# Monitoring Recovery Status and Age Structure of Cook Inlet, Alaska Belugas by Skin Color Determination 

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This is to certify that I have examined this copy of a master's thesis by

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Abstract<br>Monitoring Recovery Status and Age Structure of Cook Inlet, Alaska Belugas by Skin Color Determination<br>Laura K. Litzky<br>Chair of the Supervisory Committee:<br>Associate Professor Glenn R. VanBlaricom<br>School of Aquatic and Fishery Sciences

The Cook Inlet stock of belugas (Delphinapterus leucas) is the most isolated of five evident populations around Alaska. Declines in abundance of this stock, apparently from over harvest, have been detected since 1993. This study describes a technique developed to monitor the conservation status of the Cook Inlet stock. Belugas are gray at birth and gradually lighten with maturity. Thus, the fraction of animals in the population that are white $\left(W_{t}\right)$ is an index of the fraction of mature animals in the population $\left(\mathrm{M}_{\mathrm{t}}\right) . \mathrm{M}_{\mathrm{t}}$ is expected to increase over time from the exploited level (hunters targeted white animals) to a rebound value (harvest stopped in 1999) if population abundance recovers. Population growth was modeled using a variable Leslie matrix and $\mathrm{M}_{\mathrm{t}}$ estimated for each year from 1976-2050. Calf survival and age at sexual maturity were density dependent. Calf survival and fecundity were stochastic. Averages from 5000 simulations of the model estimated $\mathrm{M}_{1980}$ at 0.647 (CV 2.5\%), $\mathrm{M}_{2000}$ at 0.559 (CV 3.7\%), $\mathrm{M}_{2020}$ at 0.668 (CV 2.7\%). The most likely year of recovery of $\mathrm{M}_{\mathrm{t}}$ (defined as $\mathrm{M}_{\mathrm{t}}$ changing by less than $2 \%$ for at least 3 years) was 2004. The change in $M_{t}$ from its exploited to rebound level ranged from $7-15 \%$, when differing life history parameters were used in the model. To determine $\mathrm{W}_{2000}$, aerial videos of whales collected in June 2000 were analyzed using image analysis software programmed to categorize animals as gray or white. A controlled experiment, designed to provide color calibration, was conducted using aerial video of life size beluga models. Percent of control images correctly identified for color were: dark gray $=100 \%$, medium gray $=74.0 \%$, light gray $=84.3 \%$, and bright white $=$ $100 \%$. Applying the color calibration to real whale images resulted in $\mathrm{W}_{2000}=0.8109$ ( $95 \%$ CI from bootstrap: $0.7613-0.8522$ ). The value of $\mathrm{W}_{2000}$ may be positively biased due to low detection of small dark calves. Despite the bias, the increase predicted for $\mathrm{M}_{\mathrm{t}}$ with recovery, as indexed by $\mathrm{W}_{\mathrm{t}}$, should be detectable if future measurements of $\mathrm{W}_{\mathrm{t}}$ have similar variability to $\mathrm{W}_{2000}$.

## CHAPTER 1: THE COOK INLET BELUGA STOCK

## Introduction:

Beluga whales or white whales (Delphinapterus leucas) are small, toothed cetaceans considered to be Arctic specialists. They are one of the few species of cetaceans that live year round in the Northern Hemisphere's arctic and sub-arctic seas (Hazard 1988). Some stocks are thought to migrate, following the ice edge south, as it forms in the fall/winter and north, as the ice retreats in the summer. However, belugas are rarely found south of $50^{\circ} \mathrm{N}$ latitude (Rice 1998). In the summer they are mostly coastal animals, known to congregate in shallow bays, estuaries and river mouths off the shores of Greenland, Russia, Norway, Canada, and Alaska (Rice 1998).

Five discrete stocks are recognized around Alaska designated both by their primary summer locations and by genetic differentiation (O’Corry-Crowe et al. 1997). Figure 1 illustrates the summer locations of the groups generally referred to as the Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chuckchi Sea, and Beaufort Sea stocks (Hill and DeMaster 1999). All of the stocks except for the Cook Inlet whales are believed to come together in a common wintering ground. Areas the belugas can occupy are limited by the availability of open water (Lowry 1985). In the winter months, when sea ice reaches its lowest latitude and coastal areas are frozen over, groups of whales congregate near the ice edge in the Bering Sea (Harrison and Hall 1978). As the weather warms and ice retreats the belugas migrate to the distinct summering regions which constitute four of the Alaskan stock designations. Although the belugas of Cook Inlet would be physically capable of swimming the distance to the winter congregation area, there are no driving factors for the animals to make this trip and no evidence that they do so (Hazard 1988, Laidre et al. 2000). Genetic research confirms that, reproductively at least, there is no mixing (O’Corry-Crowe et al. 1997). Thus, the Cook Inlet stock is quite isolated, both geographically and genetically, making it particularly vulnerable to both anthropogenic and environmental impacts (Hill 1996, VanBlaricom et al. 2001).

## Distribution and Abundance:

Studies of the Cook Inlet beluga population started in the 1960’s. Early work focused on determining abundance and distribution. Aerial or shipboard surveys were conducted in 1964 by Klinkhart, in 1978 by Murray and Fay, and in 1982 by Calkins (Hazard 1988). In the late 1980's the National Marine Mammal Laboratory (NMML) of the U.S. National Marine Fisheries Service (NMFS) undertook research with continued focus on abundance and distribution. Systematic annual aerial surveys began by NMML in 1993 and continue at present.

Numbers of whales from the surveys done in the 1970's indicate there may have been more than 1000 animals in Cook Inlet at that time. Using a high-count number of 479 from his surveys and a correction factor of 2.7 for whales missed underwater, Calkins estimated the abundance of Cook Inlet belugas in August 1979 at 1293 animals (Calkins 1989). This number is significantly higher than the 1999 best estimate of 367 animals (Hobbs et al. 2000a). However, the techniques for counting whales and correcting those counts have been changed significantly over the years (Rugh et al. 2000). It is unknown exactly what methods were used on the original surveys and whether or not the correction factor of 2.7 is appropriate for the Cook Inlet whales. Comparing only raw counts, the number of whales counted during the NMML's 1993-99 aerial surveys (193-327) is roughly $60-80 \%$ of Klinkhart's counts from 1963 and 1964 (300-400) and Calkins’ counts from 1976-78 (approximately 400) (Rugh et al. 2000). Thus, the abundance of the Cook Inlet belugas appears to have decreased since the 1960's.

Belugas are believed to migrate seasonally within Cook Inlet (Figure 2). In the summer whales congregate around river mouths in the upper part of the inlet (Calkins 1989), most likely taking advantage of local anadromous fish runs (Rugh et al. 2000). In the fall, whales may move to the lower part of the inlet, probably to avoid heavy ice that can form in the north (Fall et al. 1984) although this has yet to be confirmed or refuted. During summer surveys conducted in the 1970's, even when animals were concentrated around river mouths in the upper inlet, animals were also sighted in the lower inlet and in non-
coastal areas of the inlet. Recent summer surveys have found whales only in the upper inlet and rarely anywhere off shore (Rugh et al. 2000).

## Harvest Information:

The U.S. Marine Mammal Protection Act (MMPA), enacted in 1972 (16 U.S.C. §§136162, 1371-84, and 1401-07 (Supp. IV 1974)) and since amended several times, allows Alaska Natives to harvest marine mammals for subsistence purposes (Hill 1996). The term Alaska Native applies to any Indian, Aleut, or Eskimo who resides in Alaska. For the natives of Alaska marine mammals are an integral part of the food supply and play a major role in cultural identities (Breton and Smith 1984). In a village setting the amount of hunting is regulated as hunters generally work together, are aware of the amount harvested, and are subject to traditional harvest limits as enforced by village elders. Anchorage, however, is no longer a small village. It has become a large city with a constant inflow of people from other areas. Hunters at present include the Dena'ina who hunt out of Tyonek, Alaska natives from small villages who have relocated permanently to the Anchorage area, and Alaska natives from small villages who visit Anchorage (Mahoney and Shelden 2000). These hunters do not tend to work together and most hunting effort is not subject to regulation by a common, village-based traditional authority.

The Cook Inlet Marine Mammal Council (CIMMC), a group formed by the local hunters of Anchorage, has attempted to record the numbers of belugas harvested each year since 1995 (summarized in Hill and DeMaster 1999). Their numbers may underestimate the total number of animals killed due to an unknown "struck and lost" rate (the fraction of animals mortally struck by hunters but not landed) and lack of recording of kills or strikes by hunters who are not members of the group (Mahoney and Shelden 2000). Based on the harvest levels reported by the CIMMC for 1995-97, Ferrero et al. (2000) estimated the average subsistence take during this period to be 87 whales per year. Using the last three reliable estimates $(1996,1997$, and 1999) of subsistence take for Cook Inlet, the average is 65 whales per year (Ferrero et al. 2000).

A major increase in the number of whales harvested became a concern due to Alaska Native commercial hunting of belugas, which began in the early 90's (Mahoney and Shelden 2000). Although the MMPA does not allow the commercial sale of marine mammal products by non-natives, an exemption permits Alaska Natives to sell marine mammal parts to other Alaska Natives for consumption (Hill 1996). This is to allow the intake of traditional foods by elderly natives who may be unable to obtain the goods themselves. In 1995 the sale of muktuk (whale skin and blubber) from whales hunted in Cook Inlet became a cause for concern (Mahoney and Shelden 2000). Alaska Native commercial hunting operations were taking more animals than the population could sustain (Hill 1996). One native commercial enterprise was observed to take more than twenty whales at one time (Schaeffer 1998). This increase in the harvest is believed to be the main reason for the decline in the abundance of the Cook Inlet stock (65 FR 34590). The NMFS has also recognized that other factors such as pollution, lack of prey, and disturbance from vessel traffic, may have additionally contributed to the observed decline in abundance between 1994 and 1998.

## Conservation Measures:

The Alaska Scientific Review Group, the Alaska Beluga Whale Committee, the CIMMC, the NMFS, and the U.S. Marine Mammal Commission all acknowledged, in the mid 1990's, a growing concern for the large numbers of belugas being taken from the Cook Inlet population. This prompted a formal comprehensive status review for the stock (63 FR 64229) initiated by the NMFS on 19 November 1998. The purpose of the review was to determine whether designation as "depleted" under the MMPA, or a change in listing classification under the U.S. Endangered Species Act (ESA) of 1973 (16 U.S.C. §§153143 (Supp. IV 1974)), as amended, would be warranted. The review resulted in the whales being listed as "depleted" under the MMPA (65 FR 34590) but not being listed as "endangered" or "threatened" under the ESA (65 FR 38778).

In early 1999 the hunters of Cook Inlet came together and made the decision to do no hunting that year. At the same time, the U.S. Congress passed legislation prohibiting the
take of Cook Inlet belugas for native subsistence for one year (P.L. 106-31 § 3022). In 2000 U.S. Congress introduced legislation passed into law permanently stopping the harvest of Cook Inlet belugas unless authorized by a cooperative agreement between NMFS and the affected Alaska Native organizations (P.L. 106-553). Thus, there was no legal harvest in 1999. A co-management agreement between the NMFS and the CIMMC was achieved for the year 2000 allowing the take of one whale. However, no animals were taken that year. In 2001, a co-management agreement between the NMFS and the CIMMC was signed allowing the native village of Tyonek a beluga harvest of one strike during that calendar year. One whale was harvested legally by Tyonek villagers in 2001.


Figure 1.1: Shaded areas show summer locations of the five recognized stocks of beluga whales in U.S. waters.


Figure 1.2: Map of Cook Inlet, Alaska.

## CHAPTER 2: USING AN AGE STRUCTURED MODEL TO DEFINE A STATISTIC FOR MONITORING RECOVERY OF THE COOK INLET STOCK OF BELUGA WHALES

## Introduction:

Long-lived species, such as belugas, often exhibit slow responses to management actions (Heppell et al. 1996). Although the Alaska Native commercial harvest, the most likely cause of the Cook Inlet belugas' decline, ended in 1999, and the average number of whales removed by year for the next decade will be less than 1.5, it may be many years before a significant increase in abundance can be detected. This can make it difficult to assess whether or not the management action is having the desired effect. Shifts in the age structure of the population, however, can occur over shorter periods (Holmes and York In review) especially when there are changes in survivorship (Caswell 2001). If one portion of the age structure is impacted differently than the others, the resulting change to the age structure can often be observed quite rapidly. The same holds true for stage structured statistics. Thus, it is useful to develop a technique to monitor recovery using an age or stage structured statistic.

One such stage structured statistic is the fraction of mature animals $\left(\mathrm{M}_{\mathrm{t}}\right)$ in the population. It is known that Cook Inlet beluga hunters targeted large mature animals. Thus, it is expected that $\mathrm{M}_{\mathrm{t}}$ would be at a reduced level, relative to an unharvested population, after being subjected to large harvests for a number of years. Cessation of the harvest should result in an increase in survivorship for mature animals and allow the population to recover. If this occurs, $\mathrm{M}_{\mathrm{t}}$ will return to a higher value characteristic of an unexploited population. This change should happen in less time than it would take for total abundance to recover.

The time frame in which the shift in $\mathrm{M}_{\mathrm{t}}(\Delta \mathrm{M})$ with recovery should occur as well as the magnitude of $\Delta \mathrm{M}$ can be predicted using age structured models (Caswell 2001). Such models simulate growth and dynamics given the input of known information about the
population of interest. Age structured models can be used to investigate the effects of varying parameters, density dependence, and stochasticity on the statistic $\mathrm{M}_{\mathrm{t}}$.

## Methods

## The Model

Initial investigations of the sensitivity of $\mathrm{M}_{\mathrm{t}}$ to varying parameters were made using Lotka's equation of unity (Lotka 1907).
$1=\sum_{x=1}^{w} \lambda^{-x} l_{x} m_{x}$
Equation 2.1
$\mathrm{x}=$ age class (beginning with 1 )
$\mathrm{w}=$ maximum age class
$\lambda=$ growth rate
$l_{\mathrm{x}}=$ survival to age class x
$\mathrm{m}_{\mathrm{x}}=$ age specific fecundity (incorporating survival of mother to next age class)

Five primary parameters were used for the initial investigations. These were calf survival, juvenile survival, adult survival, conditional fecundity (one rate for mature animals only), and harvest rate (description of values used for parameters below). The maximum age class was 35 and animals became sexually mature at age class 6. Harvest rate was incorporated into $l_{x}$ but not into conditional fecundity because the high harvest rates investigated were unsustainable. Therefore, the Lotka equation could not be reasonably solved to account for the high rates. Investigations of the effects of the life history parameters on lambda ( $\lambda$ ) and $\mathrm{M}_{\mathrm{t}}$ were conducted by holding all the parameters constant except for one, and then solving Lotka's equation for a value of 1 by changing the variable parameter.

Next, a stable age distribution (SAD) for the Cook Inlet beluga population was calculated using the Lotka equation as modified by Eberhardt and Siniff (1977).
$\frac{1}{\beta}=\sum_{x=1}^{w} \lambda^{-x} I_{x}$
Equation 2.2
$c_{x}=\beta \lambda^{-x} l_{x}$
Equation 2.3
$\beta=$ per capita birth rate
$\mathrm{c}_{\mathrm{x}}=$ the fraction of animals in age class x

If all parameters for a population stay constant for some time, the population reaches a SAD. This simply means that the portion of animals in each age class remains constant over time. It was assumed that the Cook Inlet beluga population was at a SAD in the 1970's. The SAD was calculated using the life history parameters decided upon from a literature review and the sensitivity analyses. Then $\mathrm{c}_{\mathrm{x}}$ for each age class was multiplied by the starting population size for the first year of projections to create the first column in an age structured matrix model. The first year of projections was 1976 and the starting population for that year was determined by fitting the model to the 1999 abundance estimate of 367 animals (Hobbs et al. 2000a). From 1976, the population was projected forward in time using a Leslie matrix model (Leslie 1945, 1948).
$n_{x=1, t+1}=\sum_{x=1}^{w} n_{x, t} m_{x}$
Equation 2.4
$n_{x+1, t+1}=n_{x, t} p_{x}=n_{x, t}\left(\frac{l_{x+1}}{l_{x}}\right)$
Equation 2.5
$\mathrm{t}=$ time in years
$\mathrm{n}_{\mathrm{x}, \mathrm{t}}=$ number of animals in age class x at time t
$p_{x}=$ survival from age $x$ to age $x+1$

Initially, the model was deterministic and ignored density dependence and stochasticity. This was done to ensure proper functioning of the model and to see if discrete values of $\mathrm{M}_{\mathrm{t}}$ changed as expected, from a pristine level in the 1970's down to an exploited level in the late 1990's and back up to a recovered level in the future. $\mathrm{M}_{\mathrm{t}}$ was calculated as the sum of all animals in mature age classes divided by the sum of all animals in the population.
$M_{t}=\frac{\sum_{x=A S M}^{w} n_{x, t}}{\sum_{x=1}^{w} n_{x, t}}$
Equation 2.6
$\mathrm{M}_{\mathrm{t}}=$ fraction of mature animals in the population at time t
ASM = age at sexual maturity

## Density dependence

To determine if the $\Delta \mathrm{M}$ would be detectable when life history parameters in the model were not constant, density dependence was incorporated converting the model into a variable Leslie matrix (Leslie 1945, 1948). In long-lived, large mammals, decreases in juvenile survival rates are the most probable first response to increases in population density (Eberhardt 1977) although population growth is unlikely to be regulated by a single life history parameter (Taylor and DeMaster 1993). Thus, the effects of density dependent calf survival and age at sexual maturity (ASM) were investigated. Calf survival was made density dependent such that it increased when the population declined and decreased when the population approached carrying capacity (K).
$P 1_{t+1}=P 1_{\text {min }}+\left(P 1_{\text {max }}-P 1_{\text {min }}\right)\left(1-\left(\frac{N_{t}}{K}\right)^{z}\right)$
Equation 2.7

P1 = calf survival
$\mathrm{P} 1_{\text {max }}=$ the maximum value for calf survival (from the literature)
$\mathrm{P} 1_{\text {min }}=$ the minimum value for calf survival (determined by solving Lotka's equation with $\lambda=1$ )
$\mathrm{N}_{\mathrm{t}}=$ total population size at time t
$\mathrm{K}=$ carrying capacity
$\mathrm{z}=\mathrm{a}$ shaping parameter

Conversely, ASM decreased when the population declined and increased when the population approached K.

$$
A S M_{t+1}=A S M_{\max }+\left(A S M_{\min }-A S M_{\max }\right)\left(1-\left(\frac{N_{t}}{K}\right)^{z}\right) \quad \text { Equation } 2.8
$$

ASM = age at sexual maturity
ASM $_{\text {max }}$ = the maximum value for ASM (determined by solving Lotka's equation with $\lambda=1$ )
$\mathrm{ASM}_{\text {min }}=$ the minimum value for ASM (from the literature)

A shaping parameter, z , was used to define whether density dependence was linear ( $\mathrm{z}=1$, peak production at population size of $50 \% \mathrm{~K}$ ) or not $(\mathrm{z}>1)$. It is likely that density dependence in marine mammal populations is non-linear with peak production instead occurring between 50-80\% of K (Taylor and DeMaster 1993). To attain maximum productivity at sixty percent of K, which is consistent with the NMFS definition of Optimal Sustainable Population, z was set at 2.4.

## Stochasticity

Environmental stochasticity was incorporated into the model to investigate the effects of additional variation on $\mathrm{M}_{\mathrm{t}}$. Yearly values for both calf survival and conditional fecundity (conditional on adult survival) were drawn at random from symmetrical beta distributions (Appendix A.1). A beta distribution $(0,1)$ was used because it can be defined to be symmetrical around the mean $(\mu=0.5)$ and there are no tails trailing off to plus or minus infinity for the curve (Figure 2.1). Such tails can lead to biologically impossible values being selected for the parameter of interest, or incorrect probability distributions if the tails are disregarded. The standard deviations $(\sigma)$ were varied on different trials to allow maximum ( $\sigma=0.25$ ), medium ( $\sigma=0.125$ ), and minimum ( $\sigma=0.0625$ ) variability for conditional fecundity and calf survival. The maximum standard deviation was selected such that the entire range of the distribution was included within two standard deviations. The medium and minimum standard deviations were $1 / 2$ and $1 / 4$ of the maximum standard deviation respectively. The randomly generated numbers were scaled (Appendix A.2) to appropriate ranges for the two parameters (description below).

## Simulations

The stochastic variable Leslie matrix was used to simulate population growth from 19762050. Five thousand simulations were done for each trial configuration with stochastic parameters under three primary scenarios (summarized in Table 2.1) to produce predicted averages for $\mathrm{M}_{\mathrm{t}}$ and the associated variance for each year. The primary scenarios investigated the effects of two different ways of modeling removal of harvested animals, variable versus knife-edge fecundity, and variability in the density dependent and stochastic parameters. These trials were conducted to see if modeling conditions affected the magnitude of change and time associated with $\mathrm{M}_{\mathrm{t}}$ reaching recovery. In the first two scenarios described, calf survival and conditional fecundity were stochastic with maximum variability and only calf survival was density dependent. In the third scenario fractional animals were removed to account for harvest and fecundity was knife-edge.

Two trial configurations were designed to compare the way in which harvested animals were removed from the population. The total number of animals removed in each year of projection was determined by the harvest vector (described below and summarized in Table 2.2). In trial A1, whole animals were removed from the age class vector for each year equal to the total number in the harvest vector for that year. These animals were removed at random from the mature age classes only (age class 6-35). The mature animals were selected at random from a uniform distribution such that all had an equal probability of being harvested. In trial A2 animals were removed fractionally from mature age classes only. The total harvest for each year was converted into a harvest rate by dividing the harvest value by the sum product of the age class vector for that year by the maturity vector. The harvest rate was then subtracted from 1 (to equate to survival) and multiplied by the mature age classes in the age class vector for each year.

Next, simulations were conducted to investigate the effect of variable versus knife-edge fecundity. In trial B1, juvenile animals (age class 3-5) were assigned a lower conditional fecundity rate than fully mature animals (age class 6-35). The lower rate, determined from the inflection point of a sigmoid shaped distribution with a minimum of 0 and asymptote of maximum conditional fecundity (described below) reached by age class 6 , was set at 0.0835 and was not stochastic. The lower fecundity rate was conditional on juvenile survival to the next age class. In trial B2, only mature animals reproduced, and all mature animals had the same conditional fecundity rate. Animals were removed from trial B1 and B2 fractionally (note that trial A2 = B2).

Lastly, simulations were compared in which varying parameters were density dependent, and different variability in the stochastic parameters was used. Fourteen different configurations were investigated (trials C1-C14 in Table 2.1). In these simulations, fractional animals were removed and fecundity was knife-edge (note that trial A2 = B2 = C2).

## Life History Parameters

Estimates of five life history parameters were required for the model being used. These parameters were ASM, conditional fecundity, calf survival, juvenile survival and adult survival. A vector of harvest values for each year was needed to simulate hunting mortality. Knowledge about the sex ratio of the population was also necessary so that calf production was calculated from females only. Due to the paucity of life history data available for the Cook Inlet beluga stock, estimates for parameters from other beluga populations were assumed to be comparable. Values for these parameters were either taken from the literature, calculated from values found in the literature, or determined by realistic values possible within the model framework. The life history parameters in this study are based on ages estimated from teeth assuming two growth layer groups (GLGs) are laid down per year (Appendix B.1). Generally, ages reported in the literature begin with calves assigned age 0 , while in modeling calves are assigned to age class 1 . This can lead to some confusion regarding actual ASM or maximum life span. For clarity, "age = x" will be used when calves were called age 0 , and "age class $=x$ " used if calves were termed age class 1 .

## Age at sexual maturity

ASM (Appendix B.2) for female belugas is generally reported in the range of age 4-7 years (Sergeant 1973, Braham 1984, Burns and Seaman 1985). Thus, in the deterministic model ASM was set at age 5 (age class 6). When ASM was density dependent in the variable Leslie matrix model, its minimal value was set at age 4 and its maximum value, calculated when $\lambda=1$, was age 7 .

## Fecundity

Fecundity (Appendix B.3-4) is the average rate at which female young are produced annually by females. This can be calculated by multiplying the birth rate by the proportion of females in the population (Hazard 1988) and their estimated survival, or
determined from calf counts. Using the calculation method, if 1 calf every 3 years is assumed as the birth rate and the sex ratio is $1: 1$ (Brodie 1971), the value for conditional fecundity is 0.167 . This value is conditional upon adult survival. If the calving interval is assumed to be 2 years (Burns and Seaman 1985) calculated conditional fecundity is 0.25 . Values for fecundity based on calf counts range from 0.08 (Lesage and Kingsley 1998) to 0.14 (Braham 1984). These numbers are lower than the calculated value, but do account for survival of mother through pregnancy, failed pregnancies, and some early calf mortality occurring between time of birth and time of census.

In the deterministic model, conditional fecundity was set at the calculated value of 0.167. In the variable Leslie matrix model, conditional fecundity was stochastic to account for the wide range of possible values for this parameter. Yearly values for conditional fecundity were drawn at random (Appendix A.1.2) from a range of 0.10-0.20 ( $\mu=0.15$ ). A sensitivity analysis was done to investigate the effects of this conditional fecundity range on $\mathrm{M}_{\mathrm{t}}$ and $\Delta \mathrm{M}$. Fecundity was not made density dependent because this would regulate population growth in much the same way as density dependent calf survival.

## Survival parameters

Limited knowledge about age specific survival rates provided the largest source of uncertainty for the parameters used. Many natural and anthropogenic factors can affect survival. Unfortunately, data on these variables and their associated effects are minimal (Hazard 1988). The long life span of marine mammals, however, requires that adult survival rates be high (Goodman 1981). Survival rates can be estimated in a variety of ways. These include estimation from life tables, fitting of survivorship models to agefrequency distributions, or scaling of survivorship curves by mean life span or by modal age of senescence (Barlow and Boveng 1991). Using these approaches investigators have reported a range of possible adult survival values from 0.90 to 0.97 (Appendix B.4). A range of 0.90-0.99 for adult survival was investigated in the sensitivity analyses to determine the optimal value for the parameter.

Estimates of juvenile survival for belugas are scarce. Doidge (1990) used smoothed age frequencies in a life table to obtain an estimated age-specific survival rate of 0.863 for 3 year olds. Hobbs and Shelden (1998) used a range of 0.90-0.97 for immature survival in their calculations of growth rate for Cook Inlet belugas. A range of 0.85-0.99 for juvenile survival was investigated in the sensitivity analyses to determine the optimal value for the parameter.

For calf survival Sergeant (1973) reports a possible value of 0.905 for the first half year of life excluding the first month and a half of life. This number comes from examination of age-class frequencies using a method developed by Cassie (1954). Squaring this number to convert it to an estimate for the first year of life yields an estimate of 0.819. This value was used in solving the Lotka equations and was also the maximum value for this parameter in the density dependent (Appendix A.4.1) portion of the Leslie matrix. The minimum value for calf survival, calculated when $\lambda=1$, was 0.442 . Given the importance of this parameter in recruitment, and the uncertainty associated with its value, calf survival was also stochastic. Yearly values were drawn at random (Appendix A.1-2) from a range defined as $\pm 0.05$ around the density dependent value calculated each year.

## Harvest

Harvest numbers are difficult to assess because of the uncertainties associated with reporting methods. Acknowledged minimal estimates of yearly harvest reports since the 1930's are summarized in Mahoney and Shelden (2000). These numbers were used to construct the harvest vector (Table 2.2) used in the Leslie matrix model.

## Maximum age

Belugas are a relatively long-lived species. The oldest female sampled by Burns and Seaman (1985) was estimated to be older than age 35, leading them to report beluga life span as > 30 years. Sergeant (1973) found a maximum of 50 GLGs in beluga teeth giving a life span estimate of 25 years. Due to the effect of annual wear on teeth it is
likely that the life span of belugas is longer than that estimated from GLGs. Thus, the maximum age class in the Leslie matrix was set at 35.

## Carrying capacity

Based on the 1979 abundance estimate by Calkins (1989) of 1293, the carrying capacity in the Leslie matrix for density dependent calculations was set at 1300 animals.

## Results:

## Sensitivity

Solving the Lotka equation for juvenile survival for a range of adult survival and $\lambda$ values while holding all other parameters constant (harvest rate $=0$, conditional fecundity $=$ 0.167 , calf survival $=0.819, \mathrm{ASM}=6$ ) yielded a nearly linear inverse relationship between the two survivals for each $\lambda$ value (Figure 2.2). By definition, neither adult nor juvenile survival can be greater than 1 and is unlikely that juvenile survival would be higher than adult survival. Assuming adult survival was between 0.96 and 0.98 and juvenile survival was between 0.90 and 0.95 , $\lambda_{\max }$ was between 1.04 and 1.06 (Figure 2.2) in this model when no density dependent effects were in place.

Calculation of $\mathrm{M}_{\mathrm{t}}$ after solving the Lotka equation with a range of adult survival, harvest and conditional fecundity rates indicated that $\mathrm{M}_{\mathrm{t}}$ was relatively insensitive to changes of conditional fecundity in the range 0.10-0.20 (Figure 2.3). As conditional fecundity decreased, $\mathrm{M}_{\mathrm{t}}$ increased from a range of $0.301-0.583$ to a range of 0.499-0.651, with sensitivity greater for smaller values of $\mathrm{M}_{\mathrm{t}} . \mathrm{M}_{\mathrm{t}}$ was also insensitive to changes in adult survival rate since equivalent incremental increases in adult survival produced equivalent incremental increases in $\mathrm{M}_{\mathrm{t}}$ (Figure 2.3 and 2.4). The only exception to the equivalent increases was the combination of highest harvest, lowest adult survival and lowest fecundity rates. However, the values deduced from this combination of parameters
should be disregarded, as the high harvest rate could not be sustained with such low survival and fecundity.

Considering harvest rate $(\mathrm{h})=0.20$ as an indicator of $\mathrm{M}_{\mathrm{t}}$ during heavy exploitation and $h=0$ as an indicator of $M_{t}$ after the removal of harvest, the magnitude of $\Delta M$, from exploited to rebound level, remains fairly constant for varying values of adult survival (Figure 2.3 and 2.4). Similar results were found for varying levels of juvenile survival. Because of its minimal affect on $\Delta \mathrm{M}$, adult survival was set at a constant level of 0.967 in the population projections. Solving the Lotka equation for juvenile survival when harvest rate $=0, \lambda_{\max }=1.04$, conditional fecundity $=0.167$, calf survival $=.819$, and adult survival $=0.967$ resulted in a value of 0.932 . Thus, juvenile survival was set at a constant level of 0.932 in the population projections.

Investigations on the probable range of $\lambda_{\text {max }}(1.04-1.06)$ resulted in a near constant $\Delta \mathrm{M}$ with removal of harvest throughout the range of adult survival and lambda values (Figure 2.4). Because $M_{t}$ was not observed to be sensitive to this range of values for $\lambda$, the conservative value of $\lambda_{\max }=1.04$ was used for the calculation of the SAD with which the population projections began in 1976.

## Matrix Model Projections

The two trials conducted to compare different ways of removing harvested animals in the model yielded nearly identical results for average values of $\mathrm{M}_{\mathrm{t}}$ from 5000 simulations (Figure 2.5). Similarly, the two trials conducted to compare variable versus knife-edge fecundity in the model showed comparable results (Figure 2.5). Although any sort of significance testing between the average values of $M_{t}$ predicted from the different trials was inappropriate given that variance was predetermined by the investigator, it can clearly be seen that the trends associated with $\Delta \mathrm{M}$ are consistent and of similar magnitude under each scenario (Table 2.3). Because the responses were so similar, it was unnecessary to continue to consider each trial separately. In consequent modeling,
animals were removed fractionally and fecundity was knife-edge. These configurations were chosen because both decreased the time involved in running simulations.

The results from simulations of trials C1-C10 were virtually the same, with the only difference in outcomes being the size of the error bars that resulted from the different amounts of variability in the stochastic parameters. The same was true for trials C11-C12 and C13-C14. Thus, only the averages from trials with maximum variability, trials C 2 , C12, and C14 are discussed here. Peak abundance prior to heavy exploitation in trials C2, C12, and C14 was 784, 906 and 834 whales respectively. The number of years it took for abundance to reach similar levels after removal of harvest in the three trials was 26, 11 and 19 years respectively (Figure 2.6).

The values of $\mathrm{M}_{\mathrm{t}}$ associated with the $\Delta \mathrm{M}$ from exploited to rebound level for trials C 2 , C12, and C14 are recorded in Table 2.3 and can be viewed in detail in Figure 2.6. Peak levels of $\mathrm{M}_{\mathrm{t}}$ prior to heavy exploitation were $0.66,0.64$, and 0.65 for trials $\mathrm{C} 2, \mathrm{C} 12$ and C 14 respectively. The number of years it took for $\mathrm{M}_{\mathrm{t}}$ to reach similar levels after the removal of harvest in the three trials was 5, 3, and 3 years respectively. The associated increase within the first five years after removal of harvest was $18.6 \%$ for trial C2, $11.9 \%$ for trial C12, and $15.6 \%$ for trial C14. Again, significance testing between the predicted values for the trials was inappropriate because variance was predetermined. Still, trends in $\mathrm{M}_{\mathrm{t}}$ and $\Delta \mathrm{M}$ were consistent between the three scenarios (Figure 2.6). Because the responses were so similar, it was again unnecessary to continue to consider each trial. Thus, trial C14 was selected for further analysis because it incorporated the greatest number of aspects that could be influencing the population.

If it is assumed that $\mathrm{M}_{\mathrm{t}}$ for the population would show similar variability to that set in trial C14, then the 95\% confidence intervals associated with the average $M_{t}$ for each year indicate the $\Delta \mathrm{M}$ that could be significantly detected (Figure 2.7). In trial C14 changes between $\mathrm{M}_{1999}$ and $\mathrm{M}_{2001+}$ could be significantly detected. Additionally, changes between $\mathrm{M}_{2000}$ and $\mathrm{M}_{2002+}$ could be significantly detected. The variances estimated for $\mathrm{M}_{1999}$ and
$\mathrm{M}_{2000}$ from trial C14 were 0.00056 and 0.00043 respectively. Assuming a population size of 400 , the minimum detectable difference (MDD) for $\mathrm{M}_{2001}$ (alpha $=0.05$, beta $=.15$ ) was calculated based on the estimated sample size (Table 2.4). The yearly change in $\mathrm{M}_{\mathrm{t}}$ that could be significantly detected under these scenarios ranged from 5.9-7.0\%.

After year 2003, significant detection of changes in $\mathrm{M}_{\mathrm{t}}$ became unlikely because of stabilization of the statistic. This fact was used to define recovery of $M_{t}$ as a value for $M_{t}$ at or above pristine $\mathrm{M}_{\mathrm{t}}$ (average $\mathrm{M}_{1980-85}$ ) and not changing by more than $2 \%$ for at least 3 years. This definition required stabilization of $\mathrm{M}_{\mathrm{t}}$, not just an increase to a value near the unexploited level. Under this definition, the most likely year of recovery in trial C14, accounting for $28.8 \%$ of the 5000 simulations, was 2004 (Figure 2.8). The median year of recovery was 2005 (Figure 2.9) and the mean year was 2006. Under scenario C14 virtually all simulations had reached recovery by year 2012.

## Discussion:

## Sensitivity

A value of 0.04 for $R_{\max }\left(\mathrm{R}_{\max }=\lambda_{\max }-1\right)$ is commonly accepted for the purposes of managing beluga whale populations (Hill 1996). This was consistent with the range of $\lambda_{\text {max }}$ from 1.04-1.06 predicted by solving the Lotka equations. This range was also consistent with Eberhardt's calculations for long-lived species with adult survival in the range of $0.96-0.98$ (1985).

A slight increase in $\mathrm{M}_{\mathrm{t}}$ as fecundity decreased (Figure 2.3) occurred because a decreased production of calves yielded a lower percentage of immature animals and a higher value of $\mathrm{M}_{\mathrm{t}}$. For a constant $\lambda$ (1.04) there was an inverse relationship between fecundity and juvenile survival rate. Because the first age class was larger with higher fecundity, all successive juvenile age classes were larger than the corresponding juvenile age classes at lower fecundity with higher survival (Figure 2.10). Thus, the juvenile fraction of the population was larger at higher fecundity (Figure 2.11). When fecundity was high the
magnitude of $\Delta \mathrm{M}$ when harvest was removed was greater (at reasonable levels of adult survival) because the adults initially formed a smaller portion of the population. Although $\Delta \mathrm{M}$ occurred as predicted with decreased harvest, the magnitude was not constant for varying levels of fecundity. This uncertainty in the effect of fecundity on the value of $\mathrm{M}_{\mathrm{t}}$ and magnitude $\Delta \mathrm{M}$ indicated that fecundity should be stochastic in the matrix model projections.

Increased adult survival resulted in a greater fraction of animals in mature age classes and an increased $\mathrm{M}_{\mathrm{t}}$ (Figures 2.3 and 2.4). As adult survival increased, however, the magnitude of $\Delta \mathrm{M}$ when harvest was removed stayed constant. This insensitivity indicated that this parameter could be held constant in the matrix model projections. If the actual value of adult survival was different than that estimated in the modeling work, it would not affect predictions of the magnitude of $\Delta \mathrm{M}$ as the population recovers.

Overall, the sensitivity analyses indicated that a change of $0.1-0.2$ in the statistic $\mathrm{M}_{\mathrm{t}}$ could be expected if a harvest of $20 \%$ was reduced to zero. The $\Delta \mathrm{M}$ was relatively insensitive to $\lambda$, juvenile survival and adult survival. The magnitude of $\Delta \mathrm{M}$ associated with removal of harvest was most sensitive to fecundity.

## Matrix Model Projections

Three primary scenarios, each incorporating stochastic and density dependent parameters, were investigated with population projections. These were trials A1-2, B1-2, and C1-14 defined in Table 2.1. For each scenario $\mathrm{M}_{\mathrm{t}}$ started at a constant level, decreased when harvest increased, and increased when harvest was removed. The rapid decline and rebound observed in $\mathrm{M}_{\mathrm{t}}$ were the result of drastic changes imposed on adult survival with the onset and removal of heavy harvest. The greatest $\Delta \mathrm{M}$ after removal of harvest occurred for trials A1 and A2 (B2, C2) when only calf survival was density dependent (Figure 2.5). The smallest $\Delta \mathrm{M}$ occurred for trial C 12 when only ASM was density dependent (Figure 2.6). This difference indicated that changes in calf survival affect the
age structure more than do changes in the ASM. The slightly greater change in A1 compared to A2 was the result of increased instability in the system introduced by the stochastic rather than constant removal of animals from each age class.

It is known that changes in fecundity along with survival can cause impacts on the age structure of a population (Caswell 2000). Still, the comparison of knife-edge and variable fecundity showed minimal differences in $\mathrm{M}_{\mathrm{t}}$ and $\Delta \mathrm{M}$ (Figure 2.5). Overall, $\mathrm{M}_{\mathrm{t}}$ was slightly lower in the variable fecundity scenario because more calves were being produced, increasing the percentage of immature animals. Incorporation of a gradual increase in fecundity as animals aged did not produce any change in the behavior of $\mathrm{M}_{\mathrm{t}}$.

Changes to the age structure (in the form of forced deviations from the SAD) caused by decreased adult survival were associated with the population increasing at less than its maximum growth rate (Figure 2.12). Although all parameters were defined so that $\lambda_{\max }=$ 1.04, the average growth rate over the 20 years after removal of harvest in trial C14 was only 1.02. This is one reason total abundance took longer to rebound to pre-exploitation levels than did $\mathrm{M}_{\mathrm{t}}$ in all scenarios. Trial C12 took the least number of years for abundance to rebound while trial C2 took the longest. This difference again indicates the effects of ASM and calf survival on the age structure. Additionally, abundance took longer to recover because, although removal of harvest caused an increase in adult survival, which allowed $\mathrm{M}_{\mathrm{t}}$ to rebound, the total number of mature animals producing calves was still low.

It must be noted that in trial C12 total abundance exceeded K within 25 years after the removal of harvest (Figure 2.6). It took nearly 100 years for the population to equilibrate to K when ASM was the only density dependent parameter. However, it is unlikely that this particular parameter is the only density dependent regulation on population size.

The initial peak above pre-exploitation levels that occurred in $\mathrm{M}_{\mathrm{t}}$ shortly after removal of harvest was an interesting phenomenon. The peak occurred in all trials and was a result of the relatively large juvenile portion of the exploited age structure entering the adult
portion of the age structure while total fecundity was still low. It is the inverse of the response observed in $\mathrm{M}_{\mathrm{t}}$ with the onset of harvest. This rapid response of the age structure to changes in survivorship is exactly why the statistic $\mathrm{M}_{\mathrm{t}}$ is valuable for monitoring recovery.

The variance observed in the stochastic simulations indicated that even given variability in life history parameters, the $\Delta \mathrm{M}$ associated with recovery could still be detected. In addition to variability within the population, detection of $\Delta \mathrm{M}$ from year to year will also depend on sampling error and sample size. If the variability in taking yearly measurements from the population is smaller than estimated in trial C 14 , it will be possible to detect yearly changes. If the variability is greater, then measurements may need to be taken for a number of years before significant changes are detected.

The model predicts recovery of $M_{t}$ for more than $50 \%$ of the simulations by year 2005 . Given small enough sampling error to detect a $\Delta \mathrm{M}$ of at least $5 \%$, if changes are not observed in $\mathrm{M}_{\mathrm{t}}$ within 6 years from removal of harvest, some other factor may be suppressing adult survival. Recognition of such a problem would allow for additional management actions to be taken to identify and remove the problem. Thus, $\mathrm{M}_{\mathrm{t}}$ is a useful statistic for monitoring recovery of the population.

Table 2.1: Trial configurations for population projections from year 1976-2050.
*Trials A2, B2, and C2 have the same configuration.

| Scenario | Trial | Density dependent parameter(s) | $\sigma$ value for calf survival stochasticity | $\sigma$ value for fecundity stochasticity |
| :---: | :---: | :---: | :---: | :---: |
| Whole animal removal | A1 | Calf survival | 0.25 | 0.25 |
| Fractional animal removal | A2* | Calf survival | 0.25 | 0.25 |
| Variable fecundity | B1 | Calf survival | 0.25 | 0.25 |
| Knife edge fecundity | B2* | Calf survival | 0.25 | 0.25 |
| Variable stochasticity and density dependent parameters (fractional animal removal and knife edge fecundity) | C1 | Calf survival | None | None |
|  | C2* | Calf survival | 0.25 | 0.25 |
|  | C3 | Calf survival | 0.25 | 0.125 |
|  | C4 | Calf survival | 0.25 | 0.0625 |
|  | C5 | Calf survival | 0.125 | 0.25 |
|  | C6 | Calf survival | 0.125 | 0.125 |
|  | C7 | Calf survival | 0.125 | 0.0625 |
|  | C8 | Calf survival | 0.0625 | 0.25 |
|  | C9 | Calf survival | 0.0625 | 0.125 |
|  | C10 | Calf survival | 0.0625 | 0.0625 |
|  | C11 | ASM | None | None |
|  | C12 | ASM | 0.25 | 0.25 |
|  | C13 | Calf survival \& ASM | None | None |
|  | C14 | Calf survival \& ASM | 0.25 | 0.25 |

Table 2.2 Harvest vector used in the Leslie matrix model for removal of animals.

| Years | Number harvested per year |
| :---: | :---: |
| $1979-1989$ | 8 |
| $1990-1994$ | 40 |
| $1995-1998$ | 90 |
| $1999-2000$ | 0 |
| $2001-2050$ | 2 |

Table 2.3 Average values of $\mathrm{M}_{\mathrm{t}}$ for years 1999-2010 from 5000 simulations each of trials A1, A2, B1, B2, C2, C12, and C14.

| Year | Average M via Trial A1 | Average M via Trial B1 | Average M via Trial A2, B2, C2 | Average M via Trial C12 | Average M via Trial C14 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1999 | 0.4860 | 0.5174 | 0.4928 | 0.5284 | 0.4991 |
| 2000 | 0.5983 | 0.5670 | 0.5681 | 0.5739 | 0.5588 |
| 2001 | 0.6690 | 0.6058 | 0.6282 | 0.6081 | 0.6076 |
| 2001 | 0.7004 | 0.6288 | 0.6633 | 0.6334 | 0.6368 |
| 2003 | 0.6995 | 0.6398 | 0.6790 | 0.6458 | 0.6519 |
| 2004 | 0.6743 | 0.6406 | 0.6784 | 0.6478 | 0.6552 |
| 2005 | 0.6620 | 0.6314 | 0.6645 | 0.6420 | 0.6485 |
| 2006 | 0.6580 | 0.6254 | 0.6578 | 0.6394 | 0.6461 |
| 2007 | 0.6585 | 0.6224 | 0.6561 | 0.6391 | 0.6464 |
| 2008 | 0.6612 | 0.6217 | 0.6571 | 0.6397 | 0.6478 |
| 2009 | 0.6636 | 0.6226 | 0.6592 | 0.6404 | 0.6494 |
| 2010 | 0.6642 | 0.6258 | 0.6611 | 0.6456 | 0.6504 |

Table 2.4 Minimum detectable difference (MDD) with a t-test in the value of $\mathrm{M}_{1999}$ to $\mathrm{M}_{2000}$ and from $\mathrm{M}_{2000}$ to $\mathrm{M}_{2001}$ based on variances estimated in trial 2 of the model and assuming a population size of 400 animals.

| Sample size | MDD <br> $\mathbf{1 9 9 9 - 2 0 0 0}$ <br> (equal var) | MDD <br> $\mathbf{1 9 9 9 - 2 0 0 0}$ <br> (unequal var) | MDD <br> 2000-2001 <br> (equal var) | MDD <br> 2000-2001 <br> (unequal var) |
| :---: | :---: | :---: | :---: | :---: |
| 350 | 5.86 | 6.23 | 6.67 | 6.94 |
| 300 | 5.86 | 6.23 | 6.68 | 6.95 |
| 250 | 5.87 | 6.23 | 6.68 | 6.95 |
| 200 | 5.87 | 6.24 | 6.69 | 6.96 |
| 150 | 5.89 | 6.25 | 6.70 | 6.97 |
| 100 | 5.91 | 6.28 | 6.73 | 7.00 |



Figure 2.1 The three beta distributions used in random number generation for stochastic parameters $(\alpha=\beta)$.


Figure 2.2 Juvenile versus adult survival rates for varying growth rates ( $\lambda=1.00-1.07$ ).


Figure 2.3 Results for the calculation of $\mathrm{M}_{\mathrm{t}}$ after solving the Lotka equation with a range of adult survival, harvest (h), and conditional fecundity rates when $\lambda_{\text {max }}=1.04$, calf survival $=0.819$, and conditional fecundity is $(A) 0.20$, (B) 0.15 , (C) 0.10 .


Figure 2.4 Results for the calculation of $\mathrm{M}_{\mathrm{t}}$ after solving the Lotka equation with a range of adult survival, harvest (h), and growth rates when calf survival $=0.819$, conditional fecundity $=0.167$, and $\lambda_{\text {max }}$ is (A) 1.06 , (B) 1.05 , (C) 1.04 .


Figure 2.5 Average $\mathrm{M}_{\mathrm{t}}$ values projected over time from 5000 simulations of trials comparing (A) two different ways of modeling removal of harvested animals, and (B) knife-edge versus variable fecundity.


Figure 2.6 Results from 5000 simulations of trials where varying parameters were density dependent (dd) showing averages of (A) $\mathrm{M}_{\mathrm{t}}$ and (B) abundance over time.


Figure 2.7 Average values of $\mathrm{M}_{\mathrm{t}}$ over time with associated $95 \%$ confidence intervals from 5000 simulations of trial C14 where both calf survival and ASM are density dependent and both calf survival and conditional fecundity are stochastic with maximum variability.


Figure 2.8 Frequency of years to recovery of $M_{t}$ from 5000 simulations (2004 is most likely recovery year accounting for $28.8 \%$ of simulations).


Figure 2.9 Cumulative frequency of years to recovery of $\mathrm{M}_{\mathrm{t}}$ to pristine or higher levels with subsequent fluctuations of $\leq 2 \%$ for at least 3 years.


Figure 2.10 Percent of animals in each age class at varying levels of conditional fecundity $(0.25,0.20,0.15)$ when all life history parameters are held constant except juvenile survival.


Figure 2.11 Fraction of juvenile animals in the population for varying levels of fecundity when all other life history parameters are held constant except for juvenile survival.


Figure 2.12 Changes to the age structure over time associated with the increase and removal of harvest.

## CHAPTER 3: SKIN COLOR DETERMINATION AS AN INDEX OF AGE STRUCTURE FOR COOK INLET BELUGA WHALES

## Introduction:

Traditionally, length at age frequency tables have been used to approximate aspects of the age structure of beluga populations such as the fraction of mature individuals (Burns and Seaman 1985, DeMaster et al. 1998). This technique works well in clear waters where entire body lengths can be seen and measured from aerial photographs. Unfortunately, the turbid, muddy waters of Cook Inlet make such measurements impossible (Shelden and Angliss 1995). Instead of seeing the entire length of animals from the air, only the portion of the animal exposed to air at surfacing is visible. It is possible, however, to determine the color of the animal from the exposed portion.

Beluga whales are pinkish gray at birth and become darker gray during their early years (Caron and Smith 1990). Around 4-8 years of age (depending on sex), when belugas are estimated to reach sexual maturity, they gradually turn from gray to white (Hazard 1988). Because the color change in belugas is so highly correlated with age, a measure of the fraction of white animals $\left(\mathrm{W}_{\mathrm{t}}\right)$ in the population can be used as a negatively biased, but consistent index of the fraction of mature animals $\left(\mathrm{M}_{\mathrm{t}}\right)$.

It has been shown that $\mathrm{M}_{\mathrm{t}}$ changes predictably in response to known disruptions in the age structure. In order to observe how $\mathrm{M}_{\mathrm{t}}$ changes for the Cook Inlet stock of beluga whales, a method was developed to objectively measure $\mathrm{W}_{\mathrm{t}}$ from the population.

## Methods

## Data Collection

Whale images were collected during NMML's annual aerial surveys of belugas in Cook Inlet, AK (Appendix C.1). The entire inlet was surveyed and it is believed that all whale
groups were located and video-taped. Aerial surveys are described in detail in Rugh et al. (2000).

Collection of whale color information occurred concurrently with counting passes during the survey. Images were collected using a video camera directed out of an open window on the right side of the aircraft during each pass. Passes occurred along the long axis on either edge of the whale groups (Figure 3.1) and images of whales at the surface were captured. Each video-taped pass over a group of whales was considered a random sample of the whales in that group. The speed of the aircraft in conjunction with the surfacing interval for belugas made it unlikely that any animal was resampled during a single pass (Hobbs et al. 2000a). Typically 4-8 passes were made dependent upon weather conditions, visibility, timing, and sample size requirements.

A high resolution Sony digital video camera model DSRPD100A was used for image collection (Appendix C.2). Video cameras offer the ability to view data while in the field, allowing daily determinations of sample size and video quality. Additionally, new technology has greatly increased the resolution capabilities of video cameras along with their capacity to magnify subject matter without the bulk of large lenses.

Surveys were only conducted under mild weather conditions. If sea state exceeded three (Beaufort scale), belugas became indistinguishable from "white caps" in the water. Sun angle and associated glare also played a role in visibility of belugas. High glare made detection of belugas impossible. In such situations, redirection of the aircraft occurred. When collecting images, the angle of the aircraft's passes would be modified, and data were only collected from non-glare pass directions.

From population dynamics modeling work (Chapter 2) it was known that a $\Delta \mathrm{M}$ of approximately $10 \%$ should be detectable in order to observe the rebound of $\mathrm{M}_{\mathrm{t}}$ from its exploited to recovered level. Two options were used to calculate the required sample size to significantly detect this change based upon prior knowledge of typical group sizes and locations (Table 3.1, Appendix C.3).

## Color Calibration Experiment

In order to define a whale image's color as gray or white, a color calibration experiment was conducted. Life size models of the dorsal portion of beluga whales exposed during surfacing were constructed and painted four different colors. Measurements were taken from both aerial and shipboard photos of beluga whales in Cook Inlet to determine the dimensions of the models. From these measurements the average length to width ratio was 0.35 , average length to height ratio was 0.12 and total length exposed ranged between 20-40 in. Two sizes of models within these dimensions were made to simulate adult and juvenile whales (Table 3.2). The heights of the models were larger than real whale dimensions but this had no effect on aerial image collection. More importantly, the lengths and widths fell within the calculated dimension ranges. The models were made from inner tubes cinched with plastic twist ties and weighted so that they hung vertically in the water (Figure 3.2). The tubes were painted with buoy paint (Inylon by Humboldt Treasures, U.S. Distribution, Inc., Portland, OR) so they could withstand exposure to water and be inflated and deflated without shedding paint. The four shades were mixed from black (buoy black 7-32635-4) and white (buoy white 7-32632-4) paint to approximate the range of shades in shipboard photos of Cook Inlet belugas taken at close range. Colors were defined as white, light gray, medium gray and dark gray.

Aerial imagery was collected on the models in the same way it was on actual whales. A series of trials was conducted with varying configurations of the different size and color models (Table 3.2). The first set of trials composed a controlled experiment in which known objects of each size and color ("knowns") were video-taped. These images were used during image analysis to define whale color. Next, a set of trials with random configurations of object size and color ("unknowns") was conducted. The images from these trials were used to test the criteria defined by the control. The effects of sun angle were investigated during this experiment. Sea state and weather conditions were not investigated since beluga surveys are only conducted during optimal conditions.

Assuming a binomial process in which the probability of correctly identifying a whale color is 0.90 and the desired CV is $10 \%$, a sample size of 11 images of each object per trial was required. To insure adequate sample size, trials consisted of 4 aerial circles over the objects with data being collected every $90^{\circ}$. This allowed a maximum possible collection of 16 images of each object per trial. One angle on trial 1 had glare from the sun. On all other angles and trials there was no glare. Trial 6 was conducted twice due to miscommunication between plane and boat.

## Analysis of Images

Images of both real and simulated whales were imported into a computer for editing using the software IMovie ${ }^{\circledR}$. Individual whales and whale models were identified and saved as still images using this software. Still images were created such that the object of interest was in the center of the image. These images were then analyzed using the image analysis software program Image Pro Plus®. Analysis of images consisted of defining an area of interest (AOI) for which to determine color, reading the intensity values for the pixels within the AOI, saving the pixel data into a file, and defining the image's color based on the pixel data. This set of steps was automated in Image Pro Plus® using Visual Basic® programming language.

In images, each pixel contained 24 bits of data with 8 bits for each of three color channels in the defined color model. Thus, each pixel had an intensity value from 0-255 for each color channel. The YIQ (referring to the 3 color channels: $y$-axis, in-phase, and inquadrature) color model was used in this study (Appendix C.4). AOI's were defined by pixels in the image that were within $\pm 50$ of the reference pixel's overall intensity value. The reference pixel was defined as the center pixel in the image creating AOI's that were comprised of the individual whale or model.

The images from the "known" trials of the color calibration experiment were analyzed first. Histograms for each of the four shades in the experiment were investigated in different color channels. Data from all white and light gray objects were combined to
define the white whale category. Data from all medium gray and dark gray objects were combined to define the gray whale category. Images from the "unknown" trials of the color calibration experiment were analyzed to test how well the definitions of white and gray from the "knowns" worked. Finally, images of beluga whales from the aerial passes were analyzed to estimate $\mathrm{W}_{2000}$ for the population.

## Data Analysis

The calculation of $\mathrm{W}_{2000}$ for the population was simply the sum of all white whales observed divided by the sum of all whales observed. The 95\% confidence interval for $\mathrm{W}_{2000}$ was calculated using a nested bootstrap (Efron and Tibshirani 1986). Each bootstrap entailed estimating $\mathrm{W}_{2000}$ by sampling at random with replacement from all of the passes equal to the total number of passes, and then sampling at random with replacement from the whales within a selected pass equal to the total number of whales in that pass. A total of 1000 values of $\mathrm{W}_{2000}$ were calculated using nested bootstraps. The W's were ranked smallest to largest and assigned their respective cumulative percentiles. The upper and lower 2.5 percentiles determined the end points for the confidence interval.

## Results

A total of 32 images for each whale model color were collected from the "known" trials. Images from the angles with glare were discarded (4 images of each color) because readings were inconsistent with other image readings. Water readings from the glare images had high frequencies of readings in the 240-255 intensity range in the Y (luminance) channel of the YIQ color model. Water readings from non-glare images did not have readings in the 230-255 intensity range. This fact was used to define glare in passes on groups of whales. Passes where water had readings in the 230-255 intensity range were discarded.

After discarding glare images, there were 28 images of each whale model color left for defining gray and white objects. Images of the white and light gray whale models had markedly high frequencies of readings in the intensity range of 230-255 in the Y color channel of the YIQ color model (Figure 3.3). This was distinct from the images of medium and dark gray whale models, which rarely had readings in this range at all (Figure 3.4). A series of logistic regressions on the cumulative frequencies in the 200-$255,230-255$, and 250-255 intensity ranges from all the "known" images were run. The regression with the steepest slope (17.47), and minimum uncertainty ( 0.056 ) was for the 250-255 intensity range with the $50 \%$ division point at a value of 0.1769 cumulative pixel intensity value frequency.

From the "unknown" trials there were 106 white, 121 light gray, 100 medium gray and 113 dark gray object images. Two of the small dark gray objects did not appear in the video imagery when located directly beside a large white object. Using the definition of a white object as one in which the cumulative frequencies in 250-255 intensity range were greater than 0.1769 did not work well for the "unknown" trials. Under this definition $99.5 \%$ of the gray objects were correctly identified as gray, but only $75.4 \%$ of the white objects were correctly identified as white. Visual inspection of histograms for the whale models indicated that the extremely high cumulative frequencies in the 250255 range for the white objects (average $=49.9 \%$ compared to $28.7 \%$ for light grays) had skewed the regression. Thus, light gray objects were often being misidentified. To correct for this, a series of different criteria definitions were applied to the "unknown" trials. These definitions were based on values determined from the logistic regressions and from visual inspections of the histograms (Table 3.4). When the criteria for being designated as a white object was defined as an image in which the cumulative frequencies in the 230-255 intensity range was greater than zero, object colors were correctly identified $89.8 \%$ of the time (Table 3.4). This definition provided the highest success rate for correctly identifying object color and was used in the determination of white and gray whales from imagery collected from the Cook Inlet population. Thus, any image
with a 230-255 reading greater than zero was identified as white and any image with a 230-255 reading equal to zero was identified as gray.

In 2000, aerial imagery from Cook Inlet beluga whales was collected on June 7, 8, 11, 12, and 13. A total of 132 passes were video-taped. Six passes had to be discarded because of glare from sun angle and 27 passes captured no whales. Thus, there were 99 total passes resulting in 1608 whale images available for analyses. The number of whale images ranged from 1-74 per pass. Broken down by area, 50 passes totaling 1328 whales came from the Susitna, 33 passes totaling 233 whales came from Chickaloon, and 16 passes totaling 47 whales came from Knik. Using the definitions described above, 1304 of the whale images were categorized as white and 304 as gray. This resulted in a calculation of $W_{2000}=0.810$.

A Kolmogorov-Smirnov test for normalcy (Zar 1996) on the distribution of W's resulting from the nested bootstrap (Figure 3.5) led to rejection of the null hypothesis that the values were normally distributed $(p-v a l u e=0.0765)$. The distribution was slightly left skewed ( $\mathrm{g} 1=-0.300$ ) and leptokurtic $(\mathrm{g} 2=0.313)$. Cutting of the 2.5 percentiles from the 1000 simulations gave a nonparametric 95\% confidence interval of 0.7603-0.8510. This is fairly close to the parametric $95 \%$ confidence interval constructed using the variance estimation of $0.00048(\mathrm{CI}=0.7659-0.8520)$. With this variance, a two sample ttest with 300 degrees of freedom could significantly detect a change of about $6 \%$.

Total time for the analysis of images using the automated process included time to import and watch video imagery, time to identify and save individual whale images, time to read pixel intensity values within individual whale images, and time to use the pixel intensity data to define a whale image as gray or white. The first two steps of this process, involving watching the video and identifying individual whales accounted for the majority of processing time, and would be required whether images were being read manually or using the automated system. Depending on the size of the group, these two steps could take anywhere from 1-60 minutes. Once individual whale images were saved, the time to actually read the images pixel intensity values and assign it to a color
category was minimal. These two steps took only 4-6 seconds using the automated system. This is substantially less time than the 1-2 minutes estimated for an observer to manually view an image and assign it a color category. This time is estimated from the researcher's personal experience analyzing video imagery used for abundance estimates of the Cook Inlet belugas (Hobbs et al. 2000b). Comparing only the time for the final two steps, the automated process took approximately 134 minutes while manual readings would have taken approximately 40 hours.

## Discussion

The Y color channel of the YIQ color model was used exclusively for making decisions about whether or not an image should be analyzed (regarding glare), and about defining an object as gray or white. The Y channel is a measure of luminance and as such, differences in the brightness (white and sun reflection) and darkness (gray) of images are observed this color channel. Essentially, using the Y channel is like converting the color image into a black and white one, but without the loss of any color information. All color information is stored in the I and Q channels instead of being discarded as it would be in conversion of the image to black and white. This keeps the option of analyses of the images with this information available should future studies find use for the color information.

When using the varying definitions for gray and white the main sources of error came from incorrectly identifying the medium gray and light gray objects. For the option chosen (white $=230-255>0$ ) both dark gray and white read with $100 \%$ accuracy. Medium gray objects were correctly identified as gray 74.0\% of the time, and light gray objects were correctly identified as white $83.3 \%$ of the time. In effect, the errors in reading these colors cancel each other out, although grays may be misidentified slightly more frequently. Considering $W_{t}$ as an index of $\mathrm{M}_{\mathrm{t}}$, the misidentified color designations have a parallel in the population in that some dark animals are sexually mature, while some light animals are not. There is no information available as to the fraction of dark mature or white immature animals in beluga populations to determine if the
misidentification rate introduced by the image analysis process is an accurate estimate. However, as long as the misidentification is constant throughout surveys, the predicted $\Delta \mathrm{M}$ as measured by $\mathrm{W}_{\mathrm{t}}$ should still be observed.

An interesting phenomenon was the disappearance in images of small dark gray objects when beside a large white object. The brightness of the white object apparently "washed out" the dark object. Because small dark calves swim immediately adjacent to their mothers, it is likely that such calves were missed in the collection of images to determine $\mathrm{W}_{2000}$. This would result in a positively biased estimate of $\mathrm{W}_{2000}$. Unfortunately, because the trials were not designed to compare object detection to proximity of other objects (objects were allowed to float freely during the trials and only clumped close together near the end of trial 8), a correction factor for missed animals was not a feasible outcome from this study. Using the correction factor of 1.18 for calves and yearlings developed by Brodie (1971) on the total whale image value of 1608 yields a new value of 1897.44. Using this in the calculation of $\mathrm{W}_{2000}(1304 / 1897.44)$ results in a decreased estimate of 0.687 . This value is more consistent with those predicted from the population modeling. However, if the same methodology is used in successive years, the positive bias of $\mathrm{W}_{\mathrm{t}}$ associated with missing young dark animals would be consistent, and measurements from the population would be an index of the actual value of $\mathrm{W}_{\mathrm{t}}$. Again, the predicted $\Delta \mathrm{M}$ as measured by $\mathrm{W}_{\mathrm{t}}$ should still be observable.

The value of $\mathrm{W}_{2000}$ estimated from this study was much higher than the predicted value of $\mathrm{M}_{2000}$ from modeling exercises ( 0.8109 compared to 0.5588 ). There are three probable explanations for this discrepancy. As described above, calves may not be showing up in the aerial imagery. Omitting calves in the calculation of $\mathrm{M}_{\mathrm{t}}$ from trial C14 (Figure 3.7) yields an estimate for $\mathrm{M}_{2000}$ of 0.6119 and an increase in $\mathrm{M}_{\mathrm{t}}$ associated with recovery of similar magnitude to total $\mathrm{M}_{\mathrm{t}}$ calculation. It is also possible that the average color of juvenile animals is a lighter shade of gray than that estimated by the medium gray model. If juveniles are closer in color to the light gray models, their images would be read as white. Including ages 3-4 (age classes 4-5) as mature (simulating these immature animals
being read as white or mature whales) in the calculation of $\mathrm{M}_{\mathrm{t}}$ from trial C 14 yields an estimate for $\mathrm{M}_{2000} 0.8161$ (Figure 3.7). This is quite similar to the value of $\mathrm{W}_{2000}$ collected from the population, however the magnitude $\Delta \mathrm{M}$ associated with recovery is decreased in this scenario and may not be detectable. Lastly, it is quite likely that the life history parameters for the Cook Inlet population are different than estimated in the model. Sensitivity analyses conducted in Chapter 2 indicated that the magnitude of the $\Delta \mathrm{M}$ is insensitive to all life history parameters except fecundity. Thus, even if the parameters used in the model yield a different absolute value for $\mathrm{M}_{\mathrm{t}}$, the estimated $10 \%$ increase from year 2000 should still be observed if the population recovers. The ultimate reason for the discrepancy between $\mathrm{W}_{2000}$ from the predicted $\mathrm{M}_{2000}$ is probably a combination of all of the factors described.

The ability to detect a change in $\mathrm{W}_{\mathrm{t}}$ will depend on the magnitude of the change. Given that $\mathrm{W}_{\mathrm{t}}$ is biased in some way from the model predictions of $\mathrm{M}_{\mathrm{t}}$, it is likely that the magnitude of increase from current to recovered level will be different than predicted. The non-parametric $95 \%$ confidence interval indicates that a change of about $5 \%$ could be significantly detected if future measurements of $\mathrm{W}_{\mathrm{t}}$ have similar variability. This change is smaller than any of the increases predicted from the modeling work of population recovery. Thus, it is likely that yearly increases in $\mathrm{W}_{\mathrm{t}}$ will be significantly detected, allowing $\mathrm{W}_{\mathrm{t}}$ to be used to monitor age structure recovery for the Cook Inlet stock.

## Future studies

There are many directions in which the image analysis work could be expanded. Additional color calibration experiments would be valuable to test the detection of objects under varying conditions. The use of multiple color channels in defining object color could provide improved color resolution. Comparison of manual to automated readings of images could provide validation for the objectivity of an image analysis software system.

Collection of color information from healthy beluga populations would provide more knowledge on the relationship between the fraction of white animals and the age structure of a population. This would also allow for an estimate of the pristine value of $\mathrm{M}_{\mathrm{t}}$. Photographs of harvested or stranded belugas containing some form of color calibration and collected in conjunction with a tooth for aging could yield a color at age curve (similar to a growth curve) for belugas. This would improve the understanding of the change in pigmentation associated with aging.

Clearly there is a need to continue to measure $\mathrm{W}_{\mathrm{t}}$ from the population to see if indeed it does increase as predicted. If it does not increase, investigations into probable reasons for suppression of the mature portion of the population may be warranted, which could imply the need for additional management actions. This brings up the question of the use of age structured statistics as management tools. Currently, the management of marine mammal populations focuses on total numbers of animals and does not consider the age structure of the population. However, it has been demonstrated that changes to the age structure can be observed more quickly than changes in total abundance. For this reason, age structured statistics could provide valuable information for managers and perhaps should be considered when making management decisions.

Table 3.1 Sample size requirements for collection of whale images from groups commonly identified in Cook Inlet. Option 1 samples all the groups and is preferred while option 2 focuses exclusively on the large group consistently found in the Susitna river delta.

| Group | Estimated <br> size | Option 1 <br> \# passes | Option 2 <br> \# passes | \# whales <br> per pass |
| :---: | :---: | :---: | :---: | :---: |
| Susitna | 300 | 25 | 29 | 30 |
| Knik | 50 | 7 | 0 | 5 |
| Chickaloon | 30 | 6 | 0 | 3 |
| Kachemak | 7 | 2 | 0 | 1 |

Table 3.2 Measurements of the dimensions of the whale models.

| Model | Length (in) | Width (in) | Height (in) |
| :---: | :---: | :---: | :---: |
| Large white | 34.5 | 13.5 | 20.5 |
| Large light gray | 33.5 | 13.5 | 21 |
| Large medium gray | 29.5 | 15 | 21.5 |
| Large dark gray | 32 | 15 | 21.5 |
| Small white 1 | 27 | 11 | 16 |
| Small white 2 | 28 | 11.5 | 18 |
| Small light gray 1 | 28.5 | 11 | 18 |
| Small light gray 2 | 28.5 | 10 | 18 |
| Small medium gray 1 | 26 | 11 | 17.5 |
| Small medium gray 2 | 27 | 11.5 | 16 |
| Small dark gray 1 | 28.5 | 10 | 18 |
| Small dark gray 2 | 27 | 12 | 16.5 |

Table 3.3 Configurations of whale models used in the trials conducted to define and test color criteria for gray and white objects.

| Test type | Trial | Configuration |
| :---: | :---: | :---: |
| Knowns | 1 | Large white <br> Large light gray <br> Large medium gray <br> Large dark gray |
|  | 2 | Small white <br> Small light gray <br> Small medium gray <br> Small dark gray |
| Unknowns | 3 | Large medium gray <br> Large dark gray <br> Small medium gray <br> Small dark gray |
|  | 4 | Large white <br> Large light gray <br> Small light gray |
|  | 5 | Large light gray <br> Large medium gray <br> Small white <br> Small white <br> Small dark gray |
|  | 6 | Large white <br> Large dark gray <br> Small light gray <br> Small light gray |
|  | 7 | Large light gray Large medium gray Small white |
|  | 8 | Large white <br> Large dark gray <br> Small medium gray <br> Small medium gray <br> Small dark gray |

Table 3.4 Summary of the success rate of different color criteria definitions in correctly categorizing objects from the "unknown" trials as gray or white. If the sum of the pixel intensity values in the Y channel for the range listed (i.e. 230-255) was greater than the value listed (i.e. 0.207), the object was categorized as white. If the value was less than or equal to the value listed, the object was categorized as gray.

| Definition of white | Gray correctly <br> identified | White <br> correctly <br> identified | Total correctly <br> identified |
| :--- | :---: | :---: | :---: |
| Sum 230-255 >0 | 0.8779 | 0.9163 | 0.8977 |
| Sum 250-255 >0 | 0.8685 | 0.8414 | 0.8545 |
| Sum 230-255 >0.207 | 0.9953 | 0.5242 | 0.7523 |
| Sum 230-255 >0.17 | 0.9953 | 0.7621 | 0.8750 |
| Sum $250-255>0.17$ | 0.9953 | 0.5286 | 0.7545 |



Figure 3.1 Pass configuration for collection of whale images when whale groups were encountered and for collection of images from whale models.


Figure 3.2 Design of whale model used in color calibration experiment. The models were constructed from painted inner tubes cinched with plastic ties and hung with lead weights.


Figure 3.3 Histograms of the average pixel intensity frequencies in the $Y$ color channel from the (A) 56 white and (B) 56 gray, object images.


Figure 3.5 Frequency distribution of W's (fraction white) resulting from 1000 nested bootstraps.


Figure 3.6 Cumulative percentiles from ranked W's resulting from1000 nested bootstraps. Cutting off the upper and lower 2.5 percentiles yields the non-parametric $95 \%$ confidence interval associated with $\mathrm{W}_{2000}$.


Figure 3.7 Comparison of different calculations of $\mathrm{M}_{\mathrm{t}}$ from population modeling done with trial C14 from Chapter 2 to explain positive bias of $\mathrm{W}_{2000}$ collected from the Cook Inlet beluga population.

## LITERATURE CITED

Barlow, J. and P.L. Boveng. 1991. Modeling mortality for marine mammal populations. Marine Mammal Science 7:50-65.

Bèland, P., S. De Guise, and R. Plante. 1992. Toxicologie et pathologie des mammiferes marins du Saint-Laurent. INELS, Montreal, Qc for the Fond Mondial pour la Nature (Canada), toronto. 95 pages. NTIS. (Cited in Lesage and Kingsley 1998).

Braham, H.W. 1984. Review of reproduction in the white whale, Delphinapterus leucas, narwhal, Monodon monoceros, and Irrawaddy dolphin, Orcaella brevirostris, with comments on stock assessment. Report to International Whaling Commision, Special Issue 6:81-89.

Breton, M. and T.G. Smith. 1984. Studying and Managing Arctic seals and Whales. Department of Fisheries and Oceans of Canada, Quebec, Canada. 50 pp.

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

Brodie, P.F., J.R. Geraci, and D.J. St. Aubin. 1990. Dynamics of tooth growth in beluga whales, Delphinapterus leucas, and effectiveness of tetracycline as a marker for age determination. In Advances in Research on the Beluga Whale, Delphinapterus leucas. Edited by T.G. Smith, D.J. St. Aubin, and J.R. Geraci. Canadian Bulletin of Fisheries and Aquatic Sciences 224. pp.141-148.

Burdick, H.E. 1997. Digital Imaging: Theory and Applications. McGraw Hill Text, New York, NY. 600 pp.

Burgman, M.A., S. Ferson, and H.R. Akcakaya. 1992. Risk Assessment in Conservation Biology (Population and Community Biology, No. 12). Chapman \& Hall, London, UK. 314 pp.

Burns, J.J., and G.A. Seaman. 1985. Investigations of belukha whales in coastal waters of western and northern Alaska: II. Biology and ecology. Final report prepared for the US Department of Commerce, NOAA, NOS, Anchorage, AK. Contract No. NA81RAC00049. Alaska Department of Fish and Game, Fairbanks. 129 pp.

Calkins, D.G. 1989. Status of belukha whales in Cook Inlet. In Proceedings of the Gulf of Alaska, Cook Inlet, and North Aleutian Basin Information update meeting, 7-8 Feb. 1989. Edited by L.E. Jarvela and L. K. Thorsteinson. Anchorage, AK. OCS Study, Minerals Management Service 89-0041. pp. 109-112.

Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Australian Journal of Marine and Freshwater Research 5:513-522.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second Edition. Sinauer Associates, Inc., Sunderland, MA. 722 pp.

Caron, L.M.J., and T.G. Smith. 1990. Philopatry and site tenacity of belugas, Delphinapterus leucas, hunted by the Inuit at the Nastapoka estuary, eastern Hudson Bay. In Advances in Research on the Beluga Whale, Delphinapterus leucas. Edited by T.G. Smith, D.J. St. Aubin, and J.R. Geraci. Canadian Bulletin of Fisheries and Aquatic Sciences 224. pp. 69-79.

Cochran, W.G. 1977. Sampling Techniques, Third Edition. John Wiley \& Sons, Inc. New York, NY. 428 pp.

DeMaster, D.P., W. Perryman, and L. Lowry. 1998. Beluga Whale Surveys in the eastern Chukchi Sea, July 1998. Report 98-2 submitted to Alaska Regional Office. Unpublished. 15 pp.

Doidge, D.W. 1990. Age and stage based analysis of the population dynamics of beluga whales, Delphinapterus leucas, with particular reference to the Northern Quebec population. Ph.D. Dissertation, McGill University, Montreal, Quebec. 190 pp.

Eberhardt, L.L. and D.B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 5:260263.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals. Environmental Conservation 4:205-212.

Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997-1012.

Efron, B. and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. Statistical Science 1:54-57.

Fall, J.A., D.J. Foster, and R.T. Stanek. 1983. The use of fish and wildlife resources in Tyonek, AK. Alaska Department of Fish and Game, Division of Subsistence, Anchorage. Technical Report Series 105. 219 pp.

Ferrero, R.C., D.P. DeMaster, P.S. Hill, M.M. Muto, and A.L. Lopez. 2000. Alaska marine mammal stock assessments, 2000. U.S. Department of Commerce, NOAA Technical Memo. NMFS-AFSC-119. 191 pp.

Fishman, G.S. 1996. Monte Carlo: Concepts, Algorithms and Applications (Springer Series in Operations Research). Springer-Verlag New York, Inc., New York, NY. 698 pp.

Goodman, D. 1981. Life history analysis of large mammals. In Dynamics of large mammal populations. Edited by C.W. Fowler and T.D. Smith. John Wiley \& Sons, New York, NY. pp. 415-436.

Harrison, C.S., and J.D. Hall. 1978. Alaskan distribution of the of the beluga whale, Delphinapterus leucas. Canadian Field-Naturalist. 92:235-241.

Hazard, K. 1988. Beluga whale, Delphinapterus leucas. In Selected Marine Mammals of Alaska: Species Accounts with Research and Management Recommendations. Edited by J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 195-235.

Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived species. Ecological Applications 6:556-565.

Hill, P. S. 1996. The Cook Inlet stock of beluga whales: a case for co-management. M.S. thesis. University of Washington, Seattle, WA. 107 pp.

Hill, P.S., and D.P. DeMaster. 1999. Alaska marine mammal stock assessments, 1999. U.S. Department of Commerce, NOAA Technical Memo. NMFS-AFSC-110. 166 pp.

Hobbs, R.C. and K.E.W. Shelden. 1998. Memorandum for Douglas DeMaster on the subject of Rmax for Cook Inlet Beluga Whales. National Marine Mammal Laboratory, NMFS, NOAA, Seattle, WA. Unpublished. 6 pp.

Hobbs, R.C., D.J. Rugh, and D.P. DeMaster. 2000a. Abundance of beluga in Cook Inlet, Alaska, 1994-98. Marine Fisheries Review 62:in press.

Hobbs, R. C., J. M. Waite, and D. J. Rugh. 2000b. Group size estimates of belugas, Delphinapterus leucas, in Cook Inlet, Alaska, from aerial video recordings. Marine Fisheries Review 62:inpress.

Hohn, A.A., and C. Lockyer. Unpublished report. Growth layer patterns in teeth from two known-history beluga whales: reconsideration of deposition rates. Paper SC/51/SM4 presented to the International Whaling Commission Scientific Committee. 17 pp.

Holmes, E.E., and A.E. York. In review. Using age structure to detect impacts on threatened populations: a case study using Steller sea lions. Conservation Biology.

Kelly, D.G. 1994. Introduction to Probability. Macmillan Publishing Company, New York, NY. 606 pp.

Kleinenberg, S.E., A.V. Yablokov, B.M. Bel’kovich, and M.N. Tarasevich. 1964. Beluga (Delphinapterus leucas): investigations of the species. Akademii Nauk USSR, Moscow (translated by the Israel Program for Scientific Translations Ltd., Jerusalem, 1969). 376 pp.

Laidre, K.L., K.E.W. Shelden, D.J. Rugh, and B.A. Mahoney. 2000. Beluga, Delphinapterus leucas, distribution and survey effort in the Gulf of Alaska. Marine Fisheries Review 62:in press.

Lerczak, J.A., K.E.W. Shelden, and R.C. Hobbs. 2000. Application of suction-cupattached VHF transmitters to the study of beluga whale, Delphinapterus leucas, surfacing behavior in Cook Inlet, Alaska. Marine Fisheries Review 62:in press.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Leslie, P.H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213-245.

Lesage, V., and M.C.S. Kingsely. 1998. Updated status of the St. Lawrence River population of the beluga, Delphinapterus leucas. Canadian Field-Naturalist 112:98-114.

Lotka, A.J. 1907. Relation between birth rates and death rates. Science, New Series. 26:21-22.

Lowry, L. F. 1985. The belukha whale (Delphinapterus leucas). In Marine mammals species accounts. Edited by J. J. Burns, K. J. Frost, and L. F. Lowry. Alaska Department of Fish and Game, Game Technical Bulletin No. 7. pp. 3-13.

Mahoney, B.A., and K.E.W. Shelden. 2000. The native subsistence harvest of beluga whales in Cook Inlet, Alaska. Marine Fisheries Review 62:in press.

Moore, S.E., D.J. Rugh, K.E. Shelden, B.A. Mahoney, and R.C. Hobbs. 1999. Synthesis of available information on the Cook Inlet stock of beluga whales. AFSC Processed Report 99-06. 22 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.

Ognetov, G.N. 1981. Studies on the ecology and the taxonomy of the white whale (Delphinapterus leucas Pall., 1776) inhabiting the Soviet Arctic. Report of the International Whaling Commission 31:515-520.

Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale. Report of the International Whaling Commission 29:397-406.

Reilly, S. B. and J. Barlow. 1986. Rates of increase in dolphin population size. Fishery Bulletin 84:527-533.

Rice, D.W. 1998. Marine Mammals of the World: Systematics and Distribution. Special Publication No. 4. The Society for Marine Mammalogy. Allen Press, Lawrence, KS. 231 pp.

Rugh D.J., K.E.W. Shelden, and B.A. Mahoney. 2000. Distribution of beluga, Delphinapterus leucas, in Cook Inlet, Alaska, during June/July 1993-2000. Marine Fisheries Review 62:in press.

Seargeant, D.E. 1973. Biology of white whales (Delphinapterus leucas) in western Hudson Bay. Journal of the Fisheries Research Board of Canada 30:1065-1090.

Shelden, K.E.W. and Angliss, R.P. 1995. Characterization of beluga whales (Delphinapterus leucas) habitat through oceanographic sampling of the Susitna River Delta in Cook Inlet, Alaska, 11-18 June 1994. Paper SC/47/SM13 presented to the International Whaling Commission Scientific Committee. 10 pp .

Stanek, R.T. 1994. The subsistence use of beluga whale in Cook Inlet by Alaska Natives, 1993. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper 232. 24 pp.

Taylor, B.L. and D.P. DeMaster. 1993. Implications of non-linear density dependence. Marine Mammal Science 9(4):360-371.

VanBlaricom, G.R., L.R. Gerber, and R.L. Brownell, Jr. 2001. Extinctions of marine mammals. In Encyclopedia of Biodiversity, Volume 4. Edited by S.A. Levin. Academic Press, San Diego. pp 37-69.

Zar, J.H. 1996. Biostatistical analysis, Third Edition. Prentice-Hall, Inc. Upper Saddle River, NJ. 662 pp.

## APPENDIX A: EQUATIONS USED FOR STOCHASTIC PARAMETERS

A. 1 Equations used for drawing numbers between $(0,1)$ at random from a beta distribution (Kelly 1994).

$$
\begin{array}{ll}
\mu=\frac{\alpha}{\alpha+\beta} & \text { Equation A.1.1 } \\
\sigma^{2}=\frac{\alpha \beta}{\left[(\alpha+\beta)^{2}(\alpha+\beta+1)\right]} & \text { Equation A.1.2 }
\end{array}
$$

$\mu=$ the mean of the distribution
$\sigma=$ the standard deviation of the distribution
$\alpha$ and $\beta=$ any positive numbers $>1$

The distribution is symmetrical when $\alpha=\beta$. If $\alpha=\beta$ equation A.1.2 can be solved for $\alpha$ :

$$
\alpha=\frac{1}{8 \sigma^{2}}-\frac{1}{2}
$$

Equation A.1.3

Using equation A.1.3, $\alpha$ and $\beta$ can be set to obtain any desired deviation around the mean. Random numbers were generated using an Algorithm BB from Fishman (1996).
A. 2 Equation used to scale randomly generated numbers between $(0,1)$ to the appropriate value within the parameter's given range.

$$
s=s_{\min }+R\left(s_{\max }-s_{\min }\right)
$$

Equation A.2.1
$\mathrm{s}=$ the scaled random parameter
$s_{\text {min }}=$ the minimum value for the parameter's range
$s_{\text {max }}=$ the maximum value for the parameter's range
$R=$ the randomly generated number

## APPENDIX B: LIFE HISTORY PARAMETERS

B. 1 Estimating age for belugas:

From the literature, all investigators making estimates from carcasses acknowledge the fact that any information related to age estimates may be biased downward (Burns and Seaman 1985; Lesage and Kingsley 1998; Sergeant 1973). This is because teeth, which are used to age these animals, have the possibility of being worn down. Age is estimated from carcasses by counting dentinal growth layer groups (GLGs) laid down in teeth (Burns and Seaman 1985). There is some debate as to whether one or two GLGs are laid down per year. In two different studies in which the teeth of belugas were marked with tetracycline, one concluded that two GLGs are laid down on average in a year (Brodie et al. 1990), while the other concluded a deposition rate of one GLG per year (Hohn and Lockyer unpublished). Investigators most commonly use the assumption that two GLGs are laid down per year (Braham 1984; Hazard 1988; Doidge 1990).
B. 2 Determining age at sexual maturity (ASM) for belugas:

In many mammalian species the number of ovulations (a rough indicator of the number of pregnancies) can be approximated by counting the number of corpora lutea or corpora albicantia in the ovaries (Burns and Seaman 1985). Using this number along with current age and time for gestation, ASM (meaning age of first conception) can be estimated. This method can not be used for belugas due to the presence of multiple corpora from a single pregnancy (Kleinenberg et al. 1964; Brodie 1971). Instead, investigators have looked at the percent of females pregnant at each age from available carcasses (Ognetov 1981; Burns and Seaman 1985). Burns and Seaman (1985) investigated 52 female belugas from the Bering, Chuckchi and Beaufort seas. They found no animals to be sexually mature up to age $4,33 \%$ mature at age 5 , and $94 \%$ mature at age 6 . They do note that animals were collected in the season of their births which means that some of the age 4 animals may have become pregnant before reaching age 5 .
B. 3 Equation to calculate fecundity:
$f=\frac{1}{c} * r * p$
$\mathrm{f}=$ fecundity
$\mathrm{c}=$ the calving interval
$r=$ the sex ratio (generally assumed to be 0.5)
$\mathrm{p}=$ adult survival
B. 4 Calving interval and fecundity for belugas from the literature:

The calving interval for belugas is generally reported as 3 years with gestation lasting 1214 months and lactation occurring for 18-32 months (Brodie 1971; Sergeant 1973;
Braham 1984; Burns and Seaman 1985; Lesage and Kingsley 1998). However, there is also evidence of higher conception rates, with animals conceiving while still lactating (Burns and Seaman 1985).

Using calf counts, Braham (1984) reports fecundity as 0.09-0.14, Sergeant (1973) reports it as 0.12 and Lesage and Kingsley (1998) report the range of 0.08-0.10.
B. 5 Adult survival rates for beluga from the literature:

Using the life table approach, Burns and Seamen (1985) report annual mortality for the Bering Sea population of belugas at 0.094 (giving an annual survival estimate of 0.906 ). These data come from examination of beluga carcasses taken during subsistence hunts. Using data from size and age distributions, Sergeant (1973), as cited in Ohsumi (1979), calculated an annual mortality rate for Western Hudson Bay belugas of 0.0631-0.0645 (giving an annual survival estimate of 0.9369-0.9355). These data come from examination of beluga carcasses taken during subsistence hunts and from visual aerial observations. From the relationships calculated by Ohsumi (1979) between mortality and
life span, Hazard (1988) reports an annual mortality rate for belugas in general as slightly higher than 0.10 (giving a survival estimate of slightly less than 0.90 ). She speculates, however, that this level seems high given other biological information. Braham (1984) also uses Ohsumi’s (1979) reciprocal life span calculation to estimate general beluga survival at 0.842-0.905. From the age structure of recovered carcasses Lesage \& Kingsley (1998) report an average annual mortality range of 0.065 (giving a survival estimate of 0.935) for the St Lawrence River beluga population. They also cite Beland et al. (1992) with an estimate of annual mortality at 0.03-0.04 (giving a survival estimate of $0.96-0.97$ ) for the same area.

## Appendix C: Data Collection

## C. 1 Aerial surveys:

Surveys were based out of Anchorage, Alaska and occurred during summer months. The survey aircraft used was an Aero Commander 680 FL with twin engines, high wings, ten hour flying capability, and a seating capacity for five passengers and one pilot. Coastal surveys followed a trackline approximately 1.4 km from the tideline. In an effort to see whales clearly without disturbance, an altitude of 244 m ( 800 ft .) and ground speed of approximately $185 \mathrm{~km} / \mathrm{h}$ was maintained. Saw tooth tracklines were flown up and down the inlet as well so that all potential beluga habitat was surveyed. When groups of whales were sighted the position was marked in order to categorize the group by location. The pilot would then make a series of passes along the group keeping the whales in view on the port side of the aircraft to allow observers to make counts and collect video imagery of the group.

## C. 2 Camera information:

In 1999 a Nikon F still camera equipped with a 50 mm lens and 400 speed color film was used to collect photographs of whale groups. Although the camera provided high resolution images, there was no way to determine if whales in successive pictures were the same or new individuals. This violated the assumptions for random sampling with replacement and made analysis of these images useless. Because film could not be developed until post season, the error was not realized in time to make modifications and the first season of data collection was lost. Still photography also required extra flight time because images could not be collected concurrently with counting passes. This greatly reduced the number of images that could be collected because of the high cost associated with air time. Still photography is not a recommended method for determining W for the population.

## C. 3 Sample size calculations:

In order to determine the sample size necessary to detect a $\Delta \mathrm{M}$ of $10 \%$, calculations were made using the formula for sample size in sampling for proportions (Cochran, 1977). Assumptions made for sample size calculations were that $10 \%$ of each whale group would be captured by the camera, current value of $\mathrm{M}_{\mathrm{t}}$ was 0.5 , and whale groups in the Susitna, Knik, Chickaloon, and Kachemak areas (Figure 1.2) were of sizes 300, 50, 30, and 7 respectively. Calculations were made for a $95 \%$ confidence interval. Two options for sample size were calculated (Table 3.1), both able to detect a difference in mean W of at least $7 \%$. Option 1 was preferred as it sampled all the groups, but option 2 was calculated in case the smaller groups couldn't be sampled.

## C. 4 The YIQ color model:

The most familiar color model is the RGB, referring to the three color channels red, green and blue. The YIQ color model is just the RGB matrix multiplied by a conversion matrix:

$$
\left[\begin{array}{l}
Y \\
I \\
Q
\end{array}\right]=\left[\begin{array}{ccc}
0.299 & 0.587 & 0.114 \\
0.596 & -.275 & -.321 \\
0.212 & -.528 & 0.311
\end{array}\right] *\left[\begin{array}{l}
R \\
G \\
B
\end{array}\right]
$$

The YIQ model was constructed to separate chrominance from luminance. Chrominance is the saturation and hue information contained in the color portion of a video signal. Luminance is the brightness and contrast information contained in the black and white portion of a video signal. Luminance ranges from pure black ( 0 in a 24 bit pixel) to pure white (255 in a 24 bit pixel). The Y-channel contains luminance information and the I and Q channels (in-phase and in-quadrature) carry the color or chrominance information (Burdick 1997).

