

1 USING MULTIPLE DATASETS TO ACCOUNT FOR MISALIGNMENT BETWEEN
2 STATISTICAL AND BIOLOGICAL POPULATIONS FOR ABUNDANCE ESTIMATION

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15
16 ABSTRACT

17 A fundamental aspect of ecology is identifying and characterizing population processes. Because
18 a census is rare, we almost always use sampling to make inference about the biological
19 population, and the part of the population at risk of sampling is referred to as the statistical
20 population. Ideally, the statistical population is the same as, or accurately represents its
21 corresponding biological population. However, in practice, they rarely align in space and time,
22 which can lead to biased inference. We often view a population misalignment as a temporary
23 emigration process and resolve it with replicate and/or repeat sampling, though this approach is
24 not feasible for all species and habitats. We developed a hierarchical model to estimate
25 abundance of a biological population of the Kittlitz's murrelet (*Brachyramphus brevirostris*), a
26 highly mobile, non-territorial, ice-associated seabird of conservation concern in Alaska and
27 eastern Russia. Our model combines datasets from boat and telemetry surveys to account for all
28 components of detection probability, specifically using telemetry locations to estimate
29 probability of presence (p_p) and line transect distance sampling to estimate probability of
30 detection (p_d). By estimating p_p directly, we were able to account for temporary emigration from
31 the sampled area, which changed with shifting icefloes between sampling occasions. Between
32 2007 and 2012, annual p_p was highly variable, ranging from 0.33 to 0.75 (median=0.50,
33 SE=0.02), but was not predictable using five environmental covariates. In years when two boat
34 surveys were conducted, our model reduced the coefficient of variation (CV) of abundance
35 estimates for the biological population compared to the statistical population by 13–35%, yet in
36 the year with only one boat survey (2009), the CV skyrocketed about 10-fold, emphasizing the
37 importance of a second survey if p_p varies. Although we increased the precision of annual
38 abundance estimates by accounting for p_p , we did not see the same improvement in the temporal
39 trend estimate, indicating that while we reduced within-year variance, we failed to account for a
40 source(s) of variation across years, which we suspect is related to the propensity for murrelets to
41 skip breeding in some years. Our model to account for a population misalignment is simple,
42 flexible, and scalable for generating unbiased and precise abundance estimates of highly mobile
43 species that occupy dynamic habitats where other open population models are not feasible.
44 Importantly, it improves inference of the biological population, which is the population of
45 interest. We urge ecologists to think critically about the population in which they want to draw
46 inference, especially as tracking technology improves and model complexity increases.

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KEYWORDS

temporary emigration, biological population, statistical population, abundance model, detection probability, seabird, *Brachyramphus murrelet*, superpopulation

INTRODUCTION

A fundamental aspect of ecology is identifying and characterizing population processes. While many definitions of a biological population exist, a common one is “a group of organisms of the same species occupying a particular space at a particular time that are capable of interbreeding (Krebs 1994, Williams et al. 2002); hereafter, we refer to a biological population using this definition. In studies of biological populations, it is extremely rare that all individuals in the population are under observation (i.e., a census). In most cases, where populations are not subject to census, sampling is used to make inference about the population.

The scope and strength of inference about populations in ecological studies rely on the ability to sample appropriately. For mobile species, this crucial task can be challenging. One of the important characteristics of population sampling is the portion of the population at risk of being sampled. The proportion at risk of sampling, or the proportion of the population present at the time and place of sampling, has been designated as p_p (Nichols 2009), with $p_p \leq 1$; hereafter, we refer to the part of the population at risk of sampling as the statistical population.

The conceptual distinction between a biological population and a statistical population has been around for decades, though the terminology has varied considerably (Waples and Gaggiotti 2006). In addition to biological and statistical (Krebs 1999), notable examples include target and sampled (Cochran 1977), natural and local (Andrewartha and Birch 1954), and resource and statistical (Reynolds 2012). Regardless of the terminology, the distinguishing principle is the same: one population is what we really want to know something about (biological) and the other is what we use to infer what we want to know (statistical). In practice, it is important to remember that sampling-based inference directly applies only to the statistical population; logic, assumption, or additional information are needed to extend inference to the biological population.

When $p_p=1$, the biological and statistical populations are identical, i.e., they are aligned, with direct statistical inference applying to both. However, when $p_p < 1$, the statistical population is usually a subset of the biological population (Figure 1); we refer to this situation as population misalignment. Population misalignment also has been called a frame error (Reynolds 2012), drawing from the fact that the sampling frame defines the proportion of the biological population at risk of being sampled (i.e., the statistical population).

P_p can be < 1 , i.e., the statistical population is a subset of the biological population, for a variety of reasons, including those that are physical (e.g., natural barriers), logistical (e.g., cost, safety), legal (e.g., landownership boundaries), political (e.g., international borders), and even biological (e.g., non-breeding). For example, the Pacific walrus (*Odobenus rosmarus divergens*) population ranges across marine waters of Alaska and Russia, though sampling rarely covers the entire region owing to complications with securing the necessary international permits (e.g., Beatty et

al. 2022). Consequently, assuming individuals can move freely, they may not be exposed to sampling consistently, which potentially affects inference about the biological population.

Analytically, we often view population misalignment as a form of temporary emigration, whereby individuals are temporarily not exposed to sampling (Kendall et al. 1997). Temporary emigration is an oddly vague process with biological and statistical drivers that usually are confounded. For example, individuals may temporarily emigrate for biological reasons like searching for food or avoiding predation, statistical reasons such as unequal sampling probability owing to a small or varying frame, or a combination of both. Ultimately, temporary emigration is a detection issue. If it occurs randomly with all animals equally likely to be part of the statistical population across sampling occasions, temporary emigration will cause large residual variance and reduced precision of abundance estimates; if it occurs non-randomly, e.g., with a temporal trend, it will bias estimates.

Fortunately, over the last few decades, many analytical approaches have been developed to account for temporary emigration when estimating abundance. The most notable methods are capture-recapture models that use robust design (Kendall et al. 1997) or are spatially explicit (Royle and Young 2008), extensions of N-mixture models (e.g., Chandler et al. 2011), thinned point process models (e.g., Mizel et al. 2018), and models that combine methodology (e.g., Powell et al. 2000, Amundson et al. 2014). These approaches use spatial and temporal replicates with short periods of closure (i.e., no movement into or out of the statistical population; hereafter replicate sampling) or the ability to identify individuals during sampling (hereafter repeat sampling) to estimate temporary emigration and abundance of the biological population, which is sometimes referred to in this context as the superpopulation (Schwarz and Arnason 1996). While these models are flexible and powerful, they are not feasible for all species and habitats, nor in all situations.

Some species and habitats are too complex to obtain a sufficient number of replicate or repeat samples across space or time. Species that are difficult to recapture or resight during sampling are inherently unsuitable for capture-recapture methods, as models do not produce reliable estimates with few recaptures or resights. Further, highly mobile, non-territorial species, such as many marine species, cannot satisfy the closure assumption, even for short periods, unless the study area is large relative to movement, which often makes sufficient sampling impractical. The same principle applies to species that are sampled during non-territorial portions of their life cycle, such as winter concentrations of ungulates or migrating raptors, when individuals are not tied to a particular area (e.g., breeding site). Finally, dynamic habitats that can change between sampling occasions (e.g., drift ice), are not conducive to replicate sampling; the size and shape of the sampled area (i.e., sampling frame) varies, inducing a change in the statistical population.

An alternative approach to handling a population misalignment that does not require replicate or repeat sampling is to decompose the detection process. Nichols et al. (2009) described four components of overall detection (p): (1) probability that the individual's home range includes at least a portion of the sample area (p_s); (2) probability of presence within the sample area during a survey (p_p); (3) probability of availability given presence (p_a); and (4) probability of detection given presence and availability (p_d). The first component (p_s) simply confirms that an individual is a member of the biological population, and the last component (p_d) refers to the actual

138 observation process, that is whether an individual was observed. Jointly, the second and third
139 components (p_p and p_a , respectively) describe temporary emigration, with the second component
140 (p_p), already discussed, being spatial temporary emigration, and the third component (p_a) as
141 random temporary emigration (Kery and Royle 2016). A major advantage to using this approach
142 is that each component can be estimated separately using different datasets and even different
143 data types (Hostetter et al. 2019), making it suitable for all species and habitats provided that
144 data for estimating components are available.

145

146 We applied this approach to account for population misalignment of the Kittlitz's murrelet
147 (*Brachyramphus brevirostris*), a highly mobile, non-territorial, ice-associated seabird that is
148 irregularly distributed across coastal Alaska and eastern Russia. Several aspects of this species'
149 life history complicate methods that rely on replicate or repeat sampling to estimate spatial
150 temporary emigration. Unlike most seabirds, Kittlitz's murrelets do not nest in colonies, but
151 instead nest solitarily at low densities, usually in remote inaccessible locations (Kissling et al.
152 2015a). Thus, populations cannot be monitored at colonies like most seabirds where replicate
153 and repeat sampling is practical and efficient. Additionally, owing to the small size, cryptic
154 behavior, and low and variable breeding propensity in this species, capture-recapture and resight
155 models are not feasible. It is nearly impossible to resight banded or marked murrelets on the
156 water or in flight and recapture rates are too low to be useful for estimating abundance (Kissling
157 et al. 2015b), in part because of challenges with nighttime captures during summer at high
158 latitudes.

159

160 Instead, the only viable way to monitor Kittlitz's murrelet populations is with boat-based
161 abundance surveys that are conducted during the breeding season when most murrelets
162 concentrate in bays and fjords often near tidewater glaciers (Day et al. 2020). A design challenge
163 and safety concern for these surveys is the presence of icefloes, large tidal fluctuations, glacial
164 river debris, and the possibility of rough seas. These dynamic conditions can restrict boat access
165 to portions of the study area and cause murrelets to redistribute over short time intervals,
166 resulting in time-varying statistical populations and a population misalignment that cannot be
167 handled with replicate sampling, as neither the murrelets nor the habitat can meet the closure
168 assumption.

169

170 We developed a hierarchical Bayesian model to estimate abundance of a biological population of
171 the Kittlitz's murrelet in a dynamic environment. Our model utilizes datasets from telemetry
172 flights to locate radio-tagged murrelets, boat-based distance sampling surveys, and dive behavior
173 trials to account for all components of detection probability (p_s , p_p , p_a , p_d). Our primary objective
174 was to develop an analytical tool to account for misalignment of the statistical and biological
175 populations of this unusual species so that we could generate unbiased abundance estimates for
176 later use in an integrated population model (Kissling et al. *In review*). More specifically, here, we
177 aimed to (1) estimate detection probability components and their variation across space and time;
178 (2) investigate predictability of p_p using environmental covariates; and (3) estimate abundance
179 and trend of the statistical (without p_p) and biological populations (with p_p) and identify any
180 sources of bias. We also wanted to assess whether we delineated the biological population of
181 Kittlitz's murrelets in our study area appropriately.

182

183 STUDY AREA

184 Our study was centered in Icy Bay, Alaska, USA, located in the northeastern Gulf of Alaska and
185 ~110 kilometers northwest of the town of Yakutat (Figure 2). Icy Bay is a highly dynamic glacial
186 fjord system that has experienced multiple, rapid ice advances and subsequent retreats over the
187 past ~3,800 years with the most recent retreat of approximately 40 km during the 20th century
188 (Barclay et al. 2006).

189
190 Currently, Icy Bay comprises a shallow outer bay and a deeper inner bay. The outer bay is
191 adjacent to the Gulf of Alaska and measures 6 km wide at the mouth. The inner bay is divided
192 into four distinct fjords with each terminating at an active tidewater glacier. Of these fjords, only
193 Taan Fjord is regularly accessible by boat (Figure 2) The Malaspina Glacier, the largest
194 piedmont glacier in North America, is situated to the east and empties meltwater and glacial
195 sediment into Icy Bay via the Caetani River system, which can restrict boat access to the eastern
196 side of the bay. During periods of high river flow, debris and sedimentation settle near the
197 outflow and the marine waters become too shallow to navigate a boat safely. In addition, two
198 small bays (Riou and Moraine bays) are located on the eastern side of Icy Bay and they have
199 submerged marine sills at their mouths making it difficult to access them during low tides. The
200 total surface of Icy Bay is approximately 263 km², but typically the upper half of the bay is
201 covered in thick ice floes and large icebergs, resulting in an open water surface area of ~160 km²
202 with considerable variability within and across years depending on glacial calving activity.

203

204 METHODS

205 *Data collection*

206 Boat surveys.— From 2005 to 2017, we conducted two boat-based abundance surveys between 1
207 and 15 July in each of eight years (2005, 2007–2008, 2010–2012, 2016–2017); in 2009, we
208 conducted only one survey on 17 July because of logistical constraints. The target sampling area
209 was ~160 km² and contained 19 line transects total, with 11 transects in the Main Bay and 8
210 transects in Taan Fjord (Figure 2), though actual sampling effort varied for each survey because
211 of access issues (Table 1). Generally, we completed surveys in a single day, though rarely it took
212 two days, depending on tides and other logistical factors. Boat surveys involved line transect
213 distance sampling, following the protocol described in Kissling et al. (2007, 2011), with one
214 exception; in 2016 and 2017, we estimated the angle and distance from the boat to each murrelet
215 group as opposed to estimating perpendicular distance from the line transect (all other years). We
216 also recorded group size, behavior (water, flying), and foraging activity of all *Brachyramphus*
217 murrelets observed. Both Kittlitz’s and its congeneric marbled murrelet (*B. marmoratus*) occur in
218 Icy Bay and can be difficult to distinguish, especially at a distance; if an observer was unable to
219 identify a murrelet (or group of murrelets) to species, it was recorded as an unidentified
220 murrelet(s).

221

222 Telemetry surveys.— We captured Kittlitz’s Murrelets on the water using the night-lighting
223 method (Whitworth et al. 1997) in the Icy Bay study area between 8 May and 3 June, 2007–2012
224 (Figure 2). Following capture, we transported murrelets to a larger vessel for processing, which
225 included morphometric measurements, blood sampling for sex identification, and banding. We
226 deployed very-high-frequency (VHF) radio transmitters on a subset of after-second-year
227 murrelets captured each year. We attached the transmitters (Advanced Telemetry Systems, Inc.,
228 Isanti, Minnesota; model number A4360; 110-day battery life) using a subcutaneous anchor on
229 the bird’s back between the scapulars (Newman et al. 1999). If both birds of a pair were

230 captured, we randomly selected one bird to radio-tag to ensure independence. We released
231 murrelets immediately after processing was complete.

232
233 We attempted to locate radio-tagged murrelets 2–5 times per week for at least eight weeks after
234 tagging using fixed-wing aircraft equipped with “H-style” antennas mounted on the struts. We
235 were not able to search for tagged birds using a strict design, but instead aimed for complete
236 coverage of the study area, as shown in Figure 2, in a systematic way that allowed for safe
237 flying. We first attempted to locate all murrelets on the water in the Icy Bay study area within
238 gliding distance of shore; if murrelets were not detected at sea, we flew over all assumed
239 potential nesting habitat within reason (e.g., fuel constraints) to locate incubating birds. We
240 conducted telemetry flights on the same day as boat surveys; on occasion, we had to fly the
241 telemetry survey on the following day because of aircraft availability. All telemetry flights were
242 completed in less than four hours. For more details on capture, handling, tagging, and relocating
243 see Kissling et al. (2015a, b, 2016).

244
245 During each flight, we mapped ice conditions into five categories of increasing ice density: none,
246 brash ice, open pack ice, close pack ice, and very close pack ice. We defined brash ice as
247 accumulations of floating ice made up of fragments not more than 2 m across, open pack ice as
248 low concentration pack ice with many leads and polynyas and the floes generally were not in
249 contact, close pack ice as moderate concentration pack ice with the floes generally in contact,
250 and very close pack ice as high concentration pack ice with very little water visible (Bowditch
251 classification; NOAA 2007). Following each flight, we digitized these maps in ArcGIS (ESRI,
252 v10.7.1) and estimated ice cover (km²) by category in the study area on that day. We then
253 assigned all locations of radio-tagged murrelets to an ice category using the ice condition maps
254 for each corresponding telemetry flight.

255
256 We compiled environmental data for murrelets located during telemetry flights. Using the date
257 and time of each location, we determined tide direction, which represented the vertical
258 movement of water, as ebb or flood, and tidal current strength, the horizontal movement of
259 water, following Kissling et al. (2007). We also acquired the daily precipitation (mm), which
260 affected freshwater input volume and turbidity, and average daily wind speed (m/sec), which
261 influenced icefloe movement and ocean surface conditions, from a weather station in Icy Bay
262 (<https://www.ncdc.noaa.gov/cdo-web/>). Lastly, we calculated the proportion of the Icy Bay state
263 (i.e., the area sampled during boat surveys; see below) that was covered in ice (all categories) on
264 the flight day.

265
266 *Data analysis*

267 Components of detection probability.—We considered detection probability components
268 individually, which allowed for use of different datasets, and then combined those necessary in a
269 joint likelihood model to estimate abundance (see below). This approach was efficient, as two
270 components of detection probability, p_s and p_a , were deemed to be close to 1 and unnecessary in
271 the abundance model.

272
273 We determined that p_s , the probability that an individual could be included in the sampled area
274 during a boat survey, was 1 in all years by examining both home ranges (95% utilization

275 distribution [UD]) and core use areas (50% UD) of radio-tagged murrelets (Kissling et al. In
276 revision). Therefore, we did not include p_s in our model.

277
278 We estimated p_p , the probability that an individual was present in the sampled area during a boat
279 survey, using location data from radio-tagged murrelets. Following Kissling et al. (2015b), we
280 assigned each telemetry location to one of five spatial states (Figure 2): Icy Bay, which
281 comprised Main Bay and Taan Fjord sub-states and was the core area sampled by boat; East Bay,
282 which was too shallow for a boat; Upper Bay, which was too icy; Ocean, which was too rough;
283 or at a nest. The outer limit of the Ocean state was constrained to aircraft gliding distance to
284 shore, and it was same area used for a multi-state survival analysis (Kissling et al. 2015b). Any
285 telemetry locations outside of these five states were removed from our analysis (<2% of all
286 locations); notably, none of these individuals were located again. We then merged data on spatial
287 state and ice category for each telemetry location. We considered a radio-tagged murrelet to be
288 present in the sampled area if it was in Icy Bay state and in ice categories of none, brash ice, or
289 open pack ice, where we could conduct boat surveys safely. If a radio-tagged murrelet was at a
290 nest or in the East Bay, Upper Bay, Ocean, or in close pack ice or very close pack ice, it was
291 deemed not present.

292
293 To estimate p_p , or the probability of presence, we filtered telemetry data to include locations
294 from 1 to 15 July to overlap with our boat survey protocol. We explored the use of telemetry
295 locations acquired in 1-, 3-, 5-, and 7-day windows surrounding the boat survey; for example, if a
296 boat survey was conducted on 8 July, the 3-day window was 7–9 July and the 5-day window was
297 6–10 July. All telemetry locations collected during a specific window were used to estimate a
298 single value of p_p . In 2009, we conducted a single boat survey late (17 July) because of boat
299 availability and poor weather and therefore, we shifted the windows to center on the later date. In
300 all years, we found that p_p varied little with window length, though precision improved
301 (Appendix 1), which was unsurprising given that sample size increased (i.e., number of telemetry
302 locations). Here, we report results for the 3-day window only because it was the best tradeoff
303 between improved precision while maintaining a short temporal window around each survey. For
304 comparison, we also report p_p for the entire 15-day period (1–15 July).

305
306 We conducted boat-based dive behavior trials to estimate p_a , the probability that a murrelet was
307 available for detection (i.e., not underwater) given presence. We determined that the probability
308 of a murrelet being unavailable for detection was quite low (0.032 ± 0.007 ; see details in Lukacs
309 et al. 2010). Therefore, we assumed p_a was close enough to 1 not to affect abundance estimates,
310 and, like p_s , did not include it in our model.

311
312 Finally, we estimated p_d , or the probability of being detected given presence and availability on
313 boat surveys, using conventional distance sampling. We filtered data to include murrelets
314 observed on the water only, i.e., we excluded flying birds from our analysis. We pooled data
315 across both surveys each year (except 2009) and all *Brachyramphus* murrelets to estimate p_d
316 because observers rarely changed, and we did not expect detection probability to be different by
317 species. We then truncated 5% of the data from the right-hand tail of the detection function
318 (Buckland et al. 2001). We examined the effect of group size on the scale parameter of the half
319 normal detection function, but it had no effect in any year (based on ΔAIC values and Cramer-
320 von Mises tests) and therefore, we did not include group size in our analyses.

321
 322 To allocate murrelets not identified to species (i.e., unidentified *Brachyramphus* murrelets)
 323 during boat surveys, we estimated the probability of being a Kittlitz’s murrelet (p_k), as opposed
 324 to a marbled murrelet, in two strata (m) in Icy Bay for each year (Figure 2). While Kittlitz’s
 325 murrelets are uniformly distributed throughout the bay, marbled murrelets are not; they are rarely
 326 located in Taan Fjord (Kissling et al. 2007, 2011). Therefore, we divided our sampling area into
 327 two strata, Main Bay and Taan Fjord, to satisfy the assumption of uniform distribution when
 328 estimating p_k . Note that these strata were the same as the Main Bay and Taan Fjord sub-states
 329 described for p_p , though they were not indexed for p_p ; we used different terminology to avoid
 330 confusion in the code.

331
 332 Model for biological population abundance.—We developed a hierarchical Bayesian model to
 333 estimate annual abundance of the biological population. Our model combines multiple datasets
 334 in a unified analytical framework and therefore, it fully accounts for uncertainty and error in
 335 parameter estimates, similar to an integrated model though without a shared parameter across all
 336 datasets (Zipkin et al. 2021). We used data augmentation to represent a relatively large number
 337 of potential but unobserved groups in our sampling area during each boat survey (Royle and
 338 Dorazio 2008). To estimate a single value for annual abundance, we used the following joint
 339 likelihood:

$$L[M \mid data] = [L[M \mid N_i, p_{p,i}]] [L(p_{p,i} \mid y_{p_{p,i}})] [L(p_{d,.} \mid y_{p_{d,.}})] [L(p_{k,m} \mid y_{p_{k,m}})] \quad (1)$$

343 where M is the abundance of the biological population; N_i is the statistical population abundance
 344 estimated for survey i ; $p_{p,i}$ is the probability of presence for survey i ; $y_{p_{p,i}}$ is the telemetry survey
 345 data used to estimate $p_{p,i}$; $p_{d,.}$ is the probability of detection across both surveys; $y_{p_{d,.}}$ is the boat
 346 survey data to estimate $p_{d,.}$; $p_{k,m}$ is the probability of being a Kittlitz’s murrelet across both
 347 surveys by stratum m ; $y_{p_{k,m}}$ is the boat survey data used to estimate $p_{k,m}$; and $data$ refers to the
 348 collective boat and telemetry survey data. We estimated annual abundance of the statistical
 349 population using equation 1 without the $p_{p,i}$ likelihood component, which essentially assumes $p_{p,i}$
 350 was 1.

351
 352 We modeled $p_{p,i}$ on the logit scale using telemetry survey data as $\text{logit}(p_{p,ij}) = \beta_i$, where β_i is the
 353 $\text{logit}(p_{p,i})$ and therefore,

$$y_{p_{p,ij}} \sim \text{Bernoulli}(p_{p,ij}) \quad (2)$$

357 where individual locations (j) during each survey (i) were used to estimate $p_{p,ij}$. We did not
 358 include covariates in this sub-model because we did not identify any that helped explain
 359 variation in $p_{p,ij}$ (see ‘Predicting probability of presence’ below).

360
 361 We modeled $p_{d,.}$ on the log scale using the boat survey data with perpendicular distance of each
 362 group q from the transect line (x_{iq}) and the half-normal detection function:

363

364
$$p_{d,q} = \exp\left(-\frac{x_{iq}^2}{2\sigma_{iq}^2}\right)$$

365 (3)

366 where σ_q is the scale parameter. As noted above, we did not include group size as a covariate on
 367 σ_q because it did not help explain variation in $p_{d..}$. We estimated the probability of being a
 368 Kittlitz's murrelet using the boat survey data as

369
$$y_{p_{k,m}} \sim \text{Bernoulli}(p_{k,m}),$$

370

371 (4)

372 where identified groups in each stratum across all surveys were used to estimate $p_{k,m}$. We
 373 modeled group size of the augmented groups as

374
$$y_{g,q} \sim \text{Poisson}(\lambda_g),$$

375

376 (5)

377 where $y_{g,q}$ is the observed group size q across all boat surveys and λ_g is mean group size.
 378 We ran our model (equation 1) with its components (equations 2–5) by year because of long run-
 379 times (~10–12 hours) and to accommodate slight differences in data management and storage
 380 each year. Moreover, no parameters were shared across years and therefore, we would not have
 381 gained anything by running the model with all years simultaneously.

382

383 Predicting probability of presence.—We attempted to predict p_p of radio-tagged murrelets in the
 384 sampling area using environmental covariates so that we could estimate it in years for which we
 385 lacked telemetry data (i.e. 2005, 2016, and 2017) and potentially improve our boat survey
 386 protocol to minimize variation in p_p in the future. We considered five covariates: tide direction,
 387 tidal current strength, daily precipitation, daily average wind speed, and the proportion of Icy
 388 Bay state covered in ice. We hypothesized that p_p would be higher during the flood (incoming
 389 tide) than the ebb and positively associated with tidal current strength, reasoning that these
 390 conditions would concentrate murrelet prey. We posited that p_p would be negatively associated
 391 with daily precipitation because of increased freshwater input into Icy Bay, possibly reducing
 392 prey or access to prey because of higher turbidity, and positively related to daily average wind
 393 speed, as an indicator of offshore storms. Lastly, we hypothesized that p_p would be inversely
 394 related to the proportion of ice in the Icy Bay state, as ice would displace murrelets.

395

396 We used a generalized linear mixed model (binomial error, logit link) with random effects for
 397 year and individual to explore our ability to predict p_p with environmental covariates. We filtered
 398 telemetry data to include the same dates as our boat survey protocol (1–15 July); we also
 399 excluded murrelet locations at a nest because environmental data for those records were not
 400 relevant. We scaled all covariates to have a mean of 0 and standard deviation of 1. To assess our
 401 model, we used cross-validation by randomly selecting 80% of the records to estimate p_p , then
 402 using the estimated p_p to predict presence for the remaining 20%, setting a threshold of 0.5 to
 403 denote whether a murrelet was predicted to be present or not in the sampling area. We then
 404 created a confusion matrix comparing predicted and actual presence to evaluate our ability to
 405 predict presence.

406

407 We ran this analysis separately from estimation of abundance for the statistical and biological
408 populations. Our reasoning for doing so was to manage model runtime.

409
410 Estimating trend in abundance.—We used a state space model to estimate trend in abundance, or
411 the instantaneous growth rate (r), of the statistical and biological populations (i.e. without and
412 with p_p , respectively). Our state space model included a random effect for year and weighted the
413 response variable (log abundance) by the inverse of its variance. For years with direct estimates
414 of p_p (2007–2012), we used abundance of the biological population estimated incorporating
415 telemetry data (3-day window). In years without telemetry data (2005, 2016–2017), we used
416 mean p_p from across the 15-day period in all years, with year and individual included as random
417 effects in the estimation process. We intended to predict p_p for use in these non-telemetry years,
418 but because our predictive power was low, we opted to use mean p_p . To assess the effect of
419 including p_p in our trend estimate, we examined the root-mean-square-error (RMSE) of mean r
420 and percent change of coefficients of variation (CV) of the geometric growth rate, lambda (λ),
421 converted from mean r to avoid division by 0, between models without and with p_p . We report
422 trend results across all years (2005–2017).

423
424 Because we estimated abundance for each year using separate model runs, we had to run the
425 state space model separately too. To do so, we saved the output of each model for annual
426 abundance and used it as data input for the state space model.

427
428 We fit all models using JAGS (Plummer 2003) with R 4.2.1 (R Core Team 2019) using R2jags
429 as an interface. We used weakly informative priors on all parameters and 3 chains of 50,000
430 iterations, discarding the first 15,000 per chain as burn-in (Appendix 4). We assessed model
431 convergence through visual inspection of trace plots and the Gelman-Rubin diagnostic (Brooks
432 and Gelman 1998). We assumed convergence had occurred when chains overlapped
433 substantially, and the Gelman-Rubin diagnostic was <1.1 for all parameters.

434 435 RESULTS

436 *Components of detection probability*

437 We radio-tagged 191 Kittlitz's murrelets between 12 May and 3 June, 2007–2012. Of these, 132
438 birds remained alive in the study area until at least 1 July when boat surveys commenced,
439 contributing to 516 telemetry locations that were used to estimate p_p (Table 1). Across all flights
440 and years, relocations of most radio-tagged murrelets were in the Icy Bay state (53%) where boat
441 surveys occurred, followed by the inaccessible states of Ocean (24%), East Bay (18%), Nest
442 (4%), and Upper Bay ($<1\%$; Appendix 3a). Only 5% of murrelets in the Icy Bay state were in
443 close pack ice; the remainder were in open pack ice (8%), brash ice (15%), or no ice (72%;
444 Appendix 3b).

445
446 Across all years, the median of p_p was 0.50 (SE=0.02). During the 15-day period in which boat
447 surveys were conducted, median annual estimates of p_p ranged from 0.35 (SE=0.06) to 0.65
448 (SE=0.04; Figure 3a), which was similar to median estimates from the 3-day window
449 surrounding each survey (0.32 [SE=0.10]–0.76 [SE=0.09]; Appendix 1). Within a year, p_p varied
450 little, as indicated by the points falling close to the identity line (Figure 4). Although the 95%
451 credible intervals (CrI) across surveys and within a year always overlapped, they narrowed as the

452 window widened, reflecting an increase in the number of telemetry locations used to estimate p_p
453 (Appendix 1).

454

455 Our ability to predict p_p using five environmental covariates was generally poor (Figure 5). We
456 correctly predicted 62% of the observed outcomes and incorrectly predicted 38%. Of the
457 environmental covariates examined, proportion of Icy Bay state covered in ice was the only one
458 with 95% CrI that did not include 0 ($\beta_{ice} = -0.356$, CrI = -0.665, -0.059). While our hypothesis
459 that p_p would be higher during a flood tide was not supported ($\beta_{tide} = -0.006$, CrI = -0.345,
460 0.356), we found that p_p was more variable with a flood compared to an ebb tide (Figure 5b).

461

462 Between 2005 and 2017, we conducted 17 boat surveys for *Brachyramphus* murrelets, of which
463 only one covered the sampling area completely (mean fraction of sampling area covered=0.80,
464 range=0.56–1.00; Table 1). This limitation of boat survey coverage due to shifting ice
465 underscores the dynamic nature of our study area. Median annual estimates of p_d varied from
466 0.49 to 0.77 with CVs below 9% (Figure 3b). The probability that a detected *Brachyramphus*
467 murrelet was a Kittlitz’s murrelet, not a marbled murrelet, was high in both spatial strata, but
468 lower and more variable in the Main Bay (range=0.72–1.00) compared to Taan Fjord
469 (range=0.95–1.00; Figure 3c,d).

470

471 *Abundance and trend*

472 Abundance estimates of the statistical population were positively correlated with estimates of p_p ;
473 that is, when p_p was low, abundance was low, and vice versa (Figure 6).. In all years, biological
474 population abundance estimates were generally stable across all window lengths (Appendix 2).
475 In years when two boat surveys were conducted, our model with p_p reduced CVs of annual
476 abundance estimates by 13–35%; in the year with only one boat survey (2009), CVs increased by
477 270% (Figure 7), likely because the CV of the 2009 population estimate was highly
478 underestimated.

479

480 From 2005 to 2017, the trends in abundance of the statistical and biological populations were
481 negative (Figure 8). The probability of a decline (mean $r < 0$) across our study area was 67% for
482 the statistical population and 73% for the biological population. Estimates of mean r were -0.024
483 (CrI = -0.231, 0.183) for the statistical population (i.e., without p_p) and -0.043 (CrI = -0.265,
484 0.191) for the biological population (i.e., with p_p). By including p_p in the state space model, we
485 reduced sampling variance in the estimate of annual r by 17%. However, the CV for λ increased
486 by 12% and the RMSE for r increased from 0.160 to 0.185, indicating that we reduced within-
487 year variance by accounting for p_p , but not across-year variance.

488

489 DISCUSSION

490 We developed a contemporary model to account for a population misalignment and generate
491 unbiased abundance estimates of a highly mobile, non-territorial species, the Kittlitz’s murrelet,
492 in a dynamic marine environment. By decomposing detection probability, we were able to use
493 multiple datasets of different data types that did not rely on replicate or repeat sampling, which
494 was not feasible for our study species or area without an unrealistically large number of sampling
495 occasions or sites (e.g., N-mixture models; Royle 2004, Barker et al. 2008, Hostetter et al. 2019).
496 Alternatively, we would have needed to devise a way to increase capture probabilities to utilize
497 capture-recapture or resight models effectively (Burnham et al. 1987). Moreover, the hierarchical

498 structure of our model allowed us to work within a single analytical framework and appropriately
499 account for all sources of uncertainty.

500
501 We are not aware of another abundance model that accounts for all components of detection
502 probability, especially p_p , without using replicate or repeat sampling methods. Fischbach et al.
503 (2022) developed a similar ratio estimator to account for haulout probability, which is analogous
504 to p_p , for estimating abundance of Pacific walrus, a species like *Brachyramphus* murrelets for
505 which population monitoring is notoriously difficult. Their model combined count data from
506 unoccupied aircraft systems and telemetry data, and therefore, while conceptually similar to our
507 model, it is not applicable to our situation because of differences in data types and habitat
508 dynamics, nor does it account for p_a or p_d . In these ways, our model builds on that of Fischbach
509 et al. (2022) and adds to the toolbox of demographic models that account for spatial temporary
510 emigration.

511
512 By accounting for p_p in our model, which aligned the statistical and biological populations, we
513 improved the precision of annual abundance estimates by 13–35% when we followed our
514 standard protocol of conducting two boat surveys. However, results from 2009, when only one
515 boat survey was conducted, clearly indicated that p_p and survey effort were conflated, as the CV
516 for the abundance estimate increased about tenfold. This outcome emphasizes the importance of
517 a second boat survey annually if p_p varies; otherwise, the abundance estimate from a single
518 survey can have misleadingly high precision. We suspect this implication would be true for other
519 highly mobile species and dynamic systems as well. Nonetheless, our ability to notably improve
520 CVs for abundance estimates is a major achievement for a species often plagued with imprecise
521 estimates (USFWS 2013, Hoekman 2019).

522
523 Although we increased the precision of annual abundance estimates by aligning the statistical
524 and biological populations, we did not see the same improvement in the estimate of mean r , or
525 temporal trend. Thus, while we explained and reduced variation in abundance within a year, we
526 failed to account for a source(s) of variation across years. We suspect it relates to the propensity
527 for Kittlitz’s murrelets to skip breeding in some years and resultant variable return rates to Icy
528 Bay. A modeling exercise such as a life-stage simulation analysis (Wisdom et al. 2000) or an
529 integrated population model (Schaub et al. 2007) would help approximate the potential influence
530 of these latent parameters until direct data are available (see Kissling et al. *In review*). It is worth
531 noting that while we did not increase precision of the trend estimate, we also did not reduce it
532 even though we added a parameter to the estimation process, suggesting some information about
533 p_p was useful.

534
535 Though a population misalignment existed, we found that abundance estimates for the statistical
536 population of Kittlitz’s murrelets in Icy Bay generally were proportional to those of the
537 biological population. We were somewhat surprised by this finding because, based on a survival
538 analysis with the same telemetry dataset, radio-tagged murrelets moved frequently among spatial
539 states with daily transition probabilities ranging from 0.135 to 0.279 (Kissling et al. 2015b). Yet,
540 despite these moderate movement rates, p_p varied little within a year (Figure 4). Further, p_p was
541 correlated with abundance of the statistical population across years (Figure 6), which suggests
542 that murrelets in our study area were operating as a single biological population, otherwise we
543 would have expected discordance. Importantly, we did not detect a temporal trend in p_p , the link

544 between the two types of populations, meaning that p_p in the statistical population was random
545 with respect to the biological population and inference could be extended without bias.

546
547 As with all models, our model has assumptions beyond those associated with specific methods
548 like radio telemetry (White and Garrott 1990) and distance sampling (Buckland et al. 2001).
549 Inherent to boat and telemetry surveys, we assumed that the statistical population was closed
550 with respect to p_p for survey duration and within the 3-day window used to estimate biological
551 population abundance. While we developed our model in part to avoid assumptions of closure, it
552 is not entirely possible with the survey methods used in our study; essentially, our model relaxed
553 the assumption considerably, though did not eliminate it. Even so, given that estimates of p_p did
554 not vary much within a year, we feel confident that we sufficiently met the closure assumption
555 for the purpose of estimating abundance. For trend estimation, we also assumed that mean p_p was
556 an adequate estimate of p_p in the three years with boat survey data but without telemetry data.
557 Given that p_p varied considerably across years, this assumption likely was violated, but in the
558 absence of annual telemetry data, we think that the mean and its associated variance are adequate
559 because the variance was correctly incorporated into the trend variance by the Bayesian model.
560 Also, when estimating p_k , we assumed that both murrelet species were equally likely to be
561 classed as unidentified. We think this assumption was met reasonably well in our dataset even
562 though Kittlitz's murrelets far outnumber marbled murrelets in our study area. Further, using
563 field trials, we found misidentification rates of *Brachyramphus* murrelets to be low (Schaefer et
564 al. 2015).

565
566 Our final assumption was that the tagged murrelets were representative of the biological
567 population, as we defined it. Although our boat surveys were conducted in early July, we tagged
568 murrelets in May because our capture technique requires darkness, which is not sufficiently
569 available in our study area for about 6–8 weeks surrounding summer solstice (21 June).
570 Therefore, we inevitably tagged a few birds that were transiting through Icy Bay, which we only
571 located once or twice, or never again. These birds were not included in our estimation of p_p
572 because they were not located during our boat surveys, so they are not relevant here.
573 Additionally, because we only conducted telemetry flights in the Icy Bay study area, it is
574 possible that some tagged birds could have temporarily emigrated beyond our search area, which
575 would have biased our estimation of p_p . However, we do not believe it was the case, largely
576 because it was rare for a tagged bird to leave our study area and then return, especially as late in
577 the breeding season as July. In fact, we removed eight locations (<2%) from our analysis because
578 they were not within any of the five spatial states; none of those birds were located again,
579 suggesting they permanently emigrated, or possibly the tag stopped reporting for whatever
580 reason. Therefore, we feel confident this assumption was met as best we could with VHF
581 transmitters.

582
583 Despite our poor ability to predict p_p from environmental covariates, we gained new insights into
584 the ecology of Kittlitz's murrelets. First, in previous studies of this species, we posited that, if
585 murrelets temporarily emigrated during boat surveys, they were moving into dense icefloes near
586 the tidewater glaciers (i.e., Upper Bay), presumably to search for food or avoid predation
587 (Kissling et al. 2007, Day et al. 2020). Here, we confirmed that when the proportion of ice in the
588 Icy Bay state increased, p_p decreased, but we found that instead of moving into pack ice closer to
589 the glacier(s), murrelets moved into shallow or rough waters away from the glaciers (i.e., East

590 Bay and Ocean, respectively). While this finding should be viewed cautiously until confirmed at
591 other times and locations, it appears that murrelets are less associated with ice when at sea at fine
592 spatial scales than we previously thought, at least in the Icy Bay system.

593
594 Second, although p_p varied little within a year, it varied considerably across years, revealing a
595 spatiotemporal pattern that implied an ecological driver(s) was at play but was not captured by
596 the available environmental covariates. For example, p_p was comparatively low across the 15-
597 day period in 2007 and 2010, yet in 2007, murrelets outside of the sampled area were mostly in
598 the Ocean state and in 2010, they were mostly in the East Bay state (Appendix 3). From this
599 result, we assume that variation in prey availability led murrelets to select states outside of the
600 Icy Bay state, with patterns that varied on an annual, rather than a within-year, basis. With
601 additional data on murrelet movements from Icy Bay or elsewhere, this finding may eventually
602 provide clues as to the ecological driver(s) of these patterns and improve our ability to predict p_p .

603
604 Our model to align statistical and biological populations for abundance estimation is simple,
605 flexible, and scalable and is suitable for a variety of species and habitats. It is a practical solution
606 to resolving a population misalignment when repeat and replicate sampling is not feasible and
607 increased precision of abundance and trend estimates is desired, as is the case with many species
608 of conservation concern like the Kittlitz's murrelet (USFWS 2013). Although it requires
609 telemetered animals, which can be costly compared to methods for unmarked animals, it was the
610 only reasonable way to estimate p_p for Kittlitz's murrelets in Icy Bay and we suspect the same is
611 true for other species and habitats that are difficult to sample (e.g., walrus; Fischbach et al.
612 2022). The use of satellite transmitters, which are not readily available yet for murrelets, would
613 greatly facilitate and perhaps improve estimation of p_p , especially if location data could be
614 collected at a finer temporal scale. Moreover, satellite transmitters would relax the assumption
615 related to representativeness of the tagged animals of the biological population and could
616 improve precision of trend estimates if their retention and operation extended beyond a single
617 year.

618
619 For any study reporting abundance, it is critical to clearly define the population to which
620 abundance refers (Hammond et al. 2021), though delineating populations can be difficult and
621 require substantial data (Rushing et al. 2016). Our goal here was not to provide a framework for
622 how to delineate biological populations, but instead to develop an analytical approach to account
623 for a population misalignment if one exists. However, we urge ecologists to think critically about
624 the population in which they want to draw inference, especially as tracking technology improves
625 and model complexity increases. If possible, the statistical population should be the same as the
626 biological population, or at least representative of it in terms of population processes or
627 ecological conditions, which fortunately happened in our case. Otherwise, if p_p has temporal or
628 geographic patterns, inference about abundance for the population of interest is confounded with
629 its use of the sampled area and could be misleading. This messy situation with potentially
630 misleading estimates can have conservation implications if threats or stressors vary. For
631 example, threatened grizzly bears (*Ursus arctos*) can roam outside of national park boundaries,
632 with bears outside the park being subject to differing mortality sources not captured by within-
633 park monitoring (Schwartz et al. 2010). Further, if estimates of abundance are subsequently used
634 in population models, it is imperative that they are from the same population used to estimate

635 other demographic parameters (e.g., survival and productivity) to avoid misleading inference
636 about population dynamics.

637

638 AUTHORSHIP CONTRIBUTIONS

639 Michelle Kissling, Paul Lukacs, and Scott Gende conceived ideas and designed methodology;
640 Michelle Kissling and Kelly Nesvacil collected the data; Michelle Kissling, Paul Lukacs, and
641 Grey Pendleton analyzed the data; Michelle Kissling led writing of the manuscript. All authors
642 contributed critically to drafts and gave final approval for publication.

643

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656 Tlingit Tribe.

657

658 CONFLICT OF INTEREST STATEMENT

659 The authors declare no conflict of interest.

660

661 DATA AND CODE AVAILABILITY STATEMENT

662 All data collected between 2005 and 2012 that were used in this manuscript are available via
663 Dryad at <https://doi.org/10.5061/dryad.0cfxpnw8m>. However, boat survey data from 2016 and
664 2017 were collected by the Alaska Department of Fish and Game, who considers these data to be
665 sensitive and has withheld them in accordance with Alaska State Statute 16.05.815(d). Request
666 of these data can be made to: Wildlife Science Director, Alaska Department of Fish and Game,
667 Division of Wildlife Conservation, 1255 West 8th St., Juneau, Alaska, 99802 or to
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Table 1. Sample sizes and effort by survey type for estimating abundance of a biological population of Kittlitz’s murrelets, Icy Bay, Alaska, 1–15 July 2005–2017. Truncation distance was used to model the detection function to estimate probability of detection (p_d) with distance sampling data.

Year	Boat surveys				Telemetry surveys		
	# surveys	Portion of sampling area surveyed		Truncation distance (m)	15-day period		
		Survey 1	Survey 2		# flights	# radio-tagged individuals	# locations
2005	2	0.85	0.85	250	-	-	-
2007	2	0.75	0.74	281	4	24	82
2008	2	0.75	0.70	278	8	20	137
2009 ^a	1	0.91	-	288	5	20	85
2010	2	0.67	0.91	242	3	24	58
2011	2	0.77	0.73	210	4	27	100
2012	2	0.75	0.56	181	4	17	54
2016	2	0.91	1.00	325	-	-	-
2017	2	0.91	0.90	323	-	-	-

^aBoat survey conducted on 17 July 2009; telemetry survey information presented here for 1–15 July 2009.

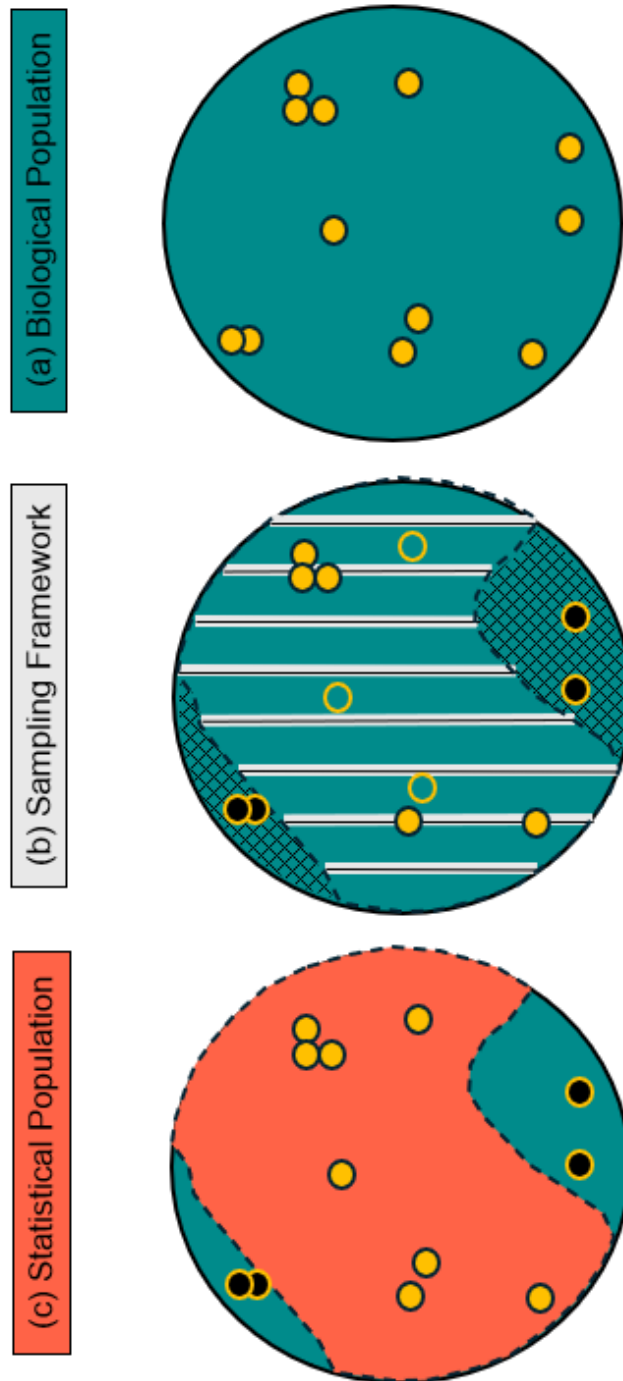


Figure 1. Schematic illustrating the relationship between the (a) biological population, or the population of interest; (b) sampling framework with line transects (black lines with gray rectangles) along which individuals are sampled (solid yellow circles) or not sampled (open yellow circles) and inaccessible areas (cross-hatching) that contain a portion of the biological population (solid black circles); and (c) statistical population, which is defined by the extent of the sampling frame in (b).

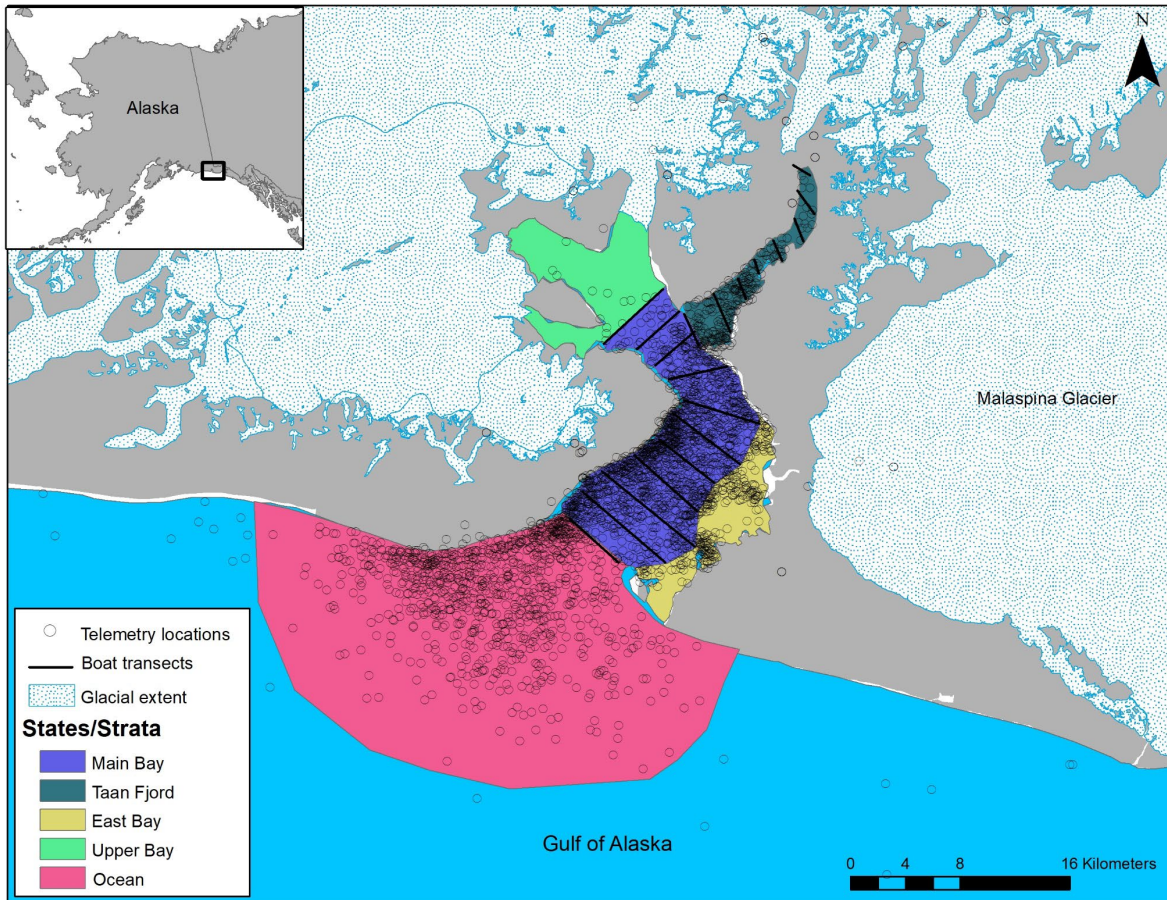


Figure 2. Map of study area, Icy Bay, Alaska, where we conducted boat and telemetry surveys to estimate abundance of Kittlitz's murrelets. Our sampling area during telemetry flights comprised five spatial states that collectively formed the extent of the biological population: Icy Bay (Main Bay and Taan Fjord sub-states combined), East Bay, Upper Bay, Ocean, and nest. During boat surveys, only the Icy Bay state, with Main Bay and Taan Fjord as strata, was regularly accessible and formed the extent of the statistical population. The gray-shaded area is land.

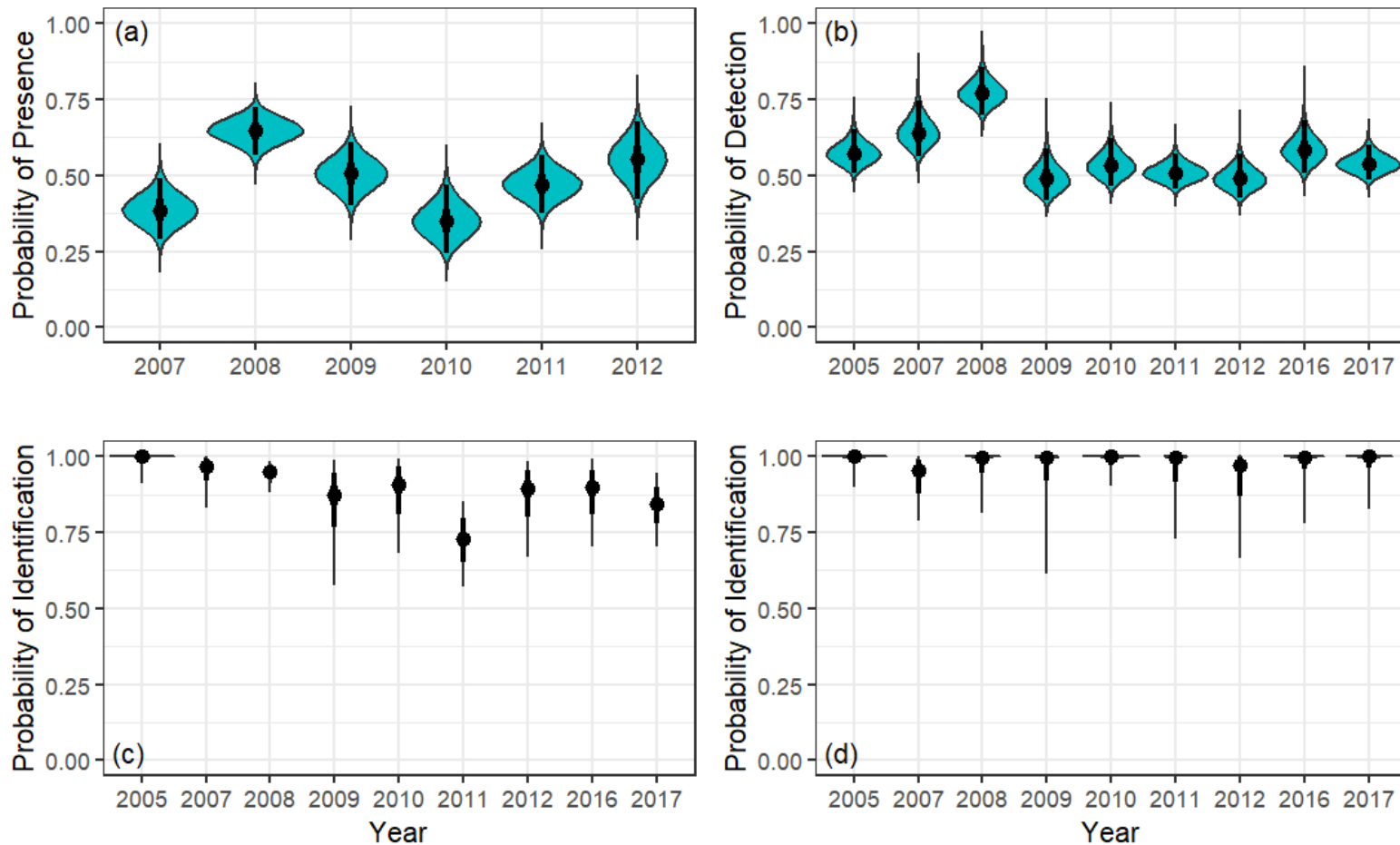


Figure 3. Posterior distributions (teal) of estimates of detection probability components for Kittlitz's murrelets, Icy Bay, Alaska, 2005–2017. Components are (a) probability of presence (p_p), (b) probability of detection (p_d), and probability of being a Kittlitz's murrelet (p_k) in (c) Main Bay and (d) Taan Fjord strata. The median of the estimate is denoted with a point, the 50% credible interval with a thick line, and the 95% credible interval with a thin line. Note that for p_d (b), truncation distance varied across years (Table 1).

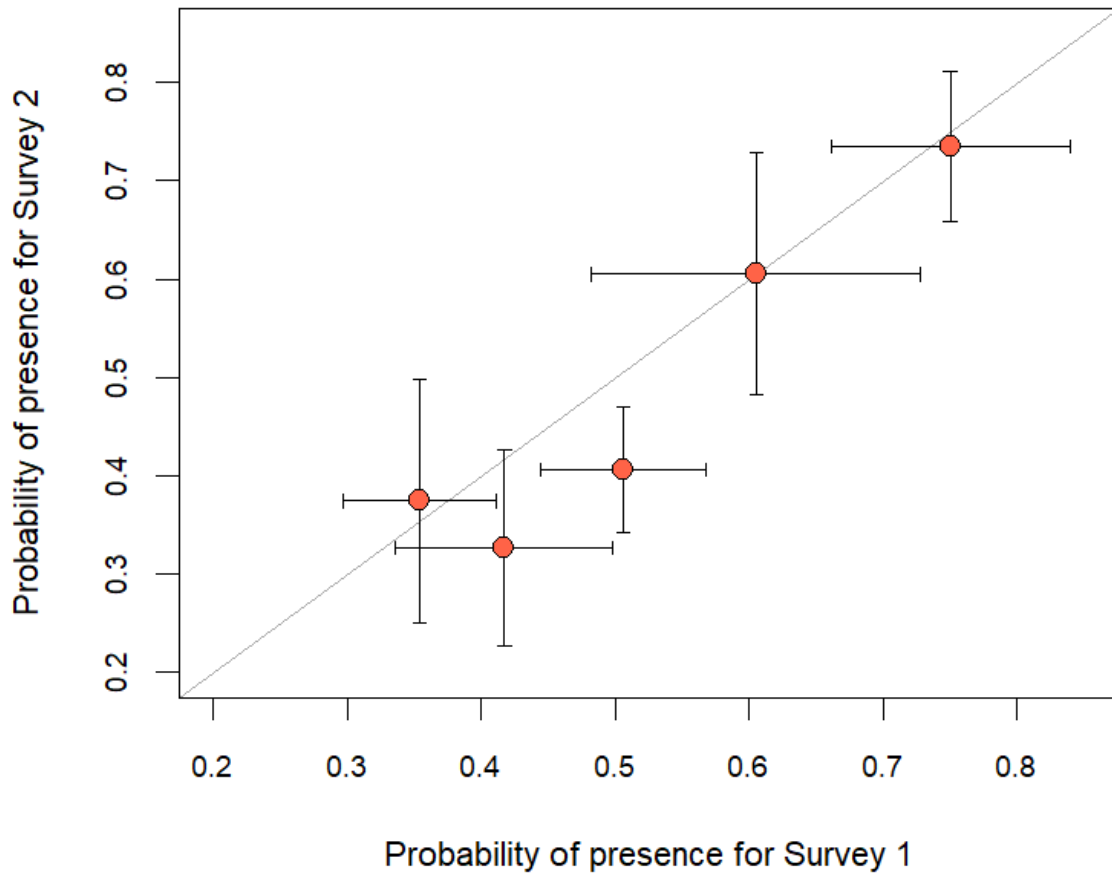


Figure 4. Probability of presence (p_p) for the 3-day window by boat survey within a year. The error bars describe the standard errors of the estimate and correspond with the respective axes. The identity, or 1:1 line, is included in gray.

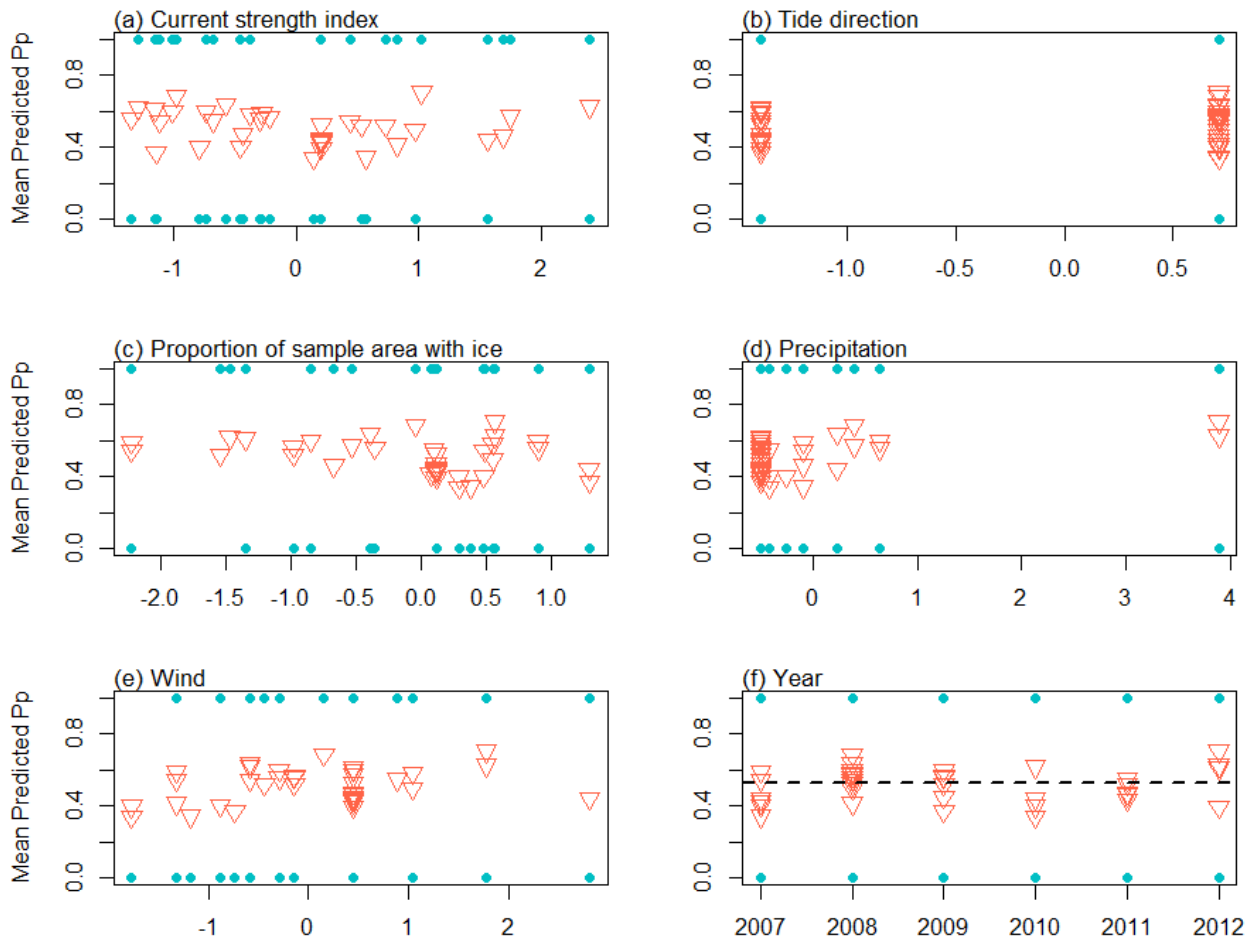


Figure 5. Distribution of observed outcomes (teal points) and predicted probability of presence (p_p ; orange triangles) using environmental covariates for Kittlitz's murrelets, Icy Bay Alaska, 2007– 2012. Covariates on x-axis are scaled; see 'Methods' text for description. For year (f), the dotted line denotes the mean p_p across all years in the observed dataset.

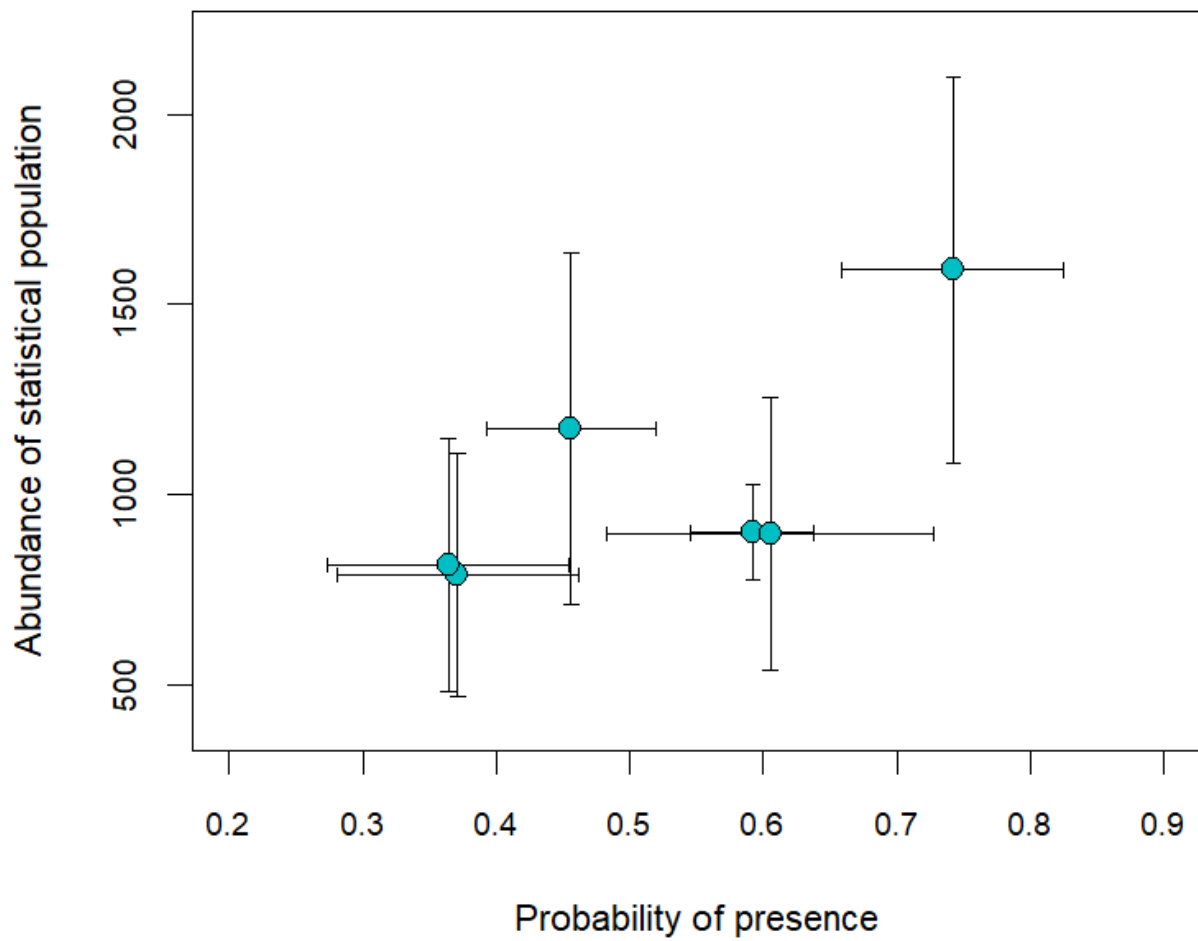


Figure 6. Probability of presence (p_p) across both surveys for the 3-day window by abundance of the statistical population, i.e., without p_p . The error bars describe the standard errors of the estimate and correspond with the axes.

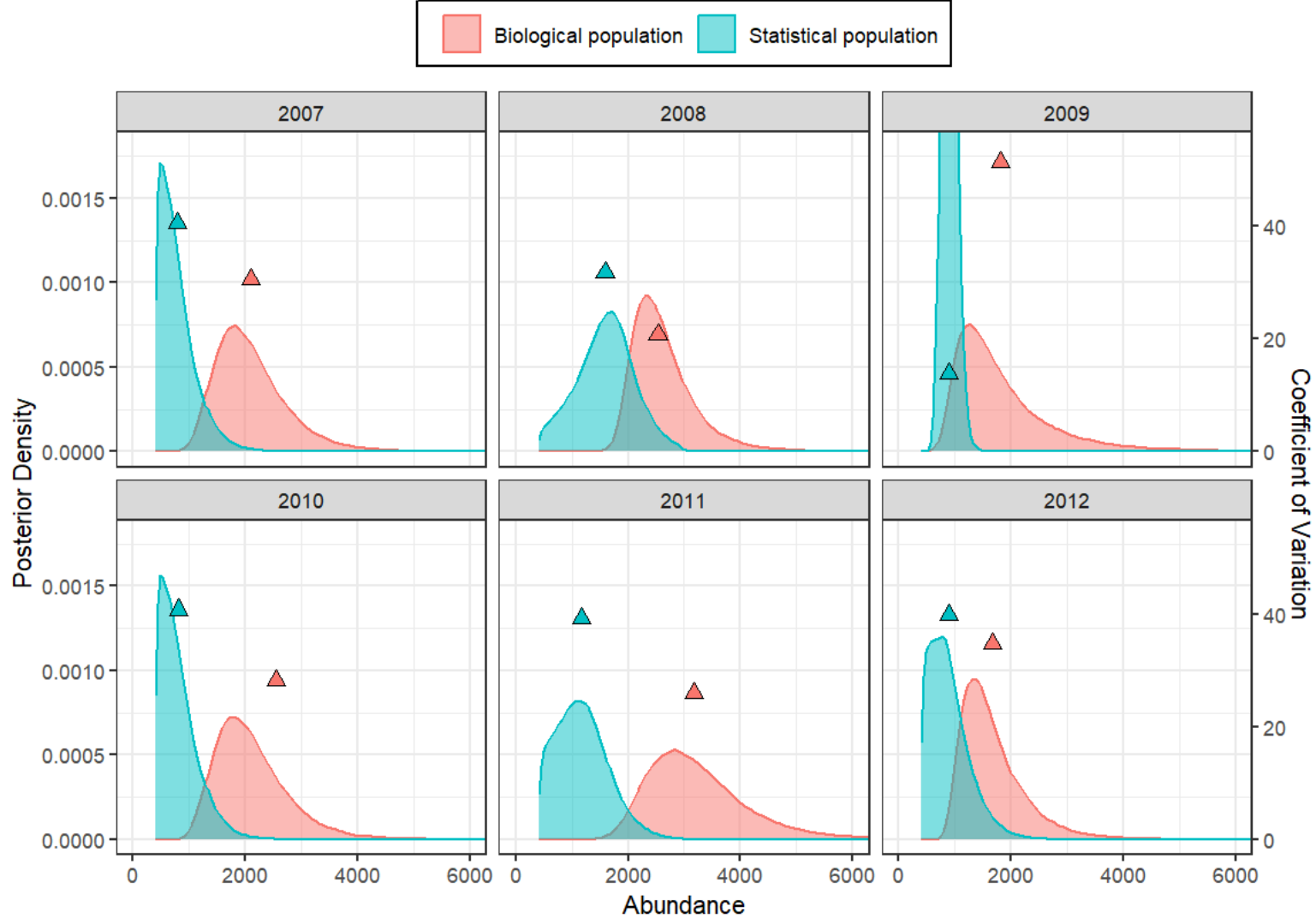


Figure 7. Posterior distributions of annual abundances estimate for the Kittlitz’s murrelet and corresponding coefficients of variation (triangles) without probability of presence (p_p ; statistical population) and with p_p (3-day window; biological population) around corresponding boat surveys, Icy Bay, Alaska. In 2009, when only one boat survey was completed, the posterior distribution was extremely narrow (overly precise) and extends beyond the y-axis limits of this figure for display purposes.

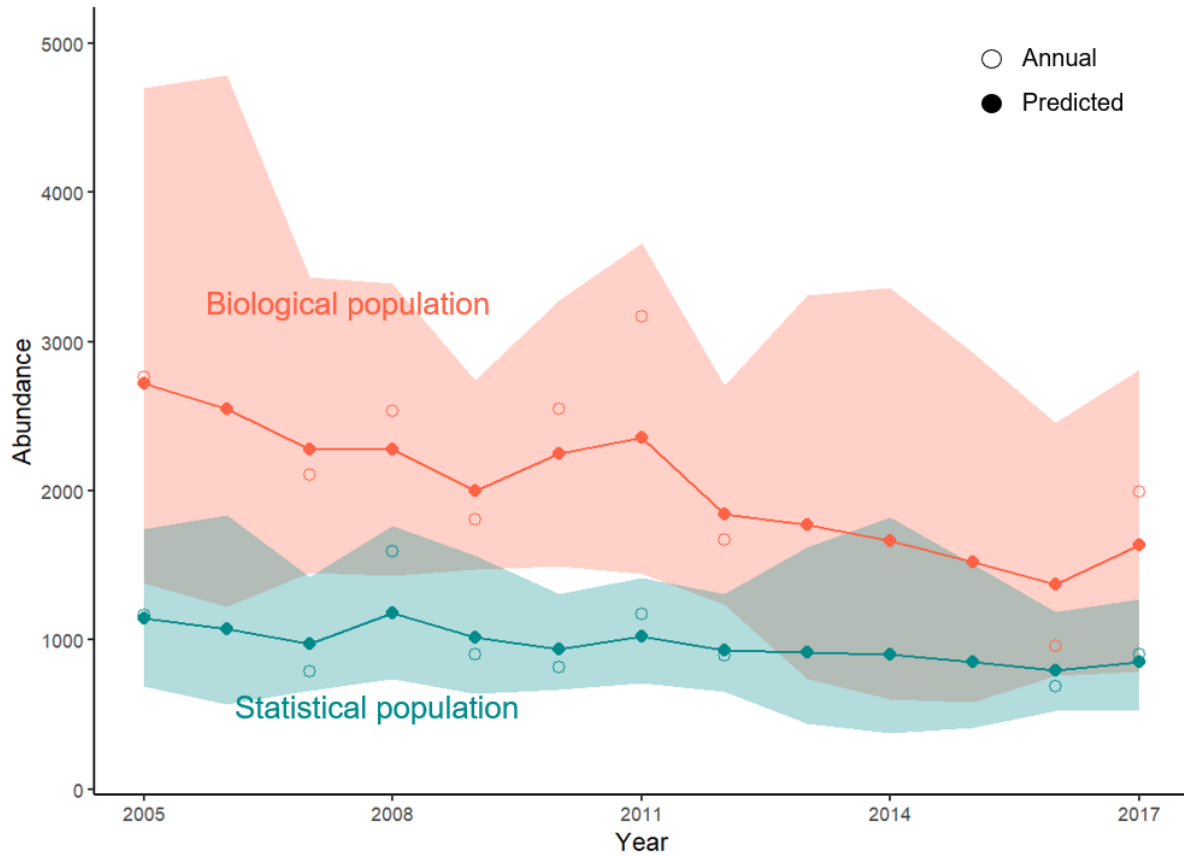
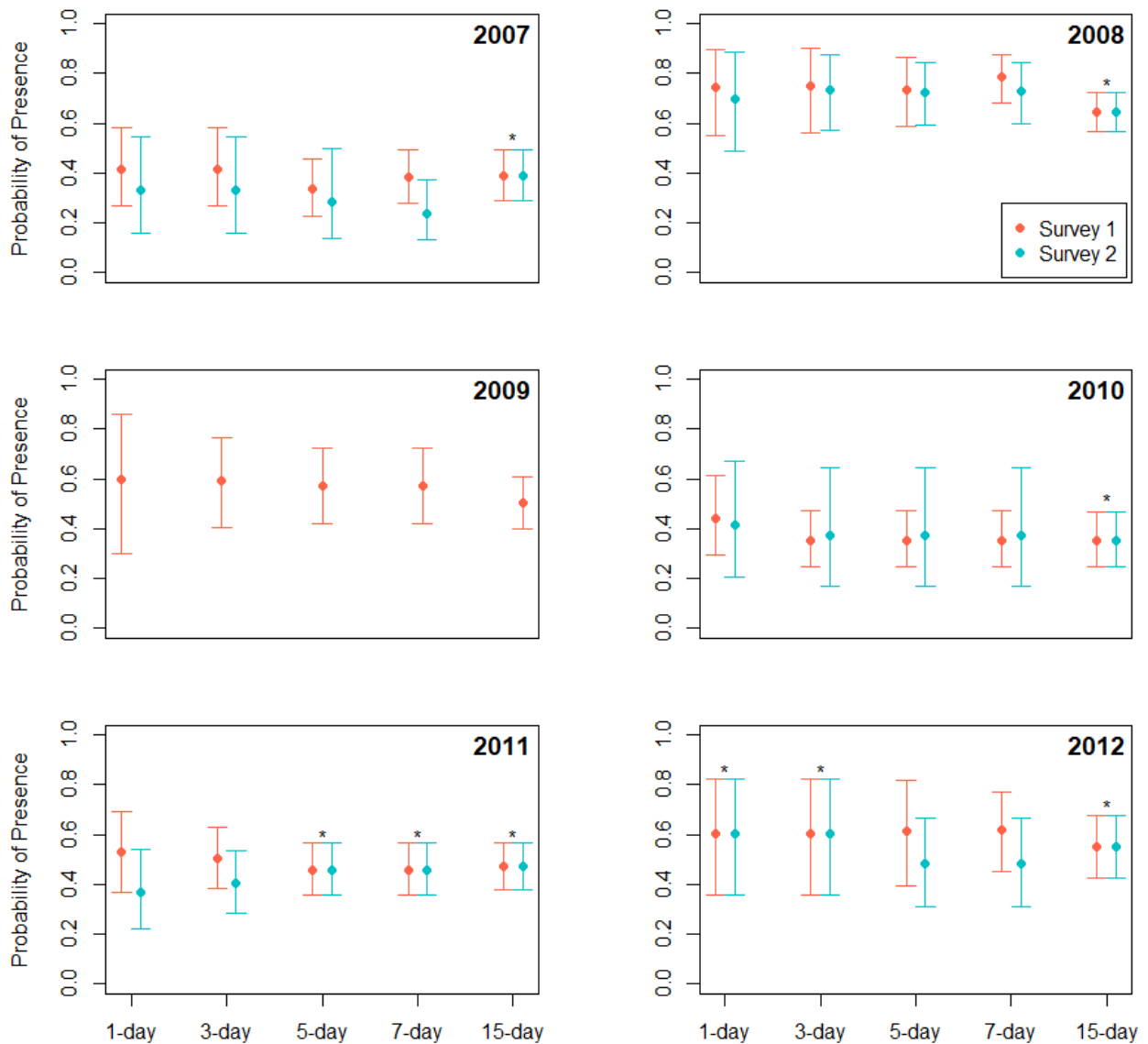
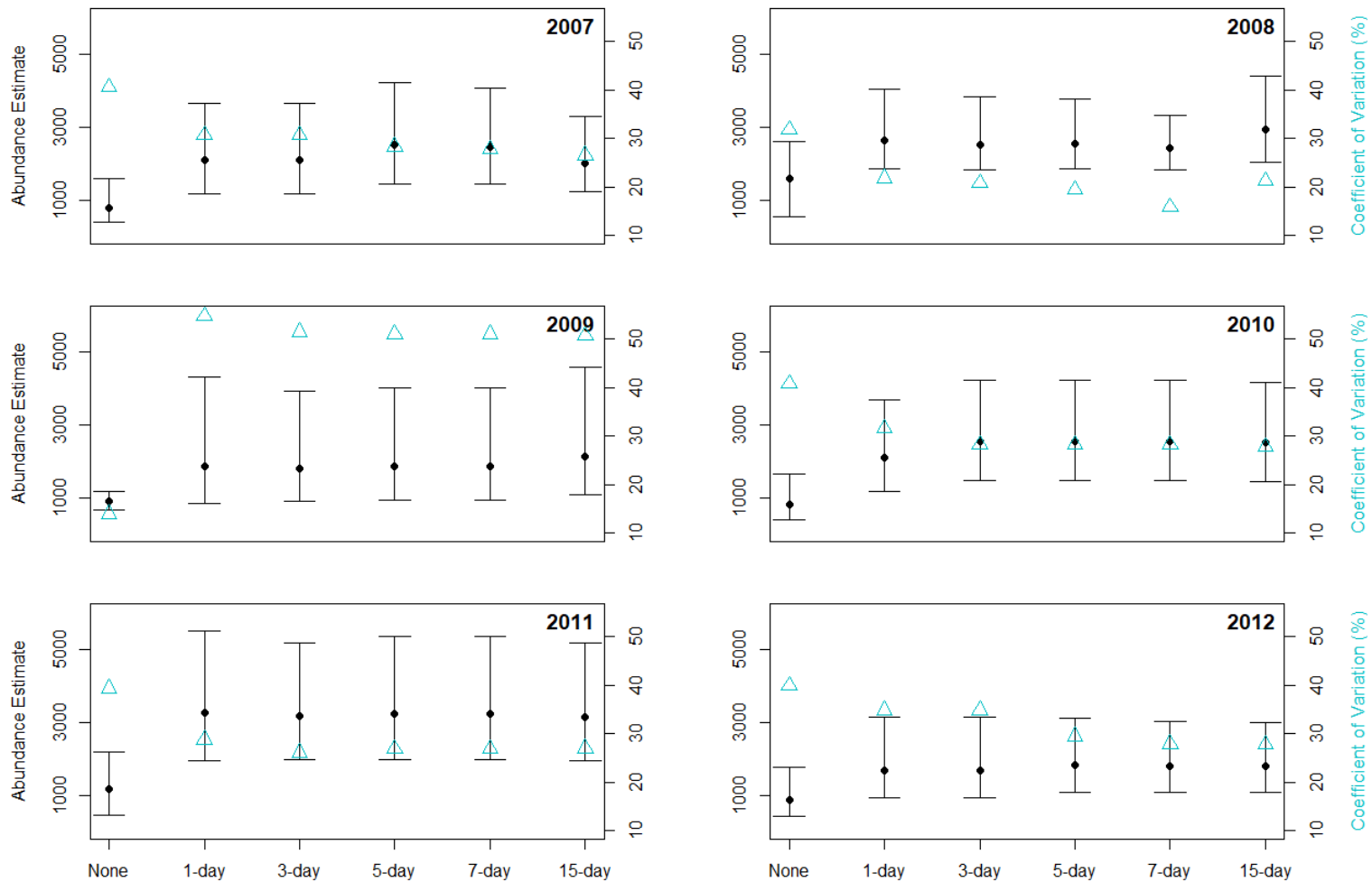


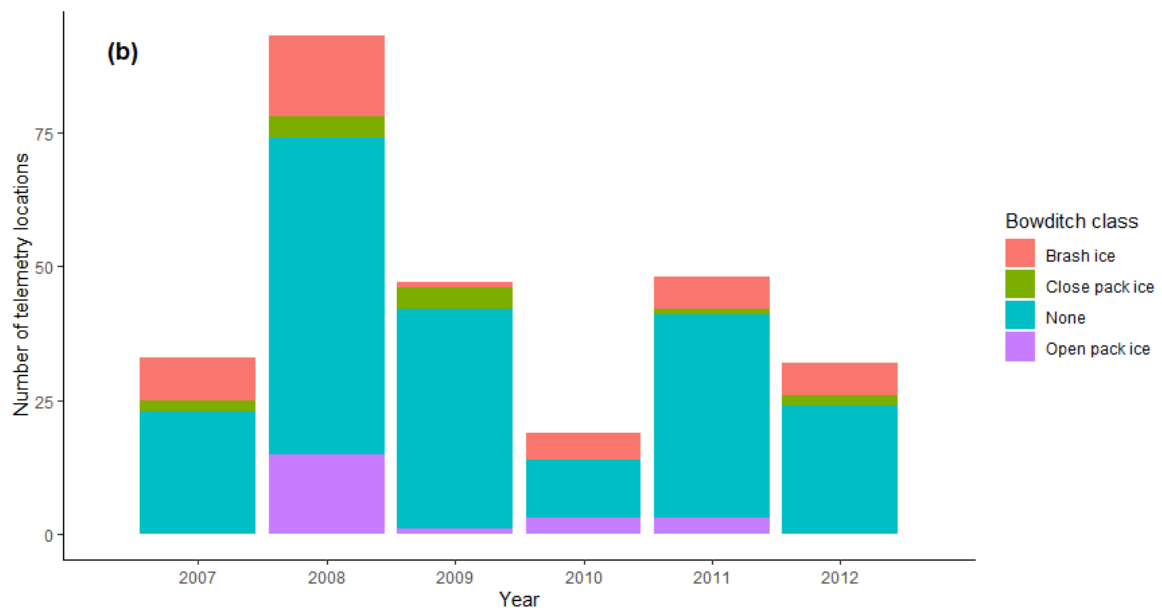
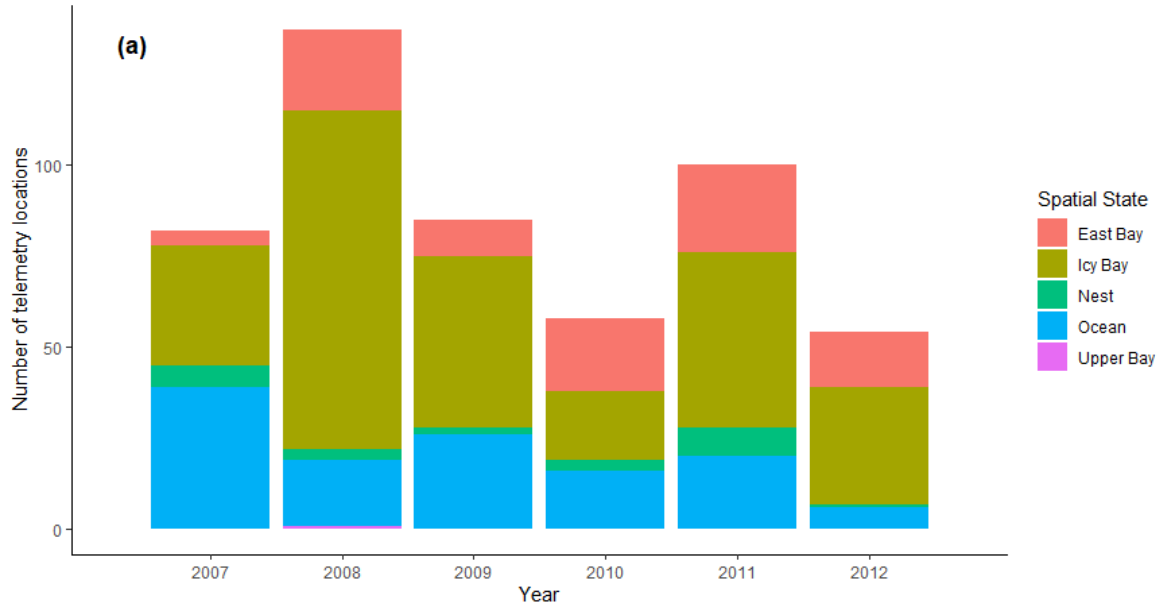
Figure 8. Annual and predicted abundance estimates of the statistical population (without probability of presence, p_p) and biological population (with p_p) of Kittlitz's murrelets, Icy Bay, Alaska, 2005–2017. Annual estimates are denoted with open circles and predicted estimates from the state-space model are identified with closed circles; the shaded areas describe the 95% credible intervals of the modeled abundance. P_p is accounted for in the biological population estimates using telemetry data surrounding a 3-day window of a boat survey.



Appendix 1. Estimates of probability of presence (p_p ; \pm 95% credible intervals) of radio-tagged Kittlitz's murrelets by window length (1-, 3-, 5-, 7-day, and 15-day) and boat survey (survey 1=orange, survey 2=teal), Icy Bay, Alaska, 1–15 July 2007–2012. Asterisks indicate windows when the same telemetry data were used to estimate p_p for boat surveys 1 and 2.



Appendix 2. Kittlitz's murrelet annual abundance estimates and 95% credible intervals (black) and corresponding coefficients of variation (blue) without probability of presence (p_p ; None; statistical population) and with p_p by window length (1-, 3-, 5-, and 7-day; biological population) around corresponding boat surveys and entire window (15-day) when boat surveys were conducted (i.e. 1–15 July), Icy Bay, Alaska. We completed two boat surveys each year except 2009 when only one survey was done.



Appendix 3. Number of telemetry locations of Kittlitz’s murrelets by year and (a) spatial state and (b) Bowditch ice class, 1–15 July 2007–2012, Icy Bay, Alaska. We did not locate any murrelets in very close pack ice.