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Assessing the abundance of Bristol Bay belugas with genetic mark-recapture methods

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Abstract

The Bristol Bay stock of beluga whales (*Delphinapterus leucas*) is genetically distinct and resides in Bristol Bay year-round. We estimated the abundance of this population using genetic mark-recapture, whereby genetic markers from skin biopsies, collected between 2002 and 2011, were used to identify individuals. We identified 516 individual belugas in two inner bays, 468 from Kvichak Bay and 48 from Nushagak Bay, and recaptured 75 belugas in separate years. Using a POPAN Jolly-Seber model, abundance was estimated at 1,928 belugas (95% CI = 1,611–2,337), not including calves, which were not sampled. Most belugas were sampled in Kvichak Bay at a time when belugas are also known to occur in Nushagak Bay. The pattern of genetic recaptures and data from belugas with satellite transmitters suggested that belugas in the two bays regularly mix. Hence, the estimate of abundance likely applies to all belugas within Bristol Bay. Simulations suggested that POPAN estimates of abundance are robust to most forms of emigration, but that emigration causes negative bias in both capture and survival probabilities. Because it is likely that some belugas do not enter the sampling area during sampling, our estimate of abundance is best considered a minimum population size.

Key words: beluga whales, *Delphinapterus leucas*, Bristol Bay, Bering Sea, genetic mark-recapture, POPAN, Program MARK.

Beluga whales (*Delphinapterus leucas*) are small cetaceans (≤5.5 m), that live in seasonally ice covered waters in arctic and subarctic regions. Populations are typically named for where they summer and, in Alaskan waters, five populations are commonly recognized by their summer ranges: Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chukchi Sea, and Beaufort Sea (Frost and Lowry 1990; O'Corry-Crowe *et al.*

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1997, 2002). The focus of this manuscript is the Bristol Bay population. The Bristol Bay population is largely restricted to an estuarine system characterized by large tidal fluctuations and turbid water. Satellite telemetry studies and aerial surveys show that Bristol Bay belugas are mostly located within Kvichak and Nushagak Bays during the ice-free seasons (Lowry *et al.* 2008; Citta *et al.* 2016*a*, *b*). When ice forms in winter, they often range into the northern and western regions of greater Bristol Bay (Citta *et al.* 2016*a*). However, even in winter, their distribution appears to be restricted to Bristol Bay (Citta *et al.* 2016*a*, *b*).

Understanding the abundance and trend of a population is important for management, especially for populations that may occupy restricted areas, exhibit low growth rates, are small, or potentially exposed to high levels of harvest or disturbance. Belugas in Bristol Bay are harvested by Alaska Natives and estimates of population abundance and trend are necessary to determine whether the harvest is sustainable. Bristol Bay also has the largest commercial sockeye salmon (*Oncorhynchus nerka*) fishery in the world; between 1992 and 2011, an average of 37.3 million sockeye salmon were commercially harvested annually (ADFG, unpublished data). Indeed, the impetus for studies of Bristol Bay belugas in the 1970s, 1980s, and early 2000s was concern that beluga predation was causing salmon stocks to decline. Belugas in Bristol Bay are known to consume both spawning salmon and outmigrating salmon smolt (Brooks 1955, Quakenbush *et al.* 2015). In order to interpret trends in salmon fisheries, information on the trend of beluga numbers, a primary salmon predator, is useful. There may also be incidental mortality of belugas due to the salmon fisheries (Frost *et al.* 1984), and potential impacts from climate change on the population are currently unknown. Finally, there is periodic interest in oil and gas development within Bristol Bay and mining within the headwaters of Bristol Bay rivers that may be detrimental to belugas, either by direct contamination or disturbance, or because development may have negative effects on prey.

Aerial surveys were conducted in Bristol Bay periodically between 1993 and 2016 (Lowry *et al.* 2008; Alaska Beluga Whale Committee [ABWC], unpublished data). Aerial surveys are prone to many sources of bias, which usually result in raw counts that underestimate the true number of animals. For example, belugas below the surface are unavailable to be sampled (availability bias) or observers might not see all the belugas at the surface due to wind or sun (perception bias). Counts from aerial surveys are commonly adjusted by "correction factors" in an attempt to calculate the true population size. However, estimating a correction factor is problematic at best. For example, many correction factors only consider availability bias, most do not incorporate measures of uncertainty, and most are based upon a small sample size that may not represent the entire population or may only reflect behavior at a particular time of year or location. Hence, it is difficult to determine how counts from aerial surveys relate to true abundance and independent methods for estimating abundance and trends are useful.

A promising technique for estimating abundance of cetaceans involves collecting skin samples from many individuals for genetic identification. In effect, molecular markers are used to genetically identify individual belugas and repeated sampling allows genetic "recaptures" to be analyzed within a mark-recapture framework. Estimates of abundance based upon mark-recapture methods are not reliant on estimating correction factors and provide an independent estimate of abundance. In addition to abundance, mark-recapture data can also be used to estimate survival rates, movements between population segments, recruitment into the population, and trends in abundance.

The beluga population in Bristol Bay is well-studied and provides a good system for the application of genetic mark-recapture methods because (1) there are aerial surveys of abundance that allow for an independent comparison between aerial surveys and genetic mark-recapture methods; (2) there are satellite tagging studies that provide information on how beluga whales move between inner bays within greater Bristol Bay and how this may affect the sampling of belugas and genetic mark-recapture estimates of abundance, and (3) ultimately it may be possible to use the genetic mark-recapture estimate of abundance to correct estimates of abundance from aerial surveys (*i.e.*, use the mark-recapture estimate to develop a correction factor for aerial surveys).

Here we report on a genetic mark-recapture study conducted in Bristol Bay from 2002 to 2011. We provide a "best" estimate of beluga abundance in Bristol Bay. We then assess the reliability of our estimate using empirical data on the movements of belugas with satellite transmitters and simulations of beluga movement patterns that may cause our estimator to be biased or yield confidence intervals with poor coverage. We also compare our best estimate of abundance for Bristol Bay belugas with correction factors that have been developed for aerial surveys conducted there. Our results are timely because the North Atlantic Marine Mammal Commission (NAMMCO) is reviewing the status of all beluga stocks worldwide.

Methods

Sampling Methods

We sampled belugas in two bays within greater Bristol Bay: (1) Kvichak Bay, near the community of Levelock, during 2002–2011, and (2) Nushagak Bay, between Dillingham and the mouth of the Snake River, in 2008 and 2011 (Fig. 1). Immediately following "break-up," when the river ice washes out into the bay, belugas are known to travel up the rivers to forage upon rainbow smelt (*Osmerus mordax*) and outmigrating salmon smolt (*Oncorhynchus* spp.; Brooks 1955). Local observers in Levelock would notify us when belugas had arrived and when ice conditions were conducive to boating, and we would begin sampling. There was one sampling session per year that typically lasted 3–7 d. When the smolt/smelt runs slowed, belugas would cease migrating up the river and would remain in the outer bay where the water was too deep to effectively sample them. We typically used two open aluminum boats with outboard motors. Each boat had a driver and a beluga sampler was located in the bow. Boat drivers were Alaska Native beluga hunters who knew where to find belugas, how to get close to them, and how to navigate the mud bars during extreme tide cycles.

The beluga sampler had a jab stick or pole that was 1.8–2.4 m long. The pole has a threaded bolt in one end to allow metal biopsy tips to be attached and detached. Biopsy tips are hollow; the outer rim has a cutting edge that allows the tip to penetrate the skin and prongs inside retain the skin biopsy. The end of the pole provides a stop so that the biopsy tip cannot penetrate deeper than the length of the tip (20–40 mm). Thickness of the skin and blubber along the back and side is ~6 cm or greater, so there was little risk of harming the beluga. Biopsy poles were tied to the boat with a long, thin line so that the pole could be thrown and retrieved. We initially experimented with other methods of collecting skin biopsies, such as using crossbows with biopsy tips mounted on crossbow bolts. We found that beluga hunters had no trouble

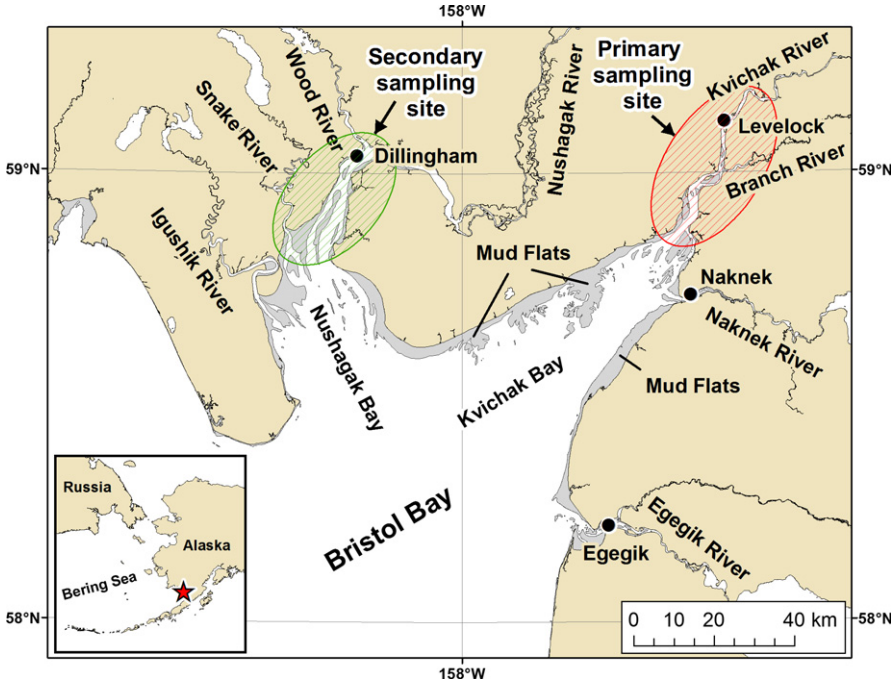

Figure 1. Bristol Bay study area; crosshatching shows the primary (red: Kvichak) and secondary (green: Nushagak) sampling locations.

getting close to belugas with boats and that using a pole to collect biopsies was much faster and safer that using a crossbow in a moving boat.

At the end of each day, the biopsy samples were removed from the tips and the skin was either placed in a solution of 20% dimethyl sulfoxide (DMSO) saturated in salt (NaCl) or frozen. A label was placed inside the bottle and the outside of the bottle was also labeled. All used tips were washed with soap and water, rinsed, dipped in bleach, and placed in a container of chlorohexidine diacetate solution for at least 20 min.

Genetic Methods

mtDNA extraction and amplification—Total cellular DNA was isolated using QIAquick Dneasy kits (QIAGEN Ltd.) or salt extraction methods. The concentration and quality of resultant DNA was estimated by spectrophotometry. Each sample was screened for polymorphism within seven unlinked, hypervariable microsatellite loci previously demonstrated to consistently amplify, be inherited in a Mendelian fashion, and have no null alleles or evidence of allelic dropout in beluga whales (O'Corry-Crowe *et al.* 2010). The original project design examined eight microsatellite loci; however, one locus, CS 468/469, proved difficult to genotype in the lab and was discontinued after 2008. PCR products were run on an Applied Biosystems Genetic Analyzer, and analyzed using Genemapper v3.7 software (Applied Biosystems). The binning option in Genemapper was used to automatically call allele sizes, although

all genotypes were inspected visually for amplification quality and calling accuracy. Roughly 10% of samples were also chosen for genotype replication (both at the PCR and screening stage).

Genetic matching and the likelihood of scoring errors—There are two types of errors that may occur when determining if two genotyped samples are from the same individual (*i.e.*, genetic matching). First, we may erroneously conclude that two samples come from the same beluga when they actually do not. Different individuals may share the same genotype at several independent loci, especially if allelic diversity within loci is low. However, if enough loci with high allelic diversity are screened, the probability that two individuals will have the same multilocus genotype, known as the probability of identity (P_{ID}; *e.g.*, Waits *et al.* 2001), becomes very low. If P_{ID} is one or two orders of magnitude lower than the inverse of population size, then the project design has sufficient discriminating power so that each individual is likely to be unique for the loci screened. When P_{ID} is high the false identification of "recaptures" artificially inflates the recapture rate and results in estimates of abundance that are biased low and levels of precision that are biased high (*e.g.*, Mills *et al.* 2000). We used the program Cervus (Kalinowski *et al.* 2007) to conduct genetic matching and to estimate P_{ID} and employed locus jackknifing to determine the minimum number of loci needed to discriminate among individuals. This equates to the minimum number of loci required where an exact match among samples indicates they are from the same individual. We also compared our multilocus estimates of P_{ID} to those estimated from an independent set of Bristol Bay samples collected prior to this study.

The second type of error occurs when we conclude that two samples came from different individuals when they are actually from the same animal. Genotyping errors due to allelic dropout, null alleles, or miss-calls may result in situations where two samples from the same animal differ at one or two loci. This results in the overestimation of unique individuals, which artificially decreases the recapture rate and results in inflated estimates of abundance (*e.g.*, Creel *et al.* 2003, McKelvey and Schwartz 2004). If genotyping error rates are low and sufficient loci are screened we expect that most errors would cause samples from the same individual to mismatch (differ) at only one locus. By contrast, if enough loci are screened, and thus P_{ID} is low, we expect different individuals to differ at two or more loci (Kalinowski *et al.* 2006). We used the program MM-Dist (Kalinowski *et al.* 2006) to distinguish between mismatches due to (1) genotyping errors between two samples and (2) genotype differences between two individuals. The program calculates probability distributions for how many loci individuals in a population will differ by. We used independent data from the Bristol Bay subsistence harvest to estimate allelic diversity, and probabilities of mismatches at different numbers of loci.

Mark-recapture Analysis

The theory for estimating abundance for open populations (*i.e.*, populations with gains and losses due to birth, death, emigration, and immigration) was developed by Jolly (1965) and Seber (1965); the models they developed became known as Jolly-Seber (JS) models. The original JS model has been reformulated a number of times (*e.g.*, Burnham 1991, Pradel 1996), with each form estimating slightly different parameters and having different assumptions.

Here, we use a version of the JS model that Schwarz and Arnason (1996) developed and originally implemented in the computer package POPAN. Schwarz and Arnason directly model the size of N, which denotes the "super-population"—a hypothetical

population that serves as a source of individuals for the population of interest. The super-population consists of the pool of all the animals that entered the population during the study, through birth and immigration, and includes animals that leave the population through death or emigration. POPAN models have four parameters, p_i, ϕ_i, b_i, and N (Fig. 2; Schwarz and Arnason 1996, 2017). The parameter p_i is the probability of capture of both marked and unmarked animals that are alive at occasion i, p_i is the survival probability of animals between occasions i and $i + 1$, and b_i is the probability that an animal from the super-population would enter (by immigration or birth) the sampled population between occasions i and $i + 1$ and would also survive to $i + 1$. N, the size of the super-population, is not specific to a specific period but is the total number of animals that existed during the study. The number of animals entering the population at time i, denoted B_i, is equal to N^*b_i. Furthermore, for K sampling occasions, $N = B_0 + B_1 + B_2 + \ldots + B_{K-1}$. Here, B_0 is the number of animals that were present in the sampled population just prior to sampling. The super-population model is of particular use for our situation because the estimate of N is not for the region being sampled (*e.g.*, Kvichak or Nushagak Bays), but for the larger super-population (*e.g.*, greater Bristol Bay). A key feature of the model is that members of the super-population need not be present within the sampling area at all times. The POPAN JS model is also available in Program MARK (White and Burnham 1999), which we used for model fitting.

The model makes the following assumptions: (1) animals retain their marks and marks are read properly; (2) sampling occasions are instantaneous and there is no birth, death, emigration, or immigration within sampling periods; (3) survival probabilities are the same for marked and unmarked animals; (4) the probability of capture is the same for marked and unmarked animals within sampling periods; (5) the size of the study area does not change over time; if the size of the study area changes, we may draw from a larger or smaller super-population and this would change the population size. More information on the super-population approach and POPAN models can be found in section 18.3 of Williams *et al.* (2002) and Schwarz and Arnason (2017).

The POPAN model is appropriate for our study design because most samples were collected in Kvichak Bay, our primary sampling area, at a time when belugas are also known to occur in Nushagak Bay. Due to logistic constraints, we only sampled in Nushagak Bay in 2008 and 2011. This is not a problem as long as all belugas have

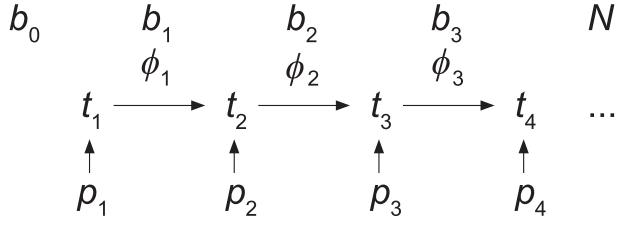

Figure 2. Process model for the POPAN parameterization of the Jolly-Seber model. For each sample occasion (t), parameter p_i is the probability of capture at occasion i; φ_i is the probability an animal surviving between occasions i and $i + 1$; and b_i is the probability that an animal from the super-population (N) would enter the population between occasions i and $i + 1$ and survive to the next sampling occasion, $i + 1$. This figure is adapted from Schwarz and Arnason (2017).

an equal chance of occurring in Kvichak Bay during sampling periods. Belugas are known to travel back and forth between Kvichak and Nushagak Bays and can do so in as little time as a day (Citta *et al.* 2016*a*). However, movement into and out of the sampling area (*i.e.*, temporary emigration) and how such movement may affect the POPAN model is largely unknown.

If temporary emigration is completely random, estimates of N should still be unbiased (Burnham 1991), although precision should decline as temporary emigration increases (Kendall *et al.* 1997). However, the probability that a beluga is outside the study area at time $i + 1$ may depend upon a beluga's location at time i (*i.e.*, a Markov process). Kendall *et al.* (1997) examined the role of Markovian temporary emigration on survival and capture probabilities and found that they were biased low if animals outside the sample area were more likely to remain outside during the next sampling period. However, the model used by Kendall *et al.* (1997) was not a POPAN model and did not estimate N for an open population. Another scenario results from the fact that belugas often travel in groups. Although the membership of groups is not well understood, it is likely that groups of females with calves travel together. As such, if one member of a group is outside the sample area, then so is the entire group. Hence, the probability an animal is a temporary emigrant may not be completely random (*i.e.*, lack independence) over time, such as with Markovian temporary emigration, and/or also not be completely random between individuals, if belugas travel in groups.

Kendall *et al.* (1997) provided methods for identifying if temporary emigration is present and if its form is random or Markovian. These methods rely on Pollock's Robust Design (Pollock 1982), where there are multiple primary periods separated by long periods of time and multiple secondary periods or capture occasions within each primary period (see description in Kendall *et al.* 1997 or Williams *et al.* 2002). Although our data collection adheres to the Robust Design in that we have multiple sampling days (secondary periods) within each year (years are primary periods), we typically do not recapture whales on different days within years. As such, there was not enough data to apply the Robust Design or use the methods of Kendall *et al.* (1997) to identify temporary emigrants. Although we cannot formally test for temporary emigration, it almost certainly exists in our study system. To explore the effects of different forms of temporary emigration, we simulated data sets generated under different patterns of emigration and then fit POPAN models to those data.

We examined five sets of simulations. All simulations assumed the true population size was 2,000 belugas, the approximate number of belugas that we think occur within the population, and were repeated for three levels of encounter probability ($p = 0.05$, 0.10, and 0.15). The first set of simulations assumed there was no temporary emigration. The second set of simulations assumed that there was random temporary emigration; we examined two levels of random temporary emigration, 0.5 and 0.75. In effect, each animal had a 50%, and 75% chance of being outside the study area in each sampling occasion. The third set of simulations assumed that emigration was random, but that belugas emigrated in groups of 50. We have no knowledge of how large groups are, so the choice of 50 is arbitrary. However, this will let us assess how a lack of independence among animals may affect our estimate of abundance. Again, we examined two levels of random temporary emigration, 0.5, and 0.75. The fourth set of simulations assumed that temporary emigration was Markovian. Belugas were randomly assigned a starting state (*i.e.*, inside or outside the sample area) with a probability of 0.5 and then given a 0.75 probability that they remained in the same state at time $i + 1$ as they were at time i. Last, we simulated the effects of Markovian

temporary emigration on groups of belugas. Again, we assumed that the probability of remaining within the prior state was 0.75 and that belugas emigrated in groups of 50. To examine how survival may affect estimation of abundance, we repeated all simulations with two levels of annual survival probability, 0.97 and 0.95. This population of belugas is thought to be increasing or stable (Lowry *et al*. 2008; ABWC, unpublished data); as such, survival rates are likely high. Assuming a population size of 2,467, the current Potential Biological Removal (PBR)[2] for this population is 59 belugas (Muto *et al*. 2016). For our simulated population size (2,000), removing 59 belugas annually would yield an annual survival probability of approximately 0.97. To determine how lower survival rates may affect estimation, we repeated our simulations with an annual survival probability of 0.95. Each simulation was repeated 1,000 times and each simulated data set was fit to a POPAN model. Mean parameters were calculated as the mean value of the 1,000 POPAN parameter sets. Confidence intervals (95%) were obtained by ordering the output and then selecting values at the upper and lower 2.5% tails with the data. For 1,000 simulations, the lower 95% confidence interval is the 25th largest observation and the upper 95% confidence interval is the 975th largest observation. Simulated data sets were generated in R (R Core Team 2017) and were fit using package *Rmark*, version 2.2.2 (Laake 2013), as an interface between R and Program MARK.

To explore how belugas may move into and out of the study area and determine which simulations may be appropriate, we also examined the pattern of genetic recaptures by bay and used movement data available from belugas tagged with satellite-linked transmitters to examine how many tagged belugas entered the sampling area while sampling was occurring. Prior to plotting the location data, we filtered it by removing locations resulting in velocities greater than a fixed threshold (McConnell *et al.* 1992); a threshold of 1.78 m/s was chosen after considering a variety of sources. Smith and Martin (1994) found belugas traveling at 1.4 m/s, Lydersen *et al.* (2001) documented 1.67 m/s as a maximum sustained velocity, and Richard *et al.* (2001) documented velocities of 1.17–1.78 m/s, which included the fastest observed velocity in any of the studies.

Results

From 2002 to 2011, 695 skin biopsies were collected from belugas in May (Table 1). Sampling methods and efficiency improved and the number of biopsies collected increased over time, as did the number of biopsies allowed by research permits. The number of biopsies we were allowed to collect increased from 30/yr during 2002–2005, to 100/yr during 2006–2009, and then to 350/yr after 2010. The low number of biopsies collected in 2009 (n = 17) occurred because few belugas were found in Kvichak Bay that year. Most of the biopsies were collected from belugas in Kvichak Bay (n = 628); fewer samples (n = 67) were collected in Nushagak Bay in 2008 and 2011. As stipulated by our permits, no newborn calves were sampled.

Within these samples, we identified 516 genetically unique belugas, 468 in Kvichak Bay and 48 in Nushagak Bay (Table 2). There were 85 recapture events in

[2]PBR is defined by the Marine Mammal Protection Act as the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population. See Wade and Angliss (1997) for information on how the PBR is calculated.

Table 1. Samples collected in the Kvichak Bay and Nushagak Bay sampling areas (see Fig. 1) during May 2002–2011.

Year	Kvichak Bay	Nushagak Bay	Total
2002	6		6
2003	5		5
2004	30		30
2005	13		13
2006	58		58
2007	93		93
2008	102	30	132
2009	17		17
2010	148		148
2011	156	37	193
Total	628	67	695

separate years, from 75 different belugas. Seventy-six recapture events occurred in Kvichak Bay and nine occurred in Nushagak Bay. A total of 67 belugas were recaptured once, six were recaptured twice, and two were recaptured three times. Eleven recaptures were based upon exact matches when only four loci were available to be compared among sample pairs, 16 were based upon five loci, 25 were based upon six loci, and 33 were based upon all seven loci.

Eight of our recaptures (*i.e.*, matching samples) were "fuzzy matches" that were the same at all but one locus. As stated in the Methods, if P_{ID} is not very low, then there is a higher likelihood of incorrectly identifying two different individuals as the same individual. Within our sample of recaptures, the P_{ID} averaged 2.3×10^{-6} and ranged from 3.6×10^{-11} to 7.6×10^{-5} (Table 3). For as few as four loci, P_{ID} averaged 1.9×10^{-5}. Similarly, in the jackknife analysis we found that the P_{ID} among matched pairs was low when as few as four loci were compared (mean $P_{ID} = 1.18 \times 10^{-4}$; Table 3). We suspect that the jackknife estimates of P_{ID} in Table 3 are biased high because we found that when two beluga samples matched at four loci, they always matched at

Table 2. Unique belugas identified in Kvichak Bay and Nushagak Bay sampling areas (see Fig. 1) and the location of between-year recapture events, during May 2002–2011. Note that there were 85 recapture events in separate years, from 75 different belugas. A total of 67 belugas were recaptured once, 6 were recaptured twice, and 2 were recaptured three times.

	Unique belugas			Recapture events		
Year	Kvichak Bay	Nushagak Bay	Total unique	Kvichak Bay	Nushagak Bay	Total recaptures
2002	6		6			
2003	5		5			
2004	28		28			
2005	11		11			
2006	46		46	5		5
2007	70		70	3		3
2008	74	25	99	21		21
2009	15		15	2		2
2010	115		115	16		16
2011	98	23	121	35	3	38
Total	468	48	516	82	3	85

many more. Based upon the independent sample of harvested belugas ($n = 66$), MM-DIST calculated that approximately 95% of belugas in Bristol Bay will differ at six or more loci. Hence, when two biopsies differ at a single locus out of the seven screened, the overwhelming probability is that they came from the same animal, thereby providing justification for including "fuzzy matches" as recaptures.

Mark-recapture Estimate

With relatively few recaptures, the POPAN models were not capable of supporting time dependent structure. Although the capture probability (p_i) and the probability that animals enter the sampled population from the super-population (b_i) almost certainly vary over time, models that included temporal variation in these parameters either did not converge or produced results that were nonsensical. Hence, we relied on a time-invariant model. Within the time-invariant model, survival probability (φ_i) was estimated to be 1.0 (95% CI = 1.0–1.0), p_i was 0.062 (95% CI = 0.050–0.075), and b_i was 0.108 (95% CI = 0.106–0.111). The estimate of b_i translates into an average annual probability of 0.110 (95% CI = 0.106–0.111) that animals from the super-population enter the sampled population. The super-population was estimated to consist of 1,928 belugas (95% CI = 1,611–2,337).

Excluding data collected in Nushagak Bay had little effect on the estimate of abundance. After removing Nushagak data, the super-population was estimated to consist of 1,801 belugas (95% CI = 1,491–2,207). Likewise, removing "fuzzy matches" from the data set had little effect on the estimate of abundance. After removing fuzzy matches, the super-population was estimated to consist of 2,145 belugas (95% CI = 1,771–2,631). This estimate does not include the number of newborn calves, as permits stipulated that no newborn calves be sampled.

Simulations

Simulations indicated that estimates of abundance from the POPAN model were largely robust to the forms of emigration that we considered (Tables 4, 5). In general, estimates of abundance were within 200 belugas of the true value (*i.e.*, a simulated population of 2,000 belugas) and 95% confidence limits contained the true value. For non-Markovian patterns of emigration, abundance was biased high, and for Markovian patterns, abundance was biased low. The largest bias occurred when belugas only had a 25% chance of being within the sampling area during any year and

Table 3. Probability of identity (P_{ID}) as a function of the number of loci amplified for the mark-recapture data set (*i.e.*, 7-locus) and from the jackknife estimator that simulates randomly dropping loci.

Data set	Number loci	n	Average P_{ID}	Minimum P_{ID}	Maximum P_{ID}
7-locus	4	11	1.9×10^{-5}	1.9×10^{-7}	7.6×10^{-5}
	5	16	1.3×10^{-6}	3.5×10^{-9}	4.3×10^{-7}
	6	25	2.9×10^{-7}	2.9×10^{-10}	1.5×10^{-6}
	7	33	4.0×10^{-8}	3.6×10^{-11}	6.1×10^{-7}
Jackknife	4	108	1.2×10^{-4}	2.9×10^{-7}	9.0×10^{-10}
	5	99	2.9×10^{-6}	1.2×10^{-8}	2.5×10^{-5}
	6	81	3.7×10^{-7}	4.2×10^{-10}	2.6×10^{-6}
	7	91	3.7×10^{-8}	2.9×10^{-11}	3.2×10^{-7}

Table 4. Estimates of abundance (N), capture probability (p), and survival (ϕ) for different simulations of beluga movement into and out of the sampling area. All simulations assume a population size of 2,000 and an annual survival probability of 0.97. Estimates are bolded when 95% confidence limits do not cover the true value.

Simulated emigration pattern	Description	Probability of being within sampling area	True p	Estimated N (95% CI)	Estimated p (95% CI)	Estimated ϕ (95% CI)
No emigration	No emigration; entire population is within the sampling area	1	0.05	2083 (1782-2448)	0.05 (0.04-0.06)	0.96 (0.92-0.99)
		1	0.1	2030 (1887-2229)	0.1 (0.09-0.11)	0.97 (0.95-0.98)
		1	0.15	2013 (1918-2117)	0.15 (0.14-0.16)	0.97 (0.96-0.98)
Random temporary	Belugas move in and out of the sampling area randomly; groups have a probability of 0.5 or 0.25 of being within the sampling area.	0.5	0.05	2192 (1593-3117)	0.03 (0.02-0.04)	0.95 (0.85-1)
		0.5	0.1	2083 (1777-2477)	0.05 (0.04-0.06)	0.96 (0.92-0.99)
		0.5	0.15	2046 (1833-2307)	**0.08 (0.07-0.09)**	0.96 (0.94-0.99)
		0.25	0.05	2438 (1282-4711)	**0.02 (0.01-0.03)**	0.92 (0.68-1)
		0.25	0.1	2198 (1593-3128)	**0.03 (0.02-0.04)**	0.95 (0.85-1)
		0.25	0.15	2110 (1706-2684)	**0.04 (0.03-0.05)**	0.96 (0.90-0.99)
Random group	Belugas move in and out of the of sampling area randomly in groups of 50; each group has a probability of 0.5 or 0.25 of being within the sampling area.	0.5	0.05	2182 (1574-3120)	**0.03 (0.02-0.04)**	0.94 (0.85-1)
		0.5	0.1	2086 (1740-2533)	**0.05 (0.04-0.07)**	0.96 (0.91-1)
		0.5	0.15	2059 (1820-2355)	**0.08 (0.07-0.09)**	0.96 (0.93-1)
		0.25	0.05	2463 (1260-5165)	**0.02 (0.01-0.04)**	0.91 (0.64-1)
		0.25	0.1	2244 (1558-3315)	**0.03 (0.02-0.05)**	0.94 (0.81-1)
		0.25	0.15	2157 (1614-2862)	**0.04 (0.03-0.06)**	0.95 (0.86-1)
Markovian	Initial state assignment (in or out of sampling area) is random; then a 0.75 probability of remaining in prior state and a 0.25 probability of switching.	See description	0.05	1980 (1431-2725)	0.04 (0.02-0.06)	0.91 (0.80-0.99)
		See description	0.1	1988 (1676-2334)	**0.07 (0.06-0.09)**	0.92 (0.87-0.97)
		See description	0.15	1977 (1781-2161)	**0.11 (0.09-0.13)**	**0.92 (0.89-0.95)**
Markovian group	Same as Markovian movement (see above), except belugas move in groups of 50.	See description	0.05	1998 (1437-2739)	0.04 (0.02-0.06)	0.91 (0.79-1)
		See description	0.1	1991 (1614-2381)	**0.07 (0.06-0.09)**	0.91 (0.85-0.98)
		See description	0.15	1987 (1706-2300)	**0.11 (0.09-0.13)**	**0.92 (0.87-0.96)**

Table 5. Estimates of abundance (N), capture probability (p), and survival (ϕ) for different simulations of beluga movement into and out of the sampling area. All simulations assume a population size of 2,000 and an annual survival probability of 0.95. Estimates are bolded when 95% confidence limits do not cover the true value.

Simulated emigration pattern	Description	Probability of being within sampling area	True p	Estimated N (95% CI)	Estimated p (95% CI)	Estimated Φ (95% CI)
No emigration	No emigration; entire population is within the sampling area	1	0.05	2082 (1772-2495)	0.05 (0.04-0.07)	0.94 (0.89-0.97)
		1	0.1	2035 (1876-2208)	0.1 (0.09-0.11)	0.95 (0.92-0.96)
		1	0.15	2015 (1904-2121)	0.15 (0.14-0.16)	0.95 (0.93-0.96)
Random temporary	Belugas move in and out of the sampling area randomly; groups have a probability of 0.5 or 0.25 of being within the sampling area.	0.5	0.05	2165 (1543-2972)	**0.03 (0.02-0.04)**	0.93 (0.83-0.98)
		0.5	0.1	2071 (1750-2476)	**0.05 (0.04-0.07)**	0.94 (0.89-0.97)
		0.5	0.15	2047 (1842-2284)	**0.08 (0.07-0.09)**	0.94 (0.92-0.97)
		0.25	0.05	2371 (1243-4700)	**0.02 (0.01-0.03)**	0.90 (0.68-0.99)
		0.25	0.1	2163 (1564-3080)	**0.03 (0.02-0.04)**	0.93 (0.82-0.98)
		0.25	0.15	2093 (1673-2656)	**0.04 (0.03-0.05)**	0.94 (0.87-0.97)
Random group	Belugas move in and out of the of sampling area randomly in groups of 50; each group has a probability of 0.5 or 0.25 of being within the sampling area.	0.5	0.05	2167 (1534-3080)	**0.03 (0.02-0.04)**	0.93 (0.80-0.99)
		0.5	0.1	2083 (1748-2530)	**0.05 (0.04-0.07)**	0.94 (0.89-0.98)
		0.5	0.15	2047 (1795-2313)	**0.08 (0.07-0.09)**	0.94 (0.90-0.98)
		0.25	0.05	2395 (1212-4855)	**0.02 (0.01-0.04)**	0.89 (0.60-1)
		0.25	0.1	2199 (1500-3185)	**0.03 (0.02-0.05)**	0.92 (0.79-1)
		0.25	0.15	2143 (1620-2851)	**0.04 (0.03-0.06)**	0.93 (0.84-1)
Markovian	Initial state assignment (in or out of sampling area) is random; then a 0.75 probability of remaining in prior state and a 0.25 probability of switching.	See description	0.05	1919 (1376-2612)	0.04 (0.02-0.06)	0.90 (0.879-0.97)
		See description	0.1	1918 (1632-2244)	**0.07 (0.06-0.09)**	0.89 (0.85-0.95)
		See description	0.15	1925 (1730-2121)	**0.11 (0.09-0.13)**	**0.90 (0.87-0.94)**
Markovian group	Same as Markovian movement (see above), except belugas move in groups of 50.	See description	0.05	1954 (1387-2765)	0.04 (0.02-0.06)	0.89 (0.76-0.98)
		See description	0.1	1926 (1558-2325)	**0.07 (0.05-0.09)**	0.90 (0.83-0.96)
		See description	0.15	1934 (1655-2227)	**0.11 (0.09-0.13)**	0.90 (0.86-0.95)

capture probabilities were lowest (0.05); in these scenarios, abundance was biased high by as many as 463 belugas (*i.e.*, 23%). However, in all cases, confidence limits widened to include the true value. In contrast, capture and survival probabilities were biased low for all forms of temporary emigration. The confidence limits for capture probability generally did not include the true value (Tables 4, 5). The confidence limits for survival probability sometimes did not include the true value for forms of Markovian emigration.

Movement Between Sampling Areas

Evidence of movement between the Kvichak and Nushagak sampling areas comes from satellite tags deployed in Nushagak Bay in the spring of 2008 and 2011 and the limited amount of genetic sampling that was also conducted there in 2008 and 2011 (Table 1). In 2008, 10 belugas were tagged in Nushagak Bay from 17 to 21 May and genetic sampling in Kvichak Bay occurred from 17 to 19 May. Two belugas tagged in 2008 were males and the rest were females. Of the belugas tagged in 2008, 50% (5 of 10) moved into the genetic sampling area during 23–28 May (*i.e.*, 2–5 d after the genetic sampling period; Fig. 3). In 2011, belugas were tagged on 18 and 20 May in Nushagak Bay and genetic sampling in Kvichak Bay occurred from 24 to 30 May. One of the belugas tagged in Nushagak Bay moved into the genetic sampling area on 24 May and was present until 9 June. This tagged beluga was not seen or biopsied.

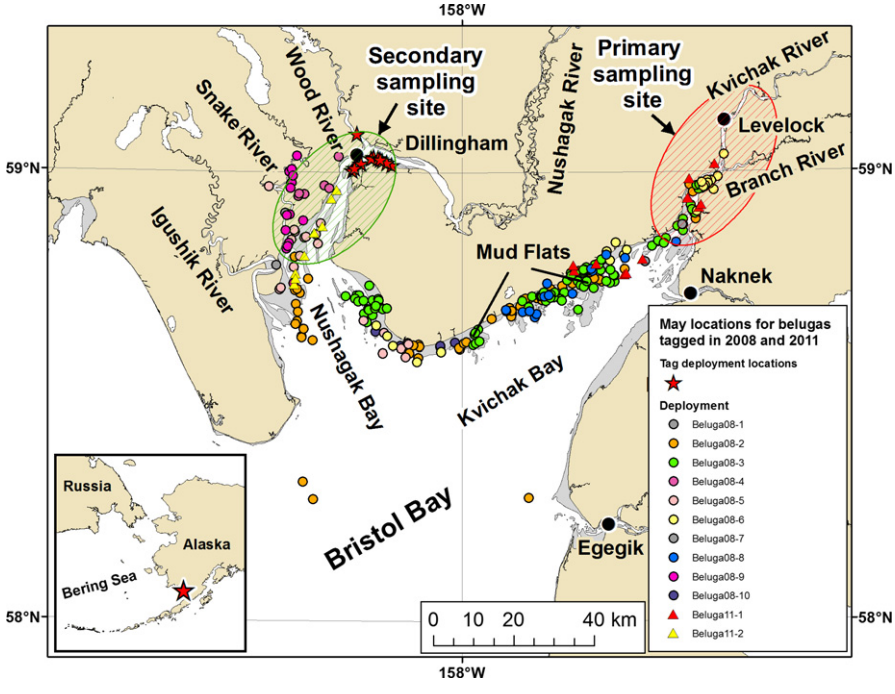

Figure 3. Locations of 12 belugas tagged in Nushagak Bay in May of 2008 ($n = 10$) and May of 2011 ($n = 2$).

Of the 25 belugas biopsied in Nushagak Bay in 2008 (Table 2), six were later recaptured in Kvichak Bay, one in 2010 and five in 2011. No belugas from the Kvichak were found in the Nushagak in 2008, however, two whales biopsied in the Kvichak were found in the Nushagak in 2011.

Discussion

Empirical Estimate of Abundance

Most of our sampling was in Kvichak Bay, thus we need to know if the estimate of abundance more appropriately applies to belugas within Kvichak Bay or belugas within all of Bristol Bay. Based upon the movements of satellite tagged belugas and the movements of genetically marked belugas, it appears that belugas readily move back and forth between bays. Likewise, the estimate of abundance that included samples from both sample areas (N = 1,928) was similar to that when only considering the Kvichak sampling area (N = 1,801). As such, we conclude that the estimate of abundance more appropriately applies to the entire population rather than just belugas found in the Kvichak River.

The high survival rate we estimated from our empirical data was clearly not possible. Mark-recapture models often have difficulty estimating parameters that are near the limits or boundaries of what is possible (*e.g.*, values of 0 or 1). With a relatively low recapture rate, the POPAN model simply cannot distinguish a very high survival rate from 1. In fact, some of our simulations that assumed survival was 0.97 and 0.95 had confidence limits that included 1, meaning that at least 2.5% of those simulations had survival rates equal to 1 (Tables 4, 5). When estimating abundance with our empirical data, fixing survival at lower values only slightly increases our estimate. If we fix the value of survival at 0.97, the estimated size of the super-population increases from 1,928 belugas (95% CI = 1,611–2,337) to 1,953 (95% CI = 1,630–2,370). If we fix the value of survival to 0.95, abundance further increases to 1,968 (95% CI = 1,641–2,390). Such increases in abundance are not biologically significant.

Exactly what time period the estimate of abundance applies to is also an important consideration. The estimate provided above applies to all belugas that were present during the study. Due to mortality, the number present at the end of the study should be less than the number present during the entire study period. However, due to immigration, this is not the case. In our model, time-specific estimates of abundance increased from 50 (95% CI = 23–108) belugas during the first sampling period to 1,925 belugas (1,597–2,320) in the last sampling period, only three belugas less than that for the entire study period. The majority of this increase is due to immigration, not birth. To illustrate how less than perfect survival affects estimation, we repeated this analysis and set survival to 0.97. Time-specific estimates of abundance increased from 46 belugas (95% CI = 21–99) in the first sampling period to 1,726 belugas (95% CI = 1,430–2,083) in the last sampling period. The overall super-population estimate is 1,982 belugas (95% CI = 1,430–2,083), approximately 250 belugas more than the final time-specific estimate. In both cases, the growth of the population is mostly due to immigration and not birth. We would need a much higher estimate of encounter probability to reliably estimate abundance for each sampling period; however, the overall population estimate in our case is equal to the final population estimate. Because the population was growing due to immigration, we

think it unlikely that all belugas were exposed to sampling risk. As such, all of these estimates are expected to be biased low by an unknown amount.

We were concerned that collecting biopsies may cause some belugas to abandon sampling areas, resulting in the probability of recapture being lower than the probability of initial capture. Current forms of the POPAN model do not allow the probability of recapture to differ from the initial probability of capture. We suspect that the probability of capture declines on days following the initial capture event. A total of 96 belugas were recaptured within years; however, only 19 of these belugas were resampled on different days within the same year. Belugas typically enter rivers and shallow areas with incoming tides and then leave with the outgoing tide; we suspect that some groups we sample do not come back up the rivers until we leave. However, for this to affect our estimate of abundance, avoidance would have to extend across years and this is highly unlikely. First, belugas are chasing seasonal food sources up the rivers; we are sampling belugas where they are finding food and belugas are found within our sampling sites every year. Second, they are exposed to small-boat traffic during the entire ice-free season, including exposure to the boats we use to sample when we are not sampling. Third, when we begin sampling varies and is probably unpredictable for belugas. Last, they are harvested before, during, and after our sampling sessions, both inside and outside our sampling areas; as such, greater levels of disturbance commonly occur inside and outside where we sampled them and they are probably familiar with being pursued by small boats. Hence, avoidance of the sampling areas seems unlikely across years.

Inferences from Simulations

In order for the POPAN estimate of abundance to be approximately unbiased, it is not necessary for all animals to be exposed to capture risk in all years. Simulations show that POPAN estimates of abundance were largely robust to emigration and were generally within 10% or 200 belugas of the true value. The exception to this was for the combination of random emigration and very low capture probabilities ($p = 0.05$), where estimates of abundance were only within 20% of the true value. These simulations yielded estimates of capture probability between 0.02 and 0.03 (Tables 4, 5). In our empirical data, the estimate of capture probability was 0.06 (95% CI = 0.05–0.08). As such, it is unlikely that the simulations with the most bias are indicative of our estimate of abundance for belugas in Bristol Bay.

Interestingly, both capture and survival probabilities were biased low in simulations that included any form of emigration. This was especially true for capture probability, estimates of which typically had confidence limits that did not include the true value. This is expected because temporary emigration functionally decreased the probability that a beluga is available to be captured. The negative bias in survival was most pronounced when emigration was Markovian (Tables 4, 5). This is because some belugas are only captured once, emigrate, and then are never encountered again. These belugas are essentially permanent emigrants within the confines of the study and the POPAN model cannot distinguish permanent emigration from death.

When emigration occurs, it has a confounding effect on the probability of capture and survival in POPAN models. Although this statistical confounding might seem to be a bad thing, and certainly results in capture and survival probabilities that are biased, the POPAN model can still provide valid estimates of abundance. One thing we discovered when fitting simulation models is that we do not want to fix parameters to constant values. In Table 4, the simulation of Markovian movements with

capture and survival probabilities of 0.1 and 0.97, respectively, yielded an abundance of 1,988 belugas (95% CI = 1,676–2,334). To illustrate how fixing parameters may affect estimation, we fixed survival within Program MARK to 0.97 (*i.e.*, the value we used to simulate the data) and then re-ran the simulation. The resulting estimate of abundance was biased low (N = 1,737) and the confidence intervals did not include the true value of 2,000 (95% CI = 1,528–1,966). This is an important finding for practitioners of mark-recapture studies. A survival probability of 0.97 will typically be statistically indistinguishable from 1. Furthermore, when using logit link functions survival is bounded between 0 and 1, and parameters near boundaries are notoriously difficult to estimate and often cause convergence issues. To avoid convergence issues, practitioners of mark-recapture analyses often fix parameters to set values (*e.g.*, 0 or 1). However, by fixing survival to the known value, we created a model that no longer accounted for belugas that emigrate out of the sampling area and provided a biased estimate of abundance and confidence intervals with poor coverage.

In order to understand how our empirical estimate may be biased, it would be useful to know what form of movement (*e.g.*, random or Markovian temporary emigration) was most likely for belugas in Bristol Bay. The satellite tag data suggested that there was extensive movement between sampling areas within years, even while we were sampling. The genetic data also suggests a high amount of movement between years. Of 25 belugas sampled in Nushagak Bay in 2008, one was recaptured in Kvichak Bay in 2010 (4%) and five (20%) in 2011. We are not suggesting that movement of belugas between Nushagak and Kvichak Bays is random. We are collecting genetic samples when belugas are moving up the bays to pursue spawning rainbow smelt and outmigrating salmon smolt. Although our efficiency in collecting biopsies from belugas certainly increased over time, the drop in the number of samples collected in 2009 (n = 15) was not due to our inability to sample belugas, rather it was because few belugas were present. Likewise, there is probably a reason why few of the Nushagak belugas biopsied in 2008 were found in the Kvichak until 2011, when we recaptured six. As such, movement between the bays is probably not random, nor Markovian. We suggest that belugas are responding to variations in food availability, which is something we did not sample.

Regardless of why belugas move between bays in our study area, we think it is very likely that some belugas never entered our sampling areas when we were sampling. Therefore, Markovian simulations are probably most appropriate because they allow for some belugas to never be exposed to sampling effort. Our Markovian simulations of abundance were only biased low by <50 belugas and were within 5% of the true value. Given that the bias in the Markovian models was small and that we observed high levels of movement between the sampling areas, our estimate of abundance should be useful. However, the estimate we provide is best considered a minimum population estimate because it is likely that some belugas were never exposed to sampling effort.

Correction Factors and Counts from Aerial Surveys

Counts from aerial surveys are typically corrected for the number of belugas that are diving and not available to be sampled and/or for the number that are available but missed by the observer. Because beluga calves and yearlings are small and gray in color and are typically not detected in the silty (*i.e.*, gray-colored) water, a separate correction is sometimes used for them (*e.g.*, Brodie 1971). In Bristol Bay, however, correction factors have only been developed to correct for the number of adults at the

surface (*i.e.*, availability correction). Frost *et al.* (1985) used VHF transmitters to estimate an availability correction factor of 2.75. This estimate was later revised to 2.62 by Frost and Lowry (1995). Citta *et al.* (ABWC, unpublished data) used satellite transmitters to estimate a correction factor of 3.3 (standard deviation = 4.52). Although such calculations are warranted because estimates of abundance are needed for management, assuming correction factors do not vary with circumstances is unrealistic. Counts of belugas often vary widely, even when surveys are conducted on the same day and cover the exact same area. In 2016, replicate counts during aerial surveys ranged from 484 to 1,024 on days with good viewing conditions (ABWC, unpublished data). In fact, these two counts were collected on the same day, within a few hours of each other. If the true number of adult belugas was 2,000, the availability correction factor for those surveys would range from approximately 1.95 to 4.13.

The estimate of abundance for Bristol Bay belugas in the most current National Marine Fisheries Service Stock Assessment Reports is 2,877 (Muto *et al.* 2016) and was derived by multiplying the average of the maximum count from surveys in 2004 (794) and 2005 (1,067) by the availability correction factor (2.62) from Frost and Lowry (1995) and by a correction for the number of calves (1.1) and yearlings (1.08) from a study of belugas in Cumberland Sound, Baffin Island, Canada (Brodie 1971). We sampled no newborn calves, so our estimate would only have to be corrected for the number of calves to be comparable. Brodie (1971) estimated that roughly 10% of a beluga population was composed of calves; after correcting the mark-recapture estimate for calves, there are 2,121 belugas (*i.e.*, 1,928 × 1.1), which is approximately 700 fewer belugas than stated in the current stock assessment report (Muto *et al.* 2016).

Comparing estimates of abundance from our genetic mark-recapture study and aerial surveys is difficult, because the implementation of each method was imperfect. The genetic mark-recapture study should have sampled belugas in each bay consistently. As a consequence, our estimate is almost certainly biased low because some belugas were likely never available to be genetically sampled. However, there is also considerable uncertainty in estimates of abundance from aerial surveys, mostly because correction factors (or survey methods) that correctly account for availability and the number calves and yearlings need to be better developed in Bristol Bay. Further discussion of how to improve upon the design of aerial surveys is outside the scope of this manuscript.

Potential Biological Removal

Under the 1994 reauthorized Marine Mammal Protection Act (MMPA), marine mammal Stock Assessment Reports (SARs) must contain an estimate of the Potential Biological Removal (PBR) level for the population and the information used to calculate it (Wade and Angliss 1997). PRB is calculated as the product of the minimum population estimate, one-half the maximum theoretical net productivity rate, and a recovery factor: $\text{PBR} = N_{\text{MIN}} \times 0.5R_{\text{MAX}} \times F_{\text{R}}$ (Wade and Angliss 1997). R_{MAX} is the maximum net productivity rate (4.8%; Lowry *et al.* 2008) and F_{R} is the "recovery factor," which is equal to 1.0 when a population is stable or increasing. N_{MIN} is the lower 20th percentile of a log-normal distribution that represents the minimum number of whales after accounting for uncertainty in the estimates. Wade and Angliss (1997) calculated N_{MIN} as: $N_{\text{MIN}} = N/\exp[0.842 \times (\ln\{1 + [\text{CV}(N)]^2\})^{1/2}]$. Because most counts of belugas do not include reliable estimates of variability, a default CV of 0.2 is typically used. Muto *et al.* (2016) used the average of the maximum counts from aerial surveys in 2004 and 2005, corrected to account for

availability and the number of calves/yearlings, to calculate a PBR of 59 belugas (2,467 × 0.024 × 1.0) in Bristol Bay.

If we calculate PBR with the genetic mark-recapture estimate, we get a lower value. We used the CV of the mark-recapture estimate (CV = 0.1) instead of the default value of 0.2. Without correcting for the number of calves, N_{MIN} equals 1,773 belugas and the PBR equals 43 belugas. If we adjust abundance by 10% to account for calves, which were not sampled, N_{MIN} equals 1,949 and the PBR equals 47 belugas (*i.e.*, 1,949 × 0.024 × 1.0). Although this calculation of PBR is lower than that calculated from aerial surveys, it is still approximately twice the current annual subsistence harvest of 23/yr (ABWC, unpublished data), even though the mark-recapture estimate is almost certainly biased low.

Fishery bycatch is another potential source of mortality for this population. Fishery observers monitored the groundfish trawl, longline, and pot fisheries within greater Bristol Bay during 1990–1997 and no incidental mortalities or injuries were observed (Muto *et al*. 2016). Aerial surveys occur in late June and early July, during the sockeye fishery, and belugas are observed swimming around gill net sets suggesting belugas could be caught in the commercial salmon set gill net and drift gill net fisheries that occur in Nushagak and Kvichak Bays. During May–July 1983, Frost *et al*. (1984) conducted beach surveys in the inner bays from airplanes and boats and found 27 dead belugas, at least 12 of which were clearly attributed to fisheries. The commercial gill net fisheries have never been monitored for bycatch and there are no current, reliable data on incidental take. There is also a large subsistence gill net fishery for salmon in Bristol Bay in which four belugas were reported taken during 2005–2012 (Allen and Angliss 2011, Muto *et al*. 2016). Some belugas caught in subsistence gill net fisheries are reported as harvest because they are consumed by Alaska Natives, however, the proportion of bycatch that is reported as harvest is unknown. Using the mark-recapture estimate, bycatch would have to be approximately 24 belugas per year, after accounting for an average annual harvest of 23 belugas, to exceed PBR as calculated from the mark-recapture study. However, as stated above, the mark-recapture estimate is almost certainly biased low. Regardless, better monitoring of bycatch is warranted.

Considerations for Future Monitoring in Bristol Bay

Approximately 25% of the population is now marked (516 marked belugas from a population size of ~2,000). This provides an opportunity to estimate population growth and survival in the future if more genetic sampling occurs. If biopsy collection in spring continues, we stress that sampling must occur simultaneously in both bays; this will help increase the probability of encounter and also help ensure that we are sampling the entire population. We cannot use simulations to overcome poor sampling design and our efforts to simulate bias in the estimate of abundance could have been avoided by consistently sampling in both Kvichak and Nushagak Bays at the same time. When the project started, we did not know if collecting biopsies was possible and permits limited us to 30 biopsies per year. Hence the project began as a pilot study to develop methods for sample collection. Later, when it was clear that many biopsies could be collected, there was neither the monetary nor the logistic support to sample both bays simultaneously. We only collected samples in the Nushagak during satellite tagging projects in 2008 and 2011. Future efforts need to better sample the complete distribution of belugas in Bristol Bay. Other parameters such as contaminant load and kinship could be explored with the existing data set.

Methods for monitoring populations are evolving and the choice of how best to proceed is not limited to aerial survey methods or mark-recapture methods as they are currently implemented in Bristol Bay. One promising approach is the "close-kin mark-recapture" method developed by Bravington *et al.* (2016), whereby abundance can be estimated by using more genetic information from captured individuals such that the capture of closely related individuals (kin) can be used as recaptures, even though they have not been captured before. In effect, this uses the samples taken from kin as recapture information and allows estimation of abundance within a single sample year.

Considerations for Other Studies Using POPAN Models

During the course of our study, we learned a number of things that may be useful for practitioners of POPAN models. First, we suggest careful consideration of how the area to be sampled relates to the range of the population (see also section 18.3 of Williams *et al.* 2002 and Schwarz and Arnason 2017). If not all animals are within the sampling area during the time of sampling, then some form of emigration is occurring. We suggest that when estimating abundance with POPAN models, parameters never be set to fixed values if there is a possibility that some animals are not within the sampling area while sampling is occurring. In simulations, confidence intervals of abundance were more likely to cover the true value if parameters were not set to fixed values. If all animals are not within the sampling area at the time of sampling, then probabilities of emigration and survival will likely be biased low. This is especially important when considering survival rates because they may be used in other studies to model population trajectories. Lastly, although estimates of abundance were generally robust to the forms of emigration we considered, this may not be true in a different system where survival is lower than what we considered or if patterns of emigration are markedly different.

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Literature Cited

Allen, B. M., and R. P. Angliss. 2012. Beluga whale (*Delphinapterus leucas*): Bristol Bay stock. Alaska marine mammal stock assessments, 2011. U.S. Department of Commerce, NOAA Technical Memorandum NOAA-TM-AFSC-234. Pp. 79–83.

Bravington, M. V., H. J. Skaug and E. C. Anderson. 2016. Close-kin mark-recapture. Statistical Science 31:259–274.

Brodie, P. F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale with reference to the Cumberland Sound, Baffin Island, population. Journal of the Fisheries Research Board of Canada 28:1309–1318.

Brooks, J. W. 1955. Beluga. 1955 annual report. Alaska Department of Fish Game, Juneau, AK. Pp. 98–106.

Burnham, K. P. 1991. On a unified theory for release-resampling of animal populations. Pages 11–36 *in* M. T. Chao and P. E. Cheng, eds. Proceedings of 1990 Taipei Symposium in Statistics. Institute of Statistical Science, Academia Sinica, Taipei, Taiwan.

Citta, J. J., L. T. Quakenbush, K. J. Frost, L. Lowry, R. C. Hobbs and H. Aderman. 2016*a*. Movements of beluga whales (*Delphinaptrus leucas*) in Bristol Bay, Alaska. Marine Mammal Science 32:1272–1298.

Citta, J. J., P. Richard, L. F. Lowry, *et al*. 2016*b*. Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. Marine Mammal Science 33:236–250.

Creel, S., G. Spong, J. Sands, *et al*. 2003. Population estimation in Yellowstone wolves with error-prone noninvasive microsatellite genotypes. Molecular Ecology 12:2003–2009.

Frost, K. J., and L. F. Lowry. 1990. Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. Canadian Bulletin of Fisheries and Aquatic Sciences 224:39–57.

Frost, K. J., and L. F. Lowry. 1995. Radio tag based correction factors for use in beluga whale population estimates. Working paper for Alaska Beluga Whale Committee Scientific Workshop, Anchorage, AK, 5–7 April 1995. 12 pp.

Frost, K. J., L. F. Lowry and R. R. Nelson. 1984. Belukha whale studies in Bristol Bay, Alaska. Pages 187–200 *in* B. R. Melteff, ed. Proceedings of the workshop on biological interactions among marine mammals and commercial fisheries in the southeastern Bering Sea. Alaska Sea Grant Report 84-1, University of Alaska, Fairbanks, AK.

Frost, K. J., L. F. Lowry and R. R. Nelson. 1985. Radiotagging studies of belukha whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. Marine Mammal Science 1:191–202.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration stochastic model. Biometrika 52:225–247.

Kalinowski, S. T., M. A. Sawaya and M. L. Taper. 2006. Individual identification and distribution of genotypic differences between individuals. Journal of Wildlife Management 70:1148–1150.

Kalinowski, S. T., M. L. Taper and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099–1006.

Kendall, W. L., J. D. Nichols and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Report 2013-01. Alaska Fisheries Science Canter, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA. 25 pp.

Lowry, L. F., K. J. Frost, A. Zerbini, D. DeMaster and R. R. Reeves. 2008. Trend in aerial counts of beluga or white whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, 1993–2005. Journal of Cetacean Research and Management 10:201–207.

Lydersen, C., A. R. Martin, K. M. Kovacs and I. Gjertz. 2001. Summer and autumn movements of white whales (*Delphinapterus leucas*) in Svalbard, Norway. Marine Ecology Progress Series 219:265–274.

McConnell, B. J., C. Chambers and M. A. Fedak. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science 4:393–398.

McKelvey, K., and M. Schwartz. 2004. Genetic error associated with population estimation using non-invasive molecular tagging: Problems and new solutions. Journal of Wildlife Management 68:439–448.

Mills, L. S., J. J. Citta, K. P. Lair, M. K. Schwartz and D. A. Tallmon. 2000. Estimating animal abundance using noninvasive DNA sampling: Promise and pitfalls. Ecological Applications 10:283–294.

Muto, M. M., V. T. Helker, R. P. Angliss, *et al*. 2016. Alaska marine mammal stock assessments, 2015. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFSAFSC-323. 300 pp.

O'Corry-Crowe, G. M., R. S. Suydam, A. Rosenberg, K. J. Frost and A. E. Dizon. 1997. Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. Molecular Ecology 6:955–970.

O'Corry-Crowe, G. M., A. E. Dizon, R. S. Suydam and L. F. Lowry. 2002. Molecular genetic studies of population structure and movement patterns in a migratory species: The beluga whale (*Delphinapterus leucas*) in the western Nearctic. Pages 53–64 *in* C. J. Pfeiffer, ed. Molecular and cell biology of marine mammals. Krieger Publishing Co., Malabar, FL.

O'Corry-Crowe, G. M., C. Lydersen, M. P. Heide-Jørgensen, L. Hansen, L. M. Mukhametov, O. Dove and K. M. Kovacs. 2010. Population genetic structure and evolutionary history of North Atlantic beluga whales (*Delphinapterus leucas*) from West Greenland, Svalbard and the White Sea. Polar Biology 33:1179–1194.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Quakenbush, L. T., R. S. Suydam, A. L. Bryan, L. F. Lowry, K. J. Frost and B. A. Mahoney. 2015. Diet of beluga whales (*Delphinapterus leucas*) in Alaska from stomach contents, March–November. Marine Fisheries Review 77:70–84.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richard, P. R., M. P. Heide-Jørgensen, J. R. Orr, R. Dietz and T. G. Smith. 2001. Summer and autumn movements and habitat use by belugas in the Canadian High Arctic and adjacent areas. Arctic 54:207–222.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of open-model capture recapture experiments. Biometrics 52:860–873.

Schwarz, C. J., and A. N. Arnason. 2017. Jolly-Seber models in MARK. Chapter 12 *in* E. G. Cooch and G. C. White, eds. Program MARK: A gentle introduction. Available at: http://www.phidot.org/software/mark/docs/book/.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52:249–259.

Smith, T. G., and A. R. Martin. 1994. Distribution and movements of belugas, *Delphinapterus leucas*, in the Canadian High Arctic. Canadian Journal of Fisheries and Aquatic Sciences 51:1653–1663.

Wade, P. R., and R. Angliss. 1997. Guidelines for assessing marine mammal stocks: Report of the GAMMS workshop April 3–5, 1996, Seattle, WA. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum. NMFS-OPR-12. 93 pp.

Waits, L. P., G. Luikart and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: Cautions and guidelines. Molecular Ecology 10:249–256.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival rate estimation from both live and dead encounters. Bird Study 46(Supplement):S120–S139.

Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. Analysis and management of animal populations: Modeling, estimation, and decision making. Academic Press, New York, NY.

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