns in the Pacific Flyway population that are described above were not linked to each other, and any one of these new management actions or changes in breeding conditions could be implemented independent of the others, or some combination of the management actions and changing conditions could be implemented. Although we limited the model simulations to the scenarios described above, other scenarios for future management of Caspian terns in the Pacific Flyway are certainly possible. Incorporation of these prospective regional management actions and various changes in breeding conditions into the population model was intended to demonstrate the population-level effects of these management options and changes in environmental conditions for breeding on the Pacific Flyway population of Caspian terns. As such, these population model simulations can provide important context for regional resource managers in planning future management actions.

Population Model Simulation

The second-generation population model for Caspian terns in the Pacific Flyway population was developed within the HexSim modeling framework/software (Schumaker 2016). HexSim is a flexible simulation modeling platform, which has been extensively used for wildlife conservation and management projects, such as the population recovery plan for the threatened northern spotted owl (*Strix occidentalis caurina*; USFWS 2011, Schumaker et al. 2014). The earlier version of the second-generation Caspian tern model developed in 2016 was population-

based and used a Leslie matrix (Caswell 2001) template in HexSim. Since then, the model has been converted to a spatially representative, fully individual-based model.

The individual-based model framework increases flexibility in model design because it more explicitly tracks the movements, traits, and fates of individuals to simulate emergent population conditions and outcomes (Grimm and Railsback 2005, DeAngelis and Grimm 2014). The individual-based approach supports the incorporation of greater ecological realism, better representing Caspian tern population biology and ecology in the Pacific Flyway. Individual-based models describe an approach to modeling where the individual is the focal unit and the mechanisms that influence an individual's outcome(s) are modeled. This bottom-up, mechanistic approach differs from a phenomenological approach in that there is not a single equation determining the model result. Rather, individual-based models track individuals through space and time and their outcomes as they respond to their environment. By summarizing output from individuals, this approach can be used to assess population-level changes and outcomes.

The latest version of the Caspian tern population model in HexSim was used to forecast population trajectories under multiple scenarios. The baseline scenario (status quo management) reflected current conditions and evaluates the current status and trend of the tern population. Several alternative scenarios were also developed to evaluate how management actions (or combinations of prospective management actions) or changes in environmental conditions for breeding were likely to affect the Pacific Flyway population. Scenarios invoked changes in region-specific carrying capacities or changes in demography, and were simulated for 30 years, and replicated 100 times. Scenario changes were invoked at the start of simulations before (e.g., carrying capacity) or during the first year of simulation (e.g., demography).

Each year, simulated terns moved through a sequence of events (Figure 4), approximating key annual life history events. Simulated terns were initialized in one of five regions, according to the estimated initial number of colony attenders and non-colony attenders (Table 1). The age of these two adult life stages at initialization was set at 10 years old because the maximum age when non-migratory pre-breeders arrive at the breeding range is nine years old. Setting adult age at 10 years for initialization also ensured that all adults were old enough at initialization to be breeding eligible. Initial numbers of juveniles and non-migratory pre-breeders in the wintering range, and migratory pre-breeders in each region of the breeding range, were obtained from the initialization model once it had reached a stable composition of life stages.

Each year, simulated terns that resided in a region were assigned a probability of remaining in their region or moving to another region, based on estimated inter-regional movement probabilities. After relocating, the number of eligible breeders was compared against the region's carrying capacity to determine how many of the breeding-eligible individuals could become colony attenders in that region. Excess breeding females and breeding ineligible (pre-breeder) terns could not reproduce. Colony attenders were probabilistically assigned a number of offspring based on their region's fledging success rate in that year, based on empirically-derived distributions of conditions for breeding (Tables 7 and 8).

The model used the estimated mean fledging success rates and standard deviations for each level of breeding conditions in each region (Table 8). These estimates were used to create normal distributions of fledging success, from which an individual's fledging success was annually drawn. These distributions represented a range of stochastic environmental and population conditions that introduce inter-annual variability in conditions for productivity and population growth. Empirical frequencies of breeding conditions in each region were used to

determine the frequency of draws from condition-specific distributions. Survival of young of the year (fledglings) from fledging to 2 years post-fledging was dependent on their natal region and conditions the year they fledged (Table 10). Individual survival rates were annually drawn from distributions created from mean estimates and standard deviations specific to their natal region to approximate inter-annual stochasticity. The distributions of survival rates were truncated to be within the range of 0-1, which could slightly reduce the range of the distributions. We expect, however, that this effect would have a minor influence, if any, on model outcomes.

During spring migration, non-migratory pre-breeders remained in the wintering range. Non-migratory pre-breeders (older than 2 years post-fledging) were assigned an annual survival rate not associated with their natal region (Table 10). As non-migratory pre-breeders matured, they probabilistically reached the age at first return to the breeding range (Table 5) and moved back to a region within the breeding range (Table 6), where they transitioned to the migratory pre-breeder life stage. Migratory pre-breeders were then assigned a breeding status (eligible or ineligible) based on their age (Table 5). In subsequent survival events, individuals are assigned a survival probability drawn from a distribution constructed from mean values and standard deviations relevant to their life stage and region (Table 10). No maximum survival age for adults was implemented as individuals experience a survival event each year, culminating in a low probability of surviving beyond the expected life span.

Because annual demographic and movement rates were drawn from distributions that were derived from empirical estimates, uncertainties in parameter estimates were directly included in model results. As individual and population outcomes were dependent on the previous year (e.g., simulated tern surviving to the next year) and sequential random draws from distributions, system variability can increase through time, yielding future long-term population

trajectories that are different than the recent past. However, examination of the 95% confidence intervals of total population size in the baseline (status quo management) scenario indicated that this effect was minimal (Figure 5). Environmental and demographic stochasticity played important roles in predicting population outcomes (e.g., Figure 5, showing the 100 replicate runs used in deriving the mean prediction). Fluctuations in fledging success and survival rates (drawn from distributions created from the mean and variance) were incorporated in the model, and induced variability in population-level outcomes (e.g., population size). To incorporate the influences of uncertain conditions and enable mean-field predictions that are informed by variability, we averaged the results of 100 random replicates.

RESULTS

The numbers of female colony attenders and female non-colony attenders in the entire Pacific Flyway population, plus the sum of these two adult life stages (all adult females), are the primary metrics presented in the results and associated figures of this report. Consistent with field observations, the proportions of migratory pre-breeders at both the regional and the Flyway-wide levels remained low (i.e. <10% of the total Flyway population) under all modeling scenarios, and this life stage was not an influential factor for population trends projected under the various scenarios of management options and environmental conditions for breeding.

Current Population Dynamics

The population model projected a gradual increase throughout the 30-year baseline simulation period in the numbers of adult Caspian terns in the breeding range of the Pacific Flyway population under scenario A (status quo management; Figure 5). The 41% increase in the total number of adults in the Flyway-wide population reflected both an increase of 25% in the number

of colony attenders and a much larger increase (261%) in the number of non-colony attenders. The proportion of the adult population that were non-colony attenders increased from 7% to 18% over the course of the 30-year simulation period. The number of adult Caspian terns in the Columbia River estuary region was projected to increase very slowly (Figure 6A), while the number of adult terns in the Columbia Plateau region was projected to increase at a slightly higher rate (Figure 6B) under status quo management. The number of adult terns in the Salish Sea region was projected to increase rapidly at first, but at a much slower rate once the number of colony attenders reaches carrying capacity (Figure 6D). In general, the increasing sub-populations within these three regions were due to increases in the numbers of non-colony attenders, because the number of colony attenders is constrained at carrying capacity.

An increasing trend in the number of adult terns was also projected for the sub-population in the SONEC region, although the carrying capacity for terns in the SONEC region was not attained during the 30-year simulation period (Figure 6C). In the Remainder of the Pacific Flyway region, the number of adult terns was projected to reach a stable state once the number of colony attenders reaches carrying capacity (Figure 6E). In model simulation runs extended beyond 30 years, the model projected that the total number of adults in the Flyway-wide population, plus the number of adults in each of the sub-populations within the Columbia River estuary, Columbia Plateau, SONEC, and Salish Sea regions, to stabilize soon after Year 30. The number of colony attenders in the SONEC region did not reach carrying capacity, however, even when the model run was extended to 100 years.

Under scenario B, the model simulated the demography of the Pacific Flyway population if the breeding colony at East Sand Island in the Columbia River estuary was not present, but all other parameters were unchanged. The model under scenario B projected that the Flyway-wide

population of adult Caspian terns would decline rapidly without any sign of recovery (Figures 7B and 9). The Flyway-wide population was projected to continue to decline beyond the 30-year simulation period, even when the model run was extended out to 100 years, albeit at lower rate of decline. The number of non-colony attenders in the Columbia River estuary initially increased rapidly due to the lack of nesting habitat on East Sand Island, followed by a rapid decline, and then a continued decline at a gradually decreasing rate. Sub-populations of adults in other regions of the Pacific Flyway also declined, while the magnitude of the declines varied by region.

Potential Management Scenarios

Under prospective management scenario C (reduced carrying capacity only in the Columbia River estuary), the adult sub-population in the Columbia River estuary stabilized at a lower level than under scenario A after an initial decline (Figure 8A). Adult sub-populations in other regions also mostly remained stable at lower levels under scenario C compared to scenario A, resulting in Flyway-wide population growth at a lower rate and stabilizing at a much lower Flyway-wide population size than under scenario A (Figure 9). The reduction in size of the East Sand Island colony under scenario C did not result in an increase in the sub-population in the Columbia Plateau region.

By reducing carrying capacity for breeding Caspian terns in only the Columbia Plateau region (management scenario D), the number of non-colony attenders in the region initially increased sharply as individuals were forced to transition from colony attenders to non-colony attenders. This initial abrupt increase was followed by a slow increase during the remainder of the model projection (Figure 8B), as additional individuals recruited and/or immigrated into this region. The smaller number of colony attenders in the Columbia Plateau region results in an

overall smaller regional sub-population of adult terns at the end of the 30-year projection compared to the baseline scenario A (Figure 7A). Although the Flyway-wide population was projected to be lower under scenario D than under scenario A, the impact of the reduction in carrying capacity in the Columbia Plateau region on the Flyway-wide population was not near as great as under scenario C (reduced carrying capacity in the Columbia River estuary; Figure 9). Two factors are involved in the large difference in Flyway-wide population model trajectories between scenario C and scenario D. First, demographic parameters and fledging success specific to the Columbia Plateau region and the Columbia River estuary are different (e.g., Tables 8 & 10). Second, the scale of reduction in carrying capacity between the two scenarios is markedly different. The Flyway-wide reduction in carrying capacity under scenario C is 2,075 breeding females, while the reduction under scenario D is only 600 breeding females.

Prospective management scenario E assumed reduced carrying capacity for Caspian terns in the SONEC region if, for example, the six Corps-constructed islands in this region became unavailable as nesting habitat for Caspian terns. Under this scenario, the total number of adult terns in the SONEC region was projected to remain stable after an initial decline, but the regional sub-population was projected to be substantially lower compared to scenario A (Figure 8C). The projected impact of this management scenario on the Flyway-wide population was similar to scenario D (Figure 9). The similarity in population projections under these two scenarios is despite the difference in reduction of Flyway-wide carrying capacity between scenarios; the reduction in carrying capacity under scenario E is 1,300 breeding females, whereas the reduction under scenario D is only 600 breeding females. This result is because the initial size of the sub-population in the SONEC region (850 breeding females) is much less than the baseline carrying capacity in the region (1,500 breeding females); thus, the impact of the reduction in carrying

capacity on the sub-population in the SONEC region, or on the Flyway-wide population as a whole, was not as pronounced as if the initial sub-population was at carrying capacity.

If carrying capacity was reduced in the Columbia River estuary and the Columbia Plateau region simultaneously (management scenario F, a combination of management scenarios C and D), a modest increase in the total population size of adult Caspian terns in the Pacific Flyway was projected, but a smaller increase than under all three management scenarios where carrying capacity was reduced in only one region (Figure 9).

Under prospective management scenario G, where carrying capacity was reduced in the Columbia River estuary region and in the SONEC region simultaneously, the Flyway-wide population was projected to follow a similar trend to scenario F, reaching a lower level at the end of the 30-year projection than all three management scenarios where carrying capacity was reduced in only one region (Figure 9).

Under prospective management scenario H, carrying capacity was reduced in the Columbia Plateau region and in the SONEC region simultaneously. The model projected an increasing trend in the total Pacific Flyway population, but at a lower rate than under scenario A (baseline), scenario D (carrying capacity reduction in the Columbia Plateau region alone), or scenario E (carrying capacity reduction in the SONEC region alone). The growth rate in the Flyway-wide population under management scenario H was greater, however, than under management scenario C, where carrying capacity was reduced only in the Columbia River estuary (Figure 9).

For the prospective management scenario where there was simultaneous reduction in carrying capacity in three regions (Columbia River estuary, Columbia Plateau, and SONEC; scenario I), the model projected no growth in the Flyway-wide population, which resulted in a

smaller Flyway-wide population size at the end of the simulation run than under any of the other prospective management scenarios described above.

Prospective management scenario J simulated reduced carrying capacity in the Columbia River estuary and an equivalent increase in carrying capacity in the Salish Sea region to reflect the potential creation of new Caspian tern nesting habitat in coastal Washington. This scenario projected an increasing Flyway-wide population, but less of an increase than under scenario A (36% vs. 41%; Figure 9). The total Pacific Flyway population size at the end of model simulations was similar to scenarios D and E (reduced carrying capacity only in one region, the Columbia Plateau or the SONEC region; 32% increases over initial sizes in both scenarios; Figure 9). When the model was run longer under scenario J, the Flyway-wide population was projected to reach a stable state around Year 50, and at a similar population size as under scenario A.

There was a correlation between the Flyway-wide carrying capacity for breeding adults and the population growth rate for adult Caspian terns in the Pacific Flyway population during years 15-30 in the population model under scenarios A-I ($R^2 = 0.94$, $p < 0.001$; Figure 10). In contrast to the growth rate observed under scenario A compared to the other management scenarios during years 1-30, when the population was simulated beyond Year 30 the population growth rate under scenario A became close to zero (stable) by Year 45 (Figure 10). The population growth rate under scenario B (elimination of nesting habitat at East Sand Island) remained negative even when the model was run out to 100 years (Figure 10).

There was a strong positive relationship between the Flyway-wide carrying capacity for breeding Caspian terns and the projected Pacific Flyway adult population under scenarios A-I ($R^2 = 0.94$, $p < 0.001$; Figure 11). The slope of the regression line was significantly greater than

1.0 ($p = 0.005$), however, indicating that the model predicts that the Pacific Flyway population of adult Caspian terns will increase at a higher rate than the Flyway-wide carrying capacity. This suggests that other life stages, such as non-colony attenders, make up a decreasing proportion of the adult population as the carrying capacity for colony attenders declines.

Lethal Control in the Columbia River Estuary

Under the K-series of management scenarios, which simulated a hypothetical 4-year program of lethal control of Caspian terns on or near the colony at East Sand Island, the annual survival rate of colony attenders in the Columbia River estuary was lower during years 1–4 of the model projection. When annual adult survival rate was reduced by 5%, which translates into an average of 257 colony attenders culled in each year of the control program, the rate of increase in the Flyway-wide population was initially lower than under baseline scenario A, followed by a steady increase in population growth rate that led to a total Flyway-wide population size that was similar to that under scenario A at the end of the 30-year model simulation period (Figure 12). Scenarios with 15% and 25% reductions in annual adult survival rate, which translates into an average removal of 682 colony attenders and 993 colony attenders, respectively, in each year of the control program, initially produced rapid declines in the Flyway-wide population. Subsequent population growth did not attain the population size at the end of the 30-year simulation period that was observed under scenarios A or K(5). The impact of scenario K(5) on the four regional sub-populations other than the Columbia River estuary was barely noticeable, while the impacts of scenarios K(15) and K(25) on the other regional sub-populations were much more pronounced.

Under all three of the K-series scenarios, the decline in number of colony attenders in the Columbia River estuary after the hypothetical 4-year culling program was less than the total number of colony attenders culled (e.g., decline of 317 colony attenders compared with 1,026 attenders culled under scenario K[5]). This major discrepancy was because a large portion of the culled individuals was replaced by recruitment, immigration from other regions, and non-colony attenders transitioning to colony attenders (when nesting habitat became available through reduced numbers of colony attenders). The discrepancy between the decline in the number of projected colony attenders and the number of colony attenders culled was proportionately less as the intensity of the cull increased.

Alternative Environmental Conditions for Breeding

Under scenario L, breeding conditions in the Columbia River estuary region were based on just empirical data collected during the previous decade (2008-2017), instead of all available data since monitoring of the Caspian tern colony at East Sand Island in the Columbia River estuary began in 2000. Breeding conditions have been poorer (as reflected by lower fledging success) during the last decade compared to pre-2008, so model projections under scenario L may be a better predictor of current and future conditions than model projections under scenario A. Under scenario L, the total Flyway-wide population of adult Caspian terns was projected to increase 30%, which is a smaller increase than under scenario A (41%; Figure 13). Although carrying capacity in each region remained the same under scenario L as under scenario A, the projected numbers of adults in each of the five regions were slightly lower under scenario L compared to scenario A.

Under scenario M, breeding conditions in the Columbia River estuary were reduced to simulate a situation where unfavorable environmental conditions for breeding predominate in the Columbia River estuary. Under this scenario, breeding conditions in the Columbia River estuary were set to vary only between “unfavorable” and “exceptionally unfavorable,” and mean fledging success from only these two levels of breeding conditions were included in the model. In the last eight years, breeding conditions in the Columbia River estuary have been classified as either “unfavorable” or “exceptionally unfavorable” in six of those years, so the poor breeding conditions simulated in scenario M are certainly possible in the future. Scenario M projected that the Flyway-wide population of adults would grow only 14%, less than in either scenarios A or L (41% and 30%, respectively; Figure 13). The numbers of adult terns in each of the five regions of the Pacific Flyway were reduced further than under scenario L, and the total Flyway-wide population was projected to be similar at Year 30 to that under prospective management scenario C, where carrying capacity of the Columbia River estuary was reduced from 5,200 pairs to 3,125 pairs.

The SONEC region (southern Oregon/northeastern California) of the Pacific Flyway has experienced severe drought conditions over the last decade, especially during the last four breeding seasons. The drought has reduced regional carrying capacity for breeding adult Caspian terns, limiting colony sizes and fledging success, and resulted in higher than normal movement rates out of the region and into neighboring regions. If the drought in the SONEC region were to end and the region experienced better environmental conditions for breeding in future years compared to recent years, we assumed that tern vital rates in the region would increase and immigration would balance emigration. To simulate the Flyway-wide population under scenario N, survival rates of all life stages, fledging success, and breeding conditions in the SONEC

region were made equal to those of the Columbia Plateau region, where those parameters have been more favorable. The projected numbers of adults in each of the five regions of the Flyway after 30 years were higher under scenario N than under scenario A, and the Pacific Flyway population increased to a higher level (an increase of 45%) than under any other scenario evaluated in this report (Figure 14). Colony attenders in the SONEC region increased throughout the 30-year model run under scenario N, and by the end of the run colony attenders were close to carrying capacity in the region.

Figures showing projections of the total adult population of Caspian terns in the Pacific Flyway and in each regional sub-population under all scenarios evaluated in this report are presented in Appendix B.

DISCUSSION

Current Population Status

Based on our estimates of current vital rates and movement rates for the Pacific Flyway population of Caspian terns, and the use of a spatially-explicit, individually-based population modeling framework, we conclude that the tern population currently has reasonable capacity for growth and is likely resilient to moderate levels of breeding habitat loss throughout its range. Our baseline model scenario suggests that, if current conditions persist, the adult portion of the population could grow up to ca. 40% before a new stable population level is reached. This capacity for growth under current conditions is a good indicator of population resiliency at the present time.

An important uncertainty when projecting any future population trend is potential changes in environmental conditions that occur during the period of projection. Our baseline

model scenario was based on the environmental conditions experienced by breeding Caspian terns in the Pacific Flyway during 2000–2017. Caspian tern breeding success in the Columbia River estuary, however, has steadily declined during this period (Collar et al. 2017), so predicting future productivity in this region is problematic. Two model scenarios that were based only on more recent conditions for breeding in the Columbia River estuary indicated substantially reduced, but still positive, capacity for growth in the Flyway-wide population.

Another important caveat to this general conclusion of population resiliency is the assumption made under our baseline model scenario (status quo management) that the availability of nesting habitat (carrying capacity) in the SONEC, Salish Sea, and Remainder of the Flyway regions remains sufficient to support the highest numbers of breeding pairs observed in each of the respective regions during the last decade. Because the current population model is not structured to permit regional carrying capacities to fluctuate based on changing environmental conditions for breeding, the model assumes the “best-case scenario” for availability of nesting habitat in all five regions. Scenarios that simulated reductions in the carrying capacity of two of the five regions in the model, based on prospective management actions, reduced the population’s capacity for growth, but did not completely eliminate it, so there is some robustness to this assumption. Nevertheless, the additive effects of reductions in available nesting habitat in multiple regions of the Pacific Flyway, plus prospective declines in conditions for breeding in more productive regions of the Flyway, has the potential to produce population declines such as those seen under scenario B.

Scenario B evaluated the population trajectory for the hypothetical case of all nesting habitat in the Columbia River estuary being lost. The dramatic decline in the modeled population under scenario B demonstrates the importance of the East Sand Island colony to the trajectory of

the Pacific Flyway population as a whole. As expected with any large decrease in Flyway-wide breeding habitat carrying capacity, the adult population declined quickly over the lifespan of the cohorts (juveniles) present at model initialization. More significantly, however, the modeled adult population continued to decline at a slow but steady rate between years 30 and 100 of an extended simulation. This persistent decline, well beyond the period when a reduction in carrying capacity would directly impact the population trajectory, indicates that rates of reproduction and recruitment in the other regions of the Pacific Flyway are currently inadequate to sustain the population in the long term. In a metapopulation context, it is likely that the Columbia River estuary currently serves as a source sub-population that sustains the other regional sub-populations within the Flyway. If further reductions in nesting habitat on East Sand Island are implemented, it would be important to provide alternative nesting habitat that offers a similar potential for the high fledgling production that East Sand Island has provided over the last two decades in order to maintain the capacity for population growth and resiliency within the Flyway-wide population.

Management of Nesting Habitat Availability

Population model simulations allow evaluation of prospective management options that can assist adaptive management planning. The potential future management scenarios evaluated using our population model highlight the ability of the model to assess how reduced carrying capacity in one region of the breeding range of the Pacific Flyway population might affect the sub-population within that region, its population dynamics in relation to that of other regional sub-populations, and the dynamics of the entire Flyway-wide population. By comparing management scenarios where only one region is subjected to a reduction in carrying capacity for

breeding terns with scenarios where multiple regions experience reductions in carrying capacity simultaneously, evaluation of any additive or synergistic population-level effects becomes possible. For example, an additive effect on the Pacific Flyway population from the simultaneous reduction in carrying capacity in both the Columbia River estuary region and the Columbia Plateau region (scenario F; reduction in population growth rate of 35 percentage points compared to scenario A) was apparent when compared to management scenarios where carrying capacity was reduced in only the Columbia River estuary region (scenario C; reduction in population growth rate of 27 percentage points compared to scenario A), or in only the Columbia Plateau region (scenario D; reduction in population growth rate of 9 percentage points compared to scenario A). Based on our population model and the prospective management scenarios evaluated in this study, a synergistic effect (greater than an additive effect) of multiple management actions on the Flyway-wide population was not evident.

Recent discussions among management agencies about potentially providing a new site for a breeding colony of Caspian terns in coastal Washington prompted the evaluation of an additional management scenario, scenario J. For the purpose of this report, we made the assumption that the conditions for breeding at the prospective new colony site would be similar to those in the Salish Sea region, where demographic parameters are not as favorable for terns as those in the Columbia River estuary. The Flyway-wide population was predicted to increase under this management scenario, but at a lower rate than under the baseline scenario. Population projections under management scenario J underline the positive effects of compensating for reduced nesting habitat in one region by increasing available nesting habitat in another region, even if vital rates and environmental conditions for breeding are not as favorable as in the region of origin. Compared to model projections under the scenario where nesting habitat was reduced

in the Columbia River estuary without providing additional nesting habitat elsewhere (scenario C), model projections under scenario J indicated much greater capacity for population growth.

Current Flyway Population Resiliency

As described above, the East Sand Island colony plays a critical role in sustaining the Pacific Flyway population of Caspian terns, due to the higher adult survival and capacity for greater rates of fledgling production there than are currently available elsewhere in the Flyway. Scenario B, which considered the population trajectory if the East Sand Island colony were lost without replacement habitat becoming available elsewhere, produced a persistent decline in the Flyway-wide population. For this report, we did not attempt to simulate a sufficient range of scenarios to identify a threshold for the size of the East Sand Island colony below which persistent population declines would occur; however, our modeling effort indicates that such a “tipping point” does in fact exist if new, high-quality habitat does not become available elsewhere. Scenario I, which examined simultaneous reductions in carrying capacity in the Columbia River estuary (2,075 breeding pairs), the Columbia Plateau region (600 breeding pairs), and the SONEC region (1,300 breeding pairs), produced a flat trajectory (no growth or decline) for the Flyway-wide population. It is likely that a similar reduction in carrying capacity occurring only in the Columbia River estuary (3,975 breeding pairs in total, leaving a colony of 1,225 breeding pairs at East Sand Island) would produce a similarly flat trajectory or potentially a decline, due to a greater loss of individuals in the estuary region where adult survival and fecundity are higher than elsewhere. It seems that a modestly larger reduction in carrying capacity in the Columbia River estuary region (e.g., 4,200 breeding pairs, leaving a colony of ca.

1,000 breeding pairs) could reasonably be expected to lead to persistent declines in the Pacific Flyway population.

Impact of Lethal Control

Flyway-wide population trajectories under the K-series of management scenarios, involving various intensities of lethal removal of breeding adults in the Columbia River estuary, suggest resilience of the Caspian tern population in the Pacific Flyway to the direct effects of a 4-year reduction in annual survival rates of breeding adults at the East Sand Island colony. However, the population projections under these scenarios only reflect the impact of reducing survival of breeding adults in one regional sub-population. As such, the population projections do not reflect the reduced fledging success that would be associated with the lethal removal of actively breeding adults. If fledging success in the Columbia River estuary was reduced, in addition to the reduction in survival rates of breeding adults, the resilience of the Flyway-wide population to culls simulated by the K-series of management scenarios would be lower than suggested by model projections presented here.

The behavioral response of breeding Caspian terns, both at the individual and the colony level, that survive the cull under a management scenario of lethal control was another factor not considered in our modeling under the K-series of management scenarios. The double-crested cormorant colony at East Sand Island, which was subjected to lethal control over a 3-year period, has experienced a dramatic and unexpected decline in nesting success during the years when a cull of the colony was conducted. The sharp decline in fledging success was associated with repeated episodes of nest abandonment by most or all of the actively nesting adults, although the causative relationship between lethal management actions and colony abandonment remains

uncertain. Simulating lethal control of any species using population models, and interpreting projected population trends from those models, require careful evaluation and appreciation of potential responses that are difficult to reliably predict and quantify.

Under the management scenarios involving lethal control (K-series), it was apparent that the number of breeding individuals culled at East Sand Island would not translate directly to the level of decline in the number of colony attenders in the Columbia River estuary. The magnitude of the decline in the regional sub-population of breeders was less than the number of colony attenders lethally removed under all of the K-series management scenarios, because some culled individuals were replaced through recruitment, breeding dispersal to the region, and non-colony attenders becoming colony attenders. These model results indicate how the prospective benefit of lethal control to the survival of salmonid smolts, on a per-tern-culled basis, could be significantly overestimated in more simplified analyses. This observation also emphasizes the importance of incorporating spatial and life stage structures in the population model for making reliable projections of population response to various management scenarios. Without such complexities, evaluating the magnitude of lethal control necessary to achieve a particular colony size set by management goals would be highly problematic.

Changing Environmental Conditions for Breeding

In addition to examining simulated population trends under different potential management scenarios, we investigated how changing environmental conditions for breeding influenced projections from population models, thereby providing another informative layer for evaluating trajectories of the Pacific Flyway population of Caspian terns. Two of these scenarios simulated less favorable environmental conditions for breeding in the Columbia River estuary

region compared to those used in scenario A. Breeding conditions for Caspian terns in the Columbia River estuary may have already transitioned to a permanently less favorable state, especially when compared with the decade of 2000-2009. By excluding the years of more favorable breeding conditions observed during the first eight years when the colony at East Sand Island was monitored (2000-2007; scenario L), and by further reducing the favorability of breeding conditions in an extrapolation of the most recent trends (scenario M), we used the model to help understand the consequences of a change in breeding conditions at one colony on the population dynamics of the Flyway-wide population.

Population trajectories under such scenarios offer useful information for managers in evaluating prospective management scenarios, because some regions might experience declines in breeding conditions concurrent with a managed reduction in nesting habitat as part of a future management plan. For example, under the additive effects of prospective management to reduce nesting habitat in several regions and declining conditions for breeding, the Flyway-wide population would be expected to decline sharply, based on the stable population trend under management scenario I (reduced nesting habitat in the Columbia River estuary, the Columbia Plateau region, and the SONEC region) and the reduction in population growth rate under scenario L (conditions for breeding in the Columbia River estuary based on only those observed during 2008-2017) compared to scenario A.

We also simulated a hypothetical scenario where environmental conditions for breeding improved in the SONEC region (scenario N); Caspian terns in the SONEC region have experienced lower survival rates and lower fledging success than other regions in recent years, associated with a severe drought in the SONEC region. As expected, the growth rate in the number of adults in the Flyway-wide population was higher under scenario N than under the

baseline scenario A, but only slightly. Evaluation of the magnitude of effects on the total Flyway-wide population from changing environmental conditions for breeding at the regional level would be extremely difficult without this type of population modeling.

Benefits of a Stage-structured Population Model

Population status assessments of colonial seabirds are generally based on enumerating breeding pairs at colonies, because estimating the numbers of non-breeding individuals is very difficult during censuses. The population model for Pacific Flyway Caspian terns presented here included pre-breeders and non-colony attenders (non-breeding life stages), in addition to breeders. Estimation of these non-breeding life stages was based on demographic parameter estimates and reasonable assumptions incorporated in the model. The results of this population model demonstrate the importance of including non-breeding Caspian terns in efforts to evaluate current population status and forecast future population trends.

The highly significant positive correlation between the carrying capacity of the Pacific Flyway for breeding adult Caspian terns (maximum number of colony attenders that can be accommodated by available nesting habitat) and the model's projected Flyway-wide population of adults (Figure 11) was expected; the Flyway-wide carrying capacity for breeders is an obvious constraint on the growth of the Pacific Flyway population. Thus, the total Flyway-wide population of adults varied under the different prospective scenarios of habitat management, but this variation was not explained solely by the carrying capacity for breeders in the Flyway. In many cases, projected increases in the Flyway-wide population or in regional sub-populations were driven mostly or entirely by increases in numbers of non-breeders (non-colony attenders). The results of model projections underline the value of including non-breeding individuals as a

separate life stage in analyses using program MARK and in the HexSim population modeling framework.

Conclusions

The individual-based model in HexSim that was used in conducting this study is an empirically-derived, structurally-rich tool to forecast population trajectories for Pacific Flyway Caspian terns. Incorporating life stage and region-based dynamics in the model allows forecasting of population trends that reflect the biology and ecology of Caspian terns in the Pacific Flyway. This robust model is designed to evaluate the response of Caspian terns at a Flyway-wide population level to prospective future management scenarios and changing environmental conditions for breeding, and will assist resource managers in developing future adaptive management plans to meet long-term management goals for the population.

Projections using this model indicate resiliency of the Pacific Flyway population of Caspian terns to a variety of prospective management options, but also suggest that the population is currently dependent on at least occasional high fledgling production in the Columbia River estuary. While we did not evaluate model projections under every possible future management scenario, certain combinations of management actions coupled with less favorable breeding conditions extrapolated from recent trends in nesting success would result in long-term declines in the Pacific Flyway population. Our population modeling framework is capable of assessing other prospective management scenarios or changes in environmental conditions; incorporating these factors in the model, either individually or in combination, would serve as a valuable tool for assisting regional resource managers in planning future management actions.

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Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed using protocols for

animal care and use that were approved by the Institutional Animal Care and Use Committee at Oregon State University.

LITERATURE CITED

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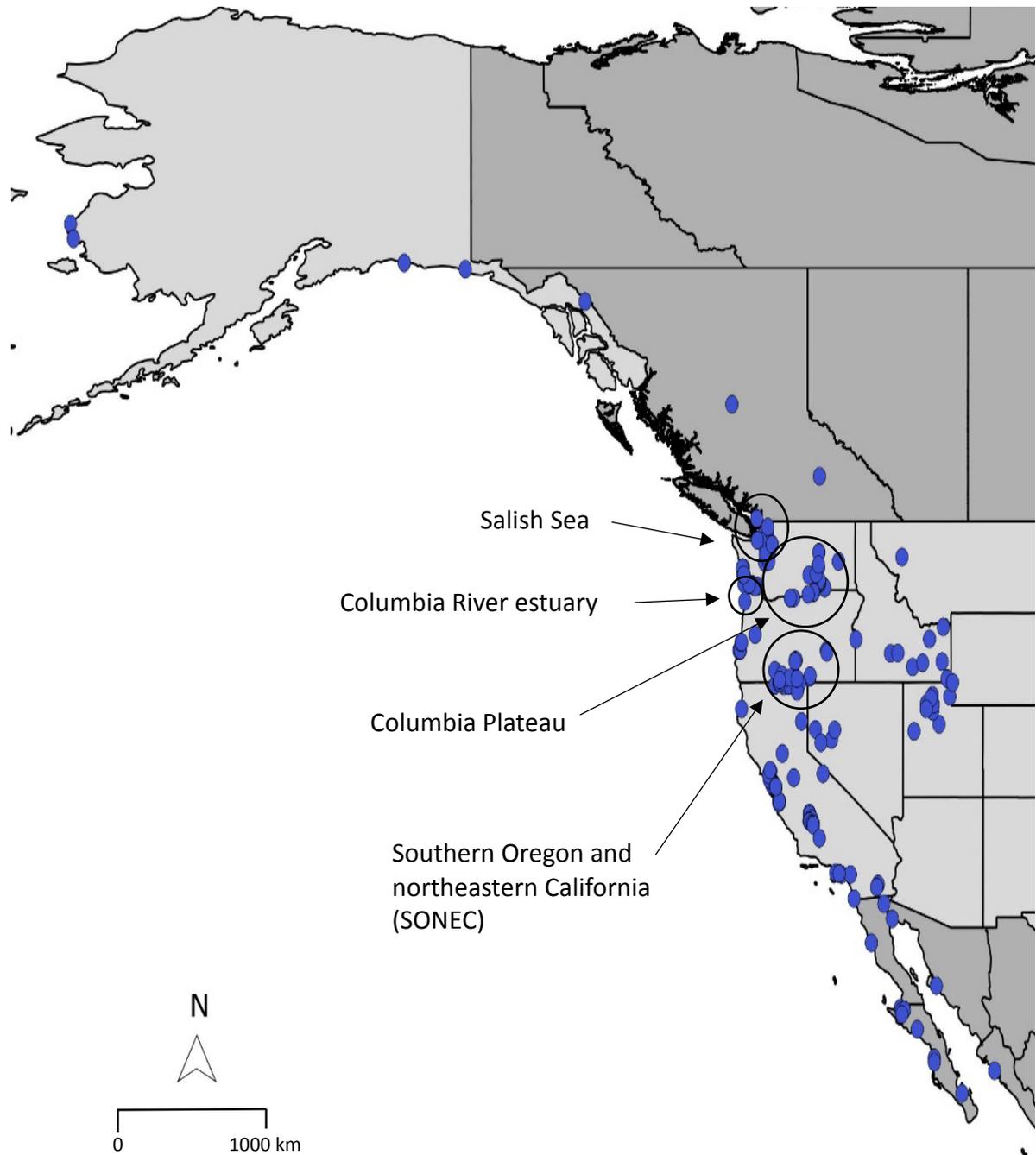


Figure 1. Caspian tern colonies (blue circles; from Collis et al. [2012] and USFWS [2015]) found in four distinct regions (black circles) within the breeding range of Caspian terns in the Pacific Flyway population that are included in the population model. The fifth region included in the population model, the Remainder of the Pacific Flyway region, includes all tern colonies located outside the four distinct regions mentioned above.

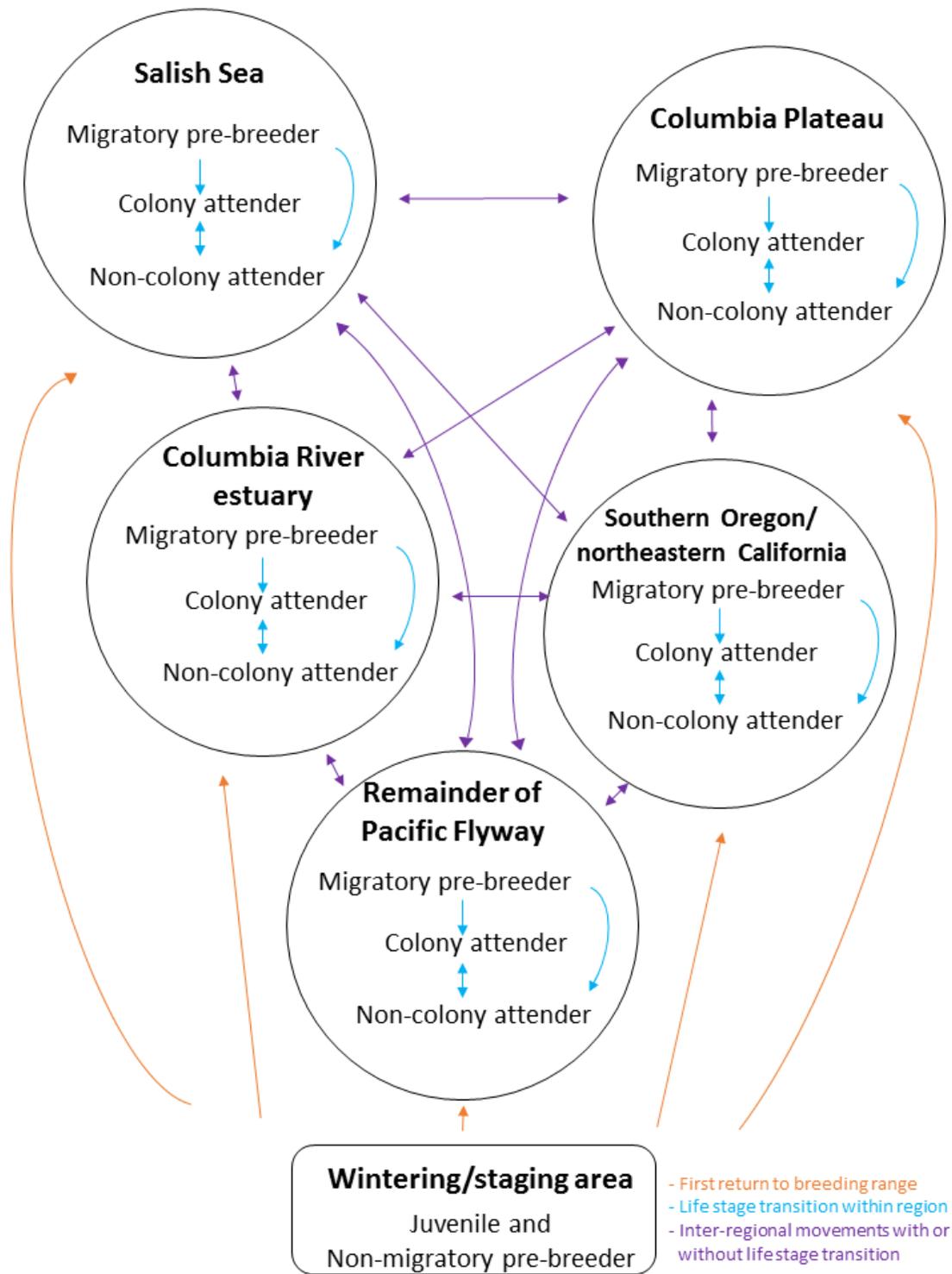


Figure 2. Transitions among regions and between life stages for individual Caspian terns in the model of the Pacific Flyway population. The southern Oregon and northeastern California (SONEC) region includes Corps-constructed tern islands in that region. The Corps-constructed tern islands in San Francisco Bay are included in the Remainder of Pacific Flyway region.

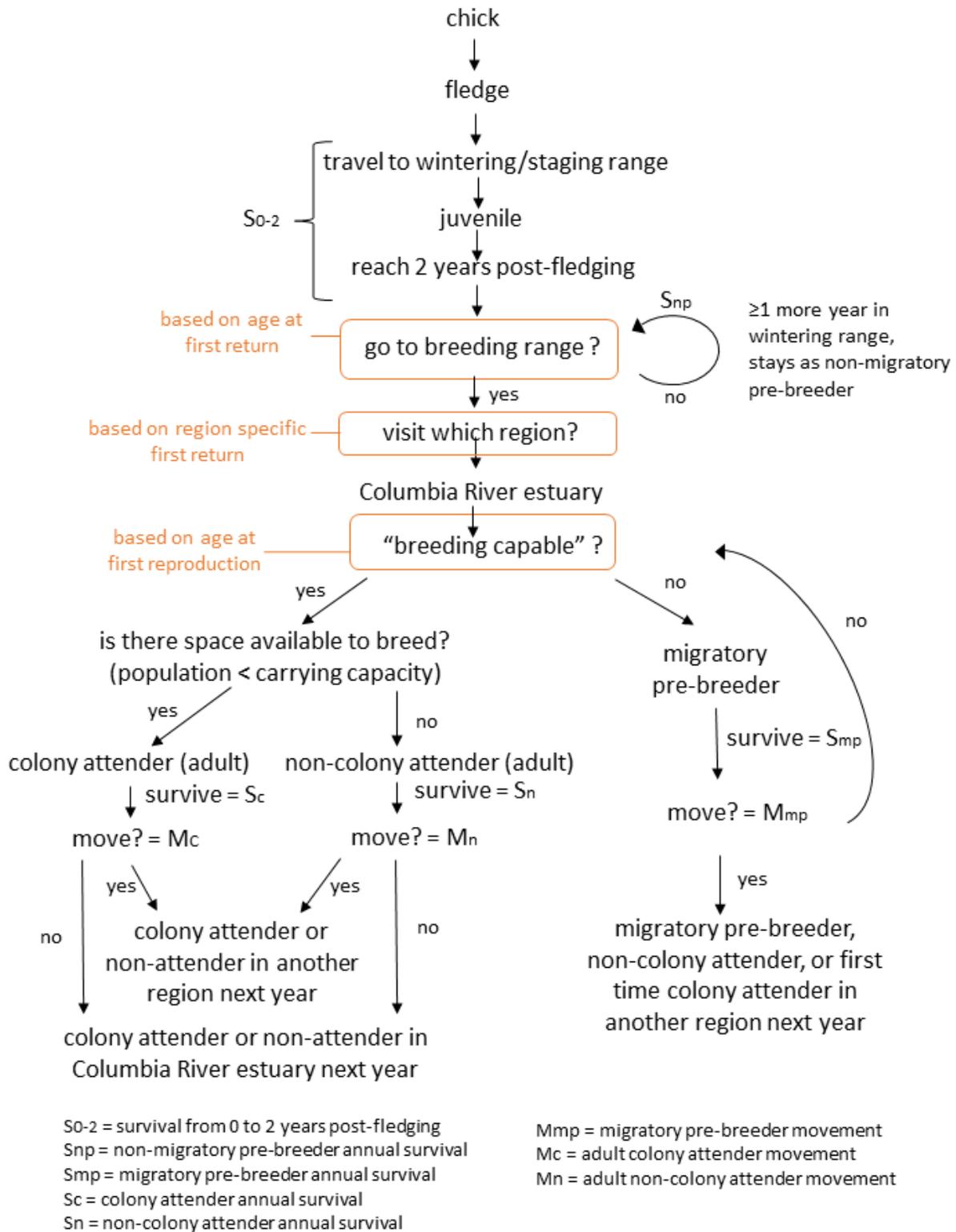


Figure 3. Progression through life stages for individual Caspian terns visiting the Columbia River estuary and the parameters used in the model of the Pacific Flyway population.

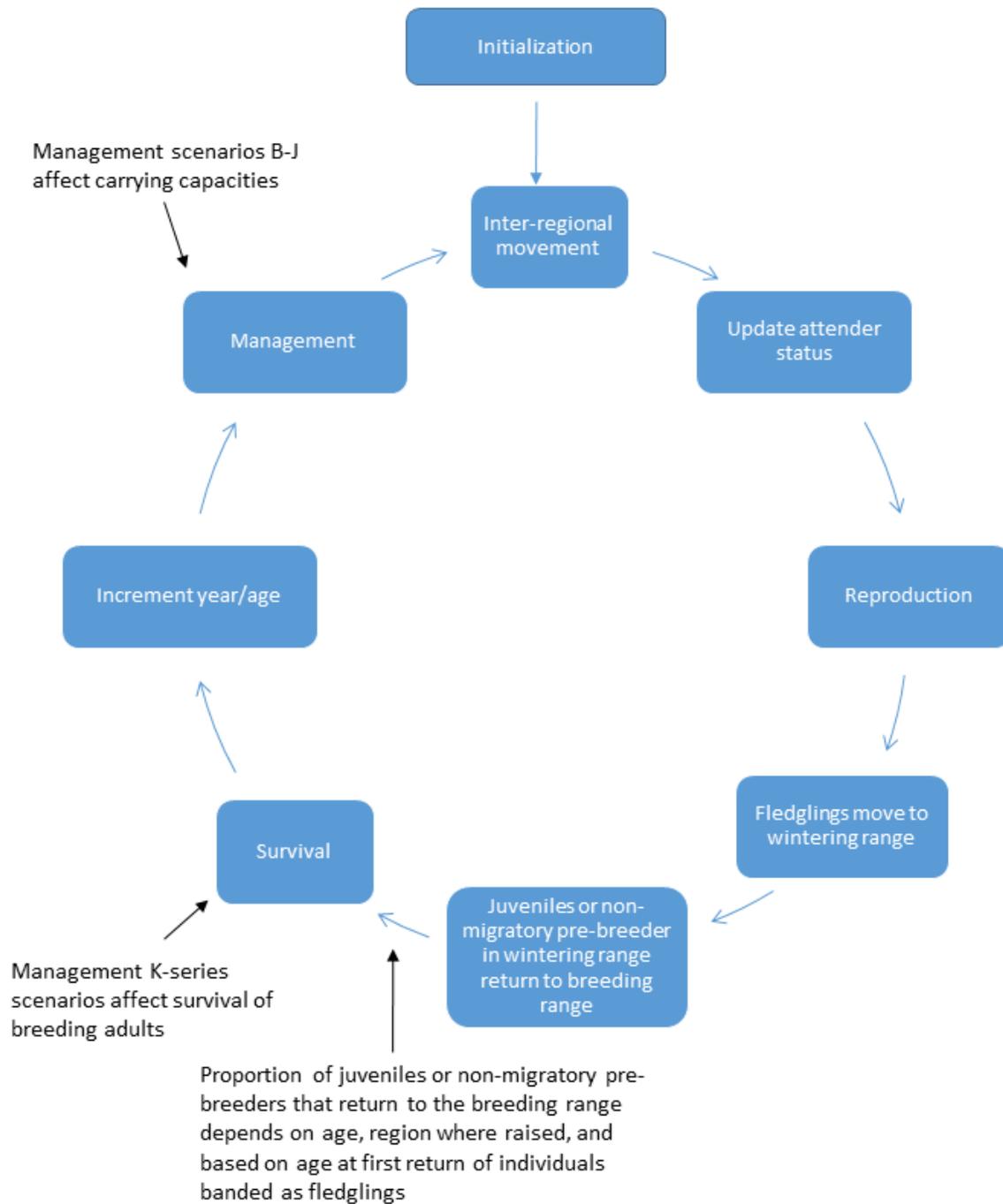


Figure 4. Cycle of life stage events in the individual-based HexSim model for Caspian terns in the Pacific Flyway population.

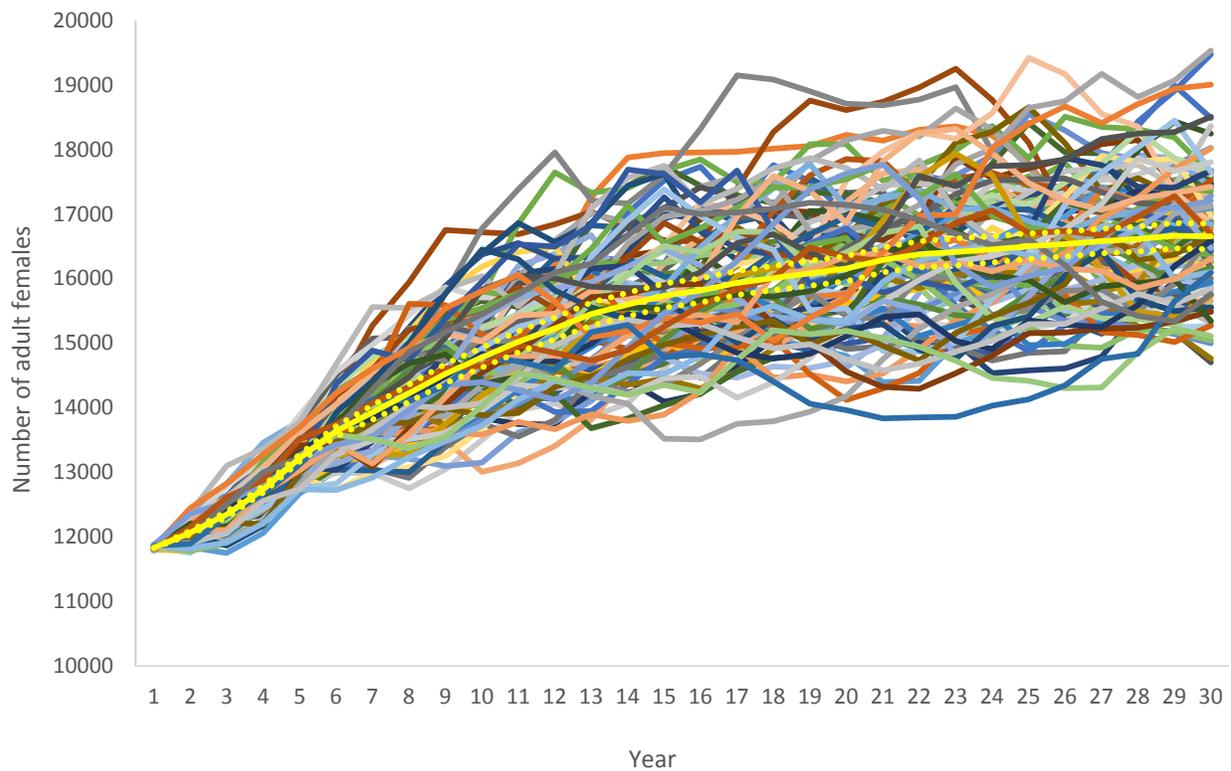


Figure 5. Plots of 100 replicate model runs of the Flyway-wide population of adult females from the model for Caspian terns in the Pacific Flyway under scenario A (status quo management or baseline). The yellow line depicts the average of the 100 replicate runs for the Flyway-wide population under scenario A, including 95% confidence intervals of the mean (dashed lines). Fluctuations within each model run and the spread of the 100 replicate runs demonstrate how the environmental stochasticity incorporated in the model can have a strong influence on individual model runs.

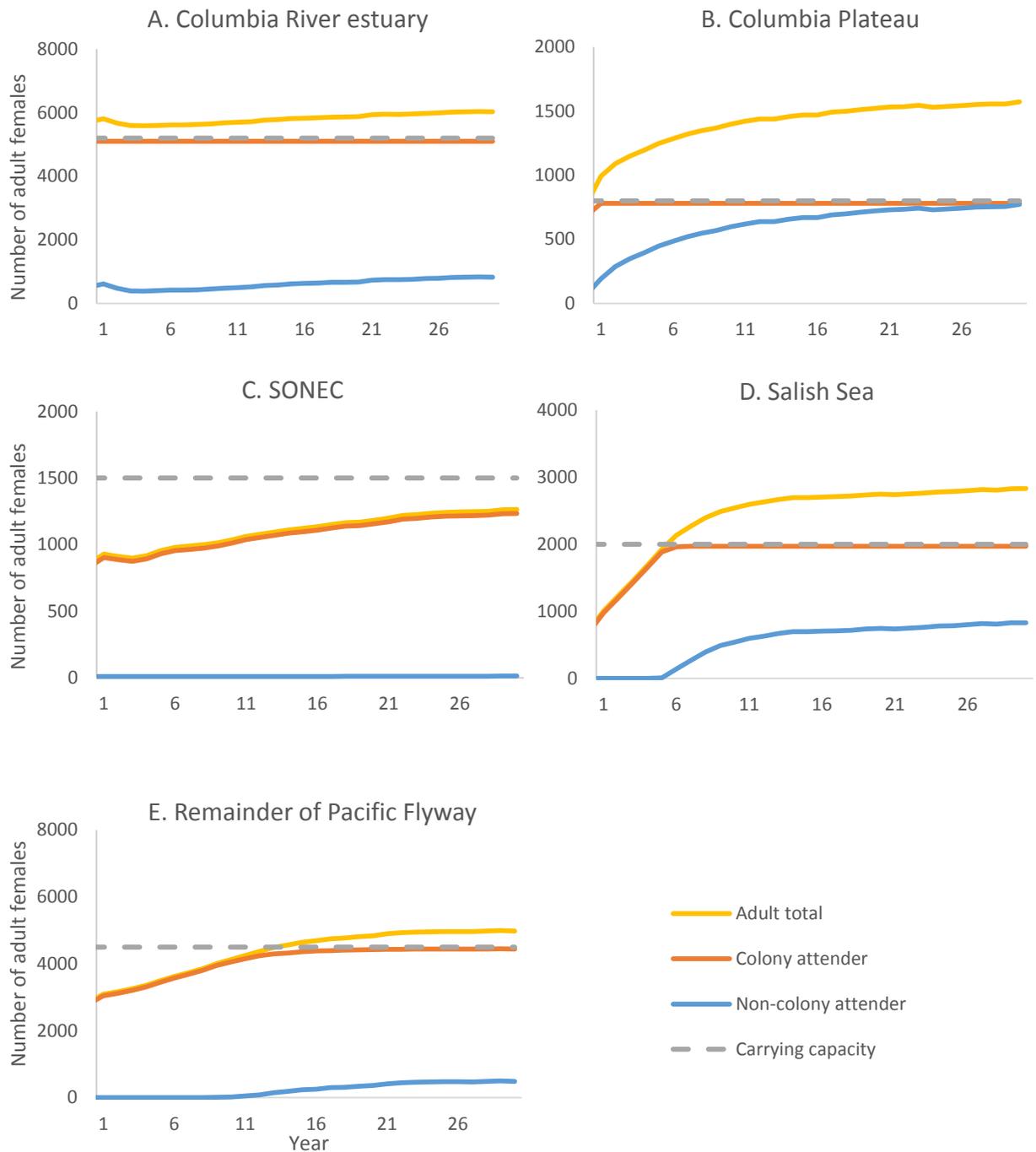


Figure 6. Projections of regional subpopulations of adult females from the model of the Pacific Flyway population of Caspian terns under management scenario A (status quo management or baseline). The five regions encompass the entire breeding range of the Pacific Flyway population.

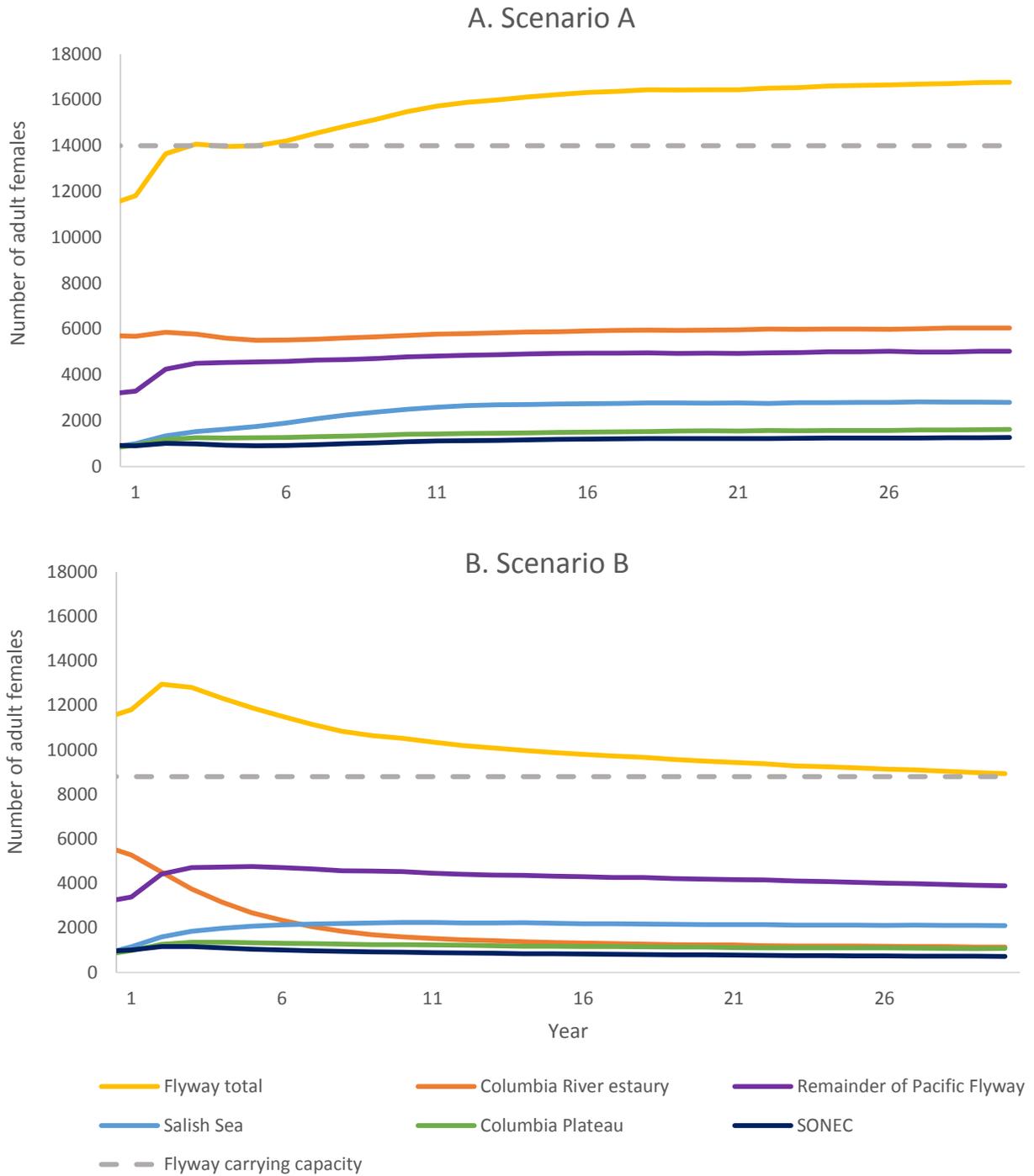


Figure 7. Projections of the total numbers of adult female Caspian terns in the Pacific Flyway population, as well as in each of five regions encompassing the entire breeding range of the Pacific Flyway population, under the baseline (status quo) management scenario (A) and under hypothetical scenario B, where the breeding colony on East Sand Island in the Columbia River estuary is completely eliminated (B; see Table 12).

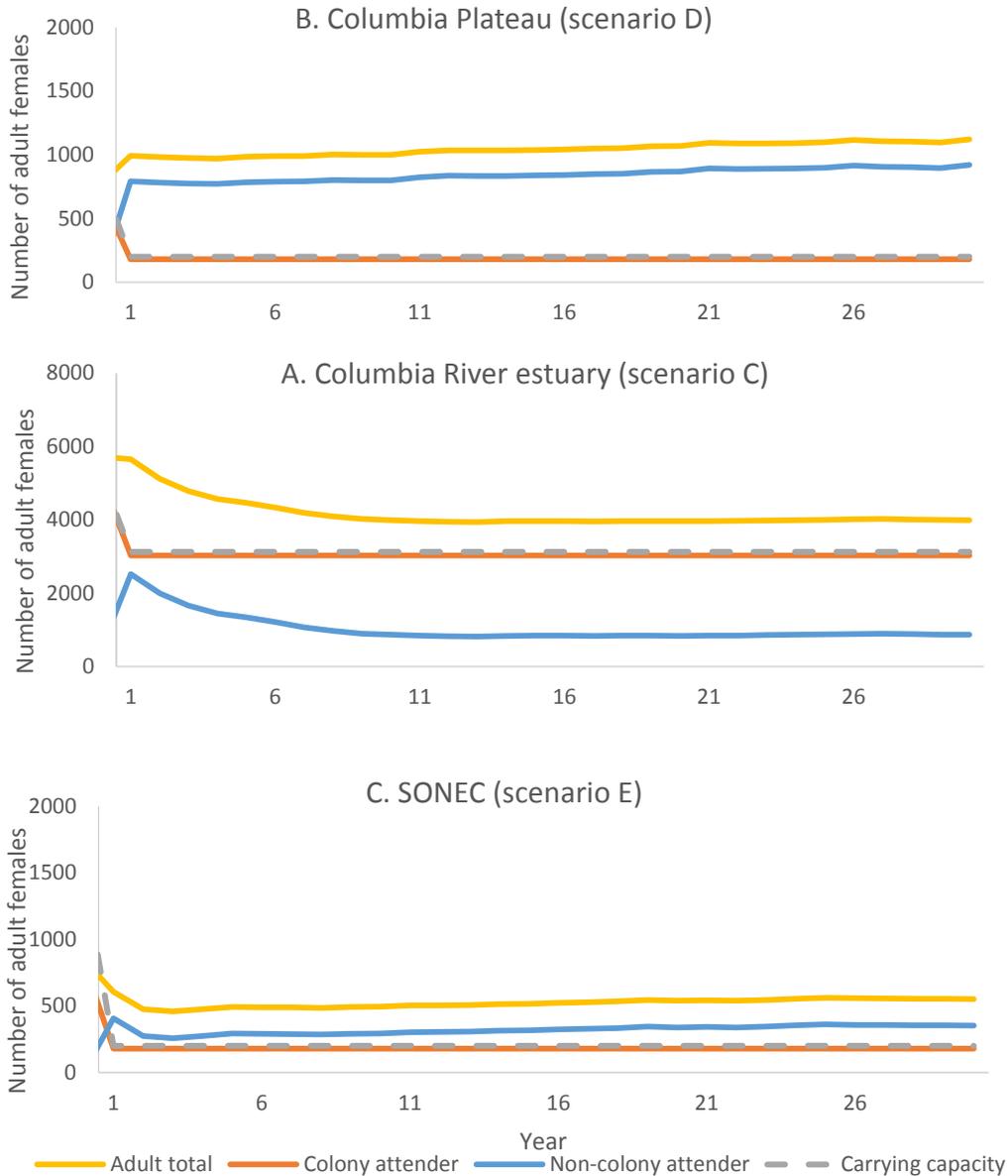


Figure 8. Regional sub-population trajectories for adult female Caspian terns in three regions of the Pacific Flyway population’s breeding range under prospective reductions in availability of nesting habitat (carrying capacity). Under management scenario C (Figure 8A), carrying capacity was reduced by 2,075 individuals from the baseline condition in the Columbia River estuary region. Under management scenario D (Figure 8B), carrying capacity was reduced by 600 individuals from the baseline condition in the Columbia Plateau region. Under management scenario E (Figure 8C), carrying capacity was reduced by 1,300 individuals from the baseline condition in the SONEC region. In each of these management scenarios (C, D, and E), carrying capacity was reduced from the baseline only in the region shown; all other regions had the same carrying capacity as in the baseline scenario.

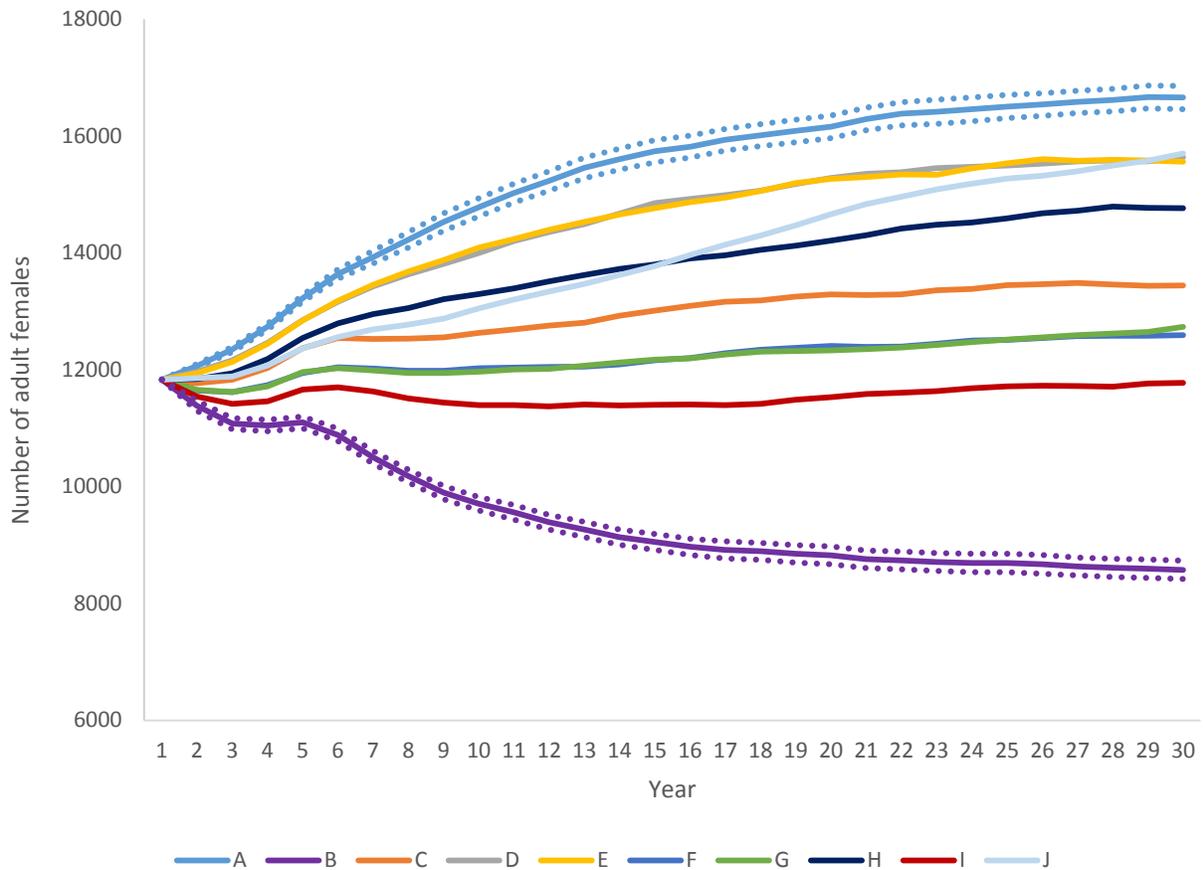


Figure 9. Projections of the total numbers of adult female Caspian terns in the Pacific Flyway population under the baseline (status quo) management scenario (A) and nine prospective management scenarios (B-J) that result in reductions in available nesting habitat in one to three of the five regions (see Table 12). The dashed lines above and below average model projections for scenarios A and B represent the 95% confidence intervals from 100 replicate runs; 95% confidence intervals for the plotted average projections from other management scenarios were similarly narrow.

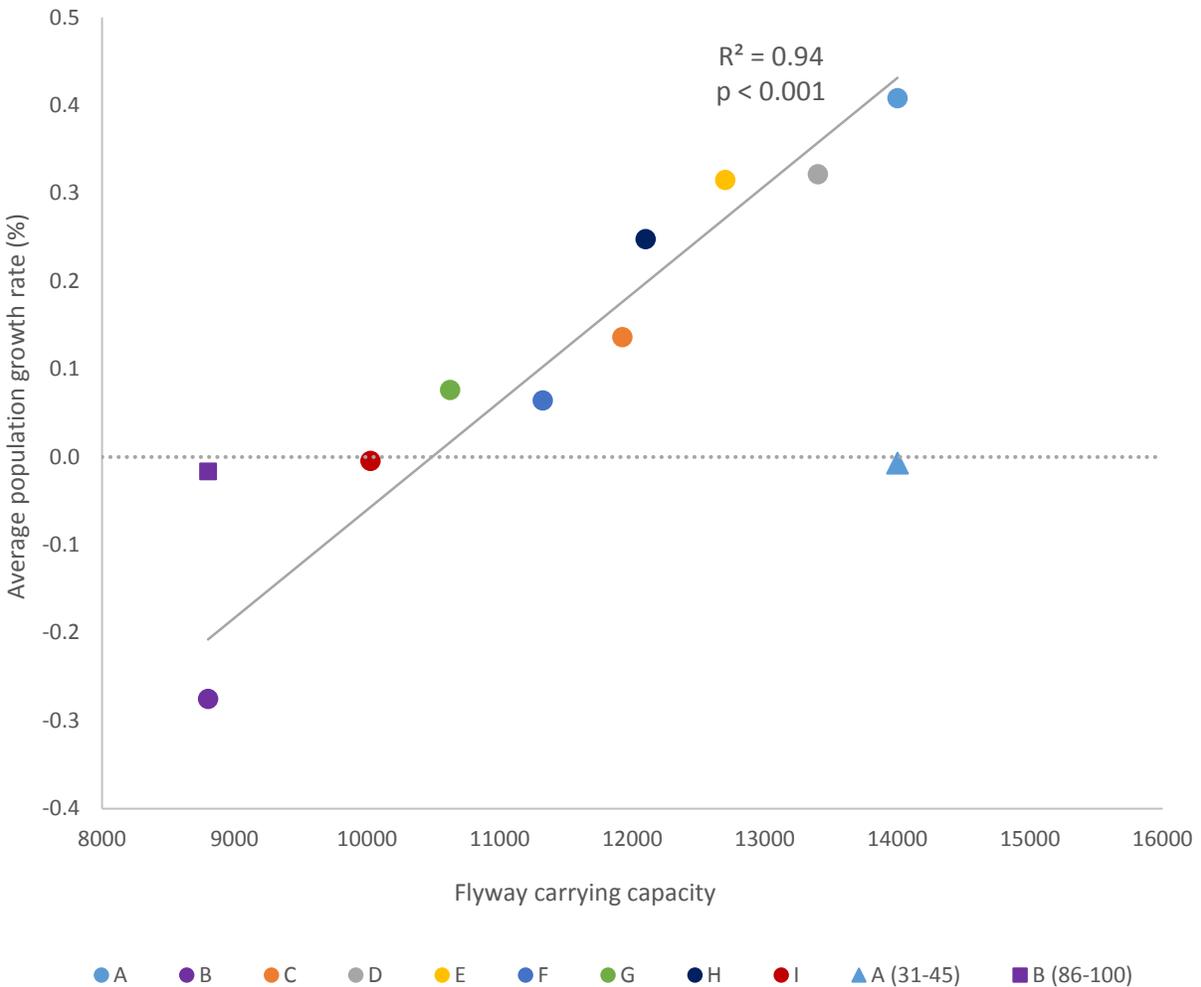


Figure 10. Population growth rate for adult Caspian terns in the Pacific Flyway population during years 1-30 (circles) of the population model projection as a function of Flyway-wide carrying capacity for numbers of breeding Caspian terns under nine different management scenarios. Management scenarios included the baseline (status quo) management scenario (A) and eight prospective management scenarios (B-I) that resulted in reductions in available nesting habitat in one to three of the five regions in the model (see Table 12). The solid line is a trend line of the relationship between Flyway-wide carrying capacity and the population growth rate. The dashed line represents a slope of zero (stable population). The population growth rate for the baseline management scenario (A) during years 31-45 (light blue triangle) and the population growth rate under scenario B during years 86-100 (purple square) were also included for comparison, but not included in the trend line. Scenario J (new nesting habitat created in coastal Washington) was excluded from this figure because the Flyway-wide carrying capacity is the same as in scenario A.

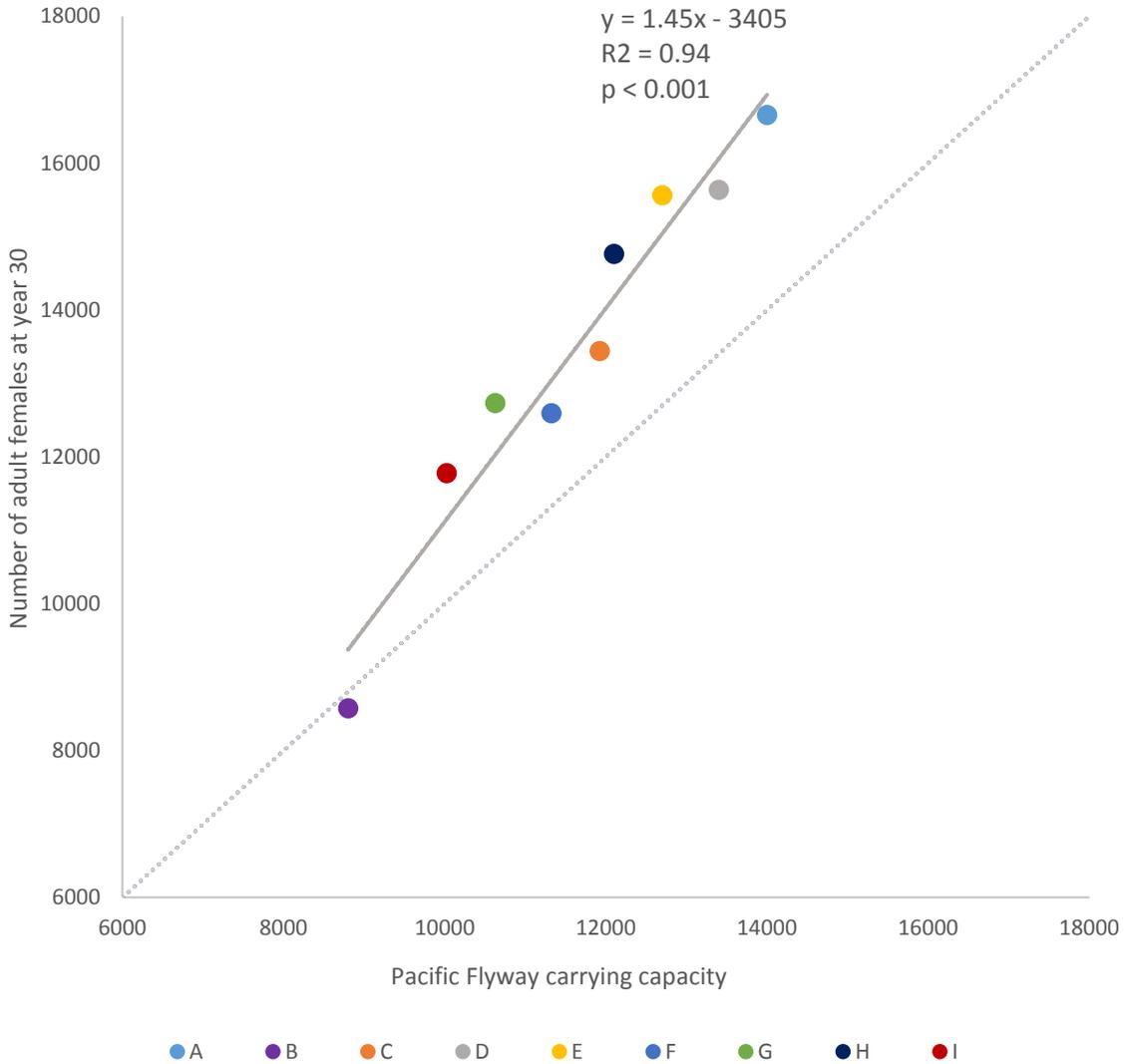


Figure 11. Numbers of adult female Caspian terns in the Pacific Flyway population at Year 30 of the population model run as a function of Flyway-wide carrying capacity for breeding adult females. The population model was run under the baseline (status quo) management scenario (A) and eight prospective management scenarios (B-I) that resulted in reductions in available nesting habitat in one to three of the five regions of the Pacific Flyway (see Table 12). The dashed line represents a slope of 1 (carrying capacity = number of adult females).

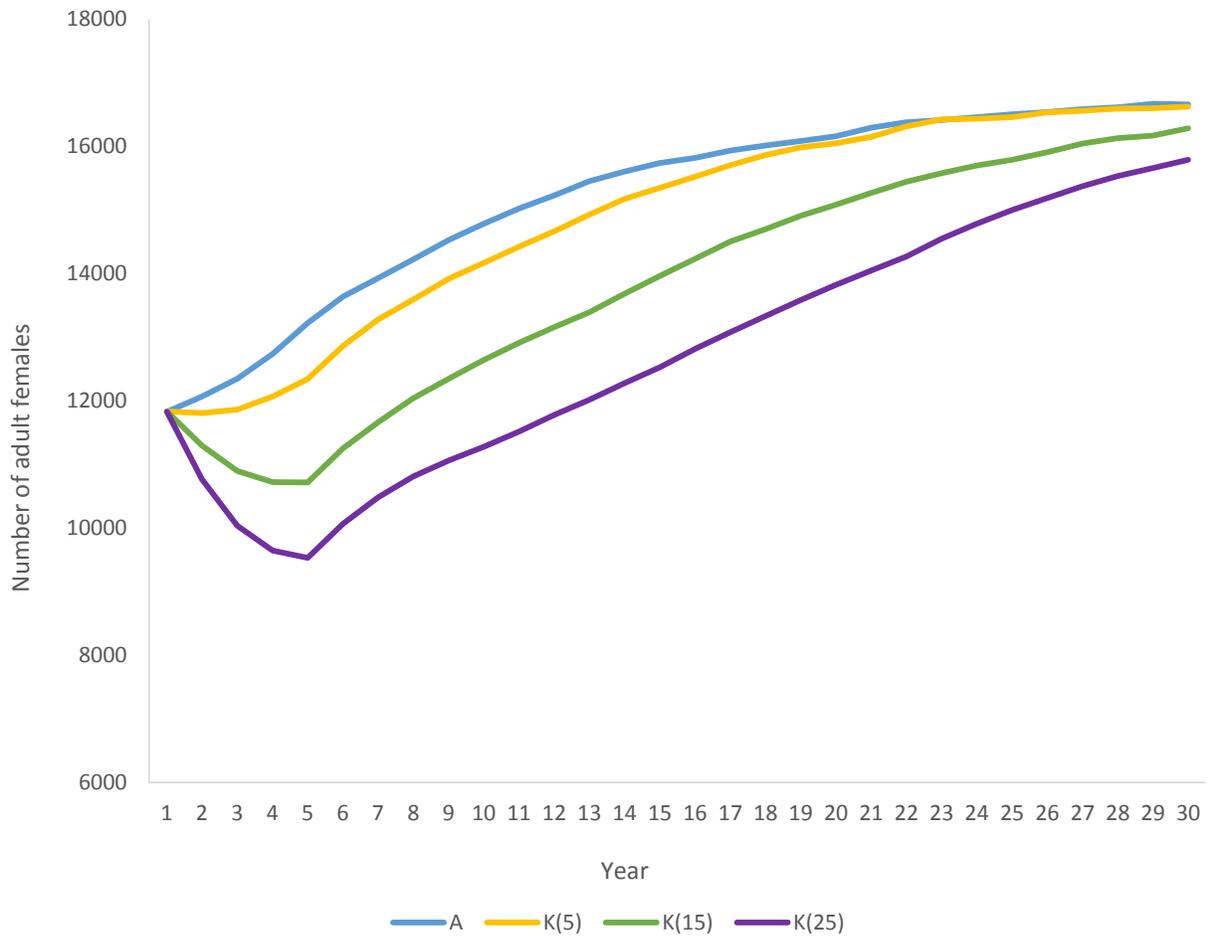


Figure 12. Projections of the total number of adult female Caspian terns in the Pacific Flyway population under the baseline (status quo) management scenario (A) and three scenarios (K series) that simulate the population response to hypothetical 4-year lethal control programs for breeding adults in the Columbia River estuary. These three cull scenarios resulted in reduced annual survival rates for female colony attenders of 5% (scenario K[5]), 15% (scenario K[15]), and 25% (scenario K[25]; see Table 12).

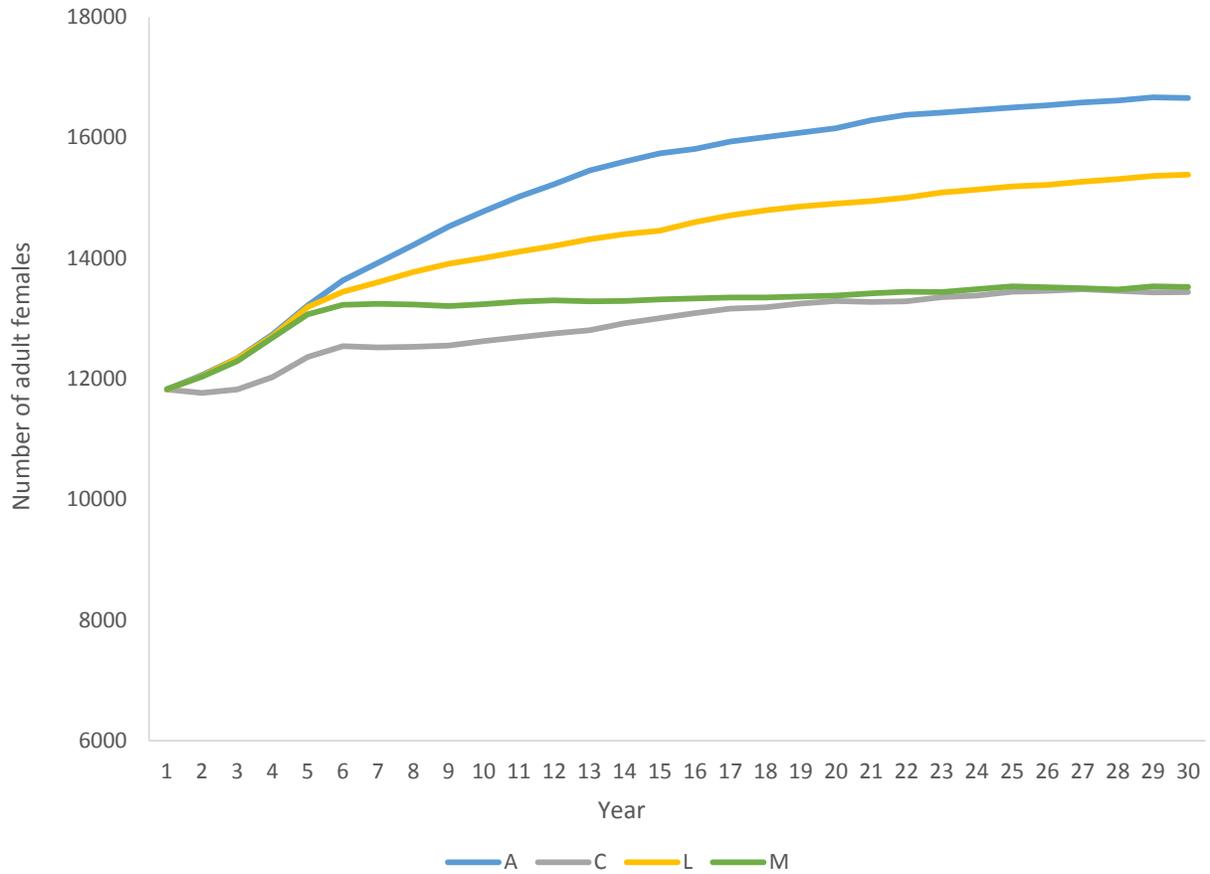


Figure 13. Projections of the total number of adult female Caspian terns in the Pacific Flyway population under the baseline (status quo) management scenario (A) and two scenarios (L and M) that reflected less favorable environmental conditions for nesting Caspian terns in the Columbia River estuary (see Table 12). The population projection under scenario C was included for comparison purposes; under this scenario the available nesting habitat in the Columbia River estuary is reduced to only what is sufficient to support 3,125 breeding females,.

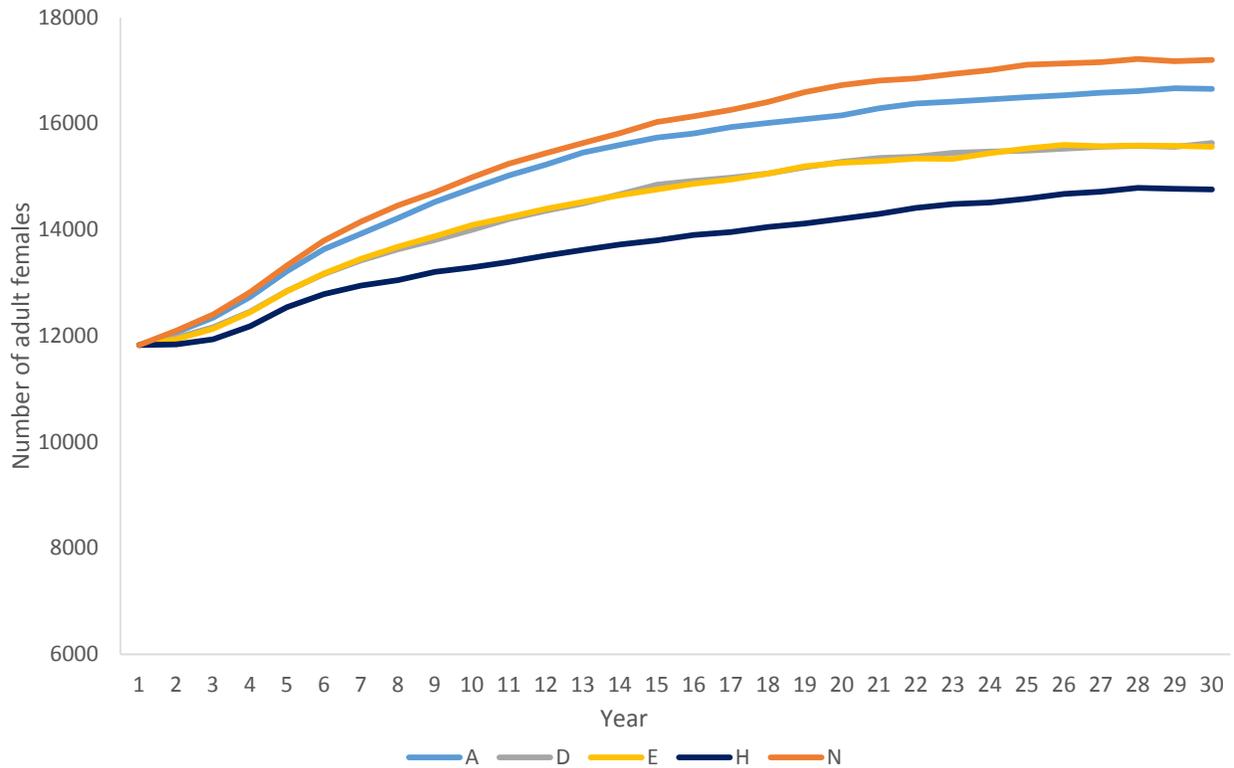


Figure 14. Projections of the total number of adult female Caspian terns in the Pacific Flyway population under the baseline (status quo) management scenario (A), and under a scenario (N) where environmental conditions for nesting Caspian terns in the SONEC region improved due to the cessation of recent drought conditions. Recent conditions for nesting and survival rates in the Columbia Plateau region were substituted for those in the SONEC region under scenario N (see Table 12). Projections under scenarios D, E, and H, which modeled Flyway-wide populations when available nesting habitat was reduced in the Columbia Plateau region, in the SONEC region, and in both regions, respectively, were also included for comparison.

Table 1. Initial population size, baseline carrying capacity, and carrying capacity under prospective management scenarios for Caspian terns in the Pacific Flyway population. Values in the regions of the breeding range are numbers of nesting females. Sex ratio of the population was assumed to be 1:1. Initial population sizes were based on the best available data collected during 2015-2017. Baseline carrying capacities were based on highest number of nesting females during the current phase of management plan (Columbia River estuary and Columbia Plateau) or during 2007-2017 (other regions).

| Region | Initial population size | Baseline carrying capacity | Carrying capacity under prospective management scenarios | Notes on carrying capacity under hypothetical management scenarios |
|--|--------------------------------|-----------------------------------|---|---|
| Columbia River estuary | 5,200 ^a | 5,200 ^a | 3,125 | Based on NOAA's Biological Opinion (2008) |
| Columbia Plateau | 705 | 800 ^b | 200 | Derived from the Environmental Assessment for the Inland Avian Predation Management Plan (2014) |
| Southern Oregon/northeastern California (SONEC) | 850 | 1,500 ^c | 200 | If Corps-constructed islands are not actively maintained as tern nesting habitat and predation and vegetation encroachment limit tern use of the islands |
| Salish Sea | 725 | 2,000 ^c | 4,075 | If a new alternative nesting site becomes available in coastal Washington for terns dispersed from Columbia River estuary, and environmental conditions are similar to Salish Sea |
| Remainder of Pacific Flyway | 2,862 | 4,500 ^c | - | |
| Total | 10,342 ^d | 14,000 | - | |

^a Colony size in 2016, when highest nesting density was observed on the 1-acre nesting area at East Sand Island (BRNW 2017a). This colony size was selected as the initial population size over the colony size in 2017 (3,500 pairs) as a conservative approach because it is suspected that the colony size in 2017 was anomalously low.

^b 31 females higher than the largest sub-population size recorded during the current management phase (2014-2017).

^c 331 females higher than the highest number observed in the region during 2008-2017.

^d Total initial population size used in the model is less than the census population size of 12,407 breeding females counted in 2015, the most recent year when the population was censused (Peterson et al. 2017), because of the inclusion of count data from 2016 and 2017. Initial population size in the model is similar, however, to the estimate of population size in 2015 based on the U.S. Fish and Wildlife Service's monitoring strategy for Caspian terns in the Pacific Flyway population (10,270 breeding females).

Table 2. Numbers of Caspian tern fledglings and adults marked with field-readable alphanumeric leg bands in the Pacific Flyway during 2005-2016. Banded fledglings that were recovered dead on or near their natal colony were not included in the dataset.

| Region where banded | Age class when banded | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | Total |
|---------------------------|-----------------------|------|------|------|------|------|------|------|------|------|------|------|------|-------|
| Columbia River estuary | Fledgling | - | 201 | 181 | 318 | 206 | 122 | - | - | 195 | - | 214 | 211 | 1,648 |
| Columbia Plateau | Fledgling | - | 94 | 304 | 86 | 240 | 186 | 253 | 117 | 234 | 141 | - | - | 1,655 |
| SONEC* | Fledgling | - | - | - | 132 | 38 | 57 | 22 | 345 | 89 | - | 64 | - | 747 |
| Salish Sea | Fledgling | - | - | - | - | - | 215 | - | - | - | - | - | - | 215 |
| Banded as fledgling total | | - | 295 | 485 | 536 | 484 | 580 | 275 | 462 | 518 | 141 | 278 | 211 | 4265 |
| Columbia River estuary | Adult | 33 | 43 | 56 | 51 | 55 | 124 | - | - | - | - | - | - | 362 |
| Columbia Plateau | Adult | 57 | 56 | - | - | - | 49 | 92 | 113 | 109 | 38 | 39 | - | 553 |
| SONEC* | Adult | - | - | - | - | 30 | 7 | 22 | - | - | - | - | - | 59 |
| Banded as adult total | | 90 | 99 | 56 | 51 | 85 | 180 | 114 | 113 | 109 | 38 | 39 | - | 974 |
| Total | | 90 | 394 | 541 | 587 | 569 | 760 | 389 | 575 | 627 | 179 | 317 | 211 | 5239 |

*SONEC: southern Oregon and northeastern California.

Table 3. Numbers of Caspian terns from the Pacific Flyway population marked with field-readable alphanumeric leg bands and resighted during 2006-2017. Although some marked individuals were observed in more than one region within a year, the numbers in the table reflect one resighting per individual per year because analyses presented in this report are based on year (e.g., inter-annual transition between regions).

| Region where resighted | Age class when banded | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
|---------------------------|-----------------------|------|------|------|------|------|------|------|-------|-------|-------|-------|------|
| Columbia River estuary | Fledgling | - | 0 | 1 | 23 | 48 | 73 | 101 | 134 | 189 | 187 | 204 | 211 |
| Columbia Plateau | Fledgling | - | 0 | 0 | 2 | 25 | 35 | 80 | 106 | 200 | 303 | 330 | 170 |
| SONEC* | Fledgling | - | - | 2 | 9 | 22 | 84 | 221 | 266 | 237 | 190 | 35 | - |
| Salish Sea | Fledgling | - | - | 0 | 0 | 27 | 13 | 16 | - | - | 82 | 131 | 40 |
| Banded as fledgling total | | - | 0 | 3 | 34 | 122 | 205 | 418 | 506 | 626 | 762 | 700 | 421 |
| Columbia River estuary | Adult | 28 | 66 | 107 | 151 | 191 | 300 | 273 | 234 | 244 | 237 | 215 | 195 |
| Columbia Plateau | Adult | 49 | 85 | 77 | 75 | 66 | 110 | 161 | 228 | 298 | 276 | 268 | 105 |
| SONEC* | Adult | - | - | 2 | 1 | 27 | 37 | 72 | 81 | 52 | 39 | 9 | - |
| Banded as adult total | | 77 | 151 | 186 | 227 | 284 | 447 | 506 | 543 | 594 | 552 | 492 | 300 |
| Total | | 77 | 151 | 189 | 261 | 406 | 652 | 924 | 1,049 | 1,220 | 1,314 | 1,192 | 721 |

* SONEC: southern Oregon and northeastern California.

Table 4. Multi-state model selection results for the top 10 models to estimate age-specific first return from the wintering range to the breeding range and age-specific first reproduction in the Pacific Flyway population of Caspian terns during 2006-2017. Apparent survival (ϕ), resighting (p), and transition (ψ) probabilities between four life stages (juvenile and non-migratory pre-breeder combined, migratory pre-breeder, colony attender, non-colony attender) were evaluated in relation to the effects of age (a), linear trend on age (A), life stage (ls), cohort (c), and year (t). The cut-off age for a difference in survival rate in younger and older individuals was assumed to be 2 years post-hatch (e.g., $\phi [a_{0-2}, a_{>2}]$: survival rates differ between age classes 0-2 years old and >2 years old), the same as the observed youngest age at first return. Age effects on transitions between four life stages (e.g. $\psi [a/a/A/.]$: age effect on transitions from juvenile or non-migratory pre-breeder to migratory pre-breeder/migratory pre-breeder to colony attender/linear trend of age effect on transition from colony attender to non-colony attender/no age effect on transition from non-colony attender to colony attender) and maximum age for first return from the wintering range (e.g., $\psi [a_9]$; ages 1-9 were estimated and then fixed to 1.0 for ages thereafter) were also evaluated. Models were ranked according to Akaike's Information Criterion adjusted for small sample size and over dispersion (QAICc). Constant (intercept only) is denoted as “.”, interactive effect as “*”, and additive effect as “+”.

| Model | QAICc | Δ QAICc | AICc Weights | Model Likelihood | No. of Parameters | Deviance |
|---|----------|----------------|--------------|------------------|-------------------|----------|
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_9/a/A/.)$ | 15301.54 | 0.000 | 0.40461 | 1.0000 | 78 | 2523.108 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_8/a/A/.)$ | 15302.19 | 0.6502 | 0.29231 | 0.7224 | 77 | 2525.800 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_{10}/a/A/.)$ | 15302.69 | 1.1568 | 0.2269 | 0.5608 | 79 | 2522.223 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_{11}/a/A/.)$ | 15305.62 | 4.0829 | 0.05253 | 0.1298 | 80 | 2523.106 |
| $\phi (a_{0-2}+c, a_{>2}*ls+t) p (ls*t) \psi (a_{11}/a/A/.)$ | 15307.66 | 6.1260 | 0.01891 | 0.0467 | 81 | 2523.106 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_{11}/a/a/.)$ | 15312.25 | 10.7118 | 0.00191 | 0.0047 | 87 | 2515.422 |
| $\phi (a_{0-2}*c, a_{>2}+ ls+t) p (ls*t) \psi (a_{11}/a/a/.)$ | 15312.37 | 10.8299 | 0.00180 | 0.0044 | 119 | 2449.769 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_{11}/a/./.)$ | 15314.93 | 13.3974 | 0.00050 | 0.0012 | 79 | 2534.464 |
| $\phi (a_{0-2}*c, a_{>2}+ ls*t) p (ls*t) \psi (a_{11}/a/./.)$ | 15315.82 | 14.2884 | 0.00032 | 0.0008 | 111 | 2469.724 |
| $\phi (a_{0-2}+c, a_{>2}+ ls+t) p (ls*t) \psi (a_{11}/a/A/.)$ | 15316.97 | 15.4307 | 0.00018 | 0.0004 | 76 | 2542.622 |

Table 5. Age-specific proportions of juvenile and non-migratory pre-breeders returning to the breeding range for the first time and for migratory pre-breeders breeding for the first time in marked Caspian terns from the Pacific Flyway population. Estimated cumulative proportions were derived from age-specific transition probabilities between life stages and survival rates estimated in the four-state analysis in program MARK using band resighting data collected during 2006-2017 (see Table 4).

| Age | Flyway-wide first return to breeding range (cumulative) | Flyway-wide first reproduction (cumulative) |
|-----|---|---|
| 1 | 0.00 | 0.00 |
| 2 | 0.10 | 0.00 |
| 3 | 0.47 | 0.03 |
| 4 | 0.70 | 0.23 |
| 5 | 0.78 | 0.58 |
| 6 | 0.85 | 0.77 |
| 7 | 0.88 | 0.88 |
| 8 | 0.94 | 0.94 |
| 9 | 0.98 | 0.97 |
| 10 | 1.00 | 0.98 |
| 11 | 1.00 | 1.00 |

Table 6. Region-specific first return rates of juvenile or non-migratory pre-breeder Caspian terns to regions within the breeding range of the Pacific Flyway population. Estimated rates of natal philopatry and natal dispersal were derived from transition probabilities between life stages and among three regions (Columbia River estuary, Columbia Plateau, and southern Oregon/northeastern California [SONEC]; Table A-7 in Appendix A) estimated from the best model in a 12-state analysis in program MARK using band resighting data collected during 2006-2017 (see Table 9). Natal philopatry and natal dispersal rates were normalized so that the sum of these rates for each natal region equaled 1.0. Prior to normalization, an averaged natal philopatry rate for the three regions was used as the natal philopatry rate for the Salish Sea region and the Remainder of Pacific Flyway region. Natal dispersal rates to/from the Salish Sea region were based on assumptions made for inter-regional movements of migratory pre-breeders and adults (see Table 11). Natal dispersal rate from a given region to the Remainder of the Pacific Flyway region is an average of natal dispersal rates from each region to the other three regions. Natal dispersal rates from the Remainder of the Pacific Flyway region to each of the four other regions were assumed to be equal.

| Natal region | Region where first return to breeding range occurred | | | | |
|-----------------------------|--|------------------|-------|------------|-----------------------------|
| | Columbia River estuary | Columbia Plateau | SONEC | Salish Sea | Remainder of Pacific Flyway |
| Columbia River estuary | 0.39 | 0.00 | 0.23 | 0.23 | 0.15 |
| Columbia Plateau | 0.00 | 0.32 | 0.51 | 0.00 | 0.17 |
| SONEC | 0.00 | 0.00 | 0.90 | 0.00* | 0.10* |
| Salish Sea | 0.32 | 0.00 | 0.00 | 0.57 | 0.11 |
| Remainder of Pacific Flyway | 0.08 | 0.08 | 0.08 | 0.08 | 0.68 |

*Natal dispersal rate from the SONEC region was zero within the three-region study area. Based on field observations, natal dispersal from the SONEC region to Salish Sea was unlikely. An assumption was made, however, that there was natal dispersal to the Remainder of Pacific Flyway at a low rate.

Table 7. Breeding conditions in five regions encompassing the entire breeding range of the Pacific Flyway population of Caspian terns during 2000-2017. Breeding conditions were assigned to five categories based on fledging success (average number of female offspring fledged per female parent): exceptionally favorable (≥ 0.6), favorable (0.40-0.59), typical (0.20-0.39), unfavorable (0.10-0.19), and exceptionally unfavorable (0.00-0.09).

| Year | Columbia River estuary | Columbia Plateau | Southern Oregon/ northeastern California (SONEC) | Salish Sea | Remainder of Pacific Flyway* |
|------|---------------------------|---------------------------|--|---------------------------|---------------------------------|
| 2000 | Typical | Typical | - | - | Typical |
| 2001 | Exceptionally favorable | Favorable | - | - | Unfavorable |
| 2002 | Favorable | Typical | - | - | Unfavorable |
| 2003 | Favorable | Typical | - | - | Typical |
| 2004 | Favorable | Typical | - | Favorable | Unfavorable |
| 2005 | Unfavorable | Typical | - | Typical | Typical |
| 2006 | Typical | Unfavorable | - | Unfavorable | Typical |
| 2007 | Typical | Typical | - | Unfavorable | Unfavorable |
| 2008 | Typical | Unfavorable | Unfavorable | Exceptionally unfavorable | Unfavorable |
| 2009 | Typical | Unfavorable | Exceptionally unfavorable | Exceptionally unfavorable | Typical |
| 2010 | Exceptionally unfavorable | Unfavorable | Typical | Typical | Unfavorable |
| 2011 | Exceptionally unfavorable | Unfavorable | Exceptionally unfavorable | Exceptionally unfavorable | Unfavorable |
| 2012 | Exceptionally unfavorable | Exceptionally unfavorable | Typical | Exceptionally unfavorable | Typical |
| 2013 | Unfavorable | Typical | Unfavorable | Exceptionally unfavorable | Typical |
| 2014 | Unfavorable | Unfavorable | Exceptionally unfavorable | Exceptionally unfavorable | Unfavorable |
| 2015 | Typical | Unfavorable | Exceptionally unfavorable | Exceptionally unfavorable | Unfavorable |
| 2016 | Typical | Unfavorable | - | Exceptionally unfavorable | Unfavorable |
| 2017 | Exceptionally unfavorable | Exceptionally unfavorable | - | Exceptionally unfavorable | Unfavorable |

*Average frequency of typical and unfavorable conditions for breeding observed in the Columbia River estuary, Columbia Plateau, SONEC, and Salish Sea regions during 2008-2015 were randomly assigned to the Remainder of the Pacific Flyway region, because data were not available for that region. Exceptionally unfavorable conditions were assumed to be unlikely in the Remainder of the Pacific Flyway region (see text).

Table 8. Mean fledging success (average number of female offspring fledged per female parent) and standard deviation (in parentheses) in relation to the regional level of breeding conditions for Caspian terns in the Pacific Flyway population during 2000-2017. Mean fledging success was estimated from empirical measurements of annual fledging success at each level of breeding conditions.

| Level of breeding conditions | Columbia River estuary | Columbia Plateau | Southern Oregon/northeastern California (SONEC) | Salish Sea | Remainder of Pacific Flyway ^a |
|------------------------------|--------------------------|--------------------------|---|--------------------------|--|
| Exceptionally favorable | 0.70 (0.08) ^b | - | - | - | - |
| Favorable | 0.51 (0.05) | 0.48 (0.12) ^b | - | 0.48 (0.08) ^b | - |
| Typical | 0.31 (0.03) | 0.25(0.06) | 0.25 (0.01) | 0.35 (0.06) | 0.29 (0.04) |
| Unfavorable | 0.14 (0.04) | 0.14 (0.03) | 0.16 (0.01) | 0.12 (0.01) | 0.14 (0.02) |
| Exceptionally unfavorable | 0.01 (0.02) | 0.05 (0.06) | 0.07 (0.02) | 0.04 (0.04) | - |

^a Mean fledging success and standard deviations were based on averages of those values in the four other regions of the Pacific Flyway because sufficient data were not available from this region.

^b Standard deviation was not estimable because only one value for fledging success was recorded at this level of breeding conditions. The coefficient of variation at another level of breeding conditions within the same region was used to estimate the standard deviation.

Table 9. Multi-state model selection results for the top 10 models to estimate survival and inter-regional movement rates of known-age and unknown-age marked Caspian terns in the Pacific Flyway population during 2005-2017. Apparent survival (ϕ), resighting (p), and transition (ψ) probabilities between four life stages (juvenile and non-migratory pre-breeders combined, migratory pre-breeder, colony attender [ct], non-colony attender [nct]) among three regions (Columbia River estuary, Columbia Plateau, southern Oregon/northeastern California [SONEC]) were evaluated in relation to the effects of cohort (c), age (a), life stage (ls), region (reg), year (t), and directional movement from one region to another ($trans$). The cut-off age for a difference in survival rate in younger and older individuals was assumed to be 2 years post-hatch (e.g., $\phi [a_{0-2}, a_{>2}]$: survival rates differ between age classes 0-2 years old and >2 years old), the same as the observed youngest age at first return. Models were ranked according to Akaike's Information Criterion adjusted for small sample size and over dispersion (QAICc). Interactive effects are denoted as "*" and additive effect as "+".

| Model | QAICc | Δ QAICc | AICc Weights | Model Likelihood | No. of Parameters | Deviance |
|---|----------|----------------|--------------|------------------|-------------------|----------|
| $\phi (a_{0-2} * reg + c, a_{>2} * reg + ls + t) p (ls * reg * t) \psi (trans * ls)$ | 22197.08 | 0.0000 | 0.98329 | 1.0000 | 167 | 8165.673 |
| $\phi (a_{0-2} + reg + c, a_{>2} + reg + ls + t) p (ls * reg * t) \psi (trans * ls)$ | 22205.37 | 8.2877 | 0.01560 | 0.0159 | 165 | 8178.073 |
| $\phi (a_{0-2} + reg + c, a_{>2} * ls + reg + t) p (ls * reg * t) \psi (trans * ls)$ | 22210.65 | 13.575 | 0.00111 | 0.0011 | 166 | 8181.304 |
| $\phi (a_{0-2} + c, a_{>2} + ls + t) p (ls * reg * t) \psi (trans * ls)$ | 22231.26 | 34.178 | 0.0000 | 0.0000 | 163 | 8208.075 |
| $\phi (a_{0-2} + c, a_{>2} * ls + t) p (ls * reg * t) \psi (trans * ls)$ | 22233.31 | 36.2334 | 0.0000 | 0.0000 | 164 | 8208.075 |
| $\phi (a_{0-2} * reg, a_{>2} * reg + ls) p (ls * reg * t) \psi (trans * ls)$ | 22255.17 | 58.0893 | 0.0000 | 0.0000 | 156 | 8246.364 |
| $\phi (a_{0-2} * reg + c, a_{>2} * reg + ls (ct = nct) + t) p (ls * reg * t) \psi (trans * ls)$ | 22291.46 | 94.3864 | 0.0000 | 0.0000 | 153 | 8288.818 |
| $\phi (a_{0-2} + reg + c, a_{>2} + reg + t) p (ls * reg * t) \psi (trans) * ls$ | 22387.87 | 190.7966 | 0.0000 | 0.0000 | 166 | 8358.526 |
| $\phi (a_{0-2} * reg + c, a_{>2} * reg + t) p (ls * reg * t) \psi (trans * ls)$ | 22441.59 | 244.5103 | 0.0000 | 0.0000 | 162 | 8420.462 |
| $\phi (a_{0-2} * reg + c, a_{>2} * reg + ls + t) p (ls * reg + t) \psi (trans * ls)$ | 22699.24 | 502.1610 | 0.0000 | 0.0000 | 90 | 8825.177 |

Table 10. Mean survival probability estimates and standard deviations (in parentheses) for Caspian terns in five regions encompassing the entire breeding range of the Pacific Flyway population. Estimates were from the best model of the 12-state analysis in program MARK, using resighting data collected from terns marked with field-readable leg bands and resighted during 2005-2017 (see Table 9). Survival probabilities across years by life stage and region are shown in Appendix A (Tables A-4, A-5, and A-6).

| Region | Juvenile survival (0-2 years post- fledging) | Annual non-migratory pre-breeder survival ^b | Annual migratory pre-breeder survival | Annual colony attender survival | Annual non-colony attender survival |
|---|--|---|--|---------------------------------------|---|
| Columbia River estuary | 0.48 (0.06) | 0.94 (0.04) | 0.89 (0.06) | 0.98 (0.01) | 0.85 (0.08) |
| Columbia Plateau | 0.60 (0.12) | 0.94 (0.04) | 0.83 (0.08) | 0.96 (0.02) | 0.77 (0.11) |
| Southern Oregon/northeastern California (SONEC) | 0.51 (0.11) | 0.94 (0.04) | 0.76 (0.11) | 0.94 (0.03) | 0.69 (0.13) |
| Salish Sea ^a | 0.53 (0.10) | 0.94 (0.04) | 0.83 (0.08) | 0.96 (0.02) | 0.77 (0.11) |
| Remainder of Pacific Flyway ^a | 0.53 (0.10) | 0.94 (0.04) | 0.83 (0.08) | 0.96 (0.02) | 0.77 (0.11) |

^a Average of survival rates from the three other regions were applied to the Salish Sea region and the Remainder of the Pacific Flyway region, where survival data were not available.

^b Annual survival rate of non-migratory pre-breeders remaining in the wintering range was estimated in the multi-state model with four states (see Table 4).

Table 11. Mean movement probabilities of Caspian terns among five regions encompassing the entire breeding range of the Pacific Flyway population during 2005-2017. Movement probabilities (Tables A-7 and A-8 in Appendix A) were estimated from the best model of the 12-state analysis in program MARK (see Table 9).

| Origination and destination regions | Pre-breeders | Colony attenders | Non-colony attenders | Assumptions |
|--------------------------------------|--------------|------------------|----------------------|---|
| From Columbia River estuary to: | | | | |
| Columbia Plateau | 0.02 | 0.009 | 0.019 | |
| SONEC | 0.11 | 0.007 | 0.027 | |
| Salish Sea | 0.13 | 0.016 | 0.046 | {Estuary to (Plateau + SONEC)} |
| Remainder of Pacific Flyway | 0.09 | 0.011 | 0.031 | Average of movement from Estuary to other regions |
| From Columbia Plateau to: | | | | |
| Columbia River estuary | 0.04 | 0.025 | 0.030 | |
| SONEC | 0.17 | 0.039 | 0.035 | |
| Salish Sea | 0.02 | 0.013 | 0.015 | (Plateau to Estuary)/2 |
| Remainder of Pacific Flyway | 0.08 | 0.026 | 0.027 | Average of movement from Plateau to other regions |
| From SONEC to: | | | | |
| Columbia River estuary | 0.08 | 0.046 | 0.155 | |
| Columbia Plateau | 0.27 | 0.116 | 0.308 | |
| Salish Sea | 0.04 | 0.023 | 0.078 | (SONEC to Estuary)/2 |
| Remainder of Pacific Flyway | 0.13 | 0.062 | 0.180 | Average of movement from SONEC to other regions |
| From Salish Sea to: | | | | |
| Columbia River estuary | 0.13 | 0.016 | 0.046 | Same as Estuary to Salish Sea |
| Columbia Plateau | 0.01 | 0.005 | 0.010 | (Estuary to Plateau)/2 |
| SONEC | 0.06 | 0.004 | 0.014 | (Estuary to SONEC)/2 |
| Remainder of Pacific Flyway | 0.07 | 0.008 | 0.023 | Average of movement from Salish Sea to others |
| From Remainder of Pacific Flyway to: | | | | |
| Columbia River estuary | 0.16 | 0.020 | 0.056 | No net movement to/from Columbia River estuary |
| Columbia Plateau | 0.02 | 0.006 | 0.007 | No net movement to/from Columbia Plateau |
| SONEC | 0.04 | 0.018 | 0.053 | No net movement to/from SONEC |
| Salish Sea | 0.02 | 0.002 | 0.006 | No net movement to/from Salish Sea |

Table 12. Population modeling scenarios under various prospective management actions and changing environmental conditions for breeding implemented at the beginning of 30-year runs of the HexSim population model for Pacific Flyway Caspian terns.

| Scenario | Reduced carrying capacity (number of female colony attenders) | | | Increased carrying capacity |
|----------------------------------|---|------------------|-------|-----------------------------|
| | Columbia River estuary | Columbia Plateau | SONEC | Salish Sea |
| Prospective management actions | | | | |
| A (status quo) | - | - | - | - |
| B | 0 | - | - | - |
| C | 3,125 | - | - | - |
| D | - | 200 | - | - |
| E | - | - | 200 | - |
| F | 3,125 | 200 | - | - |
| G | 3,125 | - | 200 | - |
| H | - | 200 | 200 | - |
| I | 3,125 | 200 | 200 | - |
| J | 3,125 | - | - | 4075 |
| Scenario | Scenario description | | | |
| Lethal control | | | | |
| K(5) | 5% lower annual survival of colony attenders in the Columbia River estuary | | | |
| K(15) | 15% lower annual survival of colony attenders in the Columbia River estuary | | | |
| K(25) | 25% lower annual survival of colony attenders in the Columbia River estuary | | | |
| Changing conditions for breeding | | | | |
| L ^a | Less favorable environmental conditions in the Columbia River estuary than under scenario A | | | |
| M ^b | Less favorable environmental conditions in the Columbia River estuary than under scenario L | | | |
| N ^c | More favorable environmental conditions in SONEC than under scenario A | | | |

^a Breeding conditions and fledging success during 2008-2017 in the Columbia River estuary were used as input data to exclude more favorable breeding conditions and fledging success in the early 2000s. Breeding conditions and fledging success during 2000-2017 were used in scenario A.

^b Typical breeding conditions and associated fledging success during 2008-2017 in the Columbia River estuary were replaced by unfavorable and exceptionally unfavorable conditions and associated fledging success.

^c Survival rates of all life stages, breeding conditions, and fledging success in the SONEC region were replaced by those of the Columbia Plateau region to simulate better environmental conditions than observed in the SONEC region due to severe drought.

Appendix A. Parameter estimates from four-state and twelve-state analyses in program MARK.

Table A-1. Two-year survival probabilities and standard errors (in parentheses) of juvenile Caspian terns 0-2 years post-fledging and residing in the wintering range of the Pacific Flyway population during 2006-2017. Survival probabilities were estimated from the best model of the four-state analysis in program MARK (see Table 4). The mean survival rate was used to estimate age-specific first return from the wintering range to the breeding range (see Table 5).

| Year banded | 0-2 years post-fledging juvenile survival |
|-------------|---|
| 2006 | 0.58 (0.05) |
| 2007 | 0.52 (0.04) |
| 2008 | 0.50 (0.04) |
| 2009 | 0.54 (0.05) |
| 2010 | 0.66 (0.06) |
| 2011 | 0.77 (0.08) |
| 2012 | 0.59 (0.07) |
| 2013 | 0.37 (0.06) |
| 2014 | 0.37 (0.07) |
| 2015 | 0.23 (0.05) |

Table A-2. Annual survival probabilities and standard errors (in parentheses) of pre-breeding Caspian terns that are older than 2 years post-fledging, including the non-migratory pre-breeder life stage (terns that reside in the wintering range) and the migratory pre-breeder life stage (terns that return to the breeding range) in the Pacific Flyway population during 2008-2017. These survival probabilities were estimated from the best model of the four-state analysis in program MARK (see Table 4). First time period when annual survival rate could be estimated for these two life stages was 2008-2009 because the oldest known-age cohort was banded in 2006. The mean annual survival rate for each life stage was used to estimate age-specific probabilities of first return from the wintering range to the breeding range, and age-specific probabilities of first reproduction (see Table 5). The mean and standard deviation of survival probabilities for the non-migratory pre-breeder life stage, which were estimated in the four-state analysis, were used directly in the population model (see Table 10).

| Year (t) | non-migratory pre-breeder in wintering range | migratory pre- breeder in breeding range |
|-------------|--|--|
| 2008 | 0.96 (0.03) | 0.87 (0.02) |
| 2009 | 0.96 (0.02) | 0.88 (0.02) |
| 2010 | 0.98 (0.01) | 0.92 (0.01) |
| 2011 | 0.99 (0.01) | 0.95 (0.01) |
| 2012 | 0.97 (0.02) | 0.90 (0.02) |
| 2013 | 0.93 (0.04) | 0.79 (0.02) |
| 2014 | 0.93 (0.04) | 0.79 (0.03) |
| 2015 | 0.87 (0.07) | 0.66 (0.03) |
| 2016 | 0.88 (0.08) | 0.69 (0.09) |

Table A-3. Life stage transition probabilities and standard errors (in parentheses) for Caspian terns in the Pacific Flyway population during 2006-2017, estimated from the best model of the four-state analysis in program MARK (see Table 4). Transition probabilities were used in estimates of age-specific probabilities of first return from the wintering range to the breeding range, and age-specific probabilities of first reproduction (see Table 5).

| Age | From juvenile or non-migratory pre-breeder (both in wintering range) to migratory pre-breeder in breeding range | From juvenile or non-migratory pre-breeder (both in wintering range) to colony attender | From migratory pre-breeder in breeding range to colony attender |
|-----|---|---|---|
| 1 | 0 ^a | 0 ^a | 0 ^a |
| 2 | 0.09 (0.01) | <0.01 (<0.01) | 0 ^a |
| 3 | 0.35 (0.03) | 0.02 (<0.01) | 0.14 (0.04) |
| 4 | 0.36 (0.04) | 0.02 (0.01) | 0.25 (0.03) |
| 5 | 0.25 (0.05) | <0.001 (-) | 0.42 (0.03) |
| 6 | 0.27 (0.05) | 0.01 (0.02) | 0.37 (0.03) |
| 7 | 0.18 (0.06) | <0.01 (<0.01) | 0.28 (0.04) |
| 8 | 0.45 (0.10) | <0.001 (-) | 0.20 (0.04) |
| 9 | 0.65 (0.20) | <0.001 (-) | 0.11 (0.04) |
| 10 | 1 ^b | <0.001 (-) | 0.03 (0.03) |
| 11 | 1 ^b | <0.001 (-) | 0.08 (0.08) |

^a Transition probability was fixed at zero because the transition was not observed in mark-resight data.

^b Transition probability was fixed at one to model the maximum age for the transition at 9 years post-fledging.

“-“ indicates a standard error was not estimable because the parameter estimate was close to zero.

Table A-4. Two-year survival probabilities and standard errors (in parentheses) of juvenile Caspian terns less than 2 years post-fledging and residing in the wintering range of the Pacific Flyway population during 2006-2017. Survival probabilities were estimated from the best model of the twelve-state analysis in program MARK (see Table 9). The mean and standard deviation of survival probabilities for each natal region were used in the population model (see Table 10).

| Year banded | Natal region | | |
|-------------|--------------------------|------------------|--------------------|
| | Columbia River estuary | Columbia Plateau | SONEC ^a |
| 2006 | 0.58 (0.05) | 0.73 (0.05) | - |
| 2007 | 0.44 (0.05) | 0.60 (0.04) | - |
| 2008 | 0.50 (0.05) | 0.66 (0.05) | 0.57 (0.06) |
| 2009 | 0.44 (0.05) | 0.60 (0.04) | 0.51 (0.07) |
| 2010 | 0.44 (0.06) | 0.61 (0.05) | 0.52 (0.07) |
| 2011 | - | 0.72 (0.06) | 0.64 (0.08) |
| 2012 | - | 0.68 (0.06) | 0.60 (0.06) |
| 2013 | 0.30 (0.05) ^b | 0.45 (0.05) | 0.36 (0.07) |
| 2014 | - | 0.36 (0.05) | - |
| 2015 | 0.28 (0.05) ^b | - | 0.35 (0.07) |

^a SONEC: southern Oregon and northeastern California.

^b When survival rates were averaged over cohorts, estimates from the Columbia River estuary in 2013 and 2015 were excluded. Only fledglings raised very late in the breeding season were banded in these two years. The survival rates for these two cohorts are likely lower than those of the majority of terns fledged during those two breeding seasons.

“-“ indicates that banding of fledglings did not occur.

Table A-5. Annual survival probabilities and standard errors (in parentheses) of Caspian terns older than 2 years post-fledging and in the migratory pre-breeder life stage (residing in the breeding range) of the Pacific Flyway population during 2008-2017. These probabilities were estimated from the best model of the twelve-state analysis in program MARK (see Table 9). The first time period when annual survival probabilities could be estimated for this life stage was 2008-2009, because the oldest known-age cohort was banded in 2006. The mean and standard deviation of survival probabilities in each region were used in the population model (see Table 10).

| Year (t) | Columbia River estuary | Columbia Plateau | SONEC* |
|----------|------------------------|------------------|-------------|
| 2008 | 0.94 (0.01) | 0.90 (0.02) | 0.85 (0.03) |
| 2009 | 0.92 (0.02) | 0.87 (0.02) | 0.81 (0.03) |
| 2010 | 0.92 (0.02) | 0.87 (0.02) | 0.82 (0.03) |
| 2011 | 0.95 (0.01) | 0.92 (0.02) | 0.88 (0.03) |
| 2012 | 0.94 (0.01) | 0.91 (0.02) | 0.86 (0.03) |
| 2013 | 0.86 (0.02) | 0.79 (0.03) | 0.70 (0.04) |
| 2014 | 0.81 (0.03) | 0.72 (0.03) | 0.62 (0.04) |
| 2015 | 0.86 (0.03) | 0.77 (0.03) | 0.69 (0.04) |
| 2016 | 0.78 (0.05) | 0.68 (0.06) | 0.57 (0.07) |

* SONEC: southern Oregon and northeastern California.

Table A-6. Annual survival probabilities and standard errors (in parentheses) of adult Caspian terns in the colony attender and non-colony attender life stages in the Pacific Flyway population during 2005-2017. Survival probabilities were estimated from the best model of the twelve-state analysis in program MARK (see Table 9). For these two life stages, known-age terns (banded as fledglings) and unknown-age terns (banded as adults) were included in the analysis. The first year when adult terns were banded was 2005. The mean and standard deviation of survival probabilities in each region and each life stage were used in the population model (see Table 10).

| Year (t) | Colony Attender | | | Non-Colony Attender | | |
|----------|------------------------|------------------|-------------|------------------------|------------------|-------------|
| | Columbia River estuary | Columbia Plateau | SONEC* | Columbia River estuary | Columbia Plateau | SONEC* |
| 2005 | 0.96 (0.02) | 0.94 (0.04) | 0.91 (0.05) | 0.76 (0.12) | 0.65 (0.15) | 0.55 (0.17) |
| 2006 | 0.99 (<0.01) | 0.98 (<0.01) | 0.98 (0.01) | 0.93 (0.02) | 0.89 (0.02) | 0.84 (0.04) |
| 2007 | 0.98 (<0.01) | 0.97 (0.01) | 0.96 (0.01) | 0.89 (0.02) | 0.82 (0.03) | 0.75 (0.04) |
| 2008 | 0.99 (<0.01) | 0.98 (<0.01) | 0.97 (0.01) | 0.91 (0.02) | 0.85 (0.02) | 0.79 (0.04) |
| 2009 | 0.98 (<0.01) | 0.97 (0.01) | 0.96 (0.01) | 0.89 (0.02) | 0.82 (0.03) | 0.75 (0.04) |
| 2010 | 0.98 (<0.01) | 0.97 (0.01) | 0.96 (0.01) | 0.89 (0.02) | 0.82 (0.03) | 0.75 (0.04) |
| 2011 | 0.99 (<0.01) | 0.98 (<0.01) | 0.98 (0.01) | 0.93 (0.02) | 0.88 (0.03) | 0.83 (0.04) |
| 2012 | 0.99 (<0.01) | 0.98 (0.01) | 0.97 (0.01) | 0.92 (0.02) | 0.87 (0.03) | 0.81 (0.04) |
| 2013 | 0.97 (0.01) | 0.95 (0.01) | 0.93 (0.01) | 0.81 (0.03) | 0.71 (0.03) | 0.61 (0.05) |
| 2014 | 0.96 (0.01) | 0.93 (0.01) | 0.90 (0.02) | 0.75 (0.03) | 0.63 (0.04) | 0.53 (0.05) |
| 2015 | 0.97 (0.01) | 0.95 (0.01) | 0.92 (0.02) | 0.80 (0.03) | 0.70 (0.03) | 0.60 (0.05) |
| 2016 | 0.95 (0.01) | 0.92 (0.02) | 0.88 (0.03) | 0.71 (0.05) | 0.58 (0.06) | 0.48 (0.07) |

* SONEC: southern Oregon and northeastern California.

Table A-7. Inter-annual transition probabilities and standard errors (in parentheses) between regions and life stages for Caspian terns in the Pacific Flyway population during 2006-2017; these probabilities were estimated from the best model of the twelve-state analysis in program MARK (see Table 9). The sum of two transition probabilities, originating from one life stage and reaching two destination life stages (e.g., sum of transitions from migratory pre-breeder in the Columbia River estuary to migratory pre-breeder and colony attender in the SONEC region), was used as an inter-regional movement rate in the population model (see Table 11). Transition probabilities for terns in the wintering range (juveniles and non-migratory pre-breeders) to the breeding range (migratory pre-breeder and colony attender) were normalized prior to estimating region-specific rates of first return (see Table 6).

| Life stage | Origination region | Migratory pre-breeder (destination region) | | | Colony attender (destination region) | | |
|--|------------------------|--|-------------------|--------------------|--------------------------------------|------------------|--------------------|
| | | Columbia River estuary | Columbia Plateau | SONEC ^a | Columbia River estuary | Columbia Plateau | SONEC ^a |
| Juvenile or non-migratory pre-breeder in the wintering range | Columbia River estuary | 0.13 (0.02) | <0.001 (-) | 0.08 (0.01) | <0.001 (-) | <0.001 (-) | <0.001 (-) |
| | Columbia Plateau | <0.001 (-) | 0.11 (0.01) | 0.18 (0.02) | <0.001 (-) | <0.001 (-) | <0.001 (-) |
| | SONEC ^a | <0.001 (-) | <0.001 (-) | 0.34 (0.05) | 0 ^b | <0.001 (-) | 0.01 (0.01) |
| Migratory pre-breeder in the breeding range | Columbia River estuary | 0.63 ^c | 0.01 (0.01) | 0.08 (0.02) | 0.24 (0.02) | 0.01 (0.01) | 0.03 (0.01) |
| | Columbia Plateau | 0.03 (0.01) | 0.46 ^c | 0.13 (0.03) | 0.01 (0.01) | 0.33 (0.03) | 0.04 (0.01) |
| | SONEC ^a | 0.08 (0.01) | 0.22 (0.03) | 0.43 ^c | <0.001 (-) | 0.05 (0.01) | 0.22 (0.02) |

^a SONEC: southern Oregon and northeastern California.

^b Transition probability was fixed at zero because the transition was not observed in mark-resight data.

^c No standard error was estimated because region and life stage philopatry was calculated as 1-sum of other transitions.

Table A-8. Inter-annual transition probabilities and standard errors (in parentheses) between regions and life stages for Caspian terns in the Pacific Flyway population during 2006-2017; these probabilities were estimated from the best model of the twelve-state analysis in program MARK (see Table 9). The sum of two transition probabilities, originating from one life stage and reaching two destination life stages (e.g., sum of transitions from colony attender in the Columbia River estuary to colony attender and non-colony attender in the Columbia Plateau region), was used as an inter-regional movement rate in the population model (see Table 11).

| Life stage | Originating region | Colony attender (destination region) | | | Non-colony attender (destination region) | | |
|---------------------|------------------------|--------------------------------------|--------------------|--------------------|--|--------------------|--------------------|
| | | Columbia River estuary | Columbia Plateau | SONEC ^a | Columbia River estuary | Columbia Plateau | SONEC ^a |
| Colony attender | Columbia River estuary | 0.796 ^b | 0.007 (0.002) | 0.005 (0.002) | 0.188 (0.010) | 0.002 (0.001) | 0.002 (0.001) |
| | Columbia Plateau | 0.016 (0.003) | 0.694 ^b | 0.029 (0.005) | 0.010 (0.003) | 0.241 (0.011) | 0.011 (0.003) |
| | SONEC ^a | 0.013 (0.005) | 0.049 (0.010) | 0.670 ^b | 0.033 (0.008) | 0.067 (0.012) | 0.168 (0.019) |
| Non-colony attender | Columbia River estuary | 0.296 (0.021) | 0.009 (0.004) | 0.012 (0.006) | 0.658 ^b | 0.010 (0.005) | 0.015 (0.007) |
| | Columbia Plateau | 0.004 (0.003) | 0.314 (0.027) | 0.010 (0.007) | 0.026 (0.010) | 0.621 ^b | 0.025 (0.012) |
| | SONEC ^a | 0.043 (0.022) | 0.125 (0.040) | 0.369 (0.063) | 0.112 (0.042) | 0.183 (0.051) | 0.168 ^b |

^a SONEC: southern Oregon and northeastern California.

^b No standard error was estimated because region and life stage philopatry was calculated as 1-sum of other transitions.

Table A-9. A portion of the encounter history matrix for Caspian terns in the Pacific Flyway population during 2005-2017 used as input data in the 12-state analyses in program MARK. In the encounter history matrix, zeros represent “not resighted” within the three-region study area (or not banded yet), and each letter represents a combination of life stage and region (e.g., G = colony attender in the Columbia River estuary).

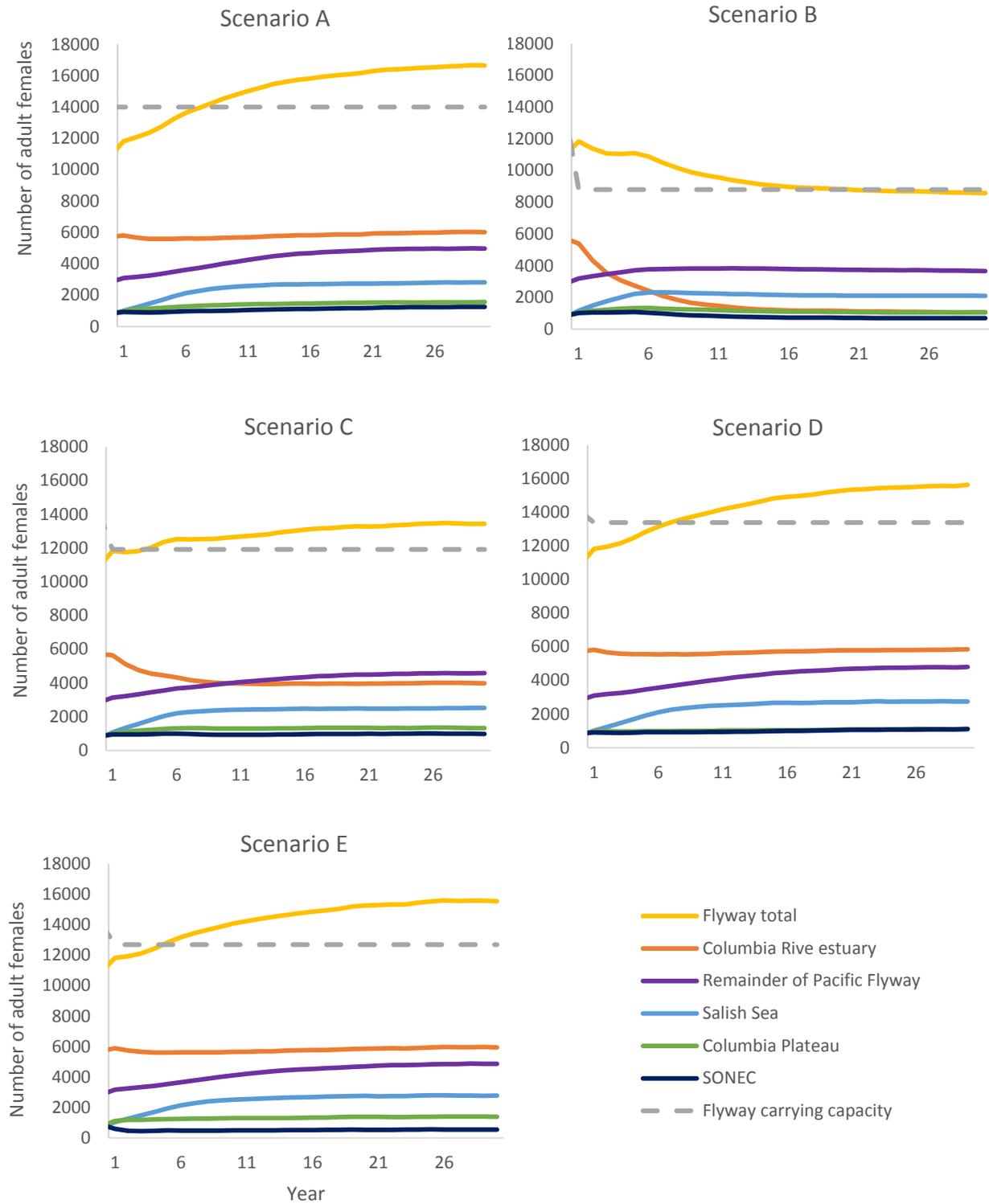
| Banding information | | | | | Encounter history | | | | | | | | | | | | |
|---------------------|---------|-----------|------------|------|-------------------|----------------|------|------|------|------|----------------|------|------|------|----------------|----------------|------|
| Year | Region | Age class | Band color | ID | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
| 2007 | Plateau | Chick | Yellow | A770 | 0 | 0 | J | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2007 | Plateau | Chick | Yellow | A771 | 0 | 0 | J | 0 | 0 | K | K | U | U | U | U | M | 0 |
| 2007 | Estuary | Chick | Yellow | A970 | 0 | 0 | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2007 | Estuary | Chick | Yellow | A971 | 0 | 0 | B | 0 | 0 | 0 | E ^a | E | U | U | U | U | 0 |
| 2008 | Plateau | Chick | Yellow | C447 | 0 | 0 | 0 | J | 0 | 0 | T | T | U | M | L | L | M |
| 2008 | Plateau | Chick | Yellow | C448 | 0 | 0 | 0 | J | 0 | 0 | 0 | T | L | 0 | L | L | 0 |
| 2008 | SONEC | Chick | Yellow | E099 | 0 | 0 | 0 | Q | 0 | 0 | 0 | U | U | U | U | U | 0 |
| 2008 | SONEC | Chick | Yellow | E100 | 0 | 0 | 0 | Q | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2008 | Estuary | Chick | Yellow | C687 | 0 | 0 | 0 | B | 0 | 0 | 0 | 0 | 0 | G | G | G | G |
| 2008 | Estuary | Chick | Yellow | C690 | 0 | 0 | 0 | B | 0 | 0 | E | T | 0 | 0 | 0 ^b | 0 ^b | 0 |
| 2005 | Plateau | Adult | Yellow | A014 | L | L | L | L | L | L | L | L | L | 0 | 0 | 0 | 0 |
| 2005 | Plateau | Adult | Yellow | A015 | L | L | L | L | L | L | L | L | L | L | V | M | 0 |
| 2005 | Estuary | Adult | Yellow | A079 | G | G | G | G | H | H | G | G | G | G | G | G | G |
| 2005 | Estuary | Adult | Yellow | A081 | G | G ^c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2006 | Plateau | Adult | Yellow | A107 | 0 | L | 0 | 0 | M | 0 | L | 0 | 0 | 0 | M | 0 | 0 |
| 2006 | Plateau | Adult | Yellow | A108 | 0 | L | L | M | M | 0 | L | L | L | L | L | 0 | 0 |
| 2006 | Estuary | Adult | Yellow | A164 | 0 | G | G | H | H | G | G | G | G | G | G | G | G |
| 2006 | Estuary | Adult | Yellow | A166 | 0 | G | G | G | G | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

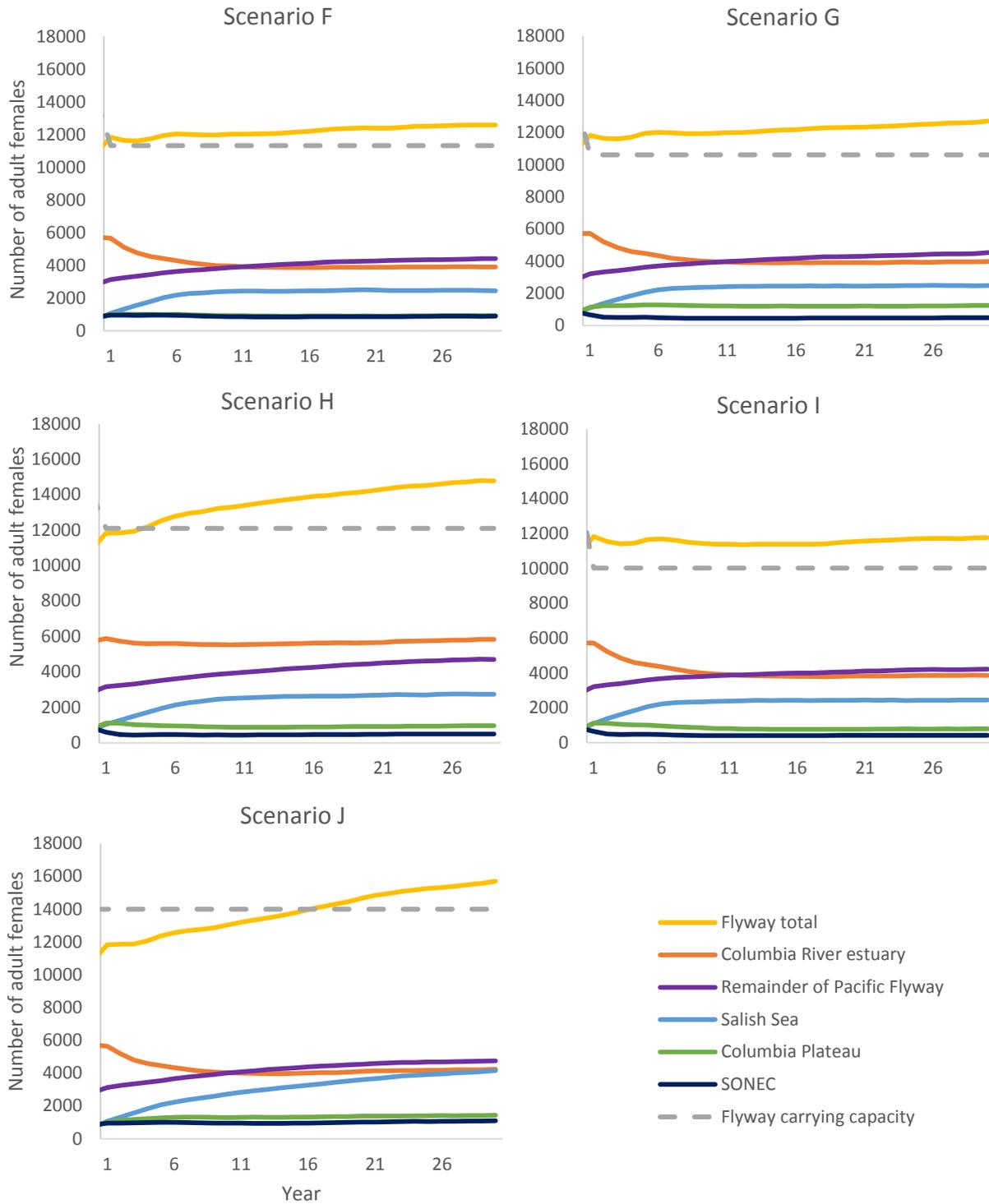
^a Resighted within the three-region study area and outside of the study area; resighting region within the study area was used for analysis.

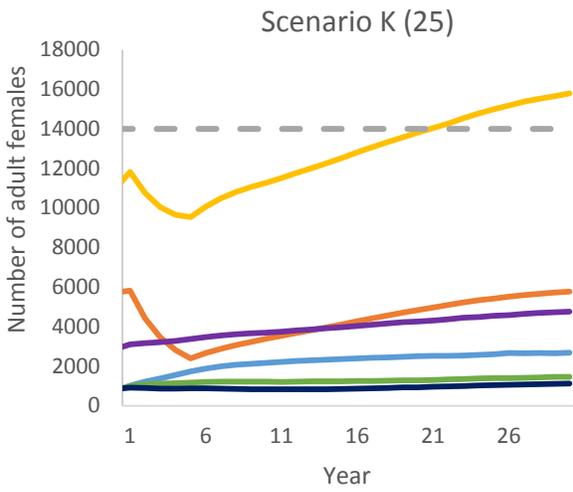
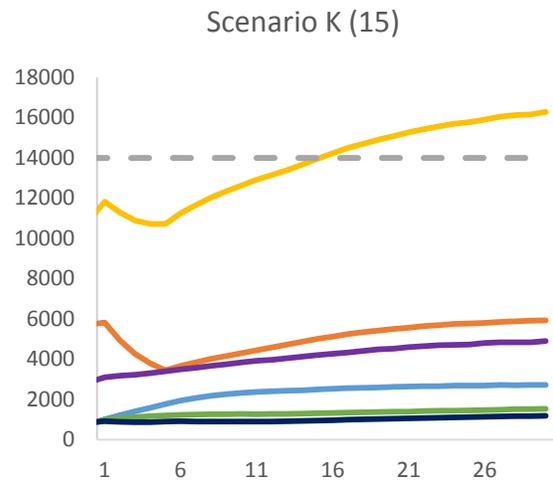
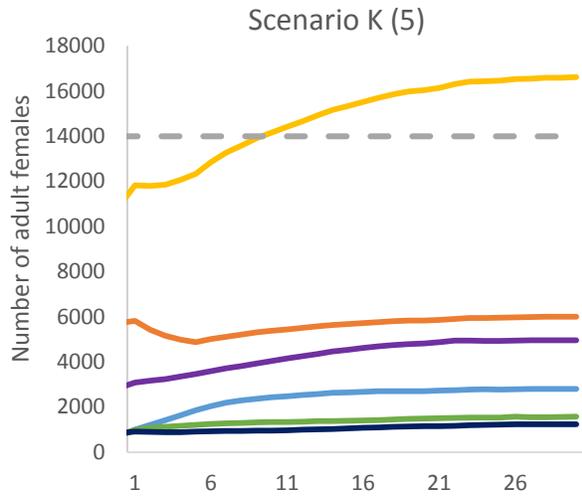
^b Resighted outside of the study area.

^c Known mortality; the individual was excluded from the analysis.

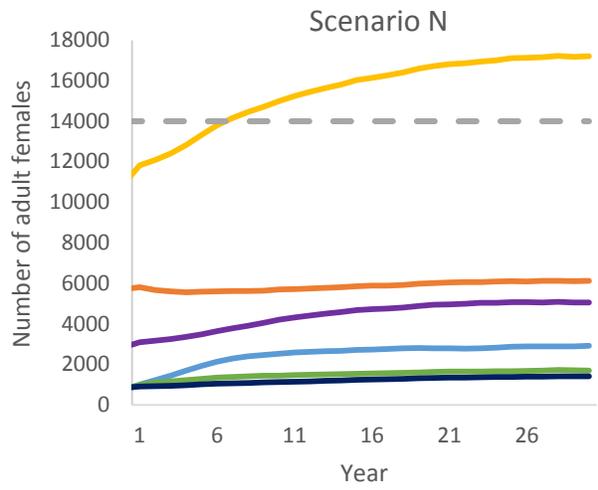
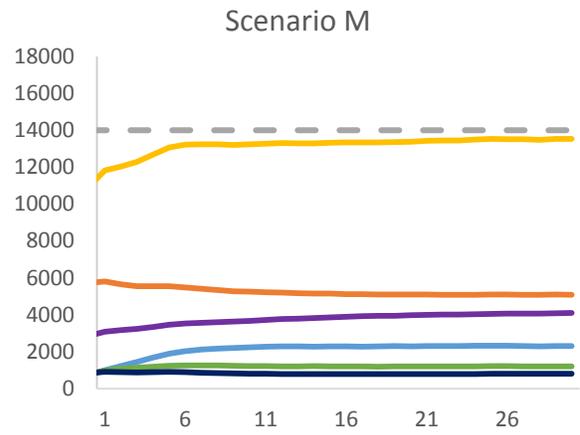
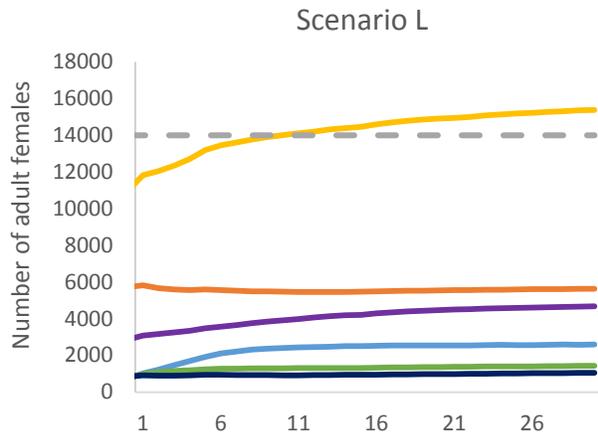
Appendix B. Model projections of the number of adult female Caspian terns in the Pacific Flyway population, as well as in sub-populations residing in each of five regions of the breeding range, under simulated scenarios A-N. Flyway carrying capacity is in numbers of breeding adult females.







- Flyway total
- Columbia River estuary
- Remainder of Pacific Flyway
- Salish Sea
- Columbia Plateau
- SONEC
- - - Flyway carrying capacity



- Flyway total
- Columbia River estuary
- Remainder of Pacific Flyway
- Salish Sea
- Columbia Plateau
- SONEC
- - - Flyway carrying capacity