

POPULATION DYNAMICS AND DEMOGRAPHY OF HUMPBACK WHALES IN GLACIER BAY AND ICY STRAIT, ALASKA

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ABSTRACT—Standardized sight-resight data of Humpback Whales (*Megaptera novaeangliae*) in Glacier Bay and Icy Strait, Alaska, have been collected since 1985. We applied closed robust design capture-recapture models to these data to provide inferences about: (1) population size; (2) population growth rate; (3) apparent survival rate; and (4) temporary emigration rate in the region during 1985–2009, while accounting for imperfect detection probability. Population size estimates ranged from a low of 49.8 (95% CI: 44.3–64.4) in 1986 to a high of 181.1 (95% CI: 173.5–196.2) in 2009, and the geometric mean of year-to-year changes in abundance suggested a rate of population growth over the 25-y period of about 4.4%/y. We estimated the annual survival rate to be 0.948 (95% CI: 0.936–0.957). We estimated the probability of temporarily emigrating from the study area to be 0.106 (95% CI: 0.086–0.128), and the probability of a temporary emigrant remaining outside the study area as 0.777 (95% CI: 0.712–0.830). Our results provide new insights into the status and dynamics of this endangered species in and around a large marine protected area and highlight the value of intensive long-term population monitoring efforts.

Key words: Alaska, capture-recapture, Glacier Bay National Park and Preserve, Humpback Whale, Icy Strait, *Megaptera novaeangliae*, population dynamics, robust design, survival rate, temporary emigration

Humpback Whales (*Megaptera novaeangliae*) that breed in tropical waters off of Hawaii migrate annually to productive feeding waters along coastal Alaska and northern British Columbia where they show strong between-year site fidelity (Straley and others 2009). A ban on commercial whaling of the species and protection under the Endangered Species Act and Marine Mammal Protection Act in the late 1960s and 1970s has resulted in recent population increases throughout the Central North Pacific (Barlow and others 2011; Hendrix and others 2012). Nevertheless, the species still faces substantial conservation threats in the region, such as vessel strikes and entanglement in fishing gear, throughout their annual cycle (Neilson and others 2009, 2012a; Gende and others 2011). Most information to inform management of Humpback Whales in the Central North Pacific is at broad ‘stock-wide’ scale; however, complementary information with finer spatial resolution (for example, within a marine protected area) would aid development

and implementation of management and conservation measures at those scales.

Individual Humpback Whales have been photographically documented in Glacier Bay and adjacent Icy Strait, Alaska, for more than 3 decades, and intensive population monitoring has been conducted in this region since 1985 (Neilson and others 2012b). Although survey effort in this region is quite high and many individuals are observed on multiple days throughout the summer, detection probability is still imperfect and may vary over time. Thus, inferences about demographic rates, population size, population dynamics, and trends based on uncorrected counts may be misleading. Better information on the demography and population dynamics of this region are needed to guide management of this protected species within Glacier Bay National Park and Preserve, a large marine protected area, and adjacent Icy Strait, an exceptionally productive marine ecosystem (Etherington and others 2007; Chenoweth and others 2011).

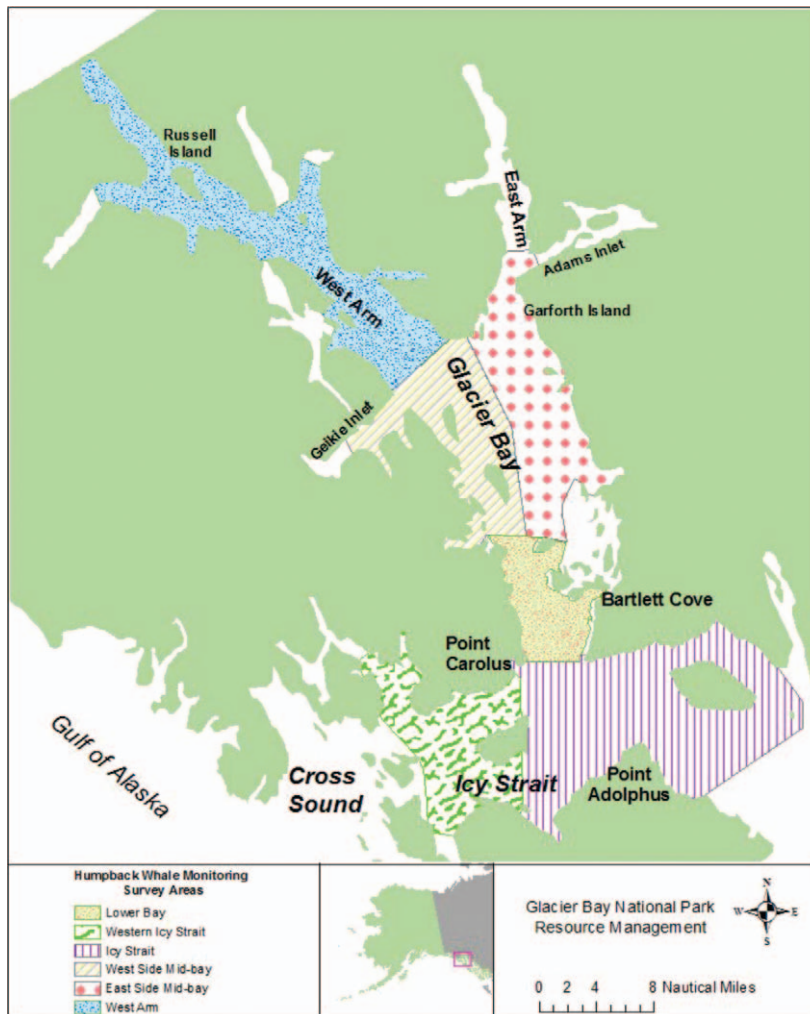


FIGURE 1. Study area encompassed by the Humpback Whale monitoring program in Glacier Bay and Icy Strait. Vessel surveys were conducted 4–5 d/wk between 1 June and 31 August in each year, 1985–2009; effort on a given day was focused on particular survey areas.

Here we apply modern capture-recapture statistical techniques to the analysis of 25 y (1985–2009) of sight-resight monitoring data to make inferences about population parameters of Humpback Whales in the Glacier Bay-Icy Strait region. Our approach improves upon earlier analyses that have examined shorter time spans within this data set (for example, Straley and others 2009) by exploiting within-year resightings in a closed robust design modeling framework to assess annual variation in abundance, survival, and temporary emigration, while accounting for temporal and group-level heterogeneity in detection probability. We

also provide an assessment of average population change (trend) for Humpback Whales in this region over the 25-y time period.

METHODS

Field Methods

Vessel surveys for Humpback Whales were conducted within Glacier Bay and Icy Strait (hereafter, GBIS; Fig. 1) 4–5 d/wk between 1 June and 31 August in each year, 1985–2009. Effort on a given day was focused within a particular survey area within the larger Glacier Bay-Icy Strait region and surveys were generally

not conducted in the same survey area on consecutive days. Individual whales were identified from photographs based on black and white pigmentation patterns on the ventral surface of the flukes (Jurasz and Palmer 1981; Katona and others 1979) or shape and scarification patterns on the flukes and dorsal fin (Blackmer and others 2000). Resightings were determined based on matching photographs to historical photographs of Humpback Whales in the study region. Age classes of individuals were assigned as calves (<1 y old), juveniles (1–4 y; for known-aged individuals first sighted as calves), or adults (≥ 5 y).

Statistical Analyses

We applied robust design capture-recapture models (Pollock and others 1990; Kendall and others 1995, 1997) to the sight-resight data collected as part of the Humpback Whale monitoring data from GBIS. These models were used to estimate and evaluate hypotheses about non-calf (adult + juvenile) population size (N), annual survival rate (S), temporary emigration rate (γ), and detection probability (p). Survival rate estimates apply to a super-population (such as southeastern Alaska and northern British Columbia; Calambokidis and others 2001; Barlow and others 2011), which includes individuals that had been identified during monitoring in GBIS, but that may or may not be available for sampling in any given year (such as temporary emigrants). Similarly, estimates of temporary emigration rate refer to the probability that an individual in the super-population is temporarily unavailable for sampling (not in GBIS) in a given year. Population size estimates, however, refer to just the portion of the super-population that is within GBIS. We estimated the average population growth rate over the 25-y period (λ) as the geometric mean of the annual year-to-year population changes in population size estimates. The standard error of $\hat{\lambda}$ was estimated using the delta method (Oehlert 1992) with the R (R Development Core Team 2011) package *msm* (Jackson 2011). We provide an approximate 95% confidence interval for $\hat{\lambda}$ based on an assumption of asymptotic normality.

Robust Design models take advantage of hierarchical sampling designs that include multiple seasons of data (primary samples) and repeated samples within seasons (secondary

samples). Primary samples are used to estimate demographic transition parameters (S and γ) under an open-population framework, while secondary samples are used to estimate abundance and detection probability parameters under a closed-population framework (Pollock and others 1990). Models applied to secondary samples generally assume no new additions or deletions (mortality and emigration) to the population across samples. A more relaxed assumption (applicable to many migratory populations) that, if met, will not bias estimates of population parameters, is that all individuals have arrived in the study area by the end of the 1st sampling period and do not begin to leave until after the final sampling period has begun (Kendall 1999). Observed residency intervals in our study area suggested that new whales arrive throughout the early season and begin leaving prior to the end of summer each year (Neilson and others 2012b). To meet the relaxed closure assumption, we aggregated daily samples at monthly resolution, and assumed that all individuals arrived in the GBIS region by the end of June and remained until at least the end of July. From these data we constructed individual encounter histories based on 25 primary sampling periods (1985–2009) and 3 secondary sampling periods (June, July, August) for a total of 75 potential encounter occasions. An additional assumption implicit in our approach is that the study region (sampled area) was consistent among secondary sampling periods.

We considered a set of 80 models that represented various hypotheses about temporal variation in survival rate and temporary emigration, and temporal variation and heterogeneity in detection probability. The model set included 2 parameterizations for survival \times 5 parameterizations for temporary emigration \times 8 parameterizations for detection probability (Table 1).

Model parameterizations for annual non-calf survival rate included models that allowed survival to vary annually (models with year-effects) and models that constrained survival to be constant among years (intercept-only models). Model parameterizations for temporary emigration included: (1) no temporary emigration (γ set equal to zero); (2) time-constant random temporary emigration; (3) annually-varying random temporary emigration; (4) time-constant Markovian emigration; and (5)

TABLE 1. Models considered for survival, temporary emigration, and detection probability parameters in closed robust design capture-recapture models applied to sight-resight data on Humpback Whales in Glacier Bay-Icy Strait, Alaska.

Parameter	Notation	Interpretation
Annual survival probability, S	$S(\cdot)$	Time-constant survival
	$S(t)$	Annually varying survival
Temporary emigration, γ (where γ'' = probability of temporarily emigrating between years; γ' = probability of staying off study areas between years)	$\gamma = 0$	No temporary emigration
	$\gamma(\cdot)$	Random time-constant temporary emigration
	$\gamma(t)$	Annually varying random temporary emigration
	$\gamma''(\cdot)\gamma'(\cdot)$ $\gamma''(t)\gamma'(t)$	Time-constant Markovian temporary emigration Annually varying Markovian temporary emigration
Detection probability, p	$p(t)$	Annually varying detection probability
	$p(\text{month})$	Monthly varying detection probability
	$p(t + \text{month})$	Additive time-varying model with year and month effects
	$p(t * \text{month})$	Full interaction model with year and month effects
	$p(t + \text{group})$	Annually-varying two-group finite mixture model
	$p(\text{month} + \text{group})$ $p(t + \text{month} + \text{group})$	Monthly-varying two-group finite mixture model Additive time-varying model with year, month, and two-group mixture effects
$p(t * \text{month} + \text{group})$	Time-varying model with full interaction year and month effects and two-group finite mixture effect	

annually-varying Markovian emigration. Random emigration parameterizations were constrained such that the probability of a whale not being present in the study in a given year (temporarily unavailable for sampling) was assumed to be the same for all whales regardless of whether they were present or absent from the study area in the previous year. Markovian movement parameterizations allowed the probability of temporary emigration between years (denoted γ'') to differ from the probability of staying out of the study area between years (remaining unavailable; denoted γ'). For annually-varying Markovian movement models, emigration and survival parameters for the final interval are not uniquely identifiable and we do not present estimates of these parameters.

For detection probability, we considered 8 model parameterizations that addressed hypotheses about temporal variation (annual, or primary sampling period, variation; and within-year, or 'secondary sampling period', variation) and heterogeneity in detection probability among whales. Four parameterizations allowed for temporal variation in detection probability and assumed that a single detection probability was applicable for the entire population. These models included: (1) annual [primary sampling period] variation only; (2) within-year [monthly

secondary sampling period] variation only; (3) an additive annual + within-year effects model; and (4) a full annual \times within-year interaction model. These 4 parameterizations will overestimate detection probability and underestimate population size if there is substantial heterogeneity in detection probability among individuals because inferences will be based largely on the easiest-to-detect individuals which provide the bulk of the data (Pollock and others 1990). For this reason we also considered the same 4 models of temporal variation, but allowing detection probability to differ between 2 groups with different detection probabilities, with groups determined using finite mixture models (Pledger 2000). These models contained an additional parameter, π , which denoted the probability of an individual being in 1 of the 2 groups (in our case, π represented probability of membership in the group with lower detection probability), as well as separate time-specific estimates of detection probability for each of the 2 groups.

We compared models using Akaike's information criterion (AIC) corrected for small sample size, AIC_c , and we assessed model support using AIC_c model weights (w_i , where $i = 1, \dots, 80$ models; Burnham and Anderson 2002). Models were run in program MARK (White and Burnham 1999) using the R (R Development Core Team 2011) package RMark (Laake 2011).

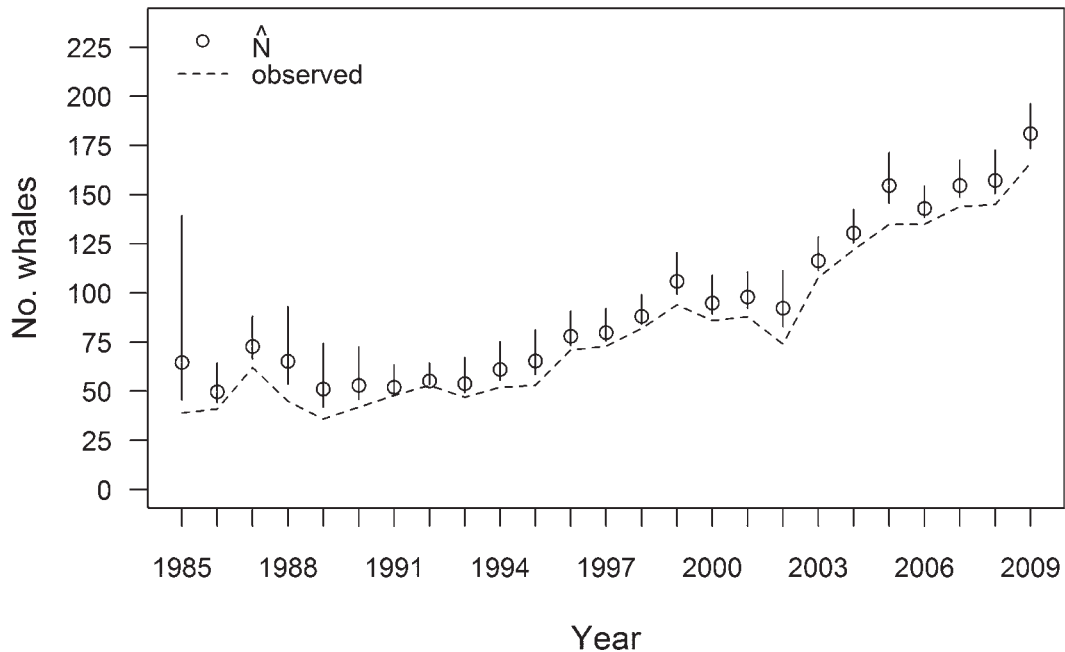


FIGURE 2. Annual estimates (and 95% confidence intervals) of non-calf population size for Humpback Whales in the Glacier Bay-Icy Strait region. Estimates are based on a robust design capture-recapture mixture model applied to sight-resight data (\hat{N}). Observed numbers of non-calf whales identified in the region (population size estimates uncorrected for imperfect detection probability) are shown for reference.

RESULTS

Of the 80 models considered, the model with time-constant survival, $S(\cdot)$, time-constant Markovian temporary emigration, $\gamma''(\cdot); \gamma'(\cdot)$, and group- and time-specific detection probability, $p(t * month + group)$, was the most strongly supported model ($w_i = 0.93$). The 2nd-best supported model differed from the top model by allowing survival to vary by year, $S(t)$, and based on AIC_c was the only other plausible model in the model set ($w_i = 0.07$; $\Delta AIC_c = 5.13$).

Population size estimates, \hat{N} , from the top model ranged from a low of 49.8 (SE = 4.7; 95% CI: 44.3–64.4) in 1986 to a high of 181.1 (SE = 5.5; 95% CI: 173.5–196.2) in 2009. These estimates were 5 to 66% larger than naive estimates based on the numbers of individuals observed. Although we found strong support for group- and time-variation in detection probabilities, population size estimates closely tracked the trajectory of the numbers of individual whales observed each year (Fig. 2). Both the observations and estimates of population size showed an increasing trend for the Humpback Whale population. The average population growth rate

over the 25-y period was about 4.4%/y ($\hat{\lambda} = 1.044$; SE = 0.0136; 95% CI = 1.017–1.070).

The annual apparent survival rate estimate, \hat{S} , from the best-supported model was 0.948 (SE = 0.005; 95% CI: 0.936–0.957). The temporary emigration probability estimate was low ($\hat{\gamma}'' = 0.106$; SE = 0.011; 95% CI: 0.086–0.128), while the estimate of the probability of a temporary emigrant remaining off of the study area between seasons was high ($\hat{\gamma}' = 0.777$; SE = 0.030; 95% CI: 0.712–0.830).

As indicated above, the 2-group heterogeneity model for detection probability was strongly supported. From the top-ranked model, the estimate of the probability of being in the lower detection probability group, $\hat{\pi}$, was 0.794 (SE = 0.020; 95% CI: 0.751–0.831). Detection probabilities for individuals in the lower detection probability group for the 3 secondary sampling periods averaged across years were 0.455, 0.512, and 0.369 for the June, July, and August sampling periods, respectively (all year- and month-specific estimates for each detectability group are presented in the Appendix). Extended out across the annual (primary) sampling

period, this would result in an average detection probability of 0.832. Thus, annual detection probability for even the lower detection probability group was, on average, high. For the group of more-easily-detected individuals, monthly detection probabilities were nearly perfect, averaging 0.994 (June), 0.995 (July), and 0.988 (August) for the 3 monthly sampling periods, June through August. The within-season pattern of average detectabilities (although variable among years) being highest in July is consistent with our assumption that individuals are still arriving in June and departing in August. Precision of detection probability estimates was high overall, with a mean coefficient of variation for the 150 group-specific sampling occasion estimates of 11%.

DISCUSSION

We provide a 25-y profile of demographic characteristics of the Humpback Whale population in the Glacier Bay-Icy Strait (GBIS) region. Our results suggested an average annual rate of increase of about 4.4%, which is slightly lower than an annual increase of 5.1% reported by Hendrix and others (2012) for 3 study regions of southeastern Alaska (including GBIS) between 1986 and 2008. Differences in population growth rate estimates between the studies could reflect differences in spatial and temporal scales of analyses or differences in analyses and how trends were assessed (see below). Even greater population increases have been reported for Humpback Whales along the Alaska Peninsula and Aleutian Islands (6.6%/y growth from 2001–2003; Zerbin and others 2006) and across the North Pacific (8.1%/y growth from early 1990s to early 2000s reported in Barlow and others 2011). Population growth in our study was not consistent across the entire time series, and increases have been especially sharp since 2002 (Fig. 2; approximately 7.7%/y).

Our estimates of population size tracked observed numbers of whales closely (Fig. 2), and reflect high detection probabilities achieved by this intensive monitoring effort. In recent years, about 90% of the estimated numbers of non-calf whales present in the study area were observed during annual surveys. Earlier in the study when whales were relatively scarce (< approximately 100 whales), detection probabilities and proportions of whales observed were

more variable. Survey effort also tended to be lower earlier in the study (Neilson and others 2012b).

Our estimates of detection probability, when extrapolated to an annual basis, were much higher, and our abundance estimates substantially lower, for GBIS than those reported by Hendrix and others (2012), who modeled movement rates, survival, and population dynamics of Humpback Whales in GBIS and 2 other southeastern Alaska study areas. We believe that an issue raised by Hendrix and others (2012), namely that of potential bias introduced by correlation between movement rates and detection probabilities, could partly explain this discrepancy. For example, if whales move from GBIS, where sampling effort and detection probabilities are relatively high, to study areas with lower detection probability where they remain for multiple years (as appears to be the case, based on our finding of high probability of emigrating whales remaining off the study area), the model of Hendrix and others (2012) could underestimate detection probabilities (and movement rates) and overestimate abundance for GBIS. Similar biases would be expected if whales moved outside of all sampled study areas, for example leaving the inside waters of the Alexander Archipelago for offshore waters in the Gulf of Alaska, a possibility not explored by Hendrix and others (2012). Rules about assignment of past and current locations of whales in the Hendrix and others (2012) analysis could also account for some differences between our population size estimates and theirs. Overall, we believe that Hendrix and others (2012) may accurately reflect the regional population trajectory and dynamics and that their findings highlight the importance of movement among feeding aggregations of Humpback Whales in southeastern Alaska. However, we believe that our analysis provides a more accurate portrayal of the status and dynamics of Humpback Whales in GBIS, which exploited a rich set of both within- and between-year resighting data. This assertion is supported by summaries of proportions of whales seen between consecutive years, which averaged 0.73 for GBIS across all years of our study (and averaged 0.80 since 2000). Such accurate sub-regional information is critical for informing management decisions that occur on

that scale (Glacier Bay National Park and Preserve).

Our survival-rate estimate of 0.948 (95% CI: 0.936–0.957) for GBIS was similar to, albeit slightly lower than, an earlier annual survival-rate estimate of 0.957 (95% CI: 0.943–0.967) of Mizroch and others (2004) for the greater southeastern Alaska region. Differences in survival estimates between the 2 studies could reflect differences in spatial scale (GBIS versus southeastern Alaska) or temporal windows (1985–2009 versus 1978–1996 in Mizroch and others 2004) of the 2 analyses. However, there were also substantial differences in analytical details between the 2 studies that could also account for discrepancies. For example, our survival estimate was derived from a model that allowed for heterogeneity in detection probability via a 2-group finite mixture, as well as multi-scale temporal variation in detection probability (within- and between-years), while Mizroch and others (2004) only considered annual variation in detection probability and variability related to sampling effort (spatial variation only considered at a scale larger than GBIS). It has been shown that such heterogeneity in detection probability among individuals, when present but unaccounted for, can introduce bias (either positive or negative) into survival-rate estimates (Pledger and others 2003). Our survival-rate estimate was also much lower than a recent estimate of 0.998 (95% credible interval: 0.985–0.999) provided by Hendrix and others (2012) for southeastern Alaska Humpback Whales during 1996–2008. Here too, differences could be due to differences in modeling approaches that could have resulted in a negative bias in detection probability in their study (see above); although differences could also have been partly due to differences in temporal and spatial extents of analyses.

We found that the rate of temporary emigration out of GBIS was low, and model selection results suggested that it was consistent among years. This finding supports results from multi-site studies that have suggested low and consistent movement rates out of the GBIS region into nearby areas of southeastern Alaska (Straley and others 2009; Hendrix and others 2012). We found that movement rates back into GBIS were also low, suggesting that whales that leave the study region tend to remain out of the

study region for multiple years. Nevertheless, movement into GBIS has probably been an important contributor to growth of the population in GBIS. For example, the increase in growth observed after 2002 might be explained in part by increased movement from nearby Frederick Sound and Lynn Canal during that time (Hendrix and others 2012).

The capture-recapture models applied here incorporate many salient features of the GBIS Humpback Whale monitoring data set (heterogeneous detectability, temporary emigration), and the data likely meet model assumptions adequately (such as population closure in mid-summer). Additional model complexities could yield greater realism and potentially improve inferences. Parameters could be included to account for misidentification of individuals (Lukacs and Burnham 2005; Yoshizaki and others 2009); however, given high overall detection probabilities, effects of small levels of misidentification would likely have little effect on inferences about population state and transition parameters. Indeed, the intensive ongoing monitoring effort of Humpback Whales in GBIS is yielding a rich detection-history database that is rarely achieved in capture-recapture studies. Future efforts at modeling these data might include incorporation of multiple age-classes (allowing for uncertain age-class assignment; Fujiwara and Caswell 2002; Pradel 2005) or exploiting the larger regional southeastern Alaska data set within a multi-state robust design framework to provide improved inferences about movement in this region (Nichols and Coffman 1999). Such analyses would further increase the value of the long-term intensive GBIS monitoring program for informing the conservation of Humpback Whales in southeastern Alaska.

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APPENDIX

Estimates of detection probability for each group from 2-group finite mixture robust-design model applied to sight-resight data of Humpback Whales in the Glacier Bay-Icy Strait region. The model for p included a group (mixture) effect, year and month effects, and a year \times month interaction term.

Year	Month	Mixture Group 1 (hard-to-detect)				Mixture Group 2 (easy-to-detect)			
		\hat{p}	\widehat{SE}	Lower 95% bound	Upper 95% bound	\hat{p}	\widehat{SE}	Lower 95% bound	Upper 95% bound
1985	June	0.313	0.171	0.087	0.685	0.990	0.033	0.144	1.000
	July	0.218	0.137	0.055	0.573	0.983	0.053	0.092	1.000
	August	0.058	0.050	0.010	0.269	0.929	0.209	0.026	1.000
1986	June	0.389	0.084	0.241	0.561	0.993	0.020	0.372	1.000
	July	0.457	0.087	0.297	0.626	0.994	0.015	0.441	1.000
	August	0.299	0.078	0.170	0.470	0.989	0.030	0.280	1.000
1987	June	0.479	0.075	0.338	0.623	0.995	0.014	0.472	1.000
	July	0.529	0.076	0.383	0.671	0.996	0.011	0.524	1.000
	August	0.209	0.061	0.114	0.351	0.982	0.048	0.200	1.000
1988	June	0.313	0.087	0.171	0.501	0.990	0.028	0.298	1.000
	July	0.291	0.084	0.156	0.478	0.989	0.031	0.278	1.000
	August	0.183	0.070	0.082	0.359	0.979	0.055	0.182	1.000
1989	June	0.272	0.086	0.137	0.468	0.988	0.035	0.222	1.000
	July	0.342	0.093	0.188	0.539	0.991	0.025	0.289	1.000
	August	0.203	0.077	0.091	0.394	0.982	0.052	0.158	1.000
1990	June	0.394	0.097	0.226	0.591	0.993	0.020	0.380	1.000
	July	0.394	0.097	0.226	0.591	0.993	0.020	0.380	1.000
	August	0.267	0.088	0.131	0.468	0.987	0.035	0.257	1.000
1991	June	0.437	0.095	0.267	0.624	0.994	0.016	0.430	1.000
	July	0.586	0.094	0.398	0.752	0.997	0.009	0.578	1.000
	August	0.536	0.095	0.353	0.710	0.996	0.011	0.529	1.000
1992	June	0.417	0.087	0.262	0.590	0.993	0.018	0.411	1.000
	July	0.778	0.075	0.600	0.891	0.999	0.004	0.769	1.000
	August	0.507	0.087	0.342	0.670	0.995	0.012	0.502	1.000
1993	June	0.425	0.085	0.272	0.593	0.994	0.017	0.410	1.000
	July	0.575	0.087	0.402	0.731	0.997	0.010	0.560	1.000
	August	0.296	0.079	0.167	0.468	0.989	0.030	0.280	1.000
1994	June	0.454	0.079	0.308	0.609	0.994	0.015	0.448	1.000
	July	0.475	0.079	0.326	0.628	0.995	0.014	0.469	1.000
	August	0.314	0.074	0.190	0.473	0.990	0.028	0.307	1.000
1995	June	0.401	0.072	0.271	0.547	0.993	0.019	0.386	1.000
	July	0.453	0.074	0.316	0.597	0.994	0.016	0.439	1.000
	August	0.246	0.063	0.143	0.390	0.986	0.039	0.228	1.000
1996	June	0.339	0.069	0.220	0.483	0.991	0.025	0.332	1.000
	July	0.737	0.068	0.585	0.847	0.998	0.005	0.729	1.000
	August	0.307	0.067	0.193	0.451	0.989	0.029	0.301	1.000
1997	June	0.402	0.069	0.277	0.542	0.993	0.019	0.398	1.000
	July	0.595	0.070	0.454	0.721	0.997	0.009	0.591	1.000
	August	0.521	0.070	0.385	0.654	0.996	0.012	0.517	1.000
1998	June	0.580	0.065	0.449	0.700	0.997	0.009	0.582	1.000
	July	0.679	0.062	0.548	0.788	0.998	0.006	0.681	1.000
	August	0.296	0.063	0.188	0.433	0.989	0.030	0.296	1.000
1999	June	0.548	0.062	0.427	0.665	0.996	0.010	0.554	1.000
	July	0.475	0.062	0.357	0.596	0.995	0.014	0.480	1.000
	August	0.378	0.061	0.268	0.503	0.992	0.021	0.382	1.000
2000	June	0.616	0.069	0.475	0.741	0.997	0.008	0.621	1.000
	July	0.372	0.071	0.246	0.518	0.992	0.021	0.378	1.000
	August	0.487	0.072	0.351	0.624	0.995	0.013	0.492	1.000
2001	June	0.542	0.061	0.423	0.657	0.996	0.011	0.542	1.000
	July	0.284	0.056	0.188	0.405	0.988	0.032	0.280	1.000
	August	0.591	0.060	0.470	0.702	0.997	0.009	0.592	1.000
2002	June	0.432	0.065	0.311	0.562	0.994	0.017	0.415	1.000
	July	0.458	0.066	0.334	0.587	0.994	0.015	0.442	1.000

APPENDIX. Continued.

Year	Month	Mixture Group 1 (hard-to-detect)				Mixture Group 2 (easy-to-detect)			
		\hat{p}	\widehat{SE}	Lower 95% bound	Upper 95% bound	\hat{p}	\widehat{SE}	Lower 95% bound	Upper 95% bound
2003	August	0.173	0.050	0.095	0.295	0.978	0.060	0.158	1.000
	June	0.430	0.058	0.322	0.546	0.994	0.017	0.431	1.000
	July	0.652	0.056	0.536	0.752	0.997	0.007	0.653	1.000
2004	August	0.515	0.058	0.401	0.626	0.996	0.012	0.516	1.000
	June	0.610	0.056	0.498	0.712	0.997	0.008	0.614	1.000
	July	0.581	0.056	0.468	0.686	0.997	0.009	0.585	1.000
2005	August	0.473	0.058	0.363	0.585	0.995	0.014	0.476	1.000
	June	0.583	0.049	0.486	0.674	0.997	0.009	0.583	1.000
	July	0.475	0.049	0.381	0.571	0.995	0.014	0.475	1.000
2006	August	0.253	0.043	0.178	0.347	0.986	0.037	0.248	1.000
	June	0.463	0.054	0.361	0.568	0.995	0.015	0.466	1.000
	July	0.672	0.050	0.567	0.761	0.998	0.006	0.675	1.000
2007	August	0.576	0.052	0.471	0.674	0.997	0.009	0.580	1.000
	June	0.500	0.053	0.398	0.602	0.995	0.013	0.506	1.000
	July	0.617	0.051	0.514	0.711	0.997	0.008	0.623	1.000
2008	August	0.525	0.053	0.422	0.626	0.996	0.011	0.531	1.000
	June	0.529	0.057	0.418	0.638	0.996	0.011	0.531	1.000
	July	0.595	0.056	0.483	0.698	0.997	0.009	0.597	1.000
2009	August	0.463	0.058	0.354	0.576	0.995	0.015	0.465	1.000
	June	0.506	0.049	0.411	0.601	0.995	0.012	0.513	1.000
	July	0.506	0.049	0.411	0.601	0.995	0.012	0.513	1.000
	August	0.556	0.049	0.460	0.649	0.996	0.010	0.563	1.000