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RESEARCH ARTICLE

A century of change in Glaucous-winged Gull (*Larus glaucescens*) populations in a dynamic coastal environment

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ABSTRACT

As conspicuous midtrophic omnivores, gulls can serve as useful indicators to characterize long-term ecological changes in marine ecosystems. Glaucous-winged Gulls (*Larus glaucescens*) have been studied in the Georgia Basin of British Columbia, Canada, an urbanized coastal zone, since the late 1800s. We collated all available information to develop a (noncontinuous) 111-year time series of counts at breeding colonies, and combined these counts with demographic vital rates to assess how changes in historical gull egg harvesting practices, forage fish abundance, and Bald Eagle (*Haliaeetus leucocephalus*) numbers affected gull population trajectories from 1900 to 2010. Mean counts at 87 breeding colonies in the Georgia Basin showed a nonlinear trend, increasing from historical low counts in the early part of the twentieth century to peak values in the 1980s, and declining thereafter to the end of the time series. Demographic models that integrated temporal trends in clutch size and nesting success, and which also included a food-related decline in first-year survival or a further reduction in nesting success as a function of eagle abundance, successfully reproduced trajectories of gull population growth rates over the study period. Glaucous-winged Gulls have thus responded to a series of changes in the Georgia Basin. These patterns are consistent with population release following cessation of egg harvesting; growing reliance by gulls on nonfish foods and resulting declines in clutch size, productivity, and first-year survival; and the effects of recovering Bald Eagle populations. These results highlight the value of compiling data from multiple retrospective studies to better understand the complex factors affecting long-term trends in animal populations.

Keywords: clutch size, *Haliaeetus*, Migratory Bird Convention Act, piscivore, population regulation, seabirds, shifting baselines

Un siglo de cambio en las poblaciones de *Larus glaucescens* en un ambiente dinámico costero

RESUMEN

En su calidad de omnívoros conspicuos y consumidores secundarios, las gaviotas pueden servir como indicadores útiles para caracterizar el cambio ecológico a largo plazo de los ecosistemas marinos. *Larus glaucescens* ha sido estudiada desde los años 1800 en la cuenca de Georgia, Columbia Británica, Canadá, una zona costera urbanizada. Cotejamos toda la información disponible para desarrollar una serie de tiempo no continua de 111 años de conteos en las colonias reproductivas, y combinamos estos datos con las tasas demográficas vitales para determinar cómo los cambios históricos en las prácticas de cosecha de huevos de gaviota, la abundancia de peces, y el número de *Haliaetus leucocephalus* afectaron la trayectoria de la población de gaviotas entre 1900 y 2010. Los conteos promedio en 87 colonias reproductivas en la cuenca de Georgia mostraron una tendencia no lineal, que se incrementó de conteos históricos bajos en la primera parte del siglo veinte a valores pico en los años 80 y luego declinó hacia el final de la serie temporal. Los modelos demográficos que integraron las tendencias temporales en tamaño de nidada y éxito reproductivo, o una mayor reducción en el éxito reproductivo en función de la abundancia de águilas, reprodujeron exitosamente la trayectoria en las tasas de crecimiento de la población de gaviotas durante el periodo de estudio. *L. glaucescens* ha respondido a una serie de cambios en la cuenca de Georgia. Estos patrones son consistentes con una liberación de la población luego del cese de la cosecha de huevos, con una creciente dependencia de las gaviotas de alimentos diferentes a los peces, y un declive resultante en el tamaño de la nidada, la productividad, y la supervivencia en el primer año, y con los efectos de la recuperación de las poblaciones de *H. leucocephalus*. Estos resultados resaltan el valor de recopilar múltiples estudios en retrospectiva para entender mejor los complejos factores que afectan las tendencias de largo plazo en las poblaciones animales.

Palabras clave: Acto de la Convención de Aves Migratorias, aves marinas, *Haliaetus*, piscívores, regulación poblacional, tamaño de nidada, líneas de referencia cambiantes

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INTRODUCTION

A key question in ecology is what constitutes a 'normal' change in animal population numbers, given the large fluctuations that may occur over time (Krebs et al. 2001). Long-term time series are critical to addressing this question because they are more likely to include multiple population or climate cycles, and thus to reveal critical underlying processes and the occurrence of rare but influential events (Wiens 1977, 1984, Ludwig 1999). Marine birds are often identified as sensitive indicators of ocean systems (Furness and Camphuysen 1997, Piatt et al. 2007, Parsons et al. 2008), with more than 200 papers in the past 2 decades showing that seabird populations are measurably affected by changes to marine environments (Grémillet and Charmantier 2010). We present an analysis aimed at identifying the range of population variation in the Glaucous-winged Gull (*Larus glaucescens*), a potential indicator species (Hebert et al. 1999, 2009, Gebbink et al. 2011), based on count data from breeding colonies spanning a period of 111 years in the Georgia Basin, British Columbia (BC), Canada.

The Glaucous-winged Gull is a long-lived marine bird described as thriving in proximity to humans, but whose numbers currently appear to be in decline over a substantial portion of its southern range (Sullivan et al 2002, Bower 2009, Hayward et al. 2010). This decline has prompted concern about future trends, although evidence exists to suggest that Glaucous-winged Gull numbers in the region were much lower at the start of the twentieth century than at present (Dawson and Bowles 1909, Drent and Guiguet 1961). Thus, it is plausible that the species responded favorably to human-induced environmental changes in the early 1900s, with these changes facilitating population growth above a baseline supported by the availability of natural foods (Vermeer 1992, Hayward et al. 2010). Under such a scenario, the recent decline would simply represent a reversal of these influences and a return to historical conditions. However, a detailed understanding of population trends to the present day is lacking.

Larus gulls worldwide often nest colonially near human population centers (Ward 1973, Pons 1992, Oro et al. 2004), and they have long drawn the attention of field biologists (Dutcher and Baily 1903, Anonymous 1908). Early studies of these species focused on behavior and demography, and only incidentally recorded population numbers (Province of British Columbia 1915, Tinbergen 1953, Vermeer 1963). To provide a definitive estimate of long-term population trends in the study region, we used colony count data for Glaucous-winged Gulls nesting in the Georgia Basin to estimate long-term changes in mean colony size from 1900 to 2010. We examined potential causes of population change based on three hypotheses developed to account for temporal trends in gull populations generally (Grandgeorge et al. 2008, Hayward and Verbeek 2008, Farmer and Leonard 2011), and that were appropriate to the history and ecology of Glaucous-winged Gulls in our region. We used a simple demographic model to generate expected population trajectories based on estimates of reproductive success and survival derived from field data and historical accounts, and compared these predicted trajectories to observed population trends derived from colony counts.

Food Limitation

Food availability may have driven both increases and decreases in Glaucous-winged Gull populations during the last century. Expanding human populations in the Georgia Basin may have increased the availability of food for gulls in the form of garbage, and by doing so may have facilitated gull population growth after 1920 (Vermeer 1992, Hayward et al. 2010), as has occurred in other systems (Spaans 1971, Pons and Migot 1995). Alternatively, changes in forage fish populations may have decreased food availability (Therriault et al. 2009, McKechnie et al. 2014), which may explain recent declines in gull populations in the Georgia Basin. Population declines have occurred in parallel with long-term decreases in egg volume and clutch size (Blight 2011), a pattern consistent with the theory that access to high-protein fish prey, as opposed to lower-quality anthropogenic garbage, may be critical for successful egg production in various gull species (Hiom et al. 1991, Bolton et al. 1992, Annett and Pierotti 1999). Food shortages may also lead to increased egg cannibalism at some colonies (Hayward et al. 2014), which has the potential to contribute to clutch size declines. These potential links between food abundance or quality and reduced clutch size, reproductive success, and population decline are hereafter referred to collectively as the 'food limitation' hypothesis.

Predation by Bald Eagles

A second hypothesis, 'predation limitation,' might also explain long-term population trends in Glaucous-winged Gulls, given that Bald Eagles (*Haliaeetus leucocephalus*) have regionally increased in number over time, presumably along with predation rates. In the first half of the twentieth century, Bald Eagles were suppressed by persecution, and, later, by exposure to DDT and PCBs (Elliott and Harris 2002). Bald Eagles can affect gull reproduction and survival directly via predation (Vermeer and Morgan 1989) and indirectly by affecting behavior and predation risk (Hipfner et al. 2012). Predation by eagles on gull eggs or young birds likely increased as eagles recovered in the mid-to-late 1900s (Sullivan et al. 2002, Elliott et al. 2011). Under this hypothesis, gull numbers should have grown or remained stable in the absence of eagles, but grown more slowly or declined as eagle populations recovered.

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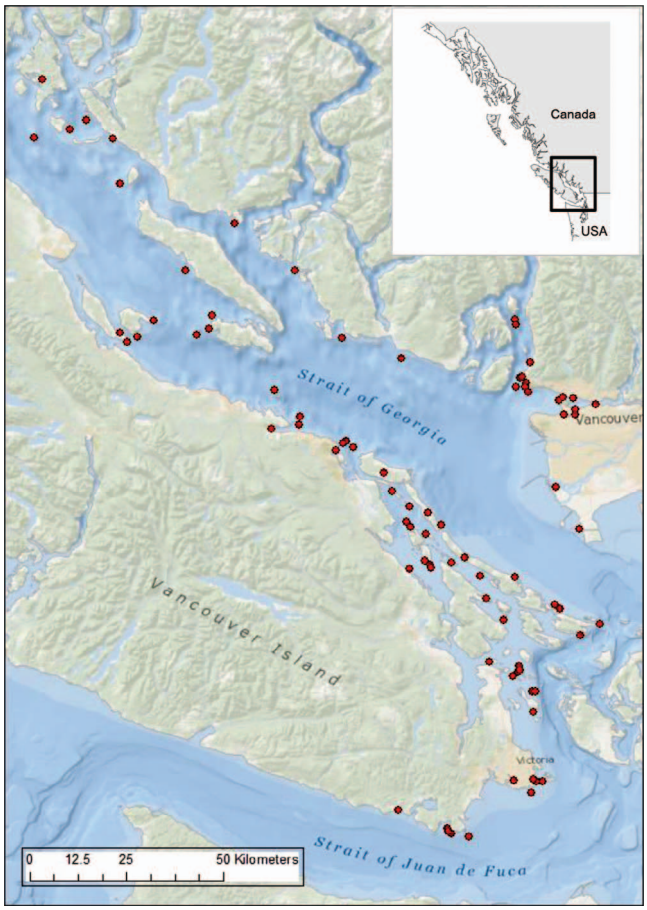


FIGURE 1. The locations of Glaucous-winged Gull colonies used to estimate population trends (1900–2010, noncontinuous data) in the Georgia Basin, British Columbia, Canada.

Cessation of Egg Harvesting

Reid (1988) suggested that increases in the productivity of Glaucous-winged Gulls in the region occurred after the adoption of the Canada–U.S. 1916 Migratory Bird Convention (Migratory Bird Treaty in the USA), which reduced or eliminated egg collecting and hunting of adults throughout the Georgia Basin. Accounts from the late 1800s suggest that, historically, harvesting of seabird eggs occurred at very high rates. On the Farallon Islands, California, USA, seabird egg hunters regularly broke all eggs found so that they could later return to collect freshly laid second clutches; in 1886 alone, 108,000 eggs were reported as having been taken from Common Murre (*Uria aalge*) nests on these islands (Doughty 1971). Seabird shooting and egg harvesting was also common in the Georgia Basin prior to legislative protection. In 1915, a warden was placed on Mandarte Island, BC, to protect nesting birds because "human beings – whites, Indians, and Japanese – carry … away the birds' eggs and young" (Province of British Columbia 1916: N15). On nearby Mitlenatch Island, Pearse (1923) noted poor reproductive success because nests were "systematically robbed" (p. 133) and that "the place was cleaned of eggs" (p. 133). Anthony (1906:130) further noted that recreational hunters would commonly "slaughter wantonly large numbers [of gulls] for the mere sport." Thus, the 'egg harvesting hypothesis' predicts that, once protected, gull populations in the Georgia Basin increased until limited by food or predators.

Each of the three general hypotheses has empirical merit, invoking factors likely to have influenced gull populations concurrently or sequentially over the last century. We evaluated their potential demographic impacts on gulls by fitting simple matrix population models and comparing trajectories of hypothesized population growth rates to observed population growth rates following the general approach of Walters (1986), Hilborn and Mangel (1997), and Walters and Martell (2004). We used a time series of gull colony counts, published demographic vital rates and our own field data, previously documented declines in clutch size, and annual eagle counts to test whether declines in gull fecundity, predation by eagles, or some combination of these two factors accounted for observed population trends within our study area. Overall, the objectives of our study were to use Glaucous-winged Gull population trends and modeled hypotheses to evaluate how gull population size changed over time in the Georgia Basin and to determine whether population trends were related to temporal variation in reproductive output, within the general context of investigating what these population trends suggested about baseline conditions in the Georgia Basin.

METHODS

Study Area and Colony Counts

The Georgia Basin refers to the Canadian portion of the Salish Sea, an inland body of water encompassing the Strait of Georgia, BC; Puget Sound, Washington, USA; the eastern portion of the Juan de Fuca Strait; and the region's islands and terrestrial watersheds (Figure 1). The area is influenced by several major urban centers and is heavily affected by human activity, being ranked as 'very high impact' in a global assessment of anthropogenic impacts of coastal ecosystems (Halpern et al. 2008).

We compiled all available published and unpublished Glaucous-winged Gull counts at breeding colonies (number of nests or breeding pairs per colony) obtained from field studies conducted between 1900 and 2010 in the inshore coastal waters of the Georgia Basin, Canada, and supplemented these data by conducting colony censuses in 2009 and 2010 (Blight 2014). In a few cases we used median values as our colony counts, when historical estimates were provided as ranges ($n = 15$). Our 2009 and 2010 counts were carried out following the methods of

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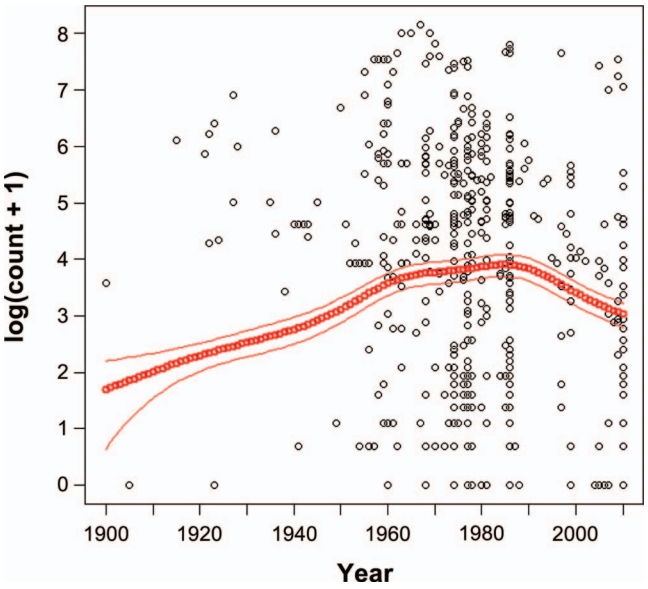


FIGURE 2. Trends in colony counts of Glaucous-winged Gulls in the Georgia Basin, British Columbia, Canada, 1900–2010. Colony counts are log-transformed as $\log_e(x+1)$ to allow plotting of 0-counts. Hollow points indicate counts of pairs or nests at 87 locations. Thick hollow points along the trend line indicate mean colony counts with 95% confidence intervals (thin lines) predicted from a Generalized Additive Model.

Vermeer and Devito (1989), who censused all nonurban Glaucous-winged Gull colonies in the Georgia Basin in 1986 (Vermeer and Devito 1989). Our censuses replicated about 60% (49 of 83) of the sites counted in 1986, but we selected these 49 sites to include most (~96% of 1986 numbers) of the breeding population. Of the 34 colonies that we did not visit, 76% historically consisted of ≤10 pairs. We conducted censuses from June 13 to June 20 in 2009 (Mandarte Island and the Chain Island group) and 2010 (remaining colonies). Four colonies of 1–5 pairs were surveyed using binoculars on July 1, 2010. The mid-June census period was chosen to most closely replicate earlier censuses and to coincide with the peak of egg laying (Vermeer and Devito 1989, Sullivan et al. 2002, Blight 2011). Conducting counts prior to hatching avoids disturbing gull chicks, which when frightened may flee into adjacent territories where they may be killed by neighboring birds (Hunt and Hunt 1976). To avoid disturbing sympatric nesting cormorants (*Phalacrocorax* spp.), we counted any gulls nesting in their vicinity using binoculars. As with previously published studies (Vermeer and Devito 1989, K. Vermeer personal communication), we counted only active nests (containing ≥1 egg, or evidence of depredation), because Glaucous-winged Gulls often build multiple nest cups prior to laying. Because count data were collected by multiple observers over more than a century, we were unable to determine the degree to which an observer effect might have affected counts, and did not attempt to correct for it. We also assumed equal nest detectability with increasing colony size, because larger colonies tended to be censused by more observers, and Glaucous-winged Gull nests are fairly visible to observers, generally being constructed in open grass or rocky areas.

Temporal Trends

Temporal trends in gull abundance were estimated using generalized additive models (GAMs) by modeling colony counts in relation to year, from 1900 to 2010. The GAM approach is an extension of the General Linear Model, in which predictors are smoothed functions rather than linear relationships (Wood 2006). This approach allowed for evaluation of nonlinear trends in mean gull colony counts over time. Year 1900 was set to a value of 0, and we used package 'mgcv' in R (Wood 2006) to fit a GAM that included a Poisson error distribution and a unique colony identifier as a random effect to account for the correlated non-normally distributed errors (all R code is available in the Supplemental Material Appendix).

Demographic Models

Using the stock reconstruction methods of Walters (1986) and Walters and Martell (2004), we tested whether observed and hypothesized changes in demographic vital rates were sufficient to explain changes in mean gull colony counts. We first calculated a time series of observed population growth rates as the ratio of successive mean predicted values from the trend model of colony counts (Figure 2), i.e. predicted mean count at year $t+1$ divided by the predicted mean count at year t. We then compared this observed population trajectory to hypothesized trajectories derived from different combinations of demographic vital rates in series of four scenarios of increasing complexity, with these scenarios determined a priori. For each scenario, a prebreeding birth-pulse deterministic matrix population model (female-only; Caswell 2001) was constructed for each year t from 1900 to 2010, similar to the matrix model built for Yellow-legged Gulls (*L. cachinnans*; Bosch et al. 2000). Each projection matrix had the general form:

$$A[t] = \begin{bmatrix} 0 & 0 & 0 & \frac{CS[t]}{2} \times NS[t] \times S1[t] \\ S2 & 0 & 0 & 0 \\ 0 & S3 & 0 & 0 \\ 0 & 0 & S4 & S4 \end{bmatrix}.$$

Clutch size ($CS[t]$) adjusted per female, nesting success ($NS[t]$), that is the proportion of eggs that hatched and survived to become fledglings (Ricklefs 1973), and survival probability ($S1[t]$) from fledging to 1 yr of age were allowed to vary by year in scenarios. Survival probabilities for the older age classes ($S2$, from 1 yr to 2 yr of age; $S3$, the

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survival of 2-yr-olds to become 3-yr-olds; and *S4*, adult survival) were assumed to be fixed in all scenarios. For the fixed survival probabilities, we used values derived from the literature. Specifically, we assumed that *S2* was 0.70 (Butler et al. 1980, Reid 1988), *S3* was 0.62 (Butler et al. 1980), and *S4* was 0.87 (Reid 1988). Where more than one value was available for an age-class, we used the mean of reported values, except for adult survival (*S4*), where 0.87 was equal to the highest estimate reported by Hayward and Verbeek (2008; range = 0.83–0.87), but was most similar to published estimates for adult temperate-breeding *Larus* gulls based on larger sample sizes and longer studies (Gaston et al. 2009).

In this matrix model, only adults (4 yr and older) were assumed to breed (Hayward and Verbeek 2008). Breeding propensity has not been described for Glaucous-winged Gulls in the study area, and we thus assumed that all adults bred. Fecundity of adult gulls varied from year to year (t), and was calculated as a function of clutch size ($CS[t]$) divided by 2. Clutch size values for year t were obtained from a time series for Glaucous-winged Gulls in the Georgia Basin from 1962 to 2009 (Blight 2011). We assumed an initial clutch size of 3 eggs in 1900, based on museum collections and the modal clutch size for the genus in early accounts of this species (Schultz 1951). We set 1900 as $Yr = 0$, and obtained a *CS* value for each year by interpolating between years 1900 to 2010 using the quadratic equation:

$$CS[t] = 3.0 + 0.003 \times Yr - 0.00009 \times Yr^2.$$

We initially fit a simple linear trend equation, but including a squared Year term (Yr^2) in this regression increased the R^2 value from 0.69 to 0.92, indicating substantial improvement and good explanatory power. This time series of *CS* values was used in all scenarios (Figure 3A).

For each year in the time series of projection matrices in each scenario, we calculated lambda ($\lambda[t]$) as the dominant eigenvalue of the population matrix, to represent the long-term growth rate of a structured population in a constant environment (Caswell 2001). We then plotted the lambda values against each year, and qualitatively compared how the observed trajectories of population growth rates based on colony counts compared with the predicted trajectories based on population models in our four scenarios. Our approach to estimating lambda assumed that detectability was constant at differing abundances and over time, and that the population state was stable. Although relying on an assumption of a stable state has the potential to introduce bias into estimated rates of change (Koons et al. 2005, 2006), we adopted this assumption due to a paucity of information on age structure from which to gauge transient dynamics.

Scenario 1: Decline in clutch size. We examined whether the temporal decline in average clutch size of Glaucous-winged Gulls in the Salish Sea (Blight 2011) could account for the population dynamics observed in colony counts. We used the values described above for demographic vital rates, and included a fixed value for nesting success (*NS*) of 0.51, based on average values in the study area (Vermeer 1963, Blight 2012). Similarly, we used a fixed value of 0.50 for *S1*, survival from fledging to 12 mo of age, based on the average of published values for the region (Butler et al. 1980, Reid 1988).

Scenario 2: Declines in clutch size and nesting success. Egg and chick production of gulls are both positively related to food availability (Mills et al. 2008), and we evaluated how including a decline in nesting success in addition to the decline in clutch size would affect the population trajectory. Data on the nesting success of Glaucous-winged Gulls in the Strait of Georgia are limited to 3 years of estimates that indicate the potential of a decline from 0.63 in 1962 (Vermeer 1963) to a mean of 0.46 in 2008 and 2009 (Blight 2012; Figure 3). We assigned *NS* values from 1963 to 2010 that interpolated between these years based on a simple linear model where:

$$NS[t] = 0.85 - 0.0036 \times Yr[t].$$

In the absence of other data, we assumed that the 0.63 value from 1962 represented the historical condition and extended this value back to 1900 (Figure 3B); this value is consistent with nesting success rates typically observed in gulls (Ricklefs 1969). All other vital rates were identical to those in Scenario 1.

Scenario 3: Declines in clutch size, nesting success, and survival to 1 yr of age. Juvenile gulls are known to be less skillful foragers than older birds (Verbeek 1977, Searcy 1978, Skórka and Wójcik 2008), and thus any declines in food availability or increases in predation over time might disproportionately affect the survival of first-year gulls (fledging to 12 mo of age). We evaluated a population trajectory based on Scenario 2, with the addition of a decline in *S1* over time from a starting value of 0.50 in 1900, such that:

$$S1[t] = 0.50 - \beta \times Yr[t].$$

To do so, we fit a range of values for the rate of decline (β) in *S1* from a sequence of values from a minimum of –0.00455 to a maximum of 0. This range allowed us to consider all options possible, from no decline in *S1* to a full collapse of juvenile survival (the minimum β was the rate of decline that would result in $S1 = 0$ by 2010). We selected the β value that resulted in the best fit to the trajectory of population growth rates estimated from count data using the lowest sum of squared deviations between the trajectory based on colony counts and the one based on

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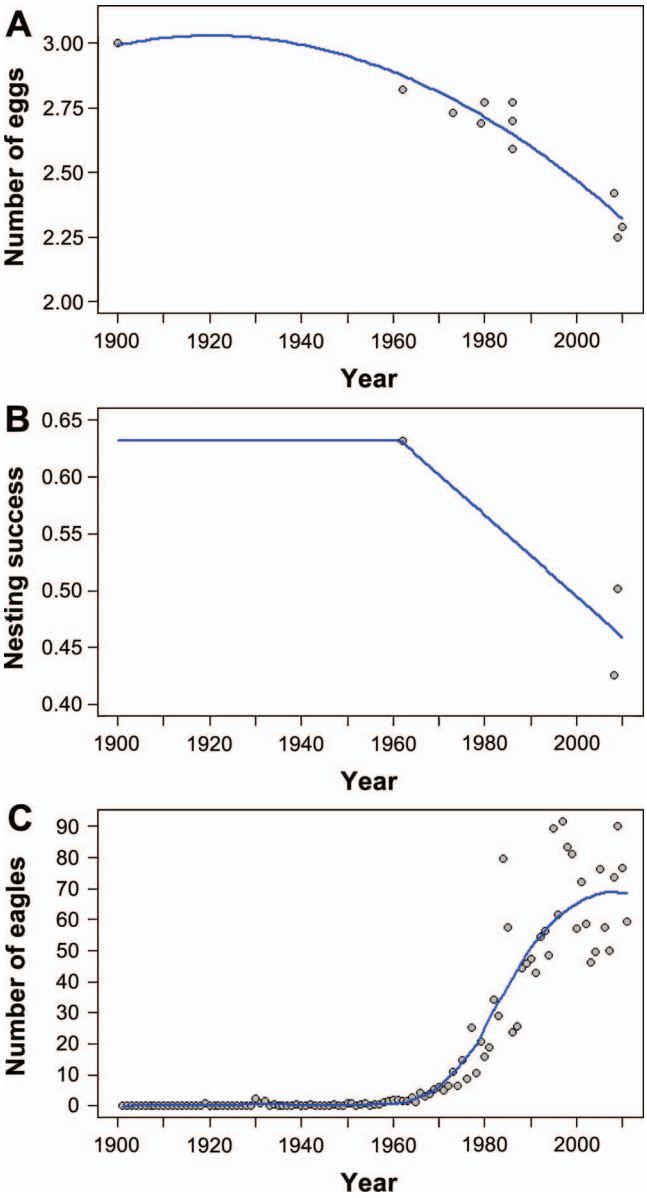


FIGURE 3. Demographic vital rates used in modeling analyses to construct population trajectories of Glaucous-winged Gulls in the Georgia Basin, British Columbia, Canada, 1900 to 2010. (**A**) Clutch size (*CS*), the number of eggs laid. (**B**) Nesting success (*NS*), the proportion of eggs that hatch and survive through the chick stage to fledging. (**C**) Bald Eagle counts, the number of eagles observed during the Christmas Bird Count for British Columbia, Canada, and Washington, USA. The solid lines indicate interpolated values used in matrix population models.

hypothesized changes in vital rates. Thus, this approach allowed us to ask how much *S1* would have had to decline over time to result in the observed gull population trends.

Scenario 4: Declines in clutch size and nesting success, and including predation by eagles. In this last scenario, we explored the potential influence of predation by eagles to ask what hypothesized rate of eagle-related mortality, indexed to eagle population size, might have resulted in the observed population growth rates as calculated from colony counts. We restricted our exploration of eagle predation to its potential detrimental effect on nesting success, *NS*. Thus, to model the effects of eagles on gulls, we added a term (γ) that further reduced *NS* probabilities from Scenario 2 as a function of eagle abundance by assuming that the annual predation rate was proportional to an index of the regional population size of Bald Eagles, such that:

$$NS.eagle[t] = NS[t] - \gamma \times EaglePop[t].$$

The $NS.eagle[t]$ sequence then took the place of $NS[t]$ in the matrix population models. For eagle population trends, we used Christmas Bird Count (CBC) data for British Columbia and Washington, adjusted for survey effort (National Audubon Society 2011). The CBC provides counts of winter rather than breeding season numbers, but winter eagle abundance provides a reasonable index of regional trend (Elliott et al. 2011). The winter counts indicated that Bald Eagles occurred at relatively low densities prior to 1950, but increased rapidly after the 1970s (Figure 3C). These eagle count data were smoothed using locally weighted regression (LOESS) and scaled to 1 by dividing by the maximum smoothed value to derive *Eagle Pop*[t]. Under this parameterization, the γ value then represents the additive mortality on eggs and chicks resulting from predation by eagles. This approach assumed that the effects of predation by eagles were not already incorporated into the time series of nesting success (*NS*) from Scenario 2. Nesting success data from 1962 were collected when eagles were nearly absent from the Georgia Basin (Figure 3), and data collected in 2008–2009 were from Mandarte Island, a site with low rates of eagle predation (L. K. Blight personal observation). Eagle predation at this site is thought to be low due the presence of an active Bald Eagle nesting territory, whereby all other eagles are excluded except the nesting pair (cf. Hipfner et al. 2012). We fit a range of values for γ from 0.00 (no effect of eagles) to 0.45 (whereby eagles at the maximum abundance would result in total reproductive failure at gull colonies [$NS.eagle = 0.00$]). As in Scenario 3, we used the least-squares approach to find the γ value that resulted in the lowest sum of squared deviations between the trajectory based on colony counts and the trajectory based on hypothesized changes in vital rates.

RESULTS

Colony Counts

We compiled 507 records of colony counts from 87 localities in the Georgia Basin over the study period, with 11 colony counts available prior to 1925. The Georgia Basin's 2 largest (historically and at present) colonies were

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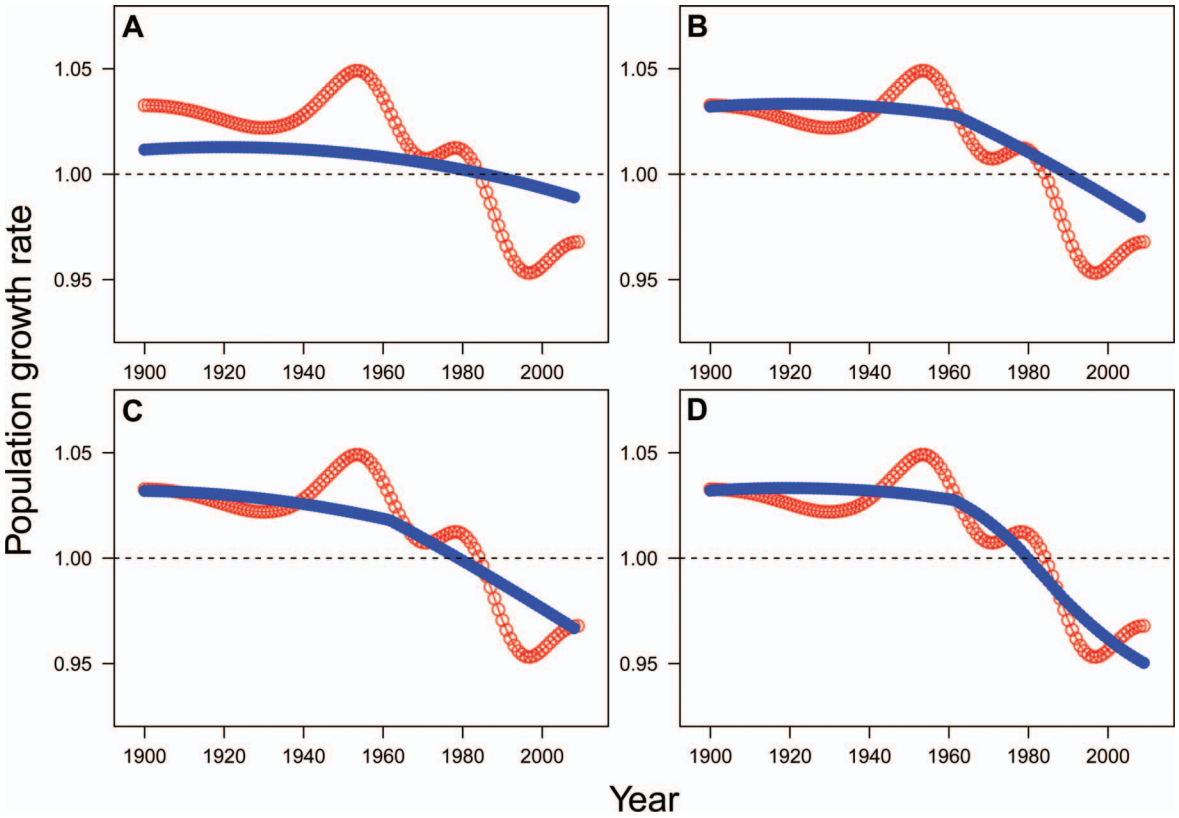


FIGURE 4. Glaucous-winged Gull population growth rate trajectory derived from counts at breeding colonies (hollow points) compared with population trajectories derived from population modeling (solid points) under 4 scenarios of increasing complexity: (**A**) Decline in clutch size only; (**B**) Decline in clutch size and nesting success; (**C**) Decline in clutch size and nesting success, and survival to 1 yr, and (**D**) Decline in clutch size and nesting success, plus inclusion of additive eagle mortality on eggs and chicks based on scaled eagle abundance.

represented in these early counts, so that our early population size estimates are likely to be representative of regional totals for that period. Colonies for which early count data were available were also among the most frequently surveyed in the region over the entire study period, and a visual inspection of the long-term trends for these and other sites showed agreement with our estimated population trend (Figure 2, Supplemental Material Figure S1).

Based on our 2009–2010 census, we estimated the 2010 Georgia Basin population at ~5,600 nesting pairs, ~7,400 fewer pairs (–57%) than were breeding during the regional census conducted in 1986 (13,002 pairs), but similar to the 5,654–6,654 pairs estimated in region-wide surveys during the middle of the population increase phase (1959–1960; Drent and Guiguet 1961, Vermeer and Devito 1989).

Temporal Trends

Glaucous-winged Gull colony numbers in the Georgia Basin ranged widely from 1900 to 2010. The GAM indicated that a smoothed function with an estimated 5.5 degrees of freedom significantly reduced model deviance ($F = 34.14$, $P < 0.001$). The smoothed function indicated that mean colony counts increased steadily from 1900 to the mid-1980s, reaching a maximum in 1986, and declining thereafter (Figure 2).

Demographic Models

Population growth rates calculated from the time series of colony counts indicated positive growth rates ($\lambda > 1$) that ranged from 1.03 to 1.05 until 1954. After that year, population growth rates remained positive but declined until 1986, after which values dropped below 1.00, indicating negative population growth. Following 1986 they continued to decline to values that ranged from 0.95 to 0.97 between 1998 and 2010 (Figure 4).

Scenario 1, which included a decline in clutch size (*CS*) but held all other vital rates constant, resulted in modeled growth rates that remained positive ($\lambda > 1$) over most of the time from 1900 to 1986, after which they dropped below 1. Modeled growth rates were lower than those calculated from the colony counts prior to 1986, and higher thereafter, and thus did not match the population trajectory derived from colony counts (Figure 4A).

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Scenario 2, which included a decline in both clutch size (*CS*) and nesting success (*NS*), resulted in a trajectory with positive growth rates that were similar to observed growth rates, approximately 3% yr^{-1}, for the early part of the time series (Figure 4B), and with mostly positive growth rates until 1993 (at $CS = 2.60$ and $NS = 0.53$), when λ values dropped below 1. This scenario did result in a reduction in population growth rates following the 1960s, as occurred in the trajectory of observed population growth rates, but overall appeared to overestimate the population growth rates derived from colony counts since the early 1990s.

Scenario 3, which assumed decreasing survival of first-year birds (*S1*) over time, produced a population trajectory that more closely fit the population growth rates modeled from colony counts than did Scenarios 1 and 2 (Figure 4C). The β value that resulted in the best fit between the 2 trajectories was −0.0007, depicting a decline in *S1* from 0.50 in 1900, to 0.44 in 1981 when projected lambda dropped below 1.00, to a value of 0.42 in 2010.

Scenario 4, which included a term that modeled additive mortality of eggs and chicks (reduction in *NS*) as a function of numbers of Bald Eagles, also resulted in a population trajectory that closely fit the population growth rates modeled from colony counts (Figure 4D). The γ value that provided the best fit between the 2 trajectories was 0.15, indicating the maximum additional reduction in *NS* that would occur when eagles were at peak abundance. This γ value resulted in overall nesting success (*NS.eagle*) that remained at 0.63 until the mid-1960s, began to decline to 0.50 in 1982 when projected lambda dropped below 1.00, and then continued to decline to a value of 0.31 in 2010.

The concurrence between the two modeled trajectories in Scenarios 3 and 4 and their concurrence with the observed population trend imply that observed declines in clutch size and nesting success, in conjunction with a similar decline in survival of first-year gulls or with further reduction of egg and chick survival proportional to eagle numbers, were sufficient to closely track long-term changes in Glaucous-winged Gull population sizes, without making additional assumptions about temporal variation in the survival of older age classes.

DISCUSSION

Colony Counts and Temporal Trends

Numbers of Glaucous-winged Gulls breeding in the Georgia Basin fluctuated widely during the 111 years from 1900 to 2010, increasing rapidly from 1900 to the mid-1980s, and then declining so that 2010 levels were ~50% of peak abundance. Our study incorporated Glaucous-winged Gull colony count data from all available sources, and represents one of the more comprehensive sets of long-term census data available for a marine bird in Canada. Compilations of marine animal count data for time periods exceeding 100 years are generally rare, and thus are valuable in studies of animal population dynamics (Pauly 1995).

These data include counts from all important colonies, totaling the majority of Glaucous-winged Gulls that nest within the region. We did not update census data for urban-nesting gulls in the Georgia Basin, but we suggest that this omission is unlikely to have markedly affected our results, i.e. that Glaucous-winged Gulls have not simply moved to more urban habitats. No large colonies are currently known to exist in urban settings in our study area, and none are known from historical records (prior to the ~1950s, when urban nesting was first documented in the region; e.g., Bowles 1906, Eddy 1982, Vermeer et al. 1988, L. K. Blight personal observation). Regional monitoring schemes counting gulls away from their colonies have also shown declines in recent decades (Bower 2009, Environment Canada 2010, National Audubon Society 2011), as has a more recent survey covering colonies in our study area that we were unable to census (Carter 2014). Further, it is unlikely that gulls emigrated to other regions because large colonies in conterminous waters in the United States also experienced rapid declines from 1993 to 2008 (44% decline on Protection Island, Washington; Hayward et al. 2010) or almost disappeared (99% decline on Colville Island, Washington, from ~1,800 pairs in the 1970s to ~20 pairs by 2000; Hayward and Verbeek 2008).

Causes of Population Trends

We used demographic models to construct population trajectories over time as a plausible, heuristic approach to conceptualizing drivers of long-term population change, and to test hypotheses about population trends (Figure 4), recognizing that more than one driver was likely to have influenced multidecadal trends. The close fit of the projected population growth rates from Scenario 3, a scenario of decreasing clutch size, nesting success, and survival of first-year birds, with the population growth rates observed at colonies, provided support for the food limitation hypothesis. Declines in egg and clutch size and nesting success have all been attributed to reductions in forage fish in other *Larus* gulls with similar life histories (Houston et al. 1983, Pierotti and Annett 1990, Hiom et al. 1991, Bolton et al. 1992), and these demographic vital rates have decreased over time in our study area (Blight 2011) concurrently with the declines and losses of forage fish populations that have occurred in the Georgia Basin (Therriault et al. 2009, McKechnie et al. 2014). Declines in forage fish availability and/or quality are also thought to have influenced reproduction and population trends in other piscivorous waterbird species in the Georgia Basin (Norris et al. 2007, Anderson et al. 2009, Wilson et al. 2013, Vilchis et al. 2014), and numerous studies have shown this link in other systems (Wanless et al. 2007, Ainley and Blight 2009, Hebert et al. 2009).

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The degree to which changes in the availability and management of human garbage may also have influenced gull fecundity and population trends in the Georgia Basin (Vermeer and Devito 1989, Vermeer 1992) remains unclear. In coastal British Columbia, the productivity of Glaucous-winged Gulls at colonies without access to garbage exceeded that of birds breeding near urban areas (Ward 1973). For Herring Gulls (*L. argentatus*), female body condition and productivity were both negatively related to the blood plasma amino acid index, an indicator of dietary garbage (Hebert et al. 2002). In contrast, other studies have shown that gulls respond to dietary garbage by increasing productivity (Spaans 1971, Pons 1992, Weiser and Powell 2010). This contrast may be explained by differences in type, quality, and availability of garbage among studies. Our study could not discriminate between reductions in productivity due to loss of fish prey vs. increases in low-quality food (i.e. garbage), and it is possible that these two factors acted in concert in the gull population decline. However, a long-term (1860–2009) reconstruction of the diet of Glaucous-winged Gulls based on stable isotope analysis of archived feather samples from the same study area showed results consistent with a gradual reduction of forage fish in gull diet since 1860, rather than increased dietary garbage during the population increase phase (Blight et al. 2014).

Including a term that linked a further reduction in nesting success to eagle abundance (Scenario 4) also resulted in a good fit of modeled and estimated population trajectories, consistent with the eagle predation hypothesis, and we suggest that recovery of eagle populations after the 1970s helped to curtail gull population growth in the Georgia Basin by increasing egg and chick mortality. Our model results indicated that predation by eagles needed to account for a further reduction of 15% in nesting success to result in a trajectory of population growth rates similar to the one observed at colonies. Cowles et al. (2012) found that eagle predation on gull nests could be as high as 51% at more southerly colonies, and thus the value of 15% appears reasonable. Eagles are capable of causing large-scale disturbance at seabird colonies, including those of Glaucous-winged Gulls (Parrish et al. 2001, Hayward et al. 2010); indeed, seabird populations are being affected in various ways by eagle population recovery throughout the northern hemisphere (Hipfner et al. 2012). However, mobbing and aggression by gulls may reduce the susceptibility of colonies to eagle attack, and to disturbance-related predation by corvids and other gulls (Hipfner et al. 2012). Gulls also do not appear frequently in the diet of nesting eagles in the Georgia Basin. For example, based on direct observations at Bald Eagle nests, Elliott et al. (2005) observed no gulls—and few birds overall—being fed to eagle chicks. Similarly, despite recording observations of eagle presence and behavior during approximately 130 field days (2008 and 2009) at the large Mandarte Island gull colony, we recorded only 5 chick predation events and 1 adult killed by an eagle (Blight 2012). Nevertheless, eagle predation may have acted synergistically with food shortages if, for example, food shortage increased predation risk to eggs and chicks because adults spent more time away from the nest to forage. Eagle predation is unlikely to have played a key role in driving gull population trends in the early 1900s, because early CBC data suggest that eagle numbers were low at that time. Human persecution of eagles and other predatory birds was commonplace in the early 1900s, as evidenced by bounties set on eagles in Alaska from 1917 until 1952 (Zwiefelhofer 2007). Thus, artificially low rates of predation by eagles may even have facilitated early gull population increases once humans stopped harvesting eggs.

The trajectory of our population model from the early 1900s to the 1960s indicates that the combination of vital demographic rates that we posited for this early period would have resulted in positive population growth rates of 2–5% per year, as could be found in any rebounding animal population. The similarity between the observed and modeled population trajectories in this early period supports the hypothesis that it was the cessation of egg harvesting and related human persecution that resulted in the strong population increases of Glaucous-winged Gulls seen during the mid-1900s (Reid 1988). Early data and anecdotes suggest that egg harvesting, and perhaps hunting, heavily affected gulls in the region at the turn of the twentieth century, with biologists of the day consistently noting that gull populations suffered from relentless persecution (Dawson and Bowles 1909, Province of British Columbia 1915, Pearse 1923). Harvest and persecution of gulls and other seabirds (e.g., Tufted Puffins [*Fratercula cirrhata*]; Province of British Columbia 1916), and resulting population effects, were globally commonplace at the time (Grandgeorge et al. 2008). Similarly, Reid (1988) suggested that population growth rates into the early 1980s at Protection Island, Washington (~5% per annum), could primarily be explained by the cessation of human persecution. Further, reduced reproductive success or total reproductive failure has been observed more recently at colonies where Glaucous-winged Gull eggs are harvested, with the timing of egg harvesting sometimes resulting in birds being unable to lay replacement eggs (Vermeer et al. 1991, Zador et al. 2006). The growth of Glaucous-winged Gull populations in the early to middle part of the twentieth century was paralleled by rapid increases of other North American populations of waterbird species (gulls, terns, alcids, cormorants, and cranes; Ludwig 1974, Reid 1988, Bird Studies Canada 2010) that were also protected by the 1916 U.S.–Canada Migratory Bird Convention, which underlines the positive effect of this legislation.

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Conclusions

Our results indicate that Glaucous-winged Gull populations in the Georgia Basin have fluctuated considerably over the 111 years of our study, with strong increases from 1900 to the early 1980s, followed by population declines to 2010. These trends could be related to declines in clutch size and reproductive success that might have resulted from changes in food resources, particularly the availability of forage fish; to changes in predation rates from recovering Bald Eagle populations; and to the cessation of egg harvesting after the implementation of the 1916 Canada–U.S. Migratory Bird Convention. Local reports and anecdotal accounts from the early 1900s suggest that Glaucous-winged Gull numbers in the region were not 'at baseline' at that time, but instead were limited by human exploitation, so that twentieth century increases at least partially represented a population recovery. Our results highlight the value of long-term, retrospective studies for providing unique perspectives on causes of population change, and indicate the need to exercise caution in assuming that historical data represent 'pristine' conditions by virtue of their age.

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