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Trends in growth of the sea otter (*Enhydra lutris*) population in British Columbia 1977 to 2017

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The BC sea otter population is estimated at 8,110 sea otters, based on a counts of 7,696 sea otters during surveys in 2017 and an additional 414 sea otters estimated to account for animals missed in three survey segments that could not be surveyed or surveyed completely as a result of weather conditions. The sea otter population in British Columbia (BC) has continued to grow in numbers and range in recent years, following patterns that are typical of recovering sea otter populations. Two main processes explain observed trends in BC: demographic growth within occupied areas, and colonization of new areas. Estimates of growth rates at smaller geographical scales than the entire BC range were obtained by fitting deterministic population models to time series of sea otter counts grouped at sub-regional scales to explore growth trends at smaller spatial scales in the population. Annual growth rates for the period 2013-2017 were lower in long occupied sub-regions of Vancouver Island and the central mainland coast (1.55% to 2.88% $year^{-1}$) than in more recently occupied areas (7.52% to 24.51% $year^{-1}$). For long-occupied sub-regions, the selection of logistic growth models confirms that density-dependent processes are acting on sea otters as carrying capacity is approached. In more recently occupied sub-regions, exponential models were selected and growth rates were, in some cases, higher than the theoretical R_{max} estimates for the species, indicating that immigration from other sub-regions was an additional factor in driving population trends of recently colonized areas. The average growth rate for the population as a whole during the period 2013-2017 was 5.26% $year^{-1}$ (SE = 1.25). Range expansion since the previous assessment in 2013, was evident in Queen Charlotte Strait primarily. No range expansion was evident during extensive survey effort on the north coast of BC, confirming that as of 2017 no further range expansion north of Aristazabal Island had occurred. Potential Biological Removal (PBR) was calculated to be 534 sea otters.

1. INTRODUCTION

Monitoring populations is fundamental to estimating abundance and growth trends, to assessing conservation status, informing harvest strategies, and examining spatial or temporal overlap with anthropogenic threats. Because of the importance of spatial structure on population processes in mammals (e.g. Ranta *et al*. 1997, Harkonen and Harding 2001), it is also important to monitor the variations in population dynamics from the centre to the margin of a population's range (Guo *et al*. 2004). This is especially relevant in the context of a species like the sea otter (*Enhydra lutris*), which has recovered from near-extinction and is now recolonizing much of its historical range (Bodkin 2015).

The intense maritime fur trade of the 17th and 18th centuries reduced the sea otter population to less than 2,000 animals throughout the North Pacific range by 1911 (Kenyon 1969). The last sea otters endemic to British Columbia (BC) were extirpated by at least 1931 (Cowan and Guiguet 1960; Nichol 2015). Canada's current sea otter population is comprised of descendants of animals from Alaska reintroduced to Checleset Bay on the west coast of Vancouver Island during three translocation efforts in 1969, 1970 and 1972 (Bigg and MacAskie 1978). Following reintroduction, the sea otter population grew at rates near the species' physiological maximum. This rapid, density independent growth was the result of abundant invertebrate prey, which had increased in the absence of sea otters (Estes 1990).

Sea otters occupy relatively shallow coastal areas and are limited, with respect to habitat, by their diving abilities and preferred foraging depth (<40 m) with the result that most sea otters are found within 1 to 2 km of shore (Riedman and Estes 1990; Bodkin *et al.* 2004). Sea otters occupy small overlapping home ranges throughout their lives and exhibit high site fidelity Bodkin 2015). They spend a large amount of time resting in floating sexually-segregated aggregations called rafts that may number over 200 animals. Because rafts form habitually in the same locations, their distribution can be an indicator of range expansion events in growing populations. The periphery, or frontal edge of the range, tends to be occupied first by male rafts. In subsequent years, females appear and form rafts in the new area (Garshelis *et al.* 1984; Jameson 1989; Lafferty and Tinker 2014).

The BC sea otter population was first surveyed in 1977 and subsequently at 1-3 year intervals thereafter to assess whether any of the re-introduced animals had survived and reproduced, although not all the range was surveyed (Bigg and MacAskie 1978; Morris *et al*. 1981; MacAskie 1987). Counts from surveys provided an index of abundance to monitor population trends and range expansion. Until 1987, sea otters were found in only two locations along the west coast of Vancouver Island, Checleset Bay and off Nootka Island (Bigg and MacAskie 1978). By 1995, the population had increased to 1,522 otters and was distributed along Vancouver Island from Estevan Point to the entrance of Quatsino Sound (Watson *et al.* 1997). By 2004 the population was distributed from Clayoquot Sound to the northwestern edge of Queen Charlotte Strait. On the central mainland coast, sea otters were first observed in 1989, and had expanded from the Goose Group to the edge of Milbanke Sound by 2001 and to Aristazabal Island by 2008 (Nichol *et al.* 2009). In 2013, the sea otter population in BC included a minimum of 6,754 sea otters, with 5,612 in the Vancouver Island region and 1,142 in the central mainland coast region (Nichol *et al.* 2015) (Figure 1).

Sea otter populations are regulated by density-dependent processes (particularly juvenile mortality) linked to food availability (Estes 1990; Thometz *et al.* 2014). Early assessments showed that the BC sea otter population initially grew exponentially (Watson *et al.* 1997). Over time, region-wide population growth has slowed and a piece-wise regression approach was needed to estimate two annual growth rates: 20.0% for the period 1977-1995, and 8.6% for the period 1996-2013 (Nichol *et al.* 2005; 2009). The change in growth rate suggested that different demographic processes were acting on sub-components in the population. Small scale population structure is increasingly recognized as an aspect of sea otter biology that should be considered in population assessment (Bodkin 2015; Davis *et. al.* 2019). Several areas of research support this assertion. Sea otters occupy small overlapping life-time home ranges of 20-45 km^2, particularly females (Tarjan and Tinker 2016; Tinker *et al.* 2019a). Dispersal distances are limited, with annual net linear displacement of 25-30km (Ralls *et al.* 1996; Tinker *et al.* 2019a). Diet and time spent foraging vary as a function of occupation time, with more time spent foraging in long occupied habitats where otter density is high (Estes *et al.* 1982; Tinker *et al.* 2012; Rechsteiner *et al.* 2019). Individual dietary specialization emerges in areas of high density as a strategy, in a species with limited dispersal and small life-time home-ranges, to compete successfully with conspecifics to meet caloric needs (Tinker *et al.* 2008; Smith *et al.* 2015). Because of these characteristics, density-dependent processes such as natural mortality and emigration are expected to act at small spatial scales within the population (Hanski 1998). Therefore, growth trends were estimated for different sub-regions within BC and were shown to be lower where sea otters had been present for many decades (reflecting density dependence), compared to growth rates in sub-regions where occupation had occurred more recently (Nichol *et al.* 2015).

The Recovery Strategy for the Sea Otter in Canada (2007), and the superseding Management Plan for the Sea Otter in Canada (2014), both identify population assessments in the form of regular surveys as required to monitor progress towards achieving the management objective for this species. Specifically, the Management Plan identifies the undertaking of “annual surveys of the Sea Otter population in index areas, areas of range expansion, and other portions of their range as needed, as well as a total population survey every five years, to monitor population trends and distribution”. In 2017, a range-wide boat survey was completed which encompassed the occupied range in BC. In this report, a minimum population estimate for 2017 is presented along with population growth trends for the population by sub-regions and as a whole for the BC population, and an estimate is provided of Potential Biological Removal (PBR).

2. METHODS

2.1 SURVEY APPROACH

Since 1988, a standardized approach has been used to survey sea otters by small boat (Watson *et al.* 1997; Nichol *et al.* 2005). The method is a direct count of sea otters in their known range whereby the range is surveyed along consistent routes that follow the coastline and include coverage of waters around all islets and reefs (habitats typically occupied by sea otters). This approach relies on characteristics of sea otter behaviour and biology that result in their distribution being predictable and showing little variability. The precision of replicate counts obtained by this method in optimal survey conditions has previously been estimated to be equivalent to a *CV* of 7 to 12% (Nichol *et al.* 2005).

Along those routes, small boat surveys were conducted by two or three observers and one boat driver. The small vessels used were 5.5-metre welded aluminum boats or 6.5-metre rigid hull inflatable boats. Observers searched for and counted sea otters on either side as well as forward of the boat. The number of otters sighted was recorded and since 2008, their location was approximated and recorded as the position of the boat at the time of the sighting using GPS. The precision of raft location was further refined by examining marine features on the marine chart relative to the boat’s position. The boats traveled at speeds of less than 10 knots (18.5 km/hour) and stopped frequently to search complex areas with binoculars and to obtain counts of the number of animals in rafts.

2.2 SURVEY AREA AND DESIGN

The goal of each coast-wide assessment is to survey the entire occupied range of sea otters in BC and to report range expansion since the previous coast-wide assessment. During intervening years, smaller surveys are conducted to assess smaller portions of the population range, to maintain index time series in some cases, and to conduct reconnaissance into new areas to record range expansion. Over time, new survey areas have been added as the sea otter range expanded. The marine mammal program at the Pacific Biological Station solicits reports of sea otter sightings from other researchers, fisheries patrol vessel personnel, fisheries enforcement officers, coastal residents and fishermen to help identify range expansion events and thereby define the extent of survey coverage needed during the range-wide surveys completed at five year intervals.

Only areas in which a raft of sea otters was observed during a survey were considered occupied. This criterion is used, for consistency, to identify range expansion events. Although single sea otters are encountered and reported outside the occupied range occasionally throughout BC (see figure in, Ford 2014), the presence of rafts during spring or summer – which is when sea otter surveys are undertaken – is used to define range of occupation. During winter months it is not uncommon for a raft of sea otters to make irregular appearances in new areas, but consistent occupation of the new area may take several years and coincides with observed occupation during spring and summer.

For logistical reasons, the sea otter range in BC was divided into *segments*. Segments boundaries are natural breaks such as points of land, or the transition from a sound to an inlet. Segments can typically be surveyed in a day by boat, although some segments delineated in the past now take more than one day to complete because of population growth, as it takes longer to count more otters. Within segments, survey coverage is defined by established survey routes. As of 2017, 24 segments comprise the BC range (Figure 2).

To investigate demographic structure in growth trends for the BC population, segments that were adjacent to each other were considered for grouping together into *sub-regions*, based on several criteria. Although these groupings do not represent distinct populations (nor do segments), it was assumed that otters within each sub-region experience similar demographic processes as well as environmental and density-dependent conditions and thus that growth rate estimates within groupings should reflect these average conditions (Tinker *et al*. 2019b). Therefore, one consideration was the similarity in occupation time. Also, segments separated by a deep sound, or relatively wide passage were more likely to be placed in different sub-regions as these were assumed to represent natural separations between suitable habitat. Finally, another requirement was to group survey segments so as to achieve a minimum of three years of survey effort over a five-year period for each sub-region, because this was needed to fit models (otherwise newly occupied segments could not have been included in the growth trend analysis). The 24 segments that comprise the BC range in 2017 were grouped into ten sub-regions (Figure 3). Annual survey counts from the member segments were summed in each sub-region.

2.3 DATA COLLECTION

During small boat surveys, rafts of sea otters were counted using 7X50 binoculars and 14X40 stabilized binoculars. Female rafts were distinguished from male rafts by the presence of pups. Rafts were counted by all observers. Each person assessed the raft size independently, making several counts when possible and then counts were compared. The final accepted count was the count most consistently reported from the observers (best overall repeatable count). This count was obtained when observers achieved an unobstructed view of the sea otter raft, as the boat and the otters rose and fell in the ground swell. Thus the best overall repeatable count was often among the higher of the initial counts (lower counts were associated with animals obscured by swell). The variation in counts from raft encounters where multiple counts were obtained in 2017 was examined by computing the differences between each of the replicate counts and the mean for that raft.

Additional counts were collected in 2009, 2013, and 2017 by observation from a large ship on Cook Bank, offshore of the Cape Scott to Hope Island segment of northern Vancouver Island where depths are 30 m at a distance of 5 km from shore. To survey the area, two observers collected sightings from the top viewing deck in 2017, (10 m above the water), and from the bridge in 2009 (7.5 m above the water) of the Canadian Coast Guard vessel *Tanu* as it made a single transit travelling parallel to the coast at 10 knots.

Sea and weather conditions were recorded during surveys and were categorized as follows. *Good* to *Excellent* survey conditions existed when sea state ranged from flat calm (Beaufort 0) to swells up to 1 m and wind speeds less than 10 knots (18 km/hr, Beaufort 3) and high overcast created ideal lighting conditions due to reduced sun glare. *Fair* conditions were defined generally as seas 1 to 1.5 m or when wind speeds ranged from 10 to 15 knots (28 km/hr, Beaufort 4). *Poor* conditions were generally defined as seas greater than 1.5 m or wind speeds greater than 15 knots (28 km/hr). Surveys did not commence in *Poor* conditions or when visibility was obscured particularly through binoculars, e.g., by rain or fog. Although *Good* to *Excellent* conditions were sought, sea states often changed during the course of a survey. If conditions deteriorated to poor, the survey was repeated at a later date whenever possible. All surveys to document minimum population size, distribution and range of occupation have been carried out from May through early September since 2004. In earlier years, surveys were conducted between April and September. Further details about survey methodology including the 2001-2004 helicopter surveys are described in Nichol *et al.* (2005).

2.4 DATA ANALYSIS

2.4.1 INCOMPLETE SURVEYS

Gaps in survey coverage occurred due to weather or for other logistical reasons. When possible, these gaps were filled by estimating the number of animals in missed segments by interpolation using the exponential equation that best fit a maximum of four counts preceding and/or succeeding the missing count for the same segment. Interpolation was restricted to survey years in which the missing segment had not been missed for more than two consecutive years and where at least 70% of the resulting population estimate for the year would be based on actual counts. These interpolated values were used only in the linear regression analysis which was restricted to years with summed BC-wide annual population estimates. Interpolated values in the data set used in the linear regression analysis accounted for 1 to 26% of the annual total for the years in which they were used (Table 1).

Missing counts in 2017 were estimated differently. Missing counts from two segments (Kains Island to Cape Scott, and Scott Islands) and an incomplete count from a third segment (Brooks Bay) in 2017, had to be estimated. In each case, the most recent survey was 2013 and thus no recent counts were available to inform the 2017 estimates. Brooks Bay has been occupied since 1989, and is nearing *K*; preliminary analysis showed that a logistic model best fits this segment up to 2013 and that growth has been slow in recent years. The portion of the Brooks Bay that was missed in 2017 had ~100 sea otters in 2013. Therefore, we assumed an additional 125 animals for this segment in 2017 (for a total of 660 sea otters). For the two un-surveyed segments, predicted numbers of otters in 2017 using the estimated recent growth rates from models fit to the two segments time series (2001 to 2013) predicted over 400 sea otters combined in 2017. This estimate seemed too high, considering that the missed segments are exposed sections of the coast of north west Vancouver Island with limited areas of quality habitat (see Figure 2 in Gregr *et al*. 2008). Fitting the past three surveys of the Kains Island to Cape Scott segment (2008, 2010, 2013) to an exponential model provided a growth rate of 3% per year, which, once extrapolated to 2017, provided an estimate of 122 additional sea otters. Applying a conservative 1% annual growth rate for the small-sized Scott Islands segment yielded an estimate of 164 additional sea otters in 2017. The estimates for missed or incomplete counts in 2017 accounted for 5% of 2017 total.

The time series for each sub-region were also inspected for gaps. If a survey had not been completed in one of the segments comprising a sub-region in a year it was considered occupied (defined as every year since a raft was first recorded during a survey), then counts for the entire sub-region for that year were excluded from the time series. In the case of estimated values for missing counts, only the estimated values for missing counts in 2017, described above were used in sub-regional analysis. Sub-regional analysis utilized many completed segment surveys particularly from years when a region wide survey had not been completed. These included surveys completed by DFO, by J. Watson prior to 2001, by Hakai Research Institute and by R. Dunlop (for Nuu-chah-nulth Tribal Council). The number of years for which sub-region counts were available for model fitting ranged from four survey years in an 11-year time series for a recently occupied sub-region, to 35 survey years in a 41-year time series for a long occupied sub-region.

2.4.2 MINIMUM POPULATION ESTIMATE FOR BC

Annual segment counts made in 2017 and counts from new areas occupied by rafts of sea otters were summed to obtain a minimum population estimate. If more than one survey had been made in a year in a segment, the survey made under the best conditions was selected (Nichol *et al.* 2005). The estimates made for the three segments that were not surveyed or completely surveyed due to weather in 2017 (described above in section 2.4.1) were also included.

2.4.3 REGION-WIDE GROWTH RATE ESTIMATES BASED ON LINEAR REGRESSION

An estimate of population growth for BC (1977-2017) based on a linear regression was provided to the 2019 COSEWIC assessment report for sea otters to maintain continuity with past COSEWIC and DFO assessments (Watson *et al.* 1997; Nichol *et al.* 2005; 2009). This linear regression estimate is included in this report along with its methodology (see Appendix A) as a supporting reference for the COSEWIC report. Growth rates for all of BC (1977-2017) were estimated by fitting the log of region-wide summed counts (and estimated values) by piece-wise linear regression. Each annual count used in the linear regression was weighted according to the square root of the proportion of the total segment counts obtained in that year. In this way the contribution of estimates for missed or incomplete segments were given less weight in the regression than the completed segment counts. There were 21 annual sea otter counts/estimates spanning the 41- year time period from 1977 to 2017 available for this analysis. Additional details are available in Nichol *et al.* (2005, 2009).

2.4.4 POPULATION MODELLING

To obtain estimates of growth rates at a finer geographical scale, a deterministic population model was fitted to the count data for every sub-region and the parameters describing its population dynamics were estimated. In each case, we fit two candidate models with discrete 1-year time steps. The first one assumes exponential growth and is described by the following equation:

$$N_t = N_{t-1} \cdot e^r \quad (1)$$

where N_t is the predicted abundance at time t in the sub-region, and r is the intrinsic rate of exponential growth. The second model assumes logistic growth and is described by:

$$N_t = N_{t-1} \cdot e^{r[1-(N_{t-1}/K)]} \quad (2)$$

where K is the carrying capacity. The parameters r, K, as well as the initial abundance at year 0 (N_0, defined as the year before the first available count for that sub-region) are estimated by the model for each sub-region.

Model fitting was accomplished using unconstrained numeric optimization to maximize the following likelihood function (Hilborn and Mangel 1997) which compared the vector of observed counts C_i to the predicted abundances N_i for a given set of parameter values (r, K and N_0):

$$\ell(C_i|N_i, r, K, N_0) = \prod_{i=1}^{n} \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma^2}} \cdot e^{-\frac{(C_i - N_i)^2}{2\sigma^2}} \quad (3)$$

We assumed that deviations between observed counts and model-predicted abundance were normally distributed with mean 0 and standard deviation σ, and thus we assumed that deviations primarily reflect observer error rather than process error (Hilborn and Mangel 1997; Tinker *et al.* 2006).

Within each sub-region, we used the Akaike Information Criterion (AIC) to select the best of the two model candidates, and report the corresponding maximum likelihood estimates for 2017 abundance (in absolute terms and as the proportion of the estimated carrying capacity for sub-regions where logistic growth was the best supported model). We expressed σ as a coefficient of variation after dividing it by the geometric mean of the predicted abundance estimates, and calculated R^2 to evaluate goodness of fit of the selected model.

Additionally, for each sub-region we calculated the estimated discrete rate of growth (r_d) for the most recent 5-year period (2013-2017) and for the previous 5-year period (2008-2012). Note that $r_{d,t}$ is a measure of the average realized annual rate of population growth over some defined interval (expressed in units of annual percent increase in population size). We calculated $r_{d,t}$ as:

$$r_{d,t} = 100 \cdot \left(\sqrt[4]{\frac{N_t}{N_{t-4}}} - 1 \right) \quad (4)$$

We calculated a standard error for $r_{d,t}$ using a resampling approach, whereby we generated 20,000 random parameter sets for equation (1) or (2) as appropriate, used these to solve equation (4), and calculated the standard deviation of $r_{d,t}$ across all iterations. Parameter sets for each iteration, were drawn randomly from a multivariate normal distribution with mean values equal to the maximum likelihood estimates and variance-covariance matrix calculated as the inverse of the hessian matrix derived from the maximum likelihood solution. The same hessian matrix was also used to provide a standard error for K.

To obtain an estimate of annual growth rate for the BC population as a whole, that could be compared with the regional growth rate estimates from previous assessments we also report $r_{d,t}$ for the entire region using equation (4) (i.e., by summing the annual expected counts derived from the best fit model for each sub-regions).

Population modelling was done in MatLab 2019.

2.5 POTENTIAL BIOLOGICAL REMOVAL

In order to estimate the upper limit to annual human-caused mortality that may be allowable without causing serious population-level consequences or prevent recovery, we followed the U.S. National Marine Fisheries Service means of calculating the maximum number of animals, excluding natural mortality, that may be removed per year while still allowing the population to reach or sustain to its ‘optimum sustainable population’ (Wade 1998). This methodology was developed originally for application to cetacean species.

Potential Biological Removal (*PBR*) is calculated as:

$$PBR = N_{min} \text{ X } ½ R_{max} * F_R$$

where:

N_{min} = the minimum population estimate, or the 20th percentile of the estimated population size in 2017

½ R_{max} = one-half the maximum theoretical or estimated net productivity of the stock at a small population size,

F_R = a recovery factor between 0.1 and 1.

3. RESULTS

3.1 SURVEY EFFORT

The 2017 sea otter survey was carried out from May 10th to September 8th 2017, and took 36 days not including days lost to weather or to other logistical considerations. Four of the days were dedicated to extensive survey of coastal areas north of the northernmost edge of the 2013 occupied range (Figure 4).

3.2 RAFT COUNT VARIATION

Among raft encounters in 2017 that had multiple counts (n = 167 encounters), 134 raft encounters had two counts, 27 raft encounters had three counts, 5 raft encounters had four counts and 1 raft encounter had five counts. There was a positive relationship between size of the raft and count differences with greater differences for larger rafts (Figure 5). However the absolute and relative differences in counts were relatively low. The difference between replicate counts and the mean count for each raft ranged from -26 otters to +42 otters. The overall mean and median were zero (Figure 6).

3.3 POPULATION COUNT 2017

A total of 7,696 sea otters were counted during surveys and a further 414 estimated for missed or incomplete segments in 2017 for a total of 8,110 sea otters (Table 1). Of the total counted sea otters, 60% (n = 4,641) were encountered in rafts, and 40% (n = 3,055) were encountered as single animals scattered in an area (including single mum-pup pairs). Among the rafted portion of the count, raft sizes ranged from groupings of 3 to 200 animals (Figure 7).

3.4 POPULATION GROWTH RATES 1977-2017 ESTIMATED BY LINEAR REGRESSION

The results of a piecewise regression indicated the recent rate of population growth region-wide remains lower than during the early years following re-introduction of sea otters to BC. From

1977 to 1995 the population grew at an average annual rate 20.1% $year^{-1}$ but has averaged 8.7% $year^{-1}$ for 1996-2017 (SE = 0.189, r^2 = 0.98, $F_{(2,21)}$ = 602.2, P < 0.0001).

3.5 POPULATION MODELLING

Counts in each sub-region in 2017 are given in Table 2. Exponential models were selected as the best models for four sub-regions (Figure 8), with growth rates (r) between 7.52 and 24.51%. The six other sub-regions exhibited logistic growth and were estimated to be between 83% and 99% of their respective carrying capacities in 2017. Goodness-of-fit of the best models to the count data ranged from R^2 values of 0.73 to 0.97.

Population modelling at the sub-regional level showed that recent growth rates were inversely related to occupation time (Figure 9). Where the population has been established for the longest period of time (sub-regions 2,3,4, and 9) the annual rate of increase was the lowest in both 5-year intervals during the period 2008 to 2017. In contrast, recently occupied sub-regions had comparatively higher rates of annual growth.

In sub-region 8, a logistic model was selected despite particularly high estimated growth rates for both 2013-2017 and 2008-2012 time periods. Previously, using the time series up to 2013, an exponential model had been selected (Nichol *et al.* 2015). Further examination of the time series showed the strong influence of new boat counts completed by researchers at Hakai Research Institute in the years 2014 and 2015, which, when added to the time series, drive this switch from an exponential model to a logistic model (Figure 10).

3.6 AGGREGATE POPULATION GROWTH FOR BRITISH COLUMBIA

The finite rate of growth for all of BC, obtained by summing the abundance estimates from the sub-regional models, was 5.26% $year^{-1}$ (SE = 1.25) over the period 2013-2017 (Figure 11). During the previous five-year period (2008-2012), the finite rate of growth was estimated at 6.37% (SE = 2.55). Figure 7, presents this trend as well as the linear regression-based trend for comparison.

3.7 RANGE EXPANSION

Since the previous assessment (Nichol *et al.* 2015), the presence of rafts of sea otters where they have not previously been seen had occurred most noticeably in eastern Queen Charlotte Strait (Segment 15), but also southward in Clayoquot Sound (Segment 1), and to another group of small islands off Aristazabal Island (Segment 22) and rafted sea otters were observed for the first time along the north coast of Price Island (Segment 24). Extensive survey effort in the coastal regions of BC's north coast yielded only four observations of single otters (during 281 km of survey effort north of Aristazabal Island), confirming that as of 2017 no further northward range expansion occurred (Figure 4).

3.8 POTENTIAL BIOLOGICAL REMOVAL

The mean abundance estimate for 2017 from summing the 10 sub-regional models was 7,816 (SE = 912.29). Using the 20th percentile of this estimate gives N_{min} = 7,087. For $R_{\max}$, we used the maximum net productivity estimated at a small population size in the BC sea otter population, equal to 20.1% as the rate for the BC population 1977 to 1995. Finally, for the recovery factor, we followed the guidelines in Hammill *et al.* (2017) for a species listed as Special Concern and not considered to be declining, and selected F_R = 0.75 . The resulting PBR is 534 sea otters.

4. DISCUSSION

In this paper we have presented the results of the 2017 sea otter survey with respect to a minimum population estimate and range of occupation, and provided a PBR estimate. We also estimated population growth trends for sub-regions within the population and provided an overall growth trend for the population from 1977 to 2017. The sea otter population in BC has continued to grow in numbers and range in recent years, following patterns that are typical of other recovering sea otter populations (e.g., Tinker *et al.* 2019b). Two main processes are at play to explain observed trends in BC: demographic growth within occupied areas, and colonization of new areas.

4.1 REGIONAL AND SUB-REGIONAL DEMOGRAPHIC PROCESSES

Because adult females, the main demographic component of the population in this highly polygynous species, exhibit strong site fidelity and occupy small life-time home ranges rarely moving more than 20km from a location in a year, (Garshelis and Garshelis 1984; Ralls *et al.* 1988; Tinker *et al.* 2019a; Tarjan and Tinker 2016) , intrinsic demographic processes are expected to operate on spatial scales much smaller than the spatial extent of the BC range (Bodkin 2015; Davis *et al*. 2019;). The results of our population modelling within sub-regions confirms previous observations that there are difference in growth trends across the geographical range of sea otters in BC and therefore that this sub-regional scale is important in regulating sea otter populations. Although these sub-regions do not represent distinct populations, these results explain the challenges associated with trying to fit a single region-wide growth trend to the entire time series (which fitted the data well in the early years following re-introductions but not after 1995). For this reason, previous assessments had to use piece-wise regression to split the time series into two periods. In contrast, summing the estimates of our population modelling at the sub-regional scale results in a better fit to the region-wide count data without having to split the time series arbitrarily. The process used to group survey segments into sub-regions was ad hoc although relying on knowledge of the population distribution and spatial structure. Nonetheless, the resulting growth rate estimates, including the overall growth rate estimate for the region, may be sensitive to the grouping decisions. Sensitivity to grouping decisions was assessed by performing the analysis using alternate groupings for some of the key areas and the overall results and conclusions were similar (not shown). Ideally, however, future work would include a data-driven approach to defining or supporting sub-regional selection.

Annual growth rates were lower in long-occupied sub-regions of Vancouver Island and the central mainland coast than in more recently occupied areas. This pattern (Figure 9) is similar to that observed in Southeast Alaska (Tinker *et al.* 2019b). For long occupied sub-regions, the selection of logistic growth models confirms that density-dependent processes are acting on sea otters as carrying capacity is approached. Carrying capacity in sea otters is thought to be mostly linked to food availability, itself influenced by habitat characteristics (Gregr *et al.* 2008; Laidre *et al.* 2002). As such, it is expected to fluctuate with pulses of invertebrate recruitment and survival. We recorded higher than expected counts, including of mothers and pups, in sub-regions 2 and 3 in 2017. These are long occupied areas with low growth rates in recent years, where it is likely the population is nearing the region's carrying capacity. Strong invertebrate recruitment was evident during subtidal surveys of long-term dive sites in Checleset Bay in 2016 and have persisted in subsequent years (J. Watson, pers. comm.), possibly influenced by the recent major die-off of sunflower stars, an important meso-predator of small invertebrates (Harvell *et al.* 2019; Schultz *et al.* 2015). Thus, higher recruitment of invertebrates may account in part for the greater number of sea otters recorded in 2017, underscoring that carrying capacity can fluctuate at fine spatio-temporal scales.

In more recently occupied sub-regions, exponential models were selected and recent growth rates were higher than in long occupied sub-regions In some cases, the estimated growth rates (*r*) were higher than the theoretical R_{max} estimates for the species (Estes 1990), indicating that immigration contributed to population growth in recently colonized areas. Emigration from “source” to “recipient” areas has two components; range expansion events which occur episodically at the range edge and are detected at longer and irregular intervals and small scale movements within colonized areas. Although limiting prey resources likely drive the population dynamics of “source” areas and influence range expansion, the timing of range expansion events is likely driven by social dynamics, the distance from occupied areas to suitable new habitat and by habitat quality (Tinker *et al.* 2008; Lafferty and Tinker 2014).

4.2 SURVEY METHODS

Because sea otters exhibit strong site fidelity and occupy small coastal home ranges, the survey methodology provides an index of abundance assumed to represent a constant proportion of the population. Similar methods have been used to assess trends in population size and growth in Alaska, Washington State, and California (Pitcher 1989; Jameson and Jeffries 2013; USGS 2014). Data collected with this survey method in BC also provide detailed, fine-scale information about the distribution of sea otters, locations of rafts by sex, and the timing of range expansion events, because parts of the range are surveyed annually in addition to the range wide survey completed at five-year intervals. However, these boat surveys do not account for availability and perception biases, and therefore an unknown proportion of the population is missing from these counts.

There are no available estimates of availability bias for BC’s small boat surveys of sea otter (how many otters are at the surface while the boat is in visual range), which is presumably compounded with perception bias as well (missing otters that are available). However, both biases are believed to be more relevant for single individuals than for large rafts (e.g., in Tinker *et al*. 2019b, detection probability was assumed to be 1 for large groups during aerial surveys in Alaska). Since 60% of sighted otters were in rafts during the 2017 survey, the impact of these biases mostly pertains to the remaining 40% of the counts. Probabilities of detection of small groups during aerial surveys have been estimated to range from 0.4 to 0.6, depending on sea otter density (Tinker *et al.* 2019b), but these values do not apply to boat surveys, which are slower and stop regularly to search areas. Another source of un-modelled uncertainty is the error in raft counts. An exploratory analysis of raft count variation showed that differences among repeated counts increased with increasing raft size, but that the overall absolute and relative differences were small and centered around zero. However, raft size and counting error could be better estimated by using UAV technology to obtain repeatable counts of the number of sea otters in rafts and compare them to boat-based counts.

An underlying assumption of our approach is that by carrying out the surveys in a consistent manner across years, and since there is strong site fidelity of sea otters and rafts, any sampling error is relatively constant over time and therefore the counts can provide a good index of population trends. Fitting population models to these counts allowed us to provide “expected” counts based on plausible population dynamics and to quantify observation error (assuming that most of the deviation between observed and expected values was primarily the result of observation error rather than process error). Quantifying this uncertainty was needed to compute PBR. Furthermore, by fitting models to sub-regional time series, we were able to use far more surveys than we have previously (segments that were surveyed completely in a year when not all segments were, resulting in incomplete counts at the coast-wide level). Next possible steps in this process would be to incorporate raft count variance from the raft count portion of each survey and include this additional uncertainty in population estimates needed for PBR since without this the PBR presented here is likely somewhat over-estimated. More broadly, this should also be included in future steps to fit a hierarchical population model, which would incorporate immigration and emigration and would better allow us to discriminate between observer and process errors (e.g., Tinker *et al.* 2019b).

A challenge for long-term population survey programmes such as this is maintaining a consistent level of effort as the population increases and expands its range (Nichol 2019[1]). In the early years of the time series when the sea otter population was limited to a small area of Checleset Bay and a small area off Nootka Island, a sea otter survey could have been accomplished over one to three days depending on weather. Recognizing the challenge of maintaining the survey effort, we previously investigated incorporating a helicopter as the observation platform (2001-2004). Helicopter surveys had the advantage of providing photographic counts of rafts, and large areas could be surveyed in one day thus potentially taking advantage of windows of good survey conditions. Such surveys, however, incurred high financial costs and could not easily be repeated multiple times, if needed (Nichol *et al.* 2005). In recent years, a ship platform has been needed to survey the shallow bank that extends offshore in Sub-region 6. The addition of this survey effort has become a standard add-on to the nearshore small boat survey.

With an analytical assessment approach that now places more emphasis on the use of sub-regional time series, it may become possible (and even necessary) to survey different sub-regions in different years rather than focus on a synchronous survey of the whole BC region in a single year. Population assessment results would still provide range of occupation, years of occupation, sub-regional growth rates and sub-regional population estimates.

4.3 MANAGEMENT IMPLICATIONS

The implications of the fine spatial scale at which sea otter populations are structured (including limited dispersal distances), are important with respect to management and understanding threats to the population. It is likely because of the relatively sedentary nature of sea otters, with small overlapping life-time home ranges that the species was extirpated by serial depletion from at least 90% of their historic range in less than 100 years during the maritime fur trade (Bodkin 2015). In the current context, spatially heterogeneous threats (e.g. oil spills, vessel strikes, entanglement in fishing gear,) may affect some sub-regions and not others, with the severity of potential impacts mediated in part by sub-regional population characteristics. From a conservation perspective, the limited nature of sea otter dispersal means that potential for a rescue effect is negligible, however, these same population structure characteristics, might be used advantageously to support small-scale management actions related to Indigenous rights to harvest sea food and sea otters, without serious region wide population effects (see as an example Tinker *et al.* 2019b).

We calculated a PBR estimate for the entire BC sea otter population. However, given that population demographic processes occur at smaller scales, and that sea otters exhibit high site fidelity, the population impact of human-caused mortality would be expected to differ across population components and sub-regions. For this reason, PBR calculated this way may not be a particularly useful measure of allowable harm in this species, unless the estimated annual allowable level of 534 animals is distributed to take into account population structure. Even so, the estimate of 534 is likely slightly over estimated because uncertainty in raft count is not included in the population estimate that is the basis of N_{min}. Future efforts to compute PBR

[1] Nichol, L.M. 2019. Conservation success, now what? – Challenges of maintaining long term population surveys for a species with an expanding range. Sea Otter Conservation Workshop XI, March 29-31, 2019. Oral presentation.

should consider whether it is possible to either calculate this by sub-region, or apportion the estimates by sub-regions.

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BC sea otter population surveys in 2017 would not have been possible without the dedicated contributions of many colleagues. We thank the following observers who work with us on the surveys, S. Hutchings, R. Abernethy (DFO), B. Wright (DFO), C. McMillan (DFO), G. Lemieux, L. Saville. We thank the captain and crew of the CCGS *Tanu* for their assistance with northern Vancouver Island surveys in May 2017, and K. Hansen and S. Hutchings for logistical support during the June 2017 central and northern BC coast surveys. We thank R. Dunlop and the Nuu-chah- nulth Tribal Council for survey data of Nootka Island (2008), and Hakai Research Institute for their survey data of central coast areas (2014 to 2017). Funding was provided by the Species-at-risk Program, Department of Fisheries and Oceans. We thank T. Tinker for analytical assistance and writing the population modelling script in 2015.

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7. TABLES

Table 1. Twenty-one summed region-wide sea otter counts for years in which survey of the entire occupied BC range was attempted. Platforms : fixed-wing aircraft - 1, helicopter - 2, small boat - 3, Coast Guard ship - 4, Estimated are values for missed or incomplete survey of some segments. See methods for explanation.

Year	Count	Estimate	Final Total	Platforms
1977	70	-	70	1
1978	67	-	67	1
1980	74	-	74	1
1982	116	-	116	1
1984	345	-	345	1,3
1987	370	-	370	1
1988	354	-	354	3
1989	582	-	582	2,3
1990	668	-	668	2,3
1991	435	-	590	3
1992	820	-	969	2,3
1993	1045	-	1045	3
1994	1188	-	1300	3
1995	1423	5	1527	3
2001	3180	-	3180	2,3
2002	2297	-	2369	2,3
2003	2777	32	2809	2,3
2004	2934	251	3185	2,3
2008	4712	-	4712	3
2013	6754	-	6754	3,4
2017	7696	414	8110	3,4

SOURCES

1977: Bigg and MacAskie 1978
1978: Morris *et al.* 1981
1980: Farr unpubl.
1982: Bigg unpubl.
1984: MacAskie 1987
1987: Bigg and Olesiuk unpubl
1988: Watson 1993
1989: Watson 1993, MacAskie unpubl.
1992: Watson *et al*. 1997, BC Parks
1993: Watson *et al* 1997
1994: Watson *et al*. 1997
1995: Watson *et al*. 1997
2001-2017: DFO, J. Watson, R. Dunlop (Nuu-chah-nulth Tribal Council)

1990: Watson 1993, Powers 1991 unpubl.
1991: Watson 1993

Table 2. Sub-regional growth trend statistics. ML: Maximum likelihood estimate. K: carrying capacity.

Sub-region	2017 count (ML estimate)	Years of occupation (no. of years)	Survey years *N*	AIC selected model	2008-2012 annual growth rate r_d (*SE*)	2013-2017 Annual growth rate r_d (*SE*)	Percent of *K* (*CV*)	R^2
1 (Hesquiat Peninsula, Clayoquot Sound)	674 (687.31)	1995 – 2017 (23)	10	Exponential	8.33(1.15)	8.33(1.15)	--	0.87
2 (Nootka Island Nuchatlitz Inlet, Catala Island, Esperanza Inlet)	1277 (1173.43)	1977 – 2017 (41)	23	Logistic (AIC, L = 269.11, E = 276.06)	4.41(1.32)	2.88 (1.12)	83 (0.18)	0.93
3 (Checleset Bay, Mission Group, Kyuquot Sound)	2367 (2088.08)	1977 – 2017 (41)	35	Logistic (AIC, L = 461.56, E = 473.46)	3.94 (0.71)	2.58 (0.73)	83 (0.15)	0.94
4 (Brooks Bay, Quatsino Sound,	893* (958.12)	1989 – 2017 (29)	15*	Logistic (AIC, L = 182.03, E = 185.09)	4.93 (2.92)	1.99 (1.71)	97 (0.11)	0.90
5 (Kains to Cape Scott, Scott Islands)	286* (301.16)	2001- 2017 (17)	6*	Exponential	8.01 (2.43	8.01 (2.43)	--	0.73
6 (Cape Scott to Hope Island)	766 (848.30)	2001 – 2017 (17)	10	Logistic (AIC, L = 124.74, E = 130.81)	29.13 (6.17)	7.52 (4.71)	99 (0.10)	0.90
7 (Queen Charlotte Strait east and Smith Sound)	306 (321.93)	2009 – 2017 (9)	5	Exponential	--	24.51 (6.19)	--	0.86
8 (Simmonds_Tribal, Kildidt Sound, Calvert Island	441 (462.20)	2007-2017 (11)	7	Logistic (AIC, L = 73.00, E = 80.63)	33.63 (5.61)	20.42 (4.60)	97 (0.09)	0.97
9 (Cape Mark McMullens_Goose Group)	800 (652.55)	1990-2017 (28)	15	Logistic (AIC, L = 183.36, E = 184.83)	2.72 (1.24)	1.55 (1.02)	93 (0.18)	0.83
10 (Seaforth, Price, Aristazabal Is)	291 (323.83)	2007-2017 (11)	4	Exponential	13.09 (4.99)	13.09 (4.99)	--	0.76

*2017 value is an estimate

8. FIGURES

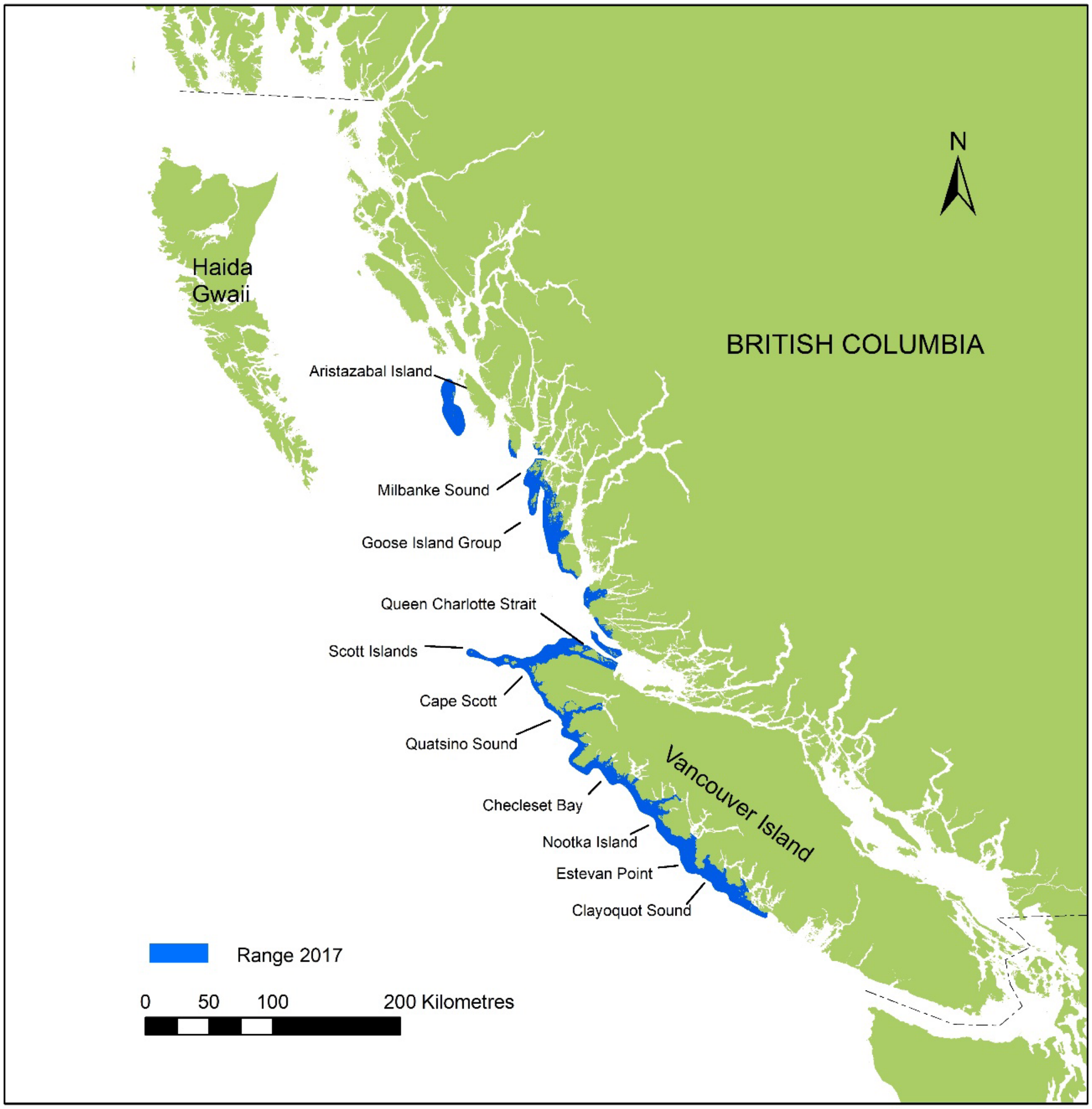

Figure 1. Sea otter range in BC in 2017 and place names mentioned in the text including Checleset Bay site of the original re-introductions 1969-1972 and Goose Island Group where groups of sea otters were first sighted on the central mainland coast in 1989. Dashed/dotted lines represent the Canada – US border.

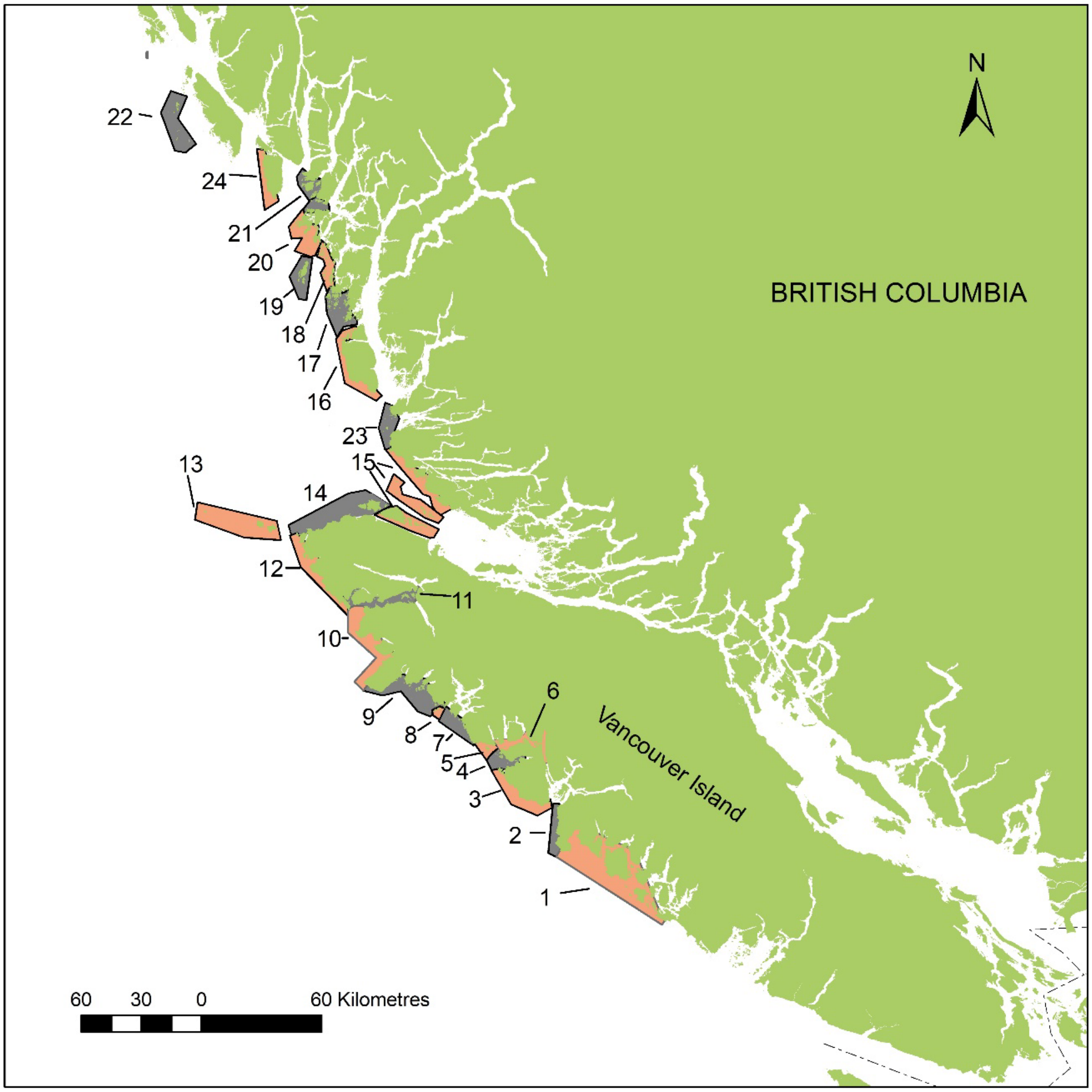

Figure 2. Twenty-four survey segments 2017. 1. Clayoquot Sound, 2. Hesquiat Peninsula, 3. Nootka Island, 4. Nuchatlitz Inlet, 5. Catala Island, 6. Esperanza Inlet, 7. Kyuquot Sound, 8. Mission Group, 9. Checleset Bay, 10. Brooks Bay, 11. Quatsino Sound, 12. Kains Island to Cape Scott, 13. Scott Islands, 14. Cape Scott to Hope Island (Queen Charlotte Strait west), 15. Queen Charlotte Strait east, 16. Calvert Island, 17. Kildidt Sound, 18. Simonds Group to Tribal Group, 19. Goose Group, 20. McMullin Group to Cape Mark, 21. Seaforth to Ivory Island and Lady Douglas Island, 22. Aristazabal Island, 23. Smith Sound, 24. Price Island. Segments are shaded orange or grey to distinguish adjoining segments.

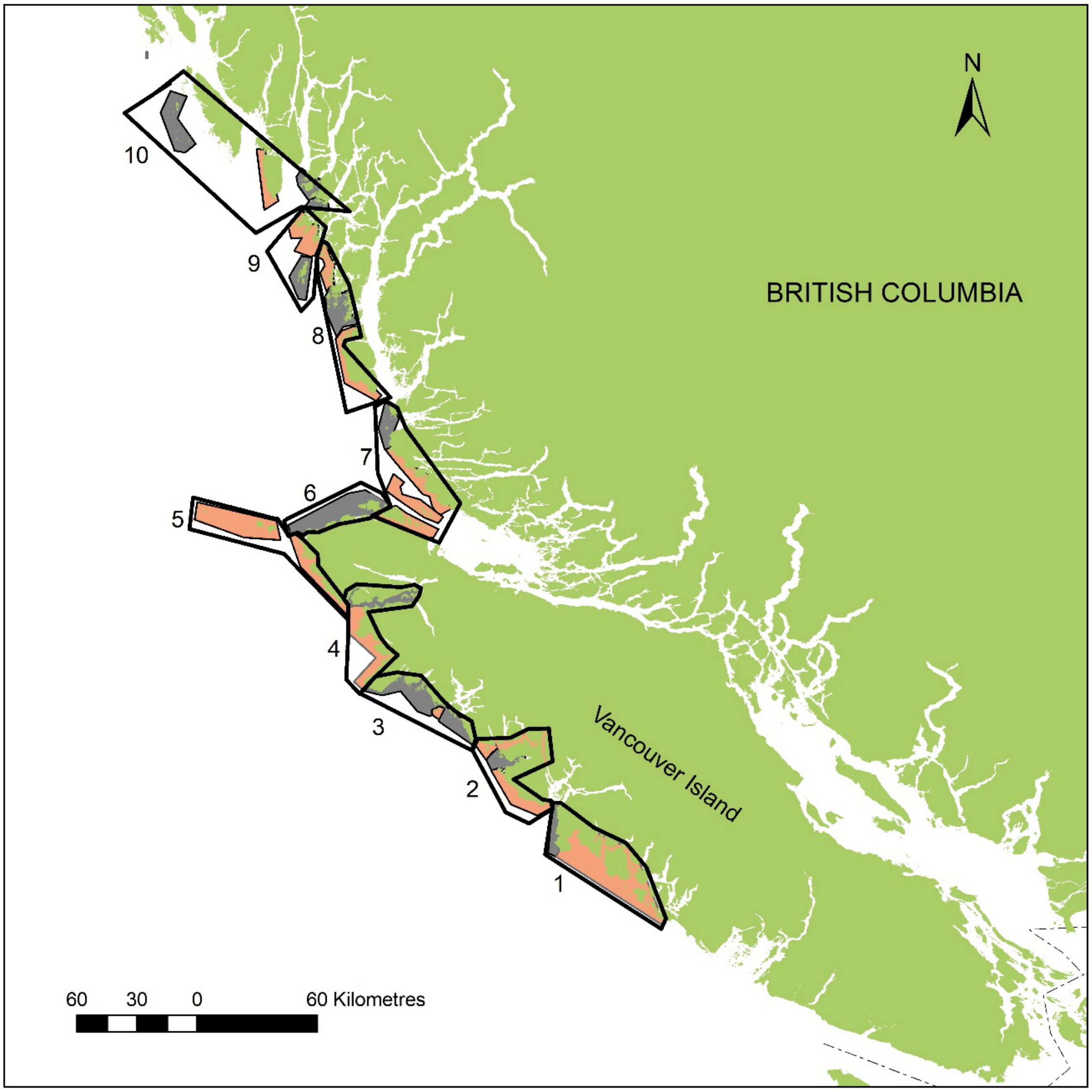

Figure 3. Twenty-four survey segments comprising the sea otter range in BC grouped into 10 sub-regions. Sub-regions are outlined in black and denoted by number. Segments within are shaded orange or grey to distinguish adjoining segments.

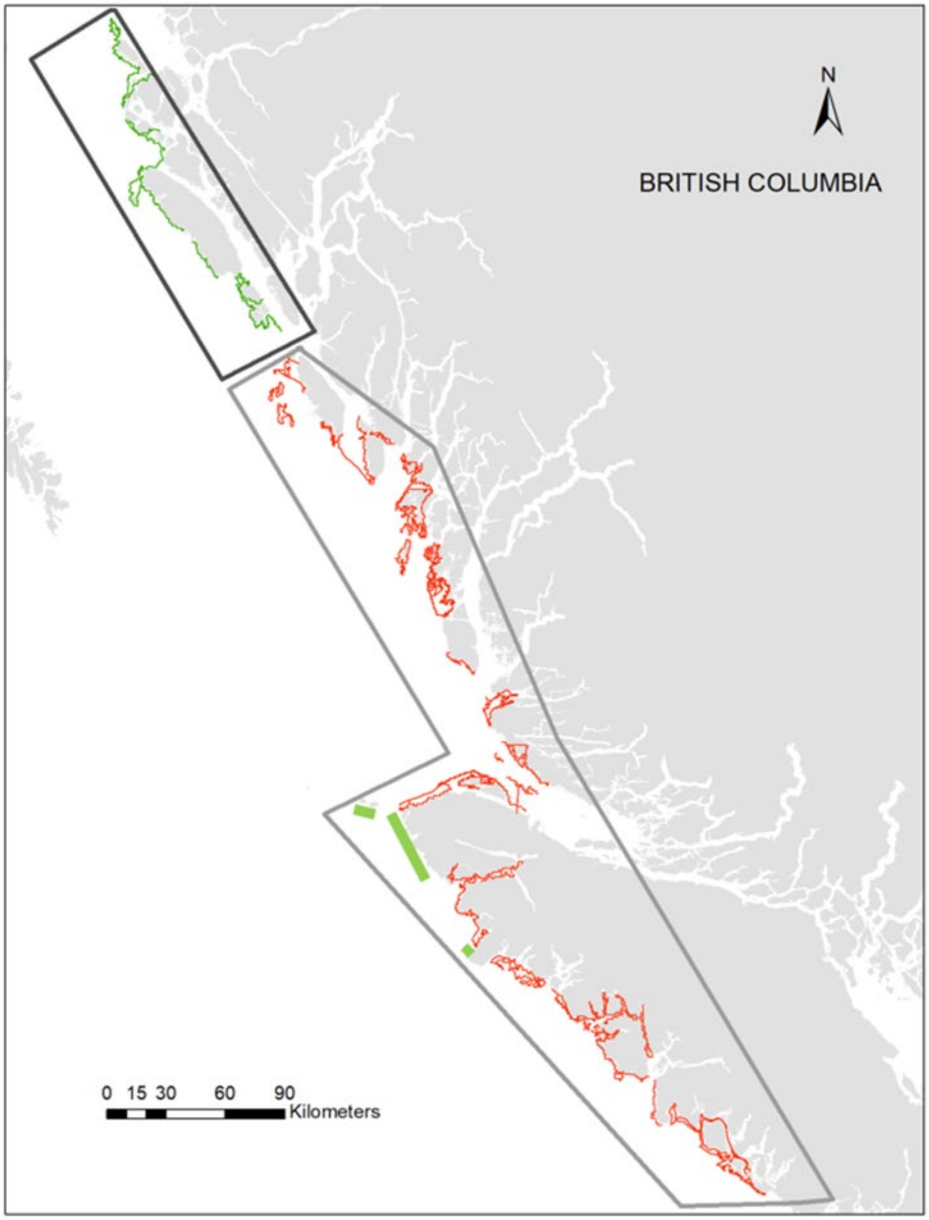

Figure 4. Survey effort on the BC coast in 2017. Black polygon outlines area of survey effort and within, green lines are kilometres of survey tracks north of the occupied range. Grey polygon outline area of survey effort and within, red lines are kilometres of survey tracks that encompasses occupied areas. Green bars indicate the areas not surveyed due to weather.

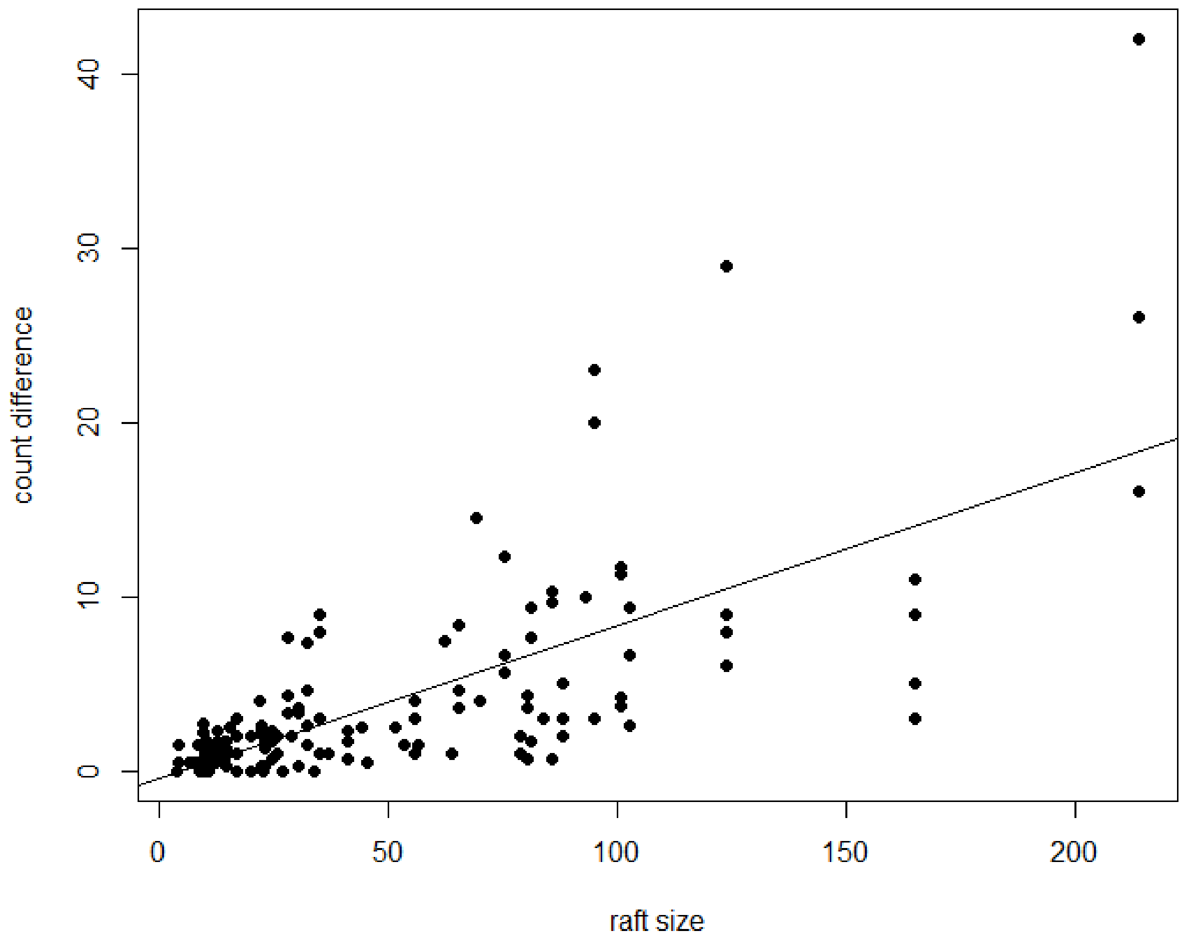

Figure 5. Count differences relative to the mean for each of 167 raft encounters (n=194 counts) in 2017. Line represents a linear regression fit with a slope of 0.087.

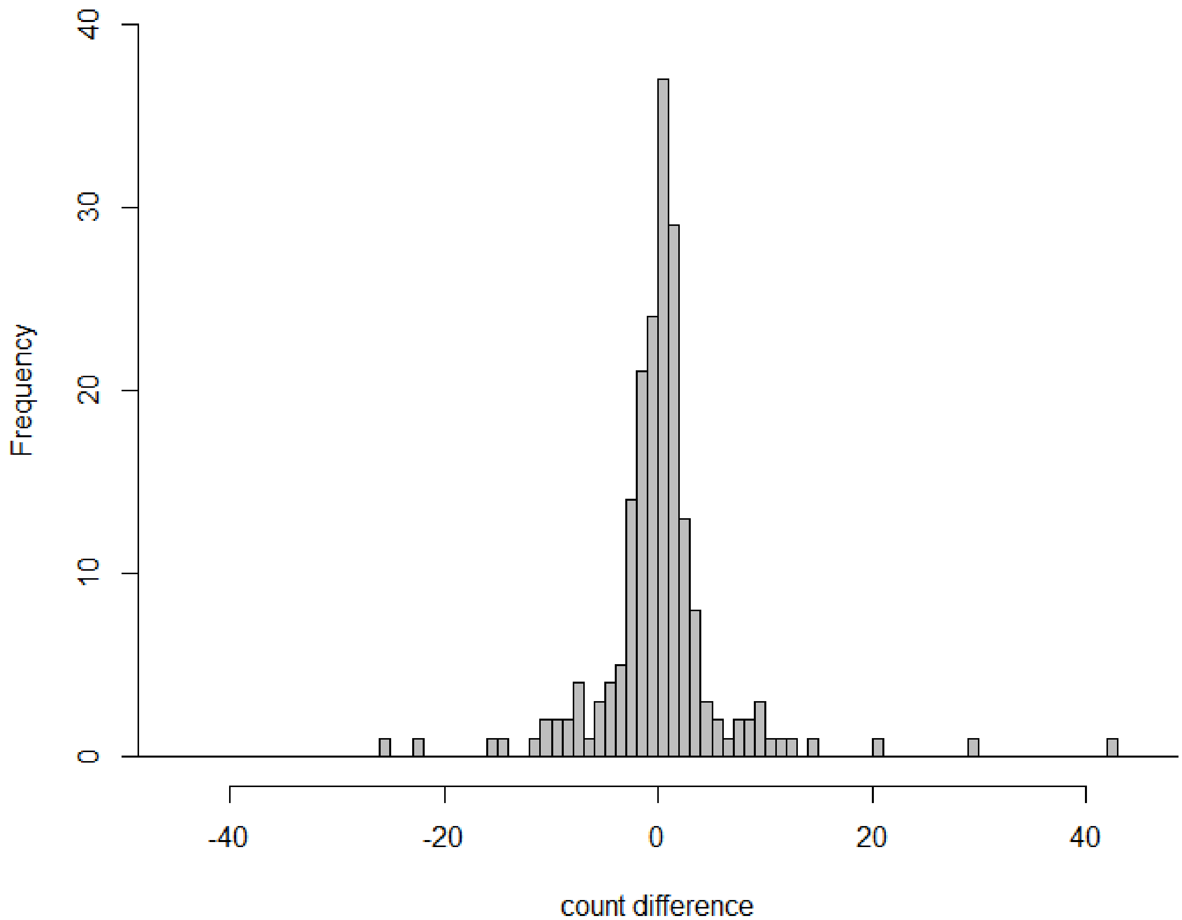

Figure 6. Frequency distribution of count differences relative to the mean for each of 167 raft encounters (n=194 counts). Differences between counts and the mean for each raft range from -26 to +42 sea otters. The overall mean and median of these count differences are zero.

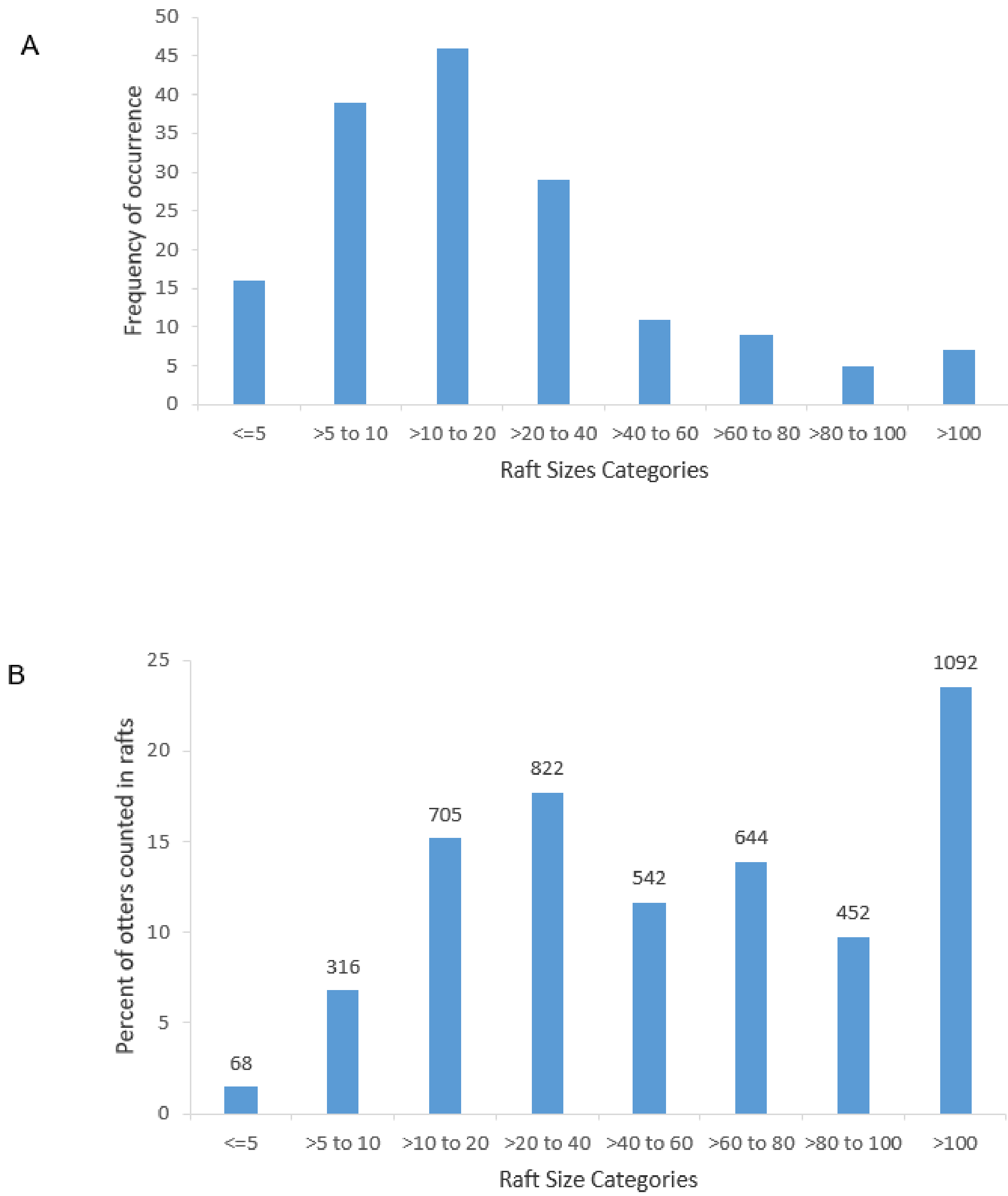

Figure 7. A. Frequency distribution of raft sizes recorded during surveys in 2017. B. Percent of all otters rafted during the 2017 surveys by raft size categories (n = 4,641) and columns labelled with the number of sea otters in each raft size category.

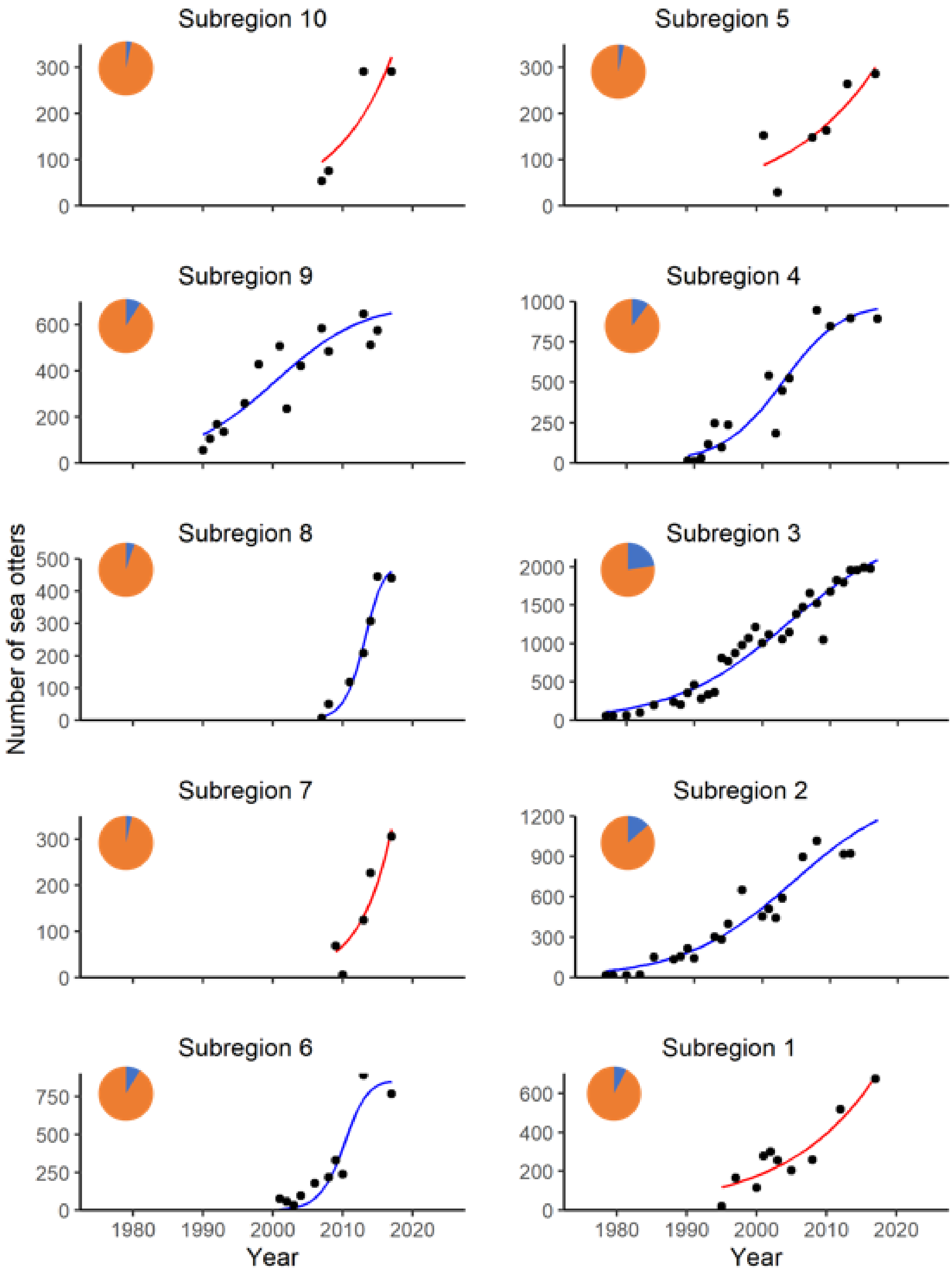

Figure 8. Sub-regional growth trends fit to survey counts 1977 to 2017. Blue line is a logistic model. Red line is an exponential model. Inset Pies illustrate the total contribution (blue) of the sub-region to the overall population estimate for 2017 (n = 8,110). Y-axis scales differ among sub-regional graphs.

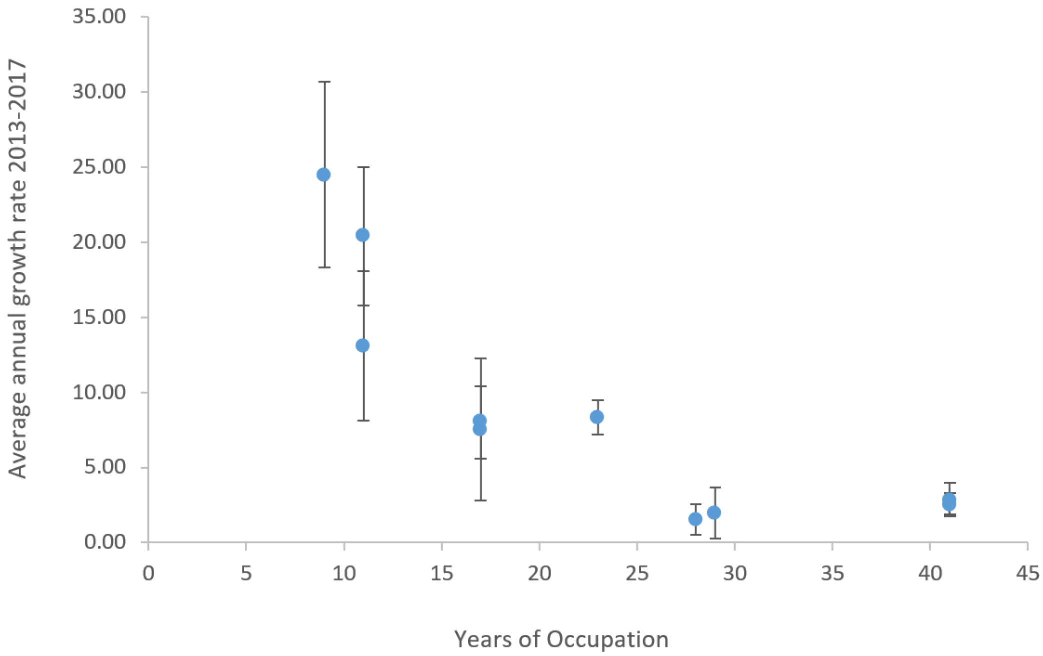

Figure 9. Sub-regional average annual growth rates in the most recent 5-year period (2013-2017), versus years of occupation. Error Bars represent plus/minus 1 Standard Error (Standard Errors for each sub-region are from Table 2).

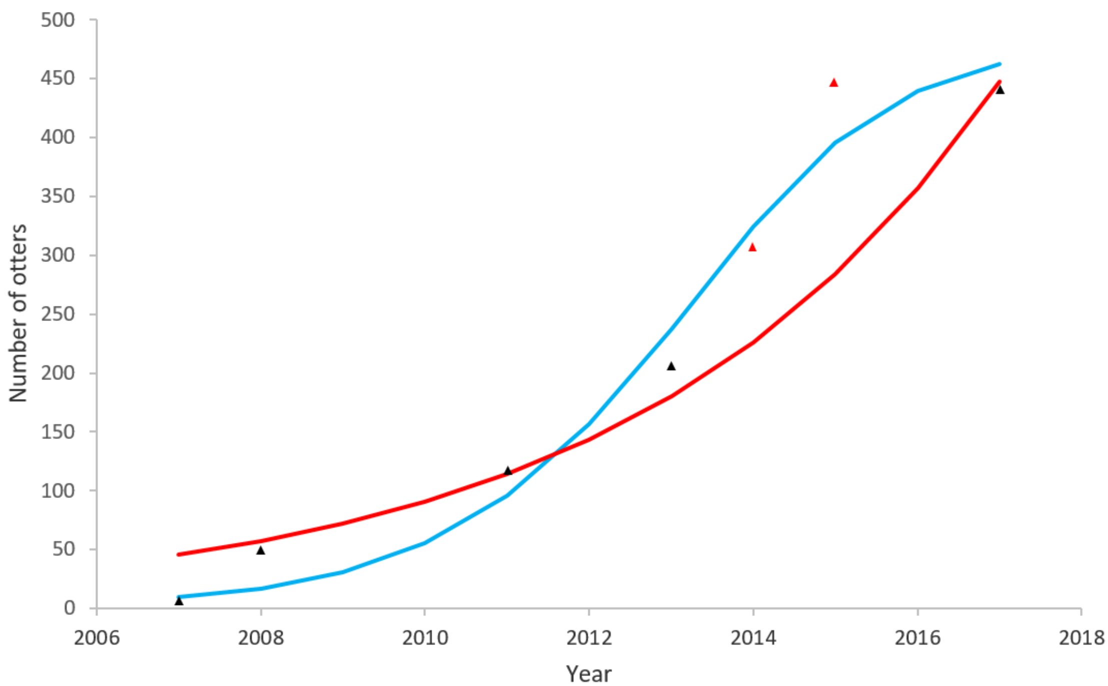

Figure 10. Effect of additional survey data in sub-region 8. Blue line represents a logistic model fit to the 2007 – 2017 time series (n = 7 counts). Red line represents an exponential model fit to the 2007 – 2017 time series excluding two counts made in 2014 and 2015 (n = 5). Triangles represent the counts. Red triangles are counts from the Hakai Research Institute surveys.

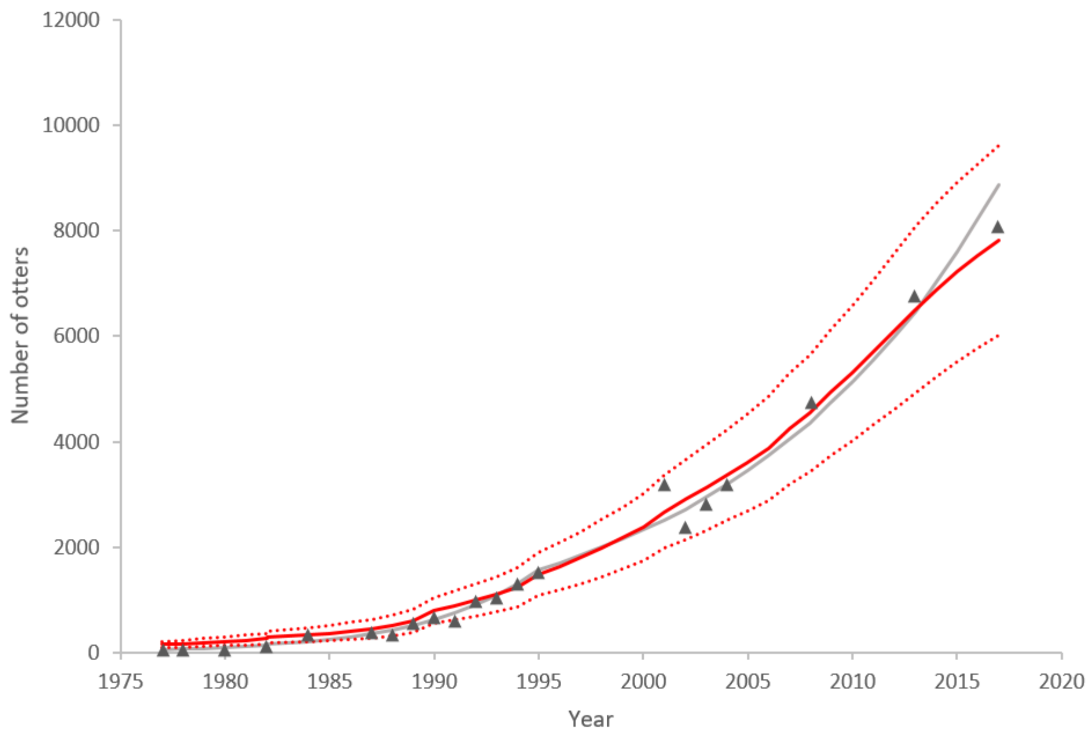

Figure 11. Comparison of BC sea otter population growth trends over the period 1977 to 2017. Red solid line represents estimated population growth for BC based on summing 10 sub-regional models. Dotted red line represents upper and lower 95% confidence intervals of this estimate. The average annual growth rate from this model for the period 2013 to 2017 was 5.26% year $^{-1}$ (SE = 1.25), and 6.37% year^{-1} (SE = 2.55) for the period 2008 to 2012. Solid grey line represents estimated population trajectory based on fitting log transformed counts on time (year) by piece-wise linear regression, which estimated growth rate up to 1995 at 20.11% year $^{-1}$, and at 8.75% year^{-1} thereafter to 2017. Black triangles represent survey counts/estimates used in the linear regression.

APPENDIX A

Analytical Method for fitting annual counts (n=21) from 1977 to 2017 by piece-wise linear regression. These are the methods followed in Nichol *et al.* (2005) and Nichol *et al.* (2009).

Annual rates of change in population size were estimated by linear regression of ln(counts) versus time to obtain the best fit to the log-transformed exponential growth equation:

$$\ln N_t = \ln N_0 + rt$$

where N_0 represents the initial population size and r the intrinsic rate of growth.

Finite rates of growth α were derived from the slope r (intrinsic rate) of the regression equation by:

$$\alpha = e^r - 1$$

The Student's *t* test was used to determine whether the slopes of two simple log-linear regressions were significantly different (Zar 1984).

Changes in population growth between 1977 and 2017, evident in the pattern of the counts over time, were evaluated by fitting piecewise linear regressions to the logarithmically transformed counts to identify the probable period of time when there was a distinct change in the growth trend:

$$\ln N_t = \ln N_0 + r_1 t + r_2(t-x)Y_t$$

where x represents the year in which growth rate changed, r_1 represents the intrinsic rate of growth before the change, and r_2 represents the amount by which the rate is adjusted after the change. Y_t is a dummy variable assigned 0 for years before the change in growth and 1 for years after. All possible regressions were fitted and those in which both coefficients were significant were evaluated by the resulting unadjusted r^2 values.