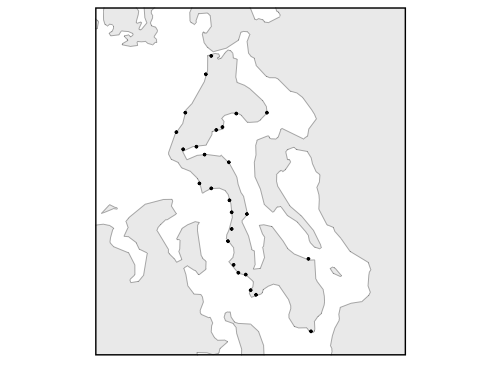
Write-Up

## OGR data source with driver: ESRI Shapefile   
## Source: "/Users/amandawarlick/Documents/SAFS/Stellers/Data/gz\_2010\_us\_040\_00\_500k", layer: "gz\_2010\_us\_040\_00\_500k"  
## with 52 features  
## It has 5 fields



#### Abstract

Pigeon guillemots (*Cepphus* columba) are an indicator species for Puget Sound in the U.S. Pacific Northwest, but existing local abundance estimates are outdated, demographic rates are unknown, and the impact of varying local oceanographic conditions on nest survival have not been investigated to date. Through an ongoing monitoring effort, a citizen science program has been recording adult colony attendance and burrow prey deliveries at known colony sites in inland waters during the breeding season from 2008-2018. The survey design and cliff-side location of burrows precludes observing if or precisely when eggs hatch or chicks fledge. I plan to use a Bayesian Jolly-Seber multievent mark-recapture model framework with uncertain nest state to estimate egg and chick survival probability based on counts of burrow visits and prey deliveries from repeated occasions and years. FIXI would like to include tidal fluctuations and environmental indices for upwelling and sea surface temperature as covariates to ascertain potential factors affecting trends in annual nest survival. The colony sites are fairly varied in terms of size, anthropogenic disturbance, cliff height, and cliff stability, and I have not yet thought fully about how and whether to include this information. This study would provide the first estimates of demographic rates with respect to oceanographic variability in this region. The results from this analysis will be foundational to developing an integrated population model for the population, which will provide important information for ongoing monitoring of indicator species in Puget Sound, particularly given observed and ongoing environmental change in the region.

#### Introduction

Understanding the processes driving trends in wildlife population abundance requires knowledge about population structure, survival, and reproductive success. Data on these demographic parameters can be obtained through capture-recapture studies, where survival probabilities and abundance can be estimated based on repeated sightings of marked or individually identifiable animals over a series of occasions. However, these studies can be cost prohibitive or logistically challenging due to species’ life history traits that might make them difficult or impossible to observe at a given time (*e.g.*, based on migratory behavior) or in a given state (*e.g.*, breeding versus non-breeding ages). This is often the case for seabird species, where individuals may only be observed at a colony during breeding season, may have unknown over-wintering locations, may exhibit a skip-breeding pattern, or may have varying degrees of site fidelity. Additionally, even when individuals are reliably detected, estimating reproductive success can be challenging if nests are inaccessible. To address some of these challenges, we develop a Bayesian multi-event mark-recapture model to estimate reproductive success of pigeon guillemots (*Cepphus* columba), a cliff-nesting seabird that has been designated as a regional indicator species for ongoing and future ecosystem-level changes occurring throughout Puget Sound.

Multi-state mark-recapture models arose to estimate age- or state-specific abundance and demographic rates and are based on the idea that we can infer information about the true latent state or ecological process of an individual based on a capture history that arises from an observation process with imperfect detection. However, biases can arise when the status of a marked individual is not observed with perfect certainty or if certain life history stages are not observable. This is the case for pigeon guillemots in Puget Sound, where individuals in the population are not marked and reproductive success cannot be observed because chicks fledge at night from nests located in cliff crevasses. Multi-event models (Kendall et al. 2004; Pradel, n.d.) arose to address these situations and have led to improved parameter estimation compared with the previous strategy of dropping cases with uncertain or hidden states (Kendall et al. 2004; Kendall and Nichols 2002) (Lebreton & Pradel 2002).  
Multi-event models have been used extensively to assess sex, reproductive status, and survival of terrestrial avian species (citations), but have been increasingly used to estimate breeding state, population structure, survival, and even the effect of oceanographic conditions for long-lived seabird species (Champagnon et al. 2018; Fay et al. 2015; Guéry et al. 2018; Payo-Payo et al. 2016; Sanz-Aguilar et al. 2017; Tavecchia, Sanz-Aguilar, and Cannell 2016) Champagnon et al. 2018). Multi-event models allow for the estimation of parameters even when observations map to multiple possible true states and can also incorporate covariates into both the state and observation processes. In this study, since pigeon guillemots are unmarked and nest fates are unobservable, we apply a novel multi-event model framework to the attendance patterns and prey deliveries made to individually-identifiable nest burrows to infer the true reproductive status and success of nests. [more specifics here, reference other study that used a similar approach, and a few demographic rate estimates for pigu]. Pigeon guillemots are one of only three alcids that nest in Puget Sound and despite having been identified as an indicator species for the region, little research has been done on the demographics of Pacific coast populations since studies in British Columbia and California throughout the 1990s. In the Pacific Northwest, Pigeon guillemots are more concentrated in eastern Juan de Fuca and central and northern Puget Sound (Nysewander et al., n.d.)2005, but their patchy distribution (Burger et al. 2008; Ewins, Morgan, and Vermeer 23AD–1994) has made estimating abundance trends difficult. Despite these challenges, there are a few rough estimates. Though some seabird species in Puget Sound have declined in recent decades (Anderson et al. 2009), survey counts suggest that abundance of pigeon guillemots has remained relatively constant since 2000 (Gaydos and Pearson 2011; Vilchis et al. 2015; Ward et al. 2015)(Bishop et al. 2016). Developing an integrated population model framework that incorporates environmental variability and is based on robust data from a citizen science program will enhance our understanding of demographic rates and abundance for this regional indicator species. This information is central to monitoring the resilience of this and other alcids in light of ongoing climatic changes and conservation and management planning throughout the region.

Methods

Study species Pigeon guillemots are cliff-nesting alcids whose range extends from California to Alaska and into Russia (Sowls 1978)CITE. Dense regional populations that breed in the Farallon Islands, CA (Nelson 1991; Nelson 1987; Press 2018), Vancouver Island in British Columbia (Ewins, Morgan, and Vermeer 23AD–1994), and Naked Island, AK (Golet et al. 2000)(Kuletz, 1983)(and others) have been the focus of numerous ecological studies, forming the foundation of our knowledge about the species to date. Insights can also be gleaned from research on two closely related species, spectacled guillemots in the northwest Pacific (Ewins, Morgan, and Vermeer 23AD–1994) and black guillemots across the Northwest Atlantic Ocean and North Sea (Asbirk 1979; Petersen 1981). Pigeon guillemots have been documented as having higher and less variable reproductive rates compared with other alcids (Cairns 1987b)(Gaston 1985)CITE. An estimated 40% of chicks survive to reach breeding age around 3-5 years (Ewins, Morgan, and Vermeer 23AD–1994; Nelson 1991) with an estimated 80% survival rate for adults (Nelson 1991)(Ewins 1993) and a total life expectancy of 8-9 years (Cormack 1964). Little is known about winter habitat or distribution, but beginning in late spring, pigeon guillemots concentrate around colony sites to nest in cliff burrows along rocky shorelines spanning coastal areas and offshore islands throughout their range.

While pigeon guillemots share many similarities with their alcid relatives, they also have unique life history traits that affect when and how many individuals are at the colony and how reliably they can be detected and counted when and if they are there. Namely, that the level of activity and the number of birds at a colony is governed by both seasonal and daily cycles. At the seasonal level, male birds arrive at the colony first to stake out burrow territory (Nelson 1987). Non-breeding individuals are also present in higher numbers at the beginning of the season (approximately 30% of total) and gradually disperse once nesting begins (Drent 1965). Eggs incubate for an average of 30 days (Drent 1965) with both sexes tending the nest (Cairns 1987a)(Cairns 1981). Once an egg hatches, adults alternately deliver food until chicks fledge after 33-45 days [K. Vermeer, Morgan, and Smith (1993a);](Thoreson%20&%20Booth%201958,%20Cairns%201981,%20Drent%201965,%20Oakley%20&%20Kuletz%201996), which is difficult to observe as it generally occurs at night. Peak prey deliveries generally occur in the early mornings and evenings, often corresponding to optimal foraging periods based on tidal fluctuations (K. Vermeer, Morgan, and Smith 1993a)(Ainley & Lewis 1972cite; Petersen 1981). Unlike other alcids, pigeon guillemots (particularly experienced breeders) often lay double clutches (where a second “beta” egg is laid ~4 days after the initial egg), an ability that likely stems from nearshore foraging (Winn 1950; Drent 1965) on demersal species with predictable distributions that allows for higher delivery rates of larger prey compared with foraging offshore on lipid-rich but less predictable pelagic species (Golet et al. 2000; Wanless et al. 2005; Cairns 1987a; Emms and Verbeek, n.d.)(Cairns 1981, Bradstreet & Brown 1985); Gaston & Jones 1998; Golet et al 1998)cite.

Data sources and characterization Pigeon guillemot breeding colonies at 40 sites on Whidbey Island, WA (Figure 1) have been observed by a citizen science program since 2008. Volunteers observe cliff sites from the beach for precisely one hour between 7:00am-10:00am (aimed at coinciding with low tide) once per week during the breeding season, ranging from mid-June to mid-September depending on the year (Kreamer, n.d.)2011. Once volunteers have waited for birds to resettle from potentially being disturbed by observer presence, volunteers record two categories of information for the duration of the one-hour survey: counts of adults and burrow activity. For the count data, volunteers record the number of adult guillemots in the water directly adjacent to the colony at the beginning, mid-point, and end of the one-hour survey. For burrow activity, volunteers record the number of times adult guillemots visit each specific cliff burrow (a) with and (b) without fish prey. Burrows are mapped and identified at the beginning of the season and are thereafter individually identifiable. Colony cliff sites differ in height, length, and aspect, with the average number of active nests observed in a given year ranging from 1 to 13.

Surveys are conducted approximately seven days apart, though the consistency and number of survey weeks varies by site due to unpredictable logistics of beach access and because nesting activities occur somewhat asynchronously across the island. Surveys extend until at least two weeks without burrow activity have been observed. Whidbey island is largely residential with public beach access and a mix of coastal land use and habitat integrity. Cliff habitat erosion and predation are the primary threats to these birds during the breeding season, though colonies are also subject to varying levels of anthropogenic disturbance from beach-goers and nearshore boat activity.

Environmental data used as covariates in this study include tidal fluctuations, local sea surface temperature, and coastal upwelling as a measure of larger-scale oceanographic processes. Daily sea surface temperatures and the timing and height of daily low and high tides were obtained from the NOAA Center for Operational Oceanographic Products and Services and extracted from the API using the noaaoceans R package (Warlick, 2019). Tidal height data in six-minute intervals was obtained from nine tidal buoys surrounding the island and the number of minutes elapsed from the morning low tide until the start of each survey was calculated. The nearest buoy with comprehensive sea-surface temperature information is 9444900 near Port Townsend, WA. Monthly upwelling anomalies were obtained from NOAA’s Pacific Fisheries Environmental Laboratory from a buoy at (45N, -124W).

Statistical analyses Multi-state mark-recapture models are powerful tools for studying wildlife population dynamics and are based on the idea that abundance at a given time t+1 can be modeled as a function of the number of individuals in a given stage at time t, along with survival and fecundity rates. State-specific survival, transition, and detection probabilities for pigeon guillemot nests were estimated using a multi-event Jolly-Seber model with uncertain state assignment (Figure 2). In this study, daily nest survival is needed in order to ascertain overall nest success using the assumption that nests receiving prey deliveries for the length of the incubation period (32-38 days) will have fledged. Using this framework allows us to estimate daily (as opposed to weekly, the level of the data) survival and account for imperfect detection and uncertain nest state, as non-prey visits to nest burrows can occur during both the egg and chick states.

Possible true states were identified as individuals that have not yet entered (pre-egg), egg, hatchling, and terminated (fledged or dead). Possible observations corresponding to these true states include birds flying into burrow nests (a) without prey, (b) with prey, and (c) not detected. Capture histories were generated for each individual, where a capture history of ‘00BV00PV0’ would represent a nest that was not seen until a non-prey burrow visit on the third week, not detected for two weeks, and subsequently detected with a prey delivery visit, and then not detected. As is typical for Jolly-Seber models, we do not condition on the first capture, where nests can ‘enter’ asynchronously, where parameter gamma represents entry probability. Using this framework also enables the estimation of egg incubation period and egg success, though we include alpha to account for the probability that nests ‘enter’ in the chick state at the first study occasion if volunteer surveys start after incubation occurs (alpha = 0 at t > 1). The state process of the model is defined as

Formula

where the state z of individual i at occasion t, conditional on the individual’s state at the previous occasion, is modeled by a categorical distribution with matrix Ω describing the probability of an individual transitioning to a new state based on its previous state and individual- and time-specific covariate effects. This transition probability is typically decomposed into survival (ϕ\_(i,t)) and state transition (ψ\_(i,t)) probabilities. For the observation process,

Formula

an observation y conditional on the true state z is modeled by a categorical distribution with probability matrix Θ, which indicates for individual i at time t the probability of detection (p\_(i,t)) and the state assignment error probability (δ\_(i,t)) (Figure 2b).

For this analysis, the typical set of JS model assumptions apply, where it is assumed that there are no identification errors, that survival and reproductive state of individuals are independent, and that there is no unmodeled heterogeneity in survival and detection probabilities. In this initial analysis, we assume that detection and assignment error probabilities remain constant throughout a given breeding season, which may not be ideal given the changing attendance and prey delivery pattern over the summer breeding season. To account for individuals that may never have been detected, capture history data was augmented with additional M individuals. The overall abundance M of nests are used as the denominator when deriving the proportion of nests with surviving fledglings. - Add statement about using weekly data and including matrix of days-between-surveys for the final daily estimate.

Clarify use of covariates – with more thought, I think the ones I have been thinking about are most relevant to attendance (counts) rather than prey deliveries. Tides: attendance (and indirectly visits/deliveries – I’m struggling to separate these two in my mental models) SST/upwelling: annual nest success rather than daily survival. I think their foraging plasticity would make it so differences would be more evident in prey type rather than delivery frequency. Normal (0, 0.001) and uniform (0, 1) distributions were used as uninformative priors for all parameters. Models were fit in JAGS using the R packages jagsUI and rjags with 50,000 iterations, 4,000 burn-in, and three MCMC chains. R-hat values were inspected for convergence (eventually see Appendix 1 for relevant JAGS code).

Results Daily survival estimates, mean Annual estimates, time-varying Detection probability, hatching success versus fledging (where is the mortality?) Overall decline in nest success over the years?

Discussion

Briefly recap and explain major results  
Questions/Issues

* What to do when see one prey delivery and no other visits?
* Excluded single burrow visits, but included single date burrow visits where bv > 1
* Haven’t trimmed total “study length” to nest level (currently year level)
* If last burrow visit was last prey delivery, could have just missed the rest of the visits?
* Contextualize major results in terms of the few other things we know about PiGu in Puget Sound, historical survival probability estimates, and the West Coast/Alaska, or related alcids. Survival (adult) similar to black gill but lower than other alcids? (Nelson 91)

What does it mean to be modeling survival based on this prey delivery/attendance pattern? What are we learning differently than if we could just see the true state? (i.e., what is the process that we are actually observing? ….attendance based on foraging/short-term ocean conditions like weather/tides, while prey delivery frequency likely based on prey availability/prey distribution/large-scale ocean conditions). Pigeon guillemots are not unique in that their demographic rates and reproductive cycle are inextricably linked to prevailing environmental conditions that influence spatio-temporal prey availability. Research suggests that oceanographic variability can impact not only reproductive success and timing, but adult survival and overall population dynamics.

Pigeon guillemot reproductive success in the Farallon Islands has been found to be lower in El Niño years (Press 2018) and lower chick growth rates and reduced brood size have coincided with years of lower prey abundance in British Columbia (K. Vermeer, Morgan, and Smith 1993b; Litzow et al. 2018; Litzow et al. 2002; Litzow and Piatt 2018). Changing prey availability due to a shift in the Pacific Decadal Oscillation index coincided with a notable decline in guillemot abundance in the Bering Sea and Gulf of Alaska in the (1990s?) (Litzow et al. 2002). Similarly, Veit and Manne (2015) found that the abundance of black guillemots in the Northeast U.S. correlated with the North Atlantic Oscillation. Guillemot responses to environmental variability are complex and nuanced (Irons et al. 2008; Burger, Hitchcock, and Davoren 2004), but one thing is clear: oceanographic conditions matter and can affect everything from nest initiation and attendance to chick provisioning and fledge weights (Nelson 1987; Press 2018).

How this relates to their naïve estimate of nest success. Sources of error/bias? Double clutching? Replacement nests? Sensitivity of model to the ‘success’ threshold number of deliveries? Survival based on hatch date? (Harris 92)  
  
Next modeling steps (IPM) and what additional information/insight that will give us. Abundance estimates can also be derived from count surveys, where variability across sampling occasions accounts for imperfect detection. While estimating a single demographic rate can be useful, simultaneously estimating survival, fecundity, and abundance through an integrated analysis yields improved understanding of how these parameters jointly vary to govern population dynamics.   
  
Scaling up to include other guillemot regions (South Sound, Vashon, Port Angeles)  
  
What the findings mean in terms of the citizen science program effort and general PSEMP work. What this program has allowed us to do/learn, but also what is missing because it is a citizen science project

Figures and Tables

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