POPULATION DYNAMICS OF PACIFIC HERRING AND HUMPBACK WHALES IN SITKA SOUND, ALASKA 1980-2011

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Abstract

Humpback whales are a major predator in Sitka Sound, possibly consuming as much as a half-ton of Pacific herring per day. These large migratory baleen whales congregate in Sitka Sound to feed on schools of Pacific herring which spawn in April. In recent decades humpback whale abundance has increased tremendously in Sitka Sound after recovering from near extinction due to commercial whaling. In order to assess the long-term impact on herring by humpback whales, I estimated humpback whale abundance from 1981 to 2011. To do so I developed a Bayesian mark-recapture method for small sample sizes. I also modified a multi-strata Hilborn model to account for sporadic availability of whales in Sitka Sound. The multi-million dollar sac roe fishery in Sitka Sound is managed by the Alaska Department of Fish and Game (ADF&G) with an Age-Structured Assessment model (ASA). I modified the standard ASA model by including the humpback whale abundance estimates as a covariate for herring natural mortality. I found that there is no significant effect of humpback whales on herring mortality. In fact, both Pacific herring and humpback whale abundance have increased together, reaching their maximum values in 2011. This suggests that some other factor, perhaps better marine survival for both species, is driving their upwards trend.

Dedication page

I dedicate this thesis to my loving wife, Melinda Liddle, who has supported my efforts patiently for ten years. Without her persistent and vigorous encouragements, I could not have arrived here. My parents, George and Nancy Liddle, supported me greatly early in my college career. Life lessons, learned from my mom and dad have paid off many times, not least in this endeavor. My two children, Amy Liddle and Nancy Liddle have been at the same time a source of love, joy, distraction but most importantly a reason to succeed in completing this thesis, if only to provide an example of how to finish a job.

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General Introduction

Each year hundreds of humpback whales arrive in Sitka Sound in order to feed on the massive schools of Pacific herring, which start to aggregate to spawn in April. It wasn't always like this, because the humpback whale population in the North Pacific was decimated by commercial whaling in Alaska (Baker *et al.*, 1992). Stomach content data from whaling records showed that whales can consume forage fishes at a rate of a half-ton per day, including Pacific herring (Witteveen *et al.*, 2006). In 1986 when humpback whale abundance was estimated to be 60 individuals (Straley, 1994), this amount of consumption was probably inconsequential in comparison to the total herring biomass. But by 2000, humpback whale abundance in Sitka Sound was almost certainly greater than 400 individuals (Straley *et al.*, 2009). And these whales, as estimated by extrapolation, possibly consumed more than 20,000 tons of herring annually in the three months leading up to the herring spawn. It is natural therefore to inquire if humpback whales might now have a consequential impact on herring mortality.

Pacific herring support a valuable sac roe fishery in Southeast Alaska (Woodby *et al.*, 2005) with annual harvests exceeding 7000 tons per year with a value of more than $10.6 million in 2009. There exists an extensive data set extending back to the 1970's which has been collected for management of this valuable fishery. The Alaska Department of Fish and Game (ADF&G), which manages the Sitka Sound sac roe herring fishery, employs a standard Age-Structured Assessment model (ASA) to estimate herring abundance, spawning biomass, recruitment, and survival (Quinn and Deriso, 1999). The current spawning biomass is estimated to be around 100,000 tons.

For this thesis, it was first necessary to create a time series of whale abundance as far back as possible in order to be included as a covariate for herring mortality in the ASA model.

Previously, estimates of humpback whale abundance had covered much shorter time spans from 1986-1992 (Straley, 1994) and 1995-2000 (Straley *et al.*, 2009). Mark-recapture data on humpback whales was available from 1981 to 2011. However there were a few problems to contend with. There were especially small sample sizes in the early 1980's and also light sampling in a handful of other years as well. Furthermore, there was a complication in that Sitka Sound whales also use other feeding areas within Southeast Alaska and consequently do not always return to Sitka Sound every year despite having a high site fidelity (Mizroch *et al.*, 2004; Straley *et al.*, 2009). Whales are sporadically available in Sitka Sound both on a seasonal basis and from year to year. Finally, another issue was that the relevant humpback whale abundance estimates needed were for the months when herring are also in Sitka Sound, specifically October to April.

I devised a Bayesian method to estimate animal abundance even if sample sizes are small, which is the subject of chapter 1 of this thesis. I applied the Bayesian method to a mark-recapture data set for sperm whales, for which there are also small sample sizes. I also conducted a variety of simulations to assess the statistical properties of the Bayesian method. I compared the Bayesian abundance estimates for sperm whales to the estimates from the standard Schnabel method. I then used the Bayesian method for small sample sizes to estimate abundance for the humpback whales from 1981 to 1989 in Sitka Sound, when sample sizes were sometimes smaller than 5.

In chapter 2 of this thesis, I developed a multi-strata, Hilborn model to account for humpback whale availability in Sitka Sound. This model was used to estimate whale abundance in the months prior to the herring spawn for the years 1981 to 2011. This time series of humpback whale abundance in Sitka Sound is second in length only to a time series of humpback whale abundances produced for Prince William Sound for 1978 to 2009 (Teerlink *et al.*, 2014).

In chapter 3, I modified the ADF&G ASA model by using these humpback whale abundance estimates as a covariate in the mortality term. I used a bootstrap algorithm to estimate the mortality term 3000 times and constructed 95% percentile confidence intervals for the mortality term, baseline natural mortality and herring spawning biomass. The bootstrap confidence intervals were used to assess the size and significance of the mortality effect.

Comparing the herring spawning biomass estimates from the ASA model together with humpback whale abundance estimates, I found that both populations have shown dramatic growth from 2002 to 2011. I have proposed several alternative models and avenues of investigation which might shed some light on the nature of the humpback whale and herring interaction.

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Chapter 1

Bayesian Mark-recapture for Small Sample Sizes[1]

1.1 Abstract

Mark-recapture methods are often used to estimate the abundance of rare or elusive populations, but produce highly uncertain results when sample sizes are small. To handle this situation, a new estimator is presented for a single-release, single-recapture experiment based on Bayesian methodology. The number of marked recaptures is assumed to have a binomial likelihood that is a function of the marked proportion of the population. The prior distribution for this proportion is chosen to be a beta distribution, the conjugate prior of the binomial, so that the posterior distribution of the marked proportion is simply an updated beta distribution. The probability density function for population abundance is derived from this posterior distribution, from which a closed-form estimator of abundance emerges, providing ease of use and general applicability. A Bayesian credible interval is found by numerically integrating the posterior density. This method is then extended to the multiple-release, multiple-recapture experiment. A sensitivity analysis showed that estimation is relatively insensitive to the choice of prior parameters. A simulation study showed that the Bayesian estimator has relative bias less than 3% even when sample size is small. The Bayesian credible interval has narrower width than the Schnabel profile likelihood interval. The method is illustrated with data from sperm whales in the Gulf of Alaska and with humpback whales in Sitka Sound, Alaska.

Keywords: Bayesian methods; mark-recapture; Petersen method; rare populations; Schnabel method; small samples; sperm whales; humpback whales

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[1] Authors are Joseph B. Liddle, Terrance J. Quinn II, Janice M. Straley and Milo Adkison. Prepared for submission to ICES Journal of Marine Science.

1.2 Introduction

Mark-recapture sampling is frequently used to estimate fish and wildlife population abundance (Schwarz and Seber, 1999; Seber, 2002). In the Petersen method for a closed population, an initial sample of animals is captured, marked, and released. After some time to allow mixing of the population, a recapture sample is taken. A maximum likelihood estimate of population abundance follows from the marked proportion of the recapture sample. The Schnabel method is an extension of the Petersen method for multiple recapture samples (Schnabel, 1938).

Often, mark-recapture methods are used with rare or elusive species, giving rise to small sample sizes making mark-recapture estimates of abundance more uncertain (Thompson, 2004). For reliable estimation, the expected number of recaptures should be greater than five (Seber, 2002) but with small samples, the number of recaptures can easily be less than five. Lower confidence limits can be less than the known number of marked animals, giving a nonsensical result. Upper confidence limits can be so large as to be meaningless (Gimenez *et al.*, 2005). Furthermore, there is a non-trivial probability of zero recaptures, for which the maximum likelihood estimator approaches infinity.

Instead, a Bayesian method that utilizes prior information about the population can be used to define a probability distribution for population abundance (Wang *et al.*, 2007). The posterior distribution, proportional to the product of the prior distribution and the likelihood of the data, is used to make inferences about parameters of interest. Bayesian methods have been successfully applied to mark-recapture situations with rare populations using numerical posterior estimation methods (Testa et. al., 1994). With more than one parameter, numerical methods for estimating the posterior distribution are necessary (Gazey and Staley, 1986; Smith, 1988, 1991). Hierarchical Bayesian models for mark-recapture data using Markov Chain Monte Carlo have been extensively developed for multi-parameter models (Mäntyniemi and Romakkaniemi, 2002; Rivot *et al.*, 2008). A limitation of these methods is that they are too difficult for many biologists to use, who then settle on using simpler methods.

Careful interaction with a subject matter expert can elicit an informative prior which is effective for subjective Bayesian estimation (Kadane and Wolfson, 1998; Winkler, 1967). One method for eliciting a prior distribution involves quantiles and modes to plot graphs interactively (Chaloner and Duncan, 1982; Gavasakar, 1988). However it is done, the expert's knowledge is a valuable resource that should not be ignored in a small sample context.

We derive a closed-form probability distribution for population abundance using a subjective Bayesian method. The closed-form distribution has the advantage that a biologist untrained in Bayesian statistics can use it directly (Karunamuni and Quinn, 1995). The probability distribution for abundance has a domain such that the lower credible limit cannot be less than the number of marked animals. The credible limits are well defined even if the number of recaptures is zero as is shown with an example involving humpback whales in Sitka Sound. The Bayesian approach allows for meaningful probability statements to be made about the population abundance. This is important for wildlife management because often what is needed is the probability that the population abundance is less than some threshold. A Bayesian posterior distribution is specifically designed to estimate probabilities about the parameters. The posterior distribution for abundance can be used to generate random values for simulations as shown with an example involving sperm whales in the Gulf of Alaska.

1.3 Methods

1.3.1 Petersen and Schnabel Maximum Likelihood Methods

Population abundance, N, is assumed to be closed to mortality, recruitment, and migration. The initial sample size is denoted n_1, the recapture sample sizes and recaptures are denoted respectively n_i and m_i for period i, and by convention $m_1 = 0$. The Schnabel estimator for estimating population abundance is derived from the binomial likelihood of the number of recaptures:

$$f(m_2,\ldots,m_s)=\prod_{i=2}^{s}\binom{n_i}{m_i}\pi_i^{m_i}(1-\pi_i)^{n_i-m_i}\ , \tag{1.1}$$

in which $\pi_i = \sum_i (n_i - m_i)/N$, the proportion of the population marked just prior to sampling and s is the number of sampling periods. The frequently-used Petersen estimator is a special case of the Schnabel with $s = 2$. It is easier to work with the kernel of the log likelihood, ignoring terms that do not contain N. For $s = 3$, the kernel reduces to:

$$\begin{aligned}L(N) &= m_2 \log\left(\frac{n_1}{N}\right) + (n_2 - m_2)\log\left(1-\frac{n_1}{N}\right) + m_3 \log\left(\frac{n_1+n_2-m_2}{N}\right)\\ &\quad + (n_3 - m_3)\log\left(1-\frac{n_1+n_2-m_2}{N}\right).\end{aligned} \tag{1.2}$$

The Schnabel estimator, denoted N_{mle}, is found by maximizing the kernel of the log likelihood. When the sample size is large, $-2[L(N) - L(N_{\text{mle}})]$, has an approximate chi-squared distribution with one degree of freedom (Rice, 1995; Seber, 2002). Numerical solutions to the equation $L(N)=L(N_{\text{mle}}) - 0.5\chi^2_{\text{df}=1,\alpha=0.05}$ give the 95% profile likelihood confidence limits (Evans *et al.*, 1996). When the number of recaptures is zero, both the upper confidence limit and the maximum likelihood estimator do not exist because the non-zero terms of (1.2) would form a monotonically increasing function of N.

1.3.2 Bayesian Method

We first consider the Petersen experiment in which $s = 2$. The posterior distribution is proportional to the product of the prior distribution and the likelihood of the data. Inferences are made as probability statements derived from the posterior distribution. The binomial likelihood from (1.1) is assumed for the number of recaptures:

$$f(m_2 \mid \pi) = \frac{n_2!}{(n_2 - m_2)!\, m_2!} \pi^{m_2} (1-\pi)^{n_2 - m_2} \quad , \qquad (1.3)$$

in which the proportion marked is $\pi = n_1 / N$. The binomial likelihood is appropriate if the proportion marked is less than 10% of the population or if sampling is done with replacement (Seber, 2002). The proportion marked is assumed to have a prior beta distribution with parameters a and b, a member of the conjugate family for the binomial likelihood:

$$g\,(\pi \mid a, b) = \frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)} \pi^{a-1} (1-\pi)^{b-1}, \qquad (1.4)$$

with expected value $\mu = a/(a+b)$.

The beta prior can be chosen after interviewing subject matter experts and examining plots for a variety of parameter values for a and b, some of which are implausible. It is preferable that the effective sample size, $a + b + 1$, is not too large, so as to not to dominate the data as expressed by the likelihood (Bolstad, 2007). In a small sample situation, the proportion marked, π, is usually expected to be less than ½, which then implies that $a < b$. The subject matter expert should be asked to provide a minimum plausible abundance N_{min} which establishes a maximum proportion marked. The inequality $\mu = a/(a+b) \leq n_1 / N_{\min}$ gives a feasible set of prior parameters for the proportion marked. Once feasible values of *a* and *b* have been chosen the analyst should examine a plot of the implied prior on the abundance. The mode of the implied prior should be near N_{min} but there should also be a heavy upper tail for large abundances which implies a large variance. If there isn't heavy upper tail, then *a* and *b* should be adjusted until there is such a tail.

The posterior distribution for the proportion marked is also a beta distribution, with parameters updated by the recapture data (Gelman *et al.*, 2004). The simple updating rules for the beta parameters are:

$$\begin{aligned} a' &= a + m_2 \\ b' &= b + n_2 - m_2 \end{aligned} . \tag{1.5}$$

These rules can be summarized as "add the marked animals to *a* and the unmarked animals to *b*", which yields the posterior distribution $g(\pi \mid a', b')$ of the proportion marked. The expected value of the proportion marked is the mean of the beta distribution:

$$\pi' = \mu' = \frac{a'}{a'+b'} . \tag{1.6}$$

The closed form posterior probability distribution for *N* is:

$$f_N(N) = \left[\frac{\Gamma(a'+b')}{\Gamma(a')\Gamma(b')} \frac{n_1^{a'}}{N^{a'+1}} \left(1 - \frac{n_1}{N}\right)^{b'-1} \right] \quad N \geq n_1 \qquad , \tag{1.7}$$

which is from the posterior distribution of the proportion marked. This is a continuous distribution over *N* and the domain includes only values of *N* greater than or equal to the number of unique animals marked. Percentiles can be found numerically from the cumulative distribution function:

$$P(N \le N_k) = \int_{n_1}^{N_k} \frac{\Gamma(a'+b')}{\Gamma(a')\Gamma(b')} \frac{n_1^{\,a'}}{N^{a'+1}} \left(1 - \frac{n_1}{N}\right)^{b'-1} dN \ . \qquad (1.8)$$

The expected value and variance, obtained from the kth moment E[N^k], are:

$$\mathrm{E}[\hat{N}] = \frac{n_1(a'+b'-1)}{(a'-1)} \text{ and} \qquad (1.9)$$

$$\mathrm{var}(\hat{N}) = \frac{n_1^2(a'+b'-1)b'}{(a'-1)^2(a'-2)} \ . \qquad (1.10)$$

These closed-form estimators ease computation and provide credible intervals for the large sample case. A symmetric credible 95% interval using (1.9) and (1.10) takes the form: $\hat{N} \pm 1.96\sqrt{\mathrm{var}(\hat{N})}$. This type of interval relies on the assumption that the distribution is approximately normal. In the small sample case this is not reasonable because there is often a heavy upper tail. This normality assumption is more reasonable if the sample sizes are larger or in multi-year studies.

Alternatively, a Bayesian estimate of abundance, $\hat{N}$, may come from any measure of central tendency of the posterior distribution (1.7), either the median using (1.8), the mean using (1.9), or the mode using the identity $\hat{N} = n_1 / \hat{\pi}$ together with (1.6). We prefer the median, because it is a robust measure of centrality when sample sizes are small. The task of finding a 95% credible interval is reduced to simply finding up the 2.5th and 97.5th percentiles from the cumulative distribution function (1.8). Although this Bayesian method was designed for a small sample case, it also has the advantages of including prior information and the ability to make probability statements in the large sample case.

The cumulative distribution function (1.8) is used to make probability statements about the value of N. One can use (1.8) to generate random values of N with the inverse CDF method (Rice, 1995). We exploited this property in the simulation studies described below.

The method is now extended to multi-year samples. The posterior distribution for the proportion marked is updated to find a highly informative prior distribution for each successive sample. At a given time period t, the proportion marked at the start of the time period is estimated from the posterior distribution of π in (1.6). At the next time period $t+1$, the proportion marked includes the new animals marked during time period t. Thus, an updated estimator of π and its variance are:

$$\hat{\mu} = \hat{\pi}_{new} = \hat{\pi} + \frac{n_2 - m_2}{\hat{N}} \tag{1.11}$$

and

$$\hat{\sigma}^2 = \mathrm{var}[\hat{\pi}_{new}] = \left(1 + \left(\frac{n_2 - m_2}{n_1}\right)^2\right) \frac{a'b'}{(a'+b')^2(a'+b'+1)}, \tag{1.12}$$

the latter of which is the variance of a beta distribution with an adjustment term to represent the uncertainty associated with the newly marked animals. Given a specific mean (1.11) and variance (1.12), the parameters of a prior beta distribution for the proportion marked can be found with these formulae:

$$\begin{aligned} a &= \frac{\mu^2(1-\mu)}{\sigma^2} - \mu \\ b &= \frac{a(1-\mu)}{\mu} \end{aligned} \tag{1.13}$$

This procedure can then be applied recursively to later time periods. In the preceding formulae, n_1 is replaced with the cumulative number of marked animals M_i, given by:

$$M_i = M_{i-1} + n_i - m_i. \tag{1.14}$$

1.4 Illustrations

1.4.1 Sperm whales 2003-2005

Commercial fishermen in Southeast Alaska have experienced economic losses due to sperm whale depredation of sablefish. Sperm whales have been frequently observed following commercial fishing vessels, removing primarily sablefish (*Anoplopoma fimbria*) and sometimes halibut (*Hippoglossus stenolepis*) as the fishing gear (demersal longlines) is recovered.

A mark-recapture experiment was conducted from 2003 to 2005 to estimate sperm whale abundance near Sitka, in the eastern Gulf of Alaska (GOA) (Straley *et al.*, 2004). Fourteen ($n_1 = 14$) whales were observed and 'marked' in 2003 by photographing unique identifying characteristics on their flukes, dorsal fins and bodies. A recapture sample was taken in 2004 in the same area. Of the 34 animals sighted ($n_2 = 34$), 5 had been previously 'marked' ($m_2 = 5$). Sampling was with replacement so that some individuals were counted more than once. The 2005 sample size was $n_3 = 20$ with $m_3 = 8$ recaptures. The standard Schnabel MLE is $\hat{N}_{\text{mle}} = 104$ with 95% confidence interval (71,174), computed with the profile likelihood method (Fig. 1.1).

To establish a prior distribution, the principal investigator (J.M. Straley) of the study gave her opinion on upper and lower bounds for abundance. Movements of sperm whales tracked through photo identification provided documentation that the sperm whales in the study area (eastern GOA) comprised a small portion of a larger population in the GOA region. She surmised (in 2004) that that there could be no fewer than 60 whales and no more than three hundred (J. Straley, personal communication). This suggested that the proportion marked must be between 5% and 25%. A large variance in the prior distribution was needed to represent great uncertainty about abundance. A beta prior distribution that summarized these beliefs had cumulative probability is in the interval 0-25% on the π axis. The implied prior on abundance has a heavy upper tail that extends well beyond $N = 200$ (Fig. 1.2). The parameter updating rules (1.5) gave $a' = 6$ and $b' = 37$, for an effective sample size of 44 after the 2004 sample. The median is a robust estimator of centrality and is insensitive to the extreme upper tail. The median population abundance (1.8) of the posterior distribution was 104 whales with a 95% Bayesian credible interval (54, 257). The comparison of the prior distribution, the likelihood, and the posterior distribution for sperm whale population abundance reveals decreasing uncertainty of the estimate of population abundance (Fig. 1.2). With the closed form estimators for the mean (1.9) and variance (1.10), estimated abundance is 118 with 95% credible interval (9, 226).

An updated estimate for the proportion marked in 2005 from (1.11) is 0.429. The variance of the 2005 prior (1.12) is 0.014. Hence, the 2005 prior parameters from (1.13) are $a = 6.8$ and $b = 9.1$. The 2005 prior is highly informative including all information from the 2004 sample and the 2004 prior. The 2005 posterior distribution reflects the increasing knowledge of the sperm whale population by having smaller variance than the 2004 posterior (Fig. 1.3). The median estimate is 105 whales with a 95% credible interval of (74,165). The 2005 posterior distribution is much narrower than the 2004 posterior (Fig. 1.3), illustrating the lower uncertainty with another year of data. The closed form estimators for the mean (1.9) and variance (1.10) produce an estimated abundance of 109 with a 95% credible interval of (62, 154).

Small endangered populations may be at high risk of extinction if the population were to fall below a certain threshold. The probability that this threshold has been reached is of interest, and the Bayesian methods provide an easy answer. For example, the probability that there are less than 85 sperm whales is found by simply evaluating the cumulative distribution function (1.8):

$$P(N \leq 85) = \int_{43}^{85} \frac{\Gamma(a'+b')}{\Gamma(a')\Gamma(b')} \frac{n_1^{a'}}{N^{a'+1}} \left(1 - \frac{n_1}{N}\right)^{b'-1} dN \approx 13\% . \tag{1.15}$$

Hence, the probability that the number of whales is less than 85 is very small.

1.4.2 Humpback whales 1981-1989

Humpback whales were driven to near extinction in Southeast Alaska by commercial whaling. However by the 1980's a few individuals were feeding on Pacific herring in Sitka Sound, enough to attract the attention of biologists (Straley, 1994). Mark-recapture sampling began at first tentatively with very small sample sizes and increasing in the late 1980's (Table 1.1). Photographs of whale flukes were painstakingly matched from year to year, eventually building up a substantial data base of uniquely identified whales. The whales in this example were in Sitka Sound during the months of October to April which is associated with Pacific herring. There was no sampling at all for two years (1982 and 1985) and in 1983 there was no recaptures. Small sample sizes, sporadic sampling, and lack of recaptures, creates challenging estimation issues for a biometrician.

We used the Bayesian method to estimate humpback whale abundance in Sitka Sound for 1981 to 1989 (Figure 1.4, Table 1.1). Confidence intervals for population abundance were at first very wide and revealed a great deal of uncertainty (Table 1.1). These early estimates were followed by more reliable abundance estimates in 1987 and afterwards as the number of known whales accumulated (Table 1.1). The humpback population in Sitka Sound grew rapidly in the late 1980's, to an estimated 131 individuals by 1989 (Table 1.1).

The versatility of the Bayesian method is demonstrated in 1983 when there was zero recaptures and again when sampling did not happen at all 1982 and 1985 (Table 1.1). In 1983 with zero recaptures the Bayesian estimator is well defined and returns values similar to previous year's estimates yet with a wider 95% credible interval. In 1982 and 1985, the Bayesian estimates were essentially the same as previous estimates, except with wider 95% credible intervals.

1.5 Sensitivity and Simulations

Several simulations were written in the R programming language to assess the statistical properties of the Bayesian method as applied to the sperm whale example. We studied model fit, bias, coverage, credible interval width, and sensitivity to prior parameters. In each simulation study the cumulative probability distribution played a key role.

The cumulative probability distribution for abundance was used to produce simulated mark-recapture data, quite similar to the observed recaptures for the sperm whale example ($m_2 = 5$ and $m_3 = 8$). For the i^{th} iteration, we drew k_i from a uniform distribution (0, 1) and solved the cumulative distribution function (1.8) to produce a random abundance N', drawn from $f_N(N)$. The number of recaptures m'_2 was drawn from a binomial distribution with parameters $n_2 = 34$ and $p'_1 = 14/N'$. For the next sampling period, m_3 had a binomial distribution with $n_3 = 20$, and such that $p'_2 = (14 + 34 - m_2)/N'$. The posterior distribution for sperm whale abundance produced simulated recaptures and proportion marked similar to the observed data.

We did a sensitivity analysis for each combination of prior parameters from $1 \leq a \leq 9$ and $1 \leq b \leq 9$. To estimate coverage of a 95% credible interval, we simulated 3000 random values of N' for each choice of prior parameters a and b. The coverage was 98% for the prior parameters we actually used in the sperm whale example. Coverage was also at least 95% for most other choices of prior parameters (Table 1.2).

We compared the relative bias and the width of the confidence intervals of the estimators as the sample sizes became smaller. For each sample size we selected an appropriate prior so that the effective sample size was less than the number marked and also the expected value of the beta distribution (1.6) was less than 1/4. For each sample size and each of the 3000 random N' values, we created a virtual population vector representing marked and unmarked animals. We then simulated recaptures, m_2 and m_3, given $n = n_1 = n_2$ and the random N'.

The relative bias was small and similar for the two estimation methods when sample size was at least 10 (Fig. 1.5). We found that with sample sizes $n<35$, the Bayesian estimator had a narrower 95% credible interval (Fig. 1.6) than the confidence interval from the Schnabel method. If the sample size was greater than 35, then the Schnabel method had similar bias and interval width as the Bayesian method.

1.6 Discussion

The core element of this work is the derivation of a Bayesian closed-form probability distribution and corresponding estimators for population abundance from a mark-recapture experiment on a closed population. Although derived mainly for use with small samples encountered in estimating population abundance, it has advantages for large samples as well. When the sample sizes are small, the asymptotic assumptions of the Schnabel method do not hold (Schnabel, 1938; Schwarz and Seber, 1999). The upper limb of the likelihood declines very slowly, resulting in excessively wide confidence intervals. The Schnabel maximum likelihood estimator and its upper confidence limit approach infinity when there are no recaptures because (1.2) becomes a monotonically increasing function.

With small sample sizes, expert opinion is essential for choosing a useful prior distribution (Gavasakar, 1988; Kadane and Wolfson, 1998). If no expert opinion is available, then one could use a uniform prior distribution on the proportion marked (Wang *et al.*, 2007). However, a uniform prior on the proportion marked gives a non-uniform prior on abundance. In our approach, the prior distribution gives voice to the researcher's experiences, while the likelihood gives weight to the actual data. The compromise is a posterior distribution that can be used to make inferences about the population abundance. Because this distribution is in closed form, one can apply our Bayesian method without knowing a great deal about the methodology used to derive it (Karunamuni and Quinn, 1995).

For small samples, our Bayesian method using percentiles (1.8) is preferable to the Schnabel profile likelihood method and also to the large-sample Bayesian method (Illustration 1.4.1). After the first year of the sperm whale study, the large-sample Bayesian method with closed-form estimators (1.9) and (1.10) produced a lower limit which is actually less than the known number of marked whales a result which is nonsensical yet very common (Evans *et al.*, 1996). In the next year of the sperm whale study, the sample size was larger, and the credible intervals produced by (1.9) and (1.10) were very similar to those produced by (1.8). The probability distribution for population abundance (1.8) also allowed for estimation of probabilities about the size of the population.

The simulation studies showed that our Bayesian method is a reliable small sample method. With simulated recapture data similar to the data actually observed, relative bias was small (Fig. 1.5). The 95% credible intervals generally had coverage of 95% or greater and a narrower width than the Schnabel method when sample size was less than 35 (Fig. 1.6). When sample size was greater than 35, both methods performed equally well in terms of width, bias, and coverage, as is expected with a large sample size. However when sample sizes are as small as 5, neither method seems to do very well with respect to interval width, bias and coverage (Fig. 1.5, Fig. 1.6).

One important advantage of the Bayesian method is that the lower confidence limit cannot be less than the number of marked animals by definition (1.8). This is because the confidence limits are computed with numerical integration of the posterior distribution where the lower limit of the integral is the total number of marked animals (1.8). An example of this occurs in 1985, when the number of previously marked animals was 7, and this also happens to be the lower limit for the confidence interval. In contrast some mark-recapture methods will sometimes produce impossible estimates for the lower confidence limit for abundance which are less than the number of marked animals or even negative (Evans *et al.*, 1996).

From the humpback whale example we also deduced a lower limit for small sample sizes using the Bayesian method. At around n=4 the Bayesian estimates are little different than what would be provided by the prior alone (Table 1.1). By 1987, sample sizes exceeded 30, and the prior had little or no influence. Nevertheless estimates are viable for the years 1981 to 1986, since the researcher's opinions are blended with the little data that was available.

Small samples can arise in several ways for mark-recapture data. For example, twelve wolverine studies were reviewed all of which had sample sizes that were less than 50, and seven sample sizes were less than 20 (Krebs *et al.*, 2003). This is what we call the 'wolverine' problem: a rare and elusive population, which simply will never yield large samples because there aren't very many wolverines and it is difficult to capture a large sample. Then there is the 'pilot study' problem: the population is large, yet researchers, perhaps due to lack of time or money, have only obtained a small sample of animals. The 'pilot study' problem can also arise within an initial sampling period, if a preliminary estimate of the abundance is desired. These two scenarios differ in the relative size of the population and the proportion marked.

In the 'wolverine' problem, the population is so small, perhaps only a few dozen, that the proportion marked can be fairly high even with small samples. In the 'pilot study' problem the proportion marked is much smaller. This can happen because the sample size is small relative to the population size since sampling has just started. The sperm whale example presented here is a 'wolverine' type of problem with the population estimated to be 104 individuals. The proportion marked was always greater than 10% and was almost 50% by the end of the study. We consider the choice of the binomial likelihood in our study to be appropriate, because sampling was done with replacement. Whales are large, mobile animals and sampling is one by one, with many days of population mixing between observation events. In the 'pilot study' problem, sampling is often done without replacement, which would make the hypergeometric likelihood appropriate

(Webster and Kemp, 2013). To use our method based on the binomial, the proportion marked should be below 10%.

In contrast the humpback whale example exhibits attributes of both the pilot study problem and the wolverine problem albeit at different times. Initially humpback whales were very rare in Sitka Sound, perhaps as few as 12 individuals (Straley, 1994). But with a sample sizes of 1 in 1981 and no sampling at all in 1982, less than 10% of the whales were marked at that time. This is characteristic of a pilot study problem where not very much data is available. However by 1989 the number of marked whales probably exceeded 50% of the abundance. This is a wolverine type of problem where the population is small enough that researchers have already identified substantial proportion of the population.

Further research is desirable to explore a hypergeometric likelihood to deal with sampling without replacement (Webster and Kemp, 2013). This would be more universal to both the 'wolverine' problem and the 'pilot study' problem. For multi-year studies the introduction of a survival parameter as in Jolly-Seber estimation would be desirable (Chavez-Demoulin, 1999; Seber, 2002). It is anticipated that a closed-form solution will not be readily available and a numerical method to estimate the posterior distribution will be needed.

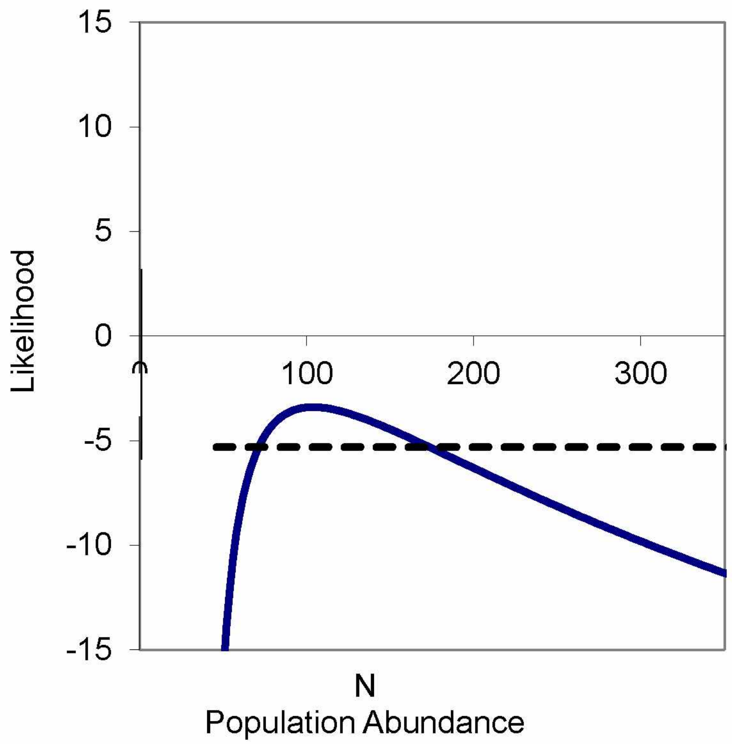

Figure 1.1 The Schnabel log likelihood. The log likelihood (solid black line) from the Schnabel method for the sperm whale example is shown. The profile likelihood confidence interval is depicted at the intersections portrayed above, with $L(N) = L(N_{\text{mle}}) - 0.5\chi^2_{\text{df}=1,\alpha=0.05}$ (dashed line).

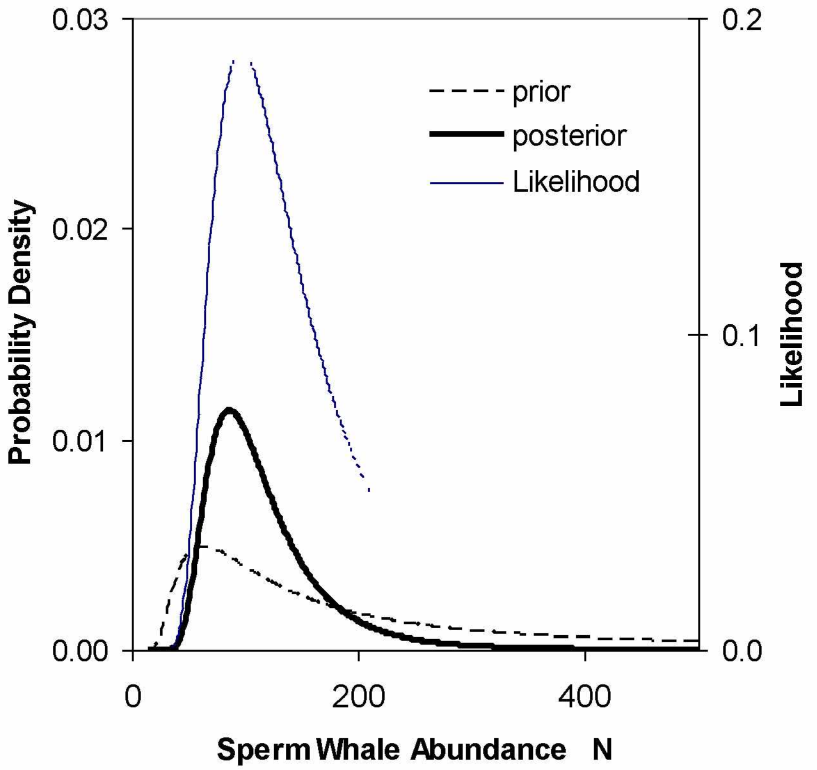

Figure 1.2 Prior and posterior distributions, sperm whales 2003-2004. The kernel of the likelihood, the prior distribution and posterior distribution are shown for the sperm whale example using data from 2003 and 2004.

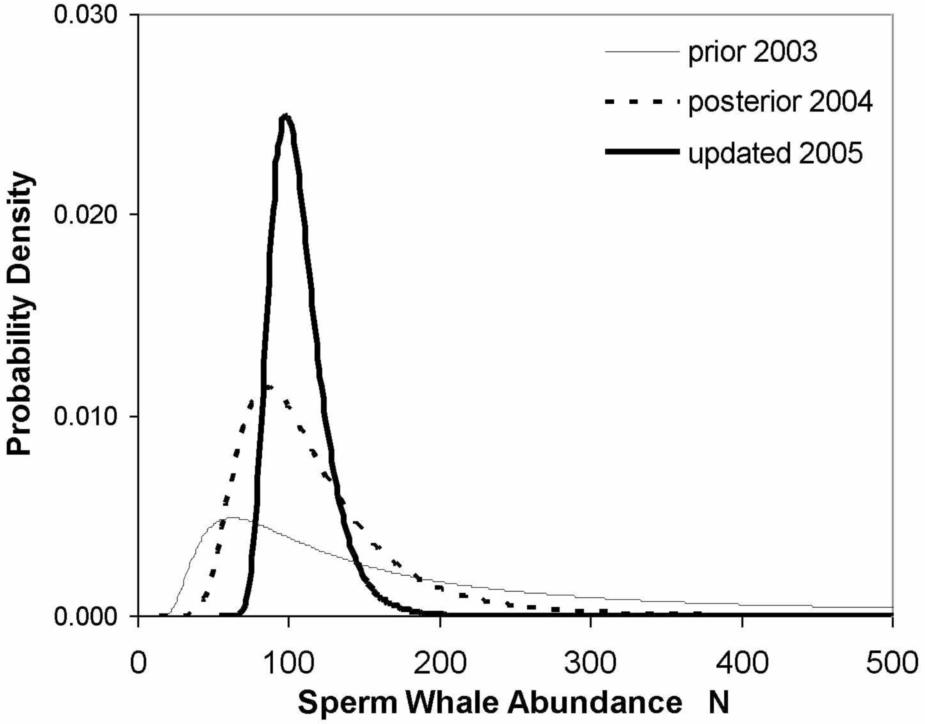

Figure 1.3 Updated posterior distributions, sperm whales 2004-2005. The posterior distribution updated in 2004 and 2005 is shown together with the prior distribution.

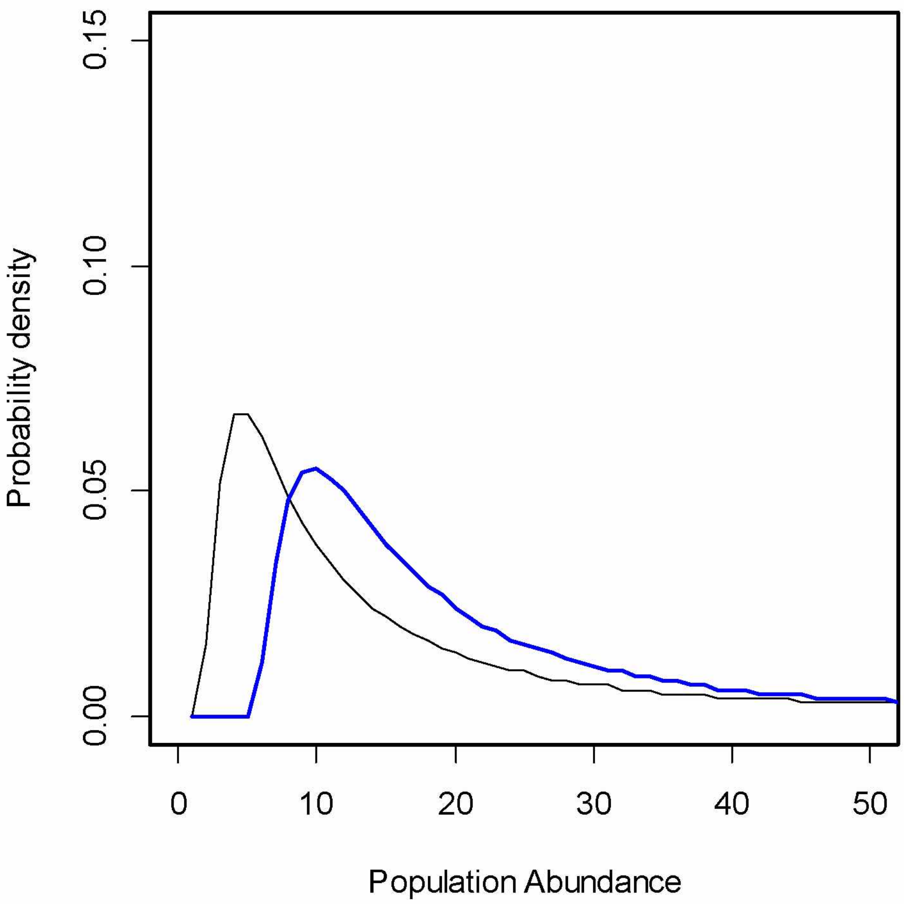

Figure 1.4 Bayesian estimates of humpback whale abundance for 1984. The prior distribution (thin black line) and the posterior distribution (thick blue line) for 1984 are shown. The median of the posterior distribution is $N = 16$, but the distribution is skewed heavily to the right, indicating that there is non-trivial probability for values of $N > 20$.

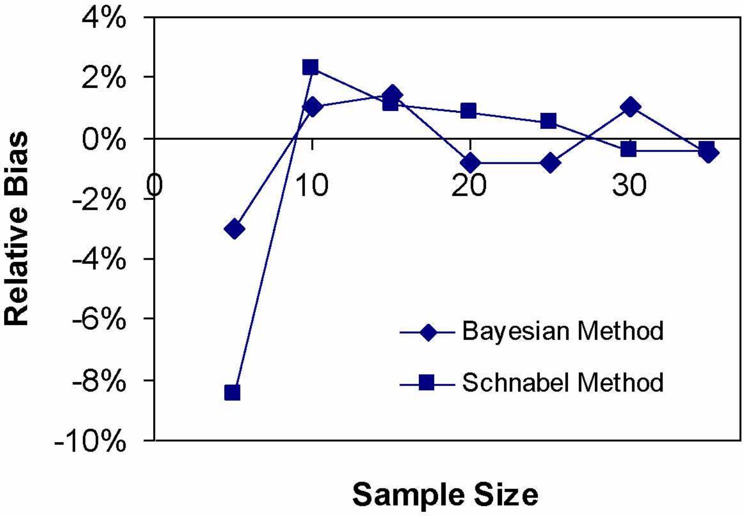

Figure 1.5 Simulation of bias. Plots of median relative bias, $\left(\hat{N} - N'\right)/ N'$, for the Schnabel and Bayesian estimators are shown as functions of sample size.

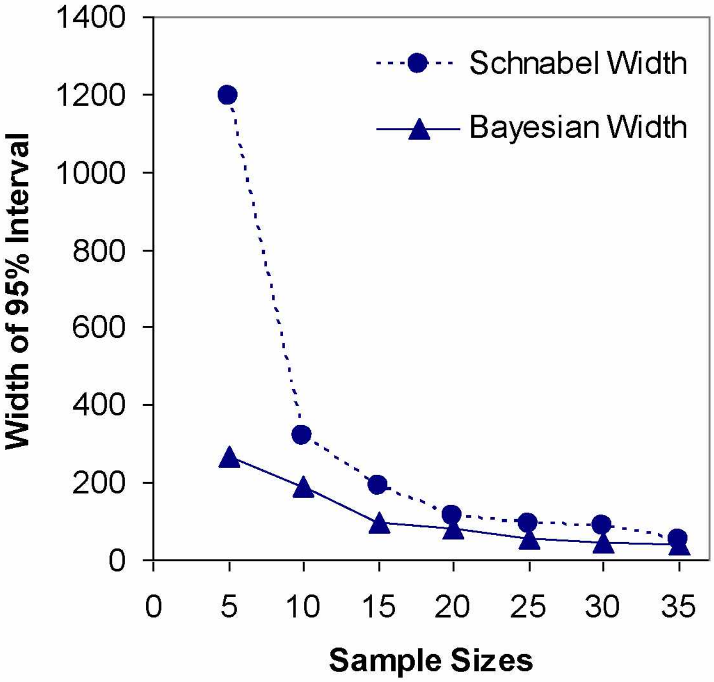

Figure 1.6 Simulation of confidence interval width. The median widths of the 95% Bayesian credible intervals and the corresponding 95% Schnabel intervals from 3000 iterations at each sample size are shown.

Table 1.1 Bayesian humpback whale abundance estimates 1981-1989.

Annual sample sizes (n_t) and recaptures (m_t) are shown along with 95% Bayesian credible intervals for humpback whale population abundance (N_t).

Year	n_t	m_t	N_t	95% CI
1981	1	0	12	(2, 258)
1982	0	0	12	(2, 258)
1983	3	0	16	(3, 436)
1984	4	1	16	(5, 169)
1985	0	0	14	(7, 264)
1986	4	1	24	(9, 172)
1987	35	1	194	(65, 267)
1988	38	9	186	(117, 301)
1989	16	12	131	(103, 186)

Table 1.2 Sensitivity of the Bayesian method to the prior. Sensitivity of median and 95% credible interval coverage to the choice of prior parameters α,β. Abundances simulated from the updated posterior distribution, given the observed data on sperm whales.

α / β	1	2	3	4	5	6	7	8	9
1	99 0.98	99 0.98	102 0.98	102 0.98	105 0.98	101 0.98	104 0.98	104 0.98	107 0.97
2	92 0.97	95 0.98	95 0.98	95 0.97	95 0.97	98 0.97	98 0.97	101 0.98	107 0.97
3	89 0.94	92 0.98	92 0.97	89 0.92	92 0.95	92 0.95	95 0.97	91 0.93	94 0.94
4	86 0.90	89 0.94	89 0.94	89 0.94	89 0.92	89 0.92	92 0.95	89 0.90	89 0.89
5	86 0.92	89 0.95	86 0.90	86 0.90	89 0.94	86 0.88	90 0.92	89 0.92	86 0.84
6	90 0.98	86 0.92	86 0.92	89 0.95	86 0.90	86 0.90	86 0.89	86 0.88	86 0.86
7	90 0.98	94 0.99	90 0.98	86 0.92	86 0.92	86 0.90	86 0.90	86 0.90	83 0.81
8	101 0.99	95 0.99	90 0.98	94 0.99	90 0.98	86 0.92	86 0.92	83 0.86	86 0.89
9	108 0.99	101 0.99	101 0.99	95 0.99	90 0.98	90 0.98	90 0.98	86 0.92	86 0.91

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Chapter 2

Humpback Whale Abundance Associated with Sitka Sound, 1981-2011[2]

2.1 Abstract

Humpback whales (*Megaptera novaeangliae*) feed seasonally upon forage fish and zooplankton in the productive waters of the higher latitudes. During the feeding season in summer, they must feed sufficiently to sustain two oceanic migrations and the energy spent in lower latitudes for mating and calving in winter where little or no feeding occurs. As large consumers, humpback whales have the ability to impact their prey and potentially the ecosystem of the surrounding ocean where they feed. Hence, to assess the impact of a predator upon their prey it is necessary to have knowledge of the numbers of feeding whales present in Sitka Sound and how that abundance changed over time. Humpback whales have increased since the end of commercial whaling in the North Pacific in 1966 (Calambokidis *et al.*, 2008), thereby changing the magnitude of the potential impact upon their target prey. We used Sitka Sound humpback whale annual sighting data in a mark-recapture analysis to estimate available whale abundance from 1981 to 2011. We created an open multi-strata Hilborn model with a negative binomial likelihood and time-varying probability of capture to account for whales that are not present in Sitka Sound each year. The strata were Sitka Sound and outside of Sitka Sound. Confidence intervals were derived using a parametric bootstrap method. We used 622 individually photo identified whales as the marked population to estimate the annual abundance of whales. The annual estimates ranged from 9 to 1044 whales for this ecologically important predator in Sitka

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Sound. By 2010 the total number of marked whales was contained within the confidence interval for the abundance estimate, suggesting that by then nearly all the humpback whales of Sitka Sound had been marked and identified.

Key words: Humpback whales, mark-recapture, abundance, Sitka Sound, Hilborn method, population dynamics, availability, parametric bootstrap.

2.2 Introduction

The study of the environmental effects on abundance of a given species generally requires a lengthy time series of abundance estimates. Humpback whales (*Megaptera novaeangliae*) are potentially having a large influence on the abundance of their prey. A mark-recapture data set of humpback whale sightings, spanning 30 years, allowed a unique opportunity to evaluate the number of whales available in Sitka Sound annually. In this paper we show how to estimate annual abundance that accounts for availability due to temporary emigration.

The humpback whales of Southeast Alaska and Northern British Columbia form a genetically discrete feeding aggregation, migrating seasonally between lower latitude mating and calving and high latitude feeding areas (Baker *et al.*, 1998; Gaskin, 1982). Known feeding areas (Fig. 2.1) within Southeast Alaska include Sitka Sound, Frederick Sound, Glacier Bay, Tenakee Inlet, Lynn Canal, and the waters west of Prince of Wales Island (Straley *et al.*, 2009). Geographically stratified models were used to estimate site fidelity and movement of whales within Southeast Alaska. The year-to-year site fidelity was 92% for Glacier Bay, 93% for Frederick Sound and 94% for Sitka Sound (Straley *et al.*, 2009). Approximately 5% of Sitka Sound whales will move to Frederick Sound each year and 6% of Frederick Sound whales will make the reverse trip (Straley *et al.*, 2009). There are also movements from Sitka Sound to Glacier Bay (1%) and back (2%). The probability that humpback whales return to the same area in future years is estimated to be greater than 0.75 (Hendrix *et al.*, 2012). In summary, individual whales display high site fidelity, yet there is a non-zero probability of moving to another area to feed perhaps depending on food availability; this feature is known as temporary emigration (Kendall *et al.*, 1997; Pollock, 1982).

Since the cessation of commercial whaling in Southeast Alaska in the 1930s, the humpback whale population has increased (Baker *et al.*, 1992; Hendrix *et al.*, 2012; Straley *et al.*, 2009). Humpback whale abundance in Sitka Sound for 1986 to 1992 ranged from 60 to 272 whales (Straley, 1994). From 1995 to 2000 the abundance estimate was updated to range from 261 to 491 (Straley *et al.*, 2009). The northern Southeast Alaska humpback whale population abundance was estimated as 1585 for 2008 (Hendrix *et al.*, 2012) with a population rate of increase of 5.1%.

The purpose of this study was to produce a lengthy time series of humpback whale abundance estimates in Sitka Sound which accounts for temporary emigration. Such a time series will allow assessment of long term trends and potential predator impacts on commercially important prey species such as Pacific herring. We constructed a multi-year multi-strata open Hilborn model with time-dependent probability of capture (Hilborn, 1990; Quinn and Deriso, 1999; Straley *et al.*, 2009). We then estimated humpback whale abundance associated with Sitka Sound from 1981 to 2011.

2.3 Methods

2.3.1 Study area

Sitka Sound is located in northern Southeast Alaska, between Kruzof Island on the west and Baranof Island on the east, and consists of a multitude of islands and bays with direct access to the Gulf of Alaska (Fig. 2.1).

2.3.2 The mark-recapture data

Notation for the data used in the Hilborn model below is now given. The mark-recapture data used in this study were accumulated from 1981 to 2011 in Sitka Sound, Southeast Alaska

(Fig. 2.1). Photographs of the ventral surface of the flukes were used as the mark that uniquely identifies each whale (see Straley et al. 2009 for effort and details regarding data collection methods). Data were used from the months of October to April, when peak aggregations of both whales and herring are present in Sitka Sound (Hulson, 2012). Each year t, a sample size of n_t whales was photographed, or 'captured' in standard mark-recapture terminology (Schwarz and Seber, 1999; Seber, 2002). Of the n_t whales in the sample, $C_{i,t}$ were identified as recaptured by comparing with whales previously photographed during the ith year. Whales not previously photographed formed the release group of year t, denoted R_t. Thus each annual sample size n_t is apportioned into recaptured whales denoted $C_{1,t}, C_{2,t}, \ldots C_{t-1,t}$ and newly photographed whales which comprise the release group R_t (Table 2.1). The mark-recapture data for thirty release groups of humpback whales from 1981 to 2011 are summarized in Table 2.2

2.3.3 Hilborn model for availability

The Hilborn approach (Hilborn, 1990; Quinn and Deriso, 1999) features a multi-strata open population dynamics model which accounts for movement between strata by using mark-recapture data. A Hilborn model has four components: (1) a population dynamics and movement model, (2) an observation model describing the process of captures, (3) a likelihood function describing the observation of captures, and (4) an algorithm for optimizing a non-linear function (Hilborn, 1990). The Hilborn method analyzes frequencies of recaptures of annual release groups rather than individual sighting histories. For the purposes of this study, we modified the usual multi-strata Hilborn model (Quinn and Deriso, 1999) for movement outside of Sitka Sound due to temporary emigration, assuming availability in a stratum where sampling occurs and non-availability in another stratum with no sampling.

2.3.4 Population dynamics model

The predicted abundance of the surviving marked whales of the *i*th release group at time *t* was:

$$M_{i,t} = \emptyset M_{i,t-1} = \emptyset^{t-i} R_i \quad , \tag{2.1}$$

where ϕ was the annual survival rate, assumed to be 0.96 (Mizroch *et al.*, 2004). Thus, the expected number of recaptures from the *i*th release group at time *t* was:

$$\hat{C}_{i,t} = \hat{p}_t \theta M_{i,t}, \tag{2.2}$$

where p_t denotes the probability of capture and θ is the proportion of whales available in Sitka Sound, assumed to be 0.94 for all release groups (Straley *et al.*, 2009). Survival, probability of capture, and availability are confounded in (2.1) and (2.2). Consequently only one of the three parameters can be estimated at a time. Availability and survival have both been estimated previously (Mizroch *et al.*, 2004; Straley *et al.*, 2009).

2.3.5 Abundance

The estimated total abundance of all whales associated with Sitka Sound was the sum of $\widehat{N}_{t,S}$ and $\widehat{N}_{t,O}$, which are the abundances available and unavailable in Sitka Sound, respectively. This sum was estimated for each year by dividing the total recaptures n_t by the product of availability θ and the estimated probability of capture $\hat{p}_t$:

$$\widehat{N}_{t,.} = \widehat{N}_{t,S} + \widehat{N}_{t,O} = n_t / [\hat{p}_t \theta] \;. \tag{2.3}$$

The abundance available in Sitka Sound during year *t* was then found by:

$$\widehat{N}_{t,S} = \theta \widehat{N}_{t,.} = n_t / \hat{p}_t. \tag{2.4}$$

Likewise the abundance which was unavailable in year *t* was the complement:

$$\widehat{N}_{t,O} = [1 - \theta] n_t / [\hat{p}_t \theta]. \tag{2.5}$$

2.3.6 Likelihood

The number of recaptures was assumed to have a negative binomial likelihood:

$$L=\sum_t\sum_i\frac{\Gamma\left(C_{i,t}+k\right)}{\Gamma(k)\Gamma\left(C_{i,t}+1\right)}\left(\frac{k}{\hat{C}_{i,t}+k}\right)^k\left(1-\frac{k}{\hat{C}_{i,t}+k}\right)^{C_{i,t}}, \tag{2.6}$$

in which k is an overdispersion parameter. The total log likelihood for the negative binomial over all release groups for all times is given by

Log L=

$$\sum_t\sum_i \log\Gamma\left(C_{i,t}+k\right)-\log\Gamma(k)-\log\Gamma\left(C_{i,t}+1\right)+k\log\left(\frac{k}{\hat{C}_{i,t}+k}\right)+C_{i,t}\log\left(1-\frac{k}{\hat{C}_{i,t}+k}\right). \tag{2.7}$$

2.3.7 Maximum likelihood estimation

We maximized the model log likelihood (2.7) using OPTIM (R v. 2.14.0), an optimization subroutine. Maximum likelihood estimates for thirty-one model parameters were found. These parameters are the probabilities of capture p_t for each of thirty years (2.2) and the overdispersion parameter k in the negative binomial likelihood (2.6). The negative binomial was used because whale mark-recapture data are usually overdispersed (Mizroch *et al.*, 2004). Availability θ and survival ϕ were not estimated as parameters, but rather fixed as constants.

2.3.8 Comparison of the various humpback whale abundance estimates

We plotted our estimates of humpback whale abundance in Sitka Sound in comparison with other studies (Liddle, 2015; Straley, 1994; Straley *et al.*, 2009). Liddle (2015) previously used a Bayesian method to estimate humpback whale abundance in Sitka Sound for 1981 to 1989 when sample sizes were especially small (Karunamuni and Quinn, 1995). Straley (1994) used an open population Jolly-Seber methods to estimate humpback whale abundance in Sitka sound for

1986 to 1992. Straley *et al.* (2009) used a multi-strata open Hilborn model to estimate humpback whale abundance in Sitka Sound, Frederick Sound and Glacier Bay for the years 1994 to 2002.

2.4 Results

A total of 662 whales were uniquely photo-identified in 30 annual release groups from 1981 to 2011 (Table 2.2). Sample sizes (n_t) ranged from 1 whale in 1981 to 114 whales in 1998 with a median of 45 whales (Table 2.2). The median annual release group (R_i) was 20 whales with a minimum of 1 in 1981 and a maximum of 54 in 1991 (Table 2.2).

Maximum likelihood estimates of the probability of capture ranged from 0.001 in 1983 to 0.493 in 1992 with a median of 0.163 (Table 2.3). The counts were so over-dispersed that the variance greatly exceeded the mean. The estimated overdispersion parameter (2.6) was k=10.9 indicating that a negative binomial likelihood is appropriate (Agresti, 2002; Mizroch *et al.*, 2004). Therefore the Poisson likelihood would not have been valid. A parametric bootstrap routine yielded 95% confidence intervals for the probability of capture which revealed rapidly decreasing widths for the estimates in the later years of the study due to the accumulating data (Fig. 2.2). Total abundance estimates from the Hilborn method (2.3) ranged from 10 whales in 1981 to 2820 whales in 1983 with median 349 (Table 2.3). The median whale abundance available in Sitka Sound from (2.4) was 328 whales, with a maximum of 2820 whales in 1983 and a minimum of 9 whales in 1981 (Fig. 2.3, Table 2.3). Meanwhile the abundance of whales that were unavailable from (2.5) ranged from 1 whale in 1981 to 180 whales in 1983 with median 21 (Table 2.3). We used the parametric bootstrap output to compute confidence intervals for the abundance of whales available in Sitka Sound (Table 2.3). By 2010, the sum of all the whales in the release groups (662) was well within the 95% confidence interval for humpback whale abundance available in Sitka Sound (Table 2.3).

Previous humpback whale abundance estimates (Liddle, 2015; Straley, 1994; Straley *et al.*, 2009) for Sitka Sound were all very similar in scale and trend (Fig. 2.3) which is not unexpected considering these estimates are drawn from the same mark-recapture data set. However, in 1983 the Bayesian upper credible limit was 436, which is much more reasonable than the 2820 obtained using the Hilborn method (Table 2.4). In addition, the Bayesian method provides abundance estimates in 1982 and 1985 when there was no sampling (Liddle, 2015) whereas the Hilborn method does not. In 1984, when there was no recaptures, the Bayesian method also performed better than the Hilborn method (Table 2.4). The overall upwards trend in humpback whale abundance in Sitka Sound is apparent in each set of estimates (Fig. 2.3). The Bayesian abundance estimates for 1981 to 1989 (Liddle, 2015) blend imperceptibly with the Jolly-Seber estimates of 1986 to 1992 (Straley, 1994). The Hilborn estimates of 1994 to 2000 (Straley *et al.*, 2009) are nearly indistinguishable from mine (Fig. 2.3).

2.5 Discussion

The purpose of this study was to develop a lengthy time series of humpback whale abundance available in Sitka Sound, sufficient information to assess long term trends. Starting with a mark-recapture data set which spanned the years 1981 to 2011, we produced thirty annual abundance estimates of humpback whale abundance in Sitka Sound, one of the longest time series of humpback whale abundance in the published scientific literature. Such consistent sampling effort provided data for excellent precision for most of the abundance estimates.

We interpret the overall upwards trend in abundance since 1981 as the gradual recovery of the humpback whale population after the cessation of commercial whaling in Alaska in the 1930s. The number of known unique whales is within the confidence interval for the abundance of whales available in Sitka Sound as of 2010. This suggests that the size of the marked population is very nearly the same as the humpback whale abundance. However, humpback whales have not yet reached the carrying capacity of Sitka Sound as the discovery curve showing new recaptures continues to increase as late as 2011 (Fig. 2.4). Factors which might eventually limit humpback carrying capacity include habitat, predators and prey (Braithwaite *et al.*, 2012; Dalla Rosa *et al.*, 2012; Pianka, 1995). If predation on humpbacks by killer whales or large sharks were to increase, or if preferred prey items such as krill or Pacific herring were to decrease, then survival or availability of humpback whales in Sitka Sound might also decrease. Finally, if either calving grounds or feeding areas were to be impacted, perhaps by human activities or climate change, then humpback whale availability in Sitka Sound could decrease.

Mark-recapture sampling of humpback whales in Sitka Sound was dedicated and persistent for over thirty years. Nonetheless, the huge abundance estimate in 1983, at a time when whales were very rare in Sitka Sound, is certainly spurious (Table 3.2). This is attributable to low sample sizes in the early 1980's. For those early years when sample sizes were very small, Bayesian abundance estimates are more realistic (Liddle, 2015). To grapple with the apparently extreme values of 2004 and 2011 (Fig. 2.3), we tried combining data from different years. But this merely moves the new whales into release groups of the year before or the year after. Incorporation of sampling effort seemed at first to be a possible avenue for improvement, but was disappointing because it didn't provide any predictive power. Although 2004 had a relatively low sampling effort, so did several other years, which did not result in extreme abundance estimates. In 2004 there was a sample size of 42, 26 of which were newly discovered whales (Table 2.2). Likewise in 2011, there was a sample size of 13, with 9 newly discovered whales (Table 2.2). The high proportion of new whales is most likely the reason for the large abundance estimates in 2004 and 2011 (Table 2.2). These high abundance estimates cannot be removed by manipulating the model or the data set. Indeed these large estimates are consistent with the upwards trend of the previous twenty years. It is possible that these large estimates indicate a population cycle as would be predicted by a predator prey differential equations model (Berryman, 2001). Discussions with biologists involved in sampling indicate that there may have been a great many whales in Sitka Sound in those years.

The published estimates of survival, availability and abundance estimates that we used (Mizroch *et al.*, 2004; Straley *et al.*, 2009) are applicable to our study because these studies overlap in time and in space and are derived from the same population of whales. Both studies used data from Sitka Sound in addition to other areas not included in our study, specifically Frederick Sound and Glacier Bay (Straley *et al.*, 2009) as well as the broader North Pacific (Mizroch *et al.*, 2004). The previous studies occurred during 1994-2000 (Straley *et al.*, 2009) and 1979-1996 (Mizroch *et al.*, 2004) substantially overlapping the period of the abundance estimates in this study, 1981-2011. One difference is that the data for this study were collected from October to April, which is when Pacific herring are present in Sitka Sound, while the other studies considered data from throughout the year.

If availability and survival constants were fixed at higher values, the trends in humpback whale abundance would not change very much. If it is assumed that availability in Sitka Sound and survival were both 100%, it would effectively remove these parameters from the model. We would still have very large estimates of whale abundance in 2004 and 2011. If the availability rate or survival rate were estimated as a parameters, they are still both constrained by the upper boundary of 100%. For example, using parts of the same mark-recapture data set, Hendrix et al. (2012) estimated the humpback adult survival rate as 0.99, which suggests that the estimation method used was pushing the survival parameter to the boundary of the parameter space, beyond which it could not go. If probability of capture was fixed (instead of availability), then similar whale abundance estimates would arise, since it is the product of availability and probability of recapture that is estimated in the Hilborn model (3.7).

We assumed that there is an overall coherent stock of whales in northern Southeast Alaska, of which about 94% of which use Sitka Sound during any given herring spawning season. In retrospect this assumption might not be justified. For evidence consider that humpback whales increased from ~600 to ~1000 from 2009 to 2011. Such a rate of increase cannot possibly be attributed to recruitment alone in a species where only about 17% of females calve each year (Gabriele *et al.*, 2001; Glockner-Ferrari and Ferrari, 1984). Even if every adult female of 2009 (~300) gave birth once between 2009 and 2010, and that all of these juveniles survived, and that all of these showed up in Sitka Sound, it would still be insufficient to explain the 1044 whales estimated for 2011 (Table 3.2). This suggests that there has been an influx of whales from other areas, for example the Gulf of Alaska (Witteveen *et al.*, 2011).

An improvement to our model would be to include data from the three feeding areas with extensive sampling (Sitka Sound, Glacier Bay, Frederick Sound) as in Straley et al. (2009), using a fourth stratum for the un-sampled regions (Fig. 2.1). Sampling in the hitherto un-sampled regions, especially the Gulf of Alaska, would be valuable. Another possibility is that availability could be modeled so that Pacific herring is an explanatory variable, thus expressing the idea that whales might arrive in greater numbers when the herring spawning biomass is larger. Similarly, the model could include a recruitment function where juvenile survival depends on previous herring spawning biomass. Climate change may provide an explanation for why the humpback whale population has increased in recent years, as humpback whale abundance is responsive to seasonal upwelling (Thompson *et al.*, 2012). Another plausible influence on humpback whale availability is the surface water temperatures in Sitka Sound (Dalla Rosa *et al.*, 2012). A Hilborn model which exploits these ideas might incorporate such climate variables into the survival parameter or the availability parameter.

A time series model, either univariate or multi-variate, would allow for forecasting abundance. A variety of variables such as sea surface temperature, herring biomass and humpback whale abundance could be included in a multi-variate time series model (Berryman, 2001; Chatfield, 2004). Such an approach would allow for hypothesis testing to exclude variables which have no effect on humpback whale abundance and thereby direct attention to those variables which remain. The drawback of time series models is that the parameters are not always interpretable from a biological point of view (Chatfield, 2004).

Humpback whales have a high survival species (Mizroch *et al.*, 2004, 2011), and also have high site fidelity (Straley *et al.*, 2009), consequently whales from the 1980's release groups continue to show up in Sitka Sound. As a case in point, consider the lone whale of the 1981 release group which was recaptured in 2005, a full 24 years after first being observed (Table 2.2). Likewise whales from the 1987 release group continue to be recaptured as recently as 2010

(Table 2.2). These recaptures from the 1980's release groups emphasize the importance of a long term sampling program for such a long-lived species.

Pollock's robust design is a mark-recapture method (Pollock, 1982) which allows estimation of availability directly by using two or more periods of recapture within each annual sampling period. However, Pollock's robust design relies on a closure assumption, that it is the same animals each subinterval, which is possibly not the case with the highly mobile humpback whale population. Perhaps if the subintervals were close enough together in time, or if there is a way to test the closure assumption, Pollack's robust design might be a fruitful approach.

Knowledge of humpback whale abundance could be useful to managers of Sitka Sound's herring population. For example, some observers have speculated that the humpback whale population consumes a significant proportion of the herring biomass and this removal should therefore be taken into consideration when managers undertake assessment to assign an annual fishing quota. Alternatively, a decline in humpback whale abundance might signal a reduction in the size of the herring biomass. Using predator abundance to assess or signal changes in prey availability is not a new concept but perhaps needs further exploration.

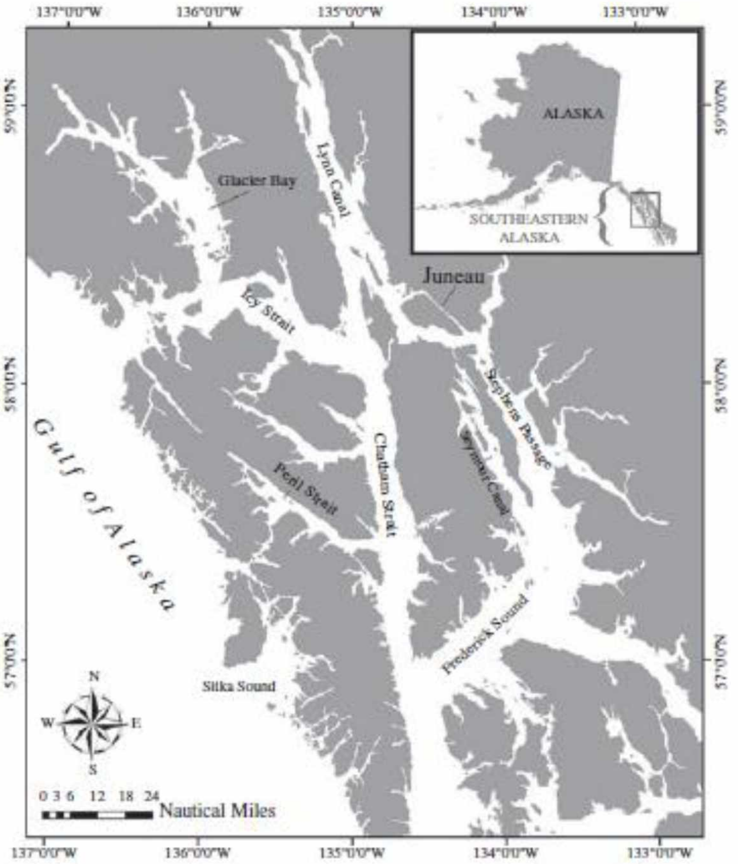

Figure 2.1 Map of northern Southeast Alaska. Some of the known feeding areas of humpback whales are shown including Sitka Sound.

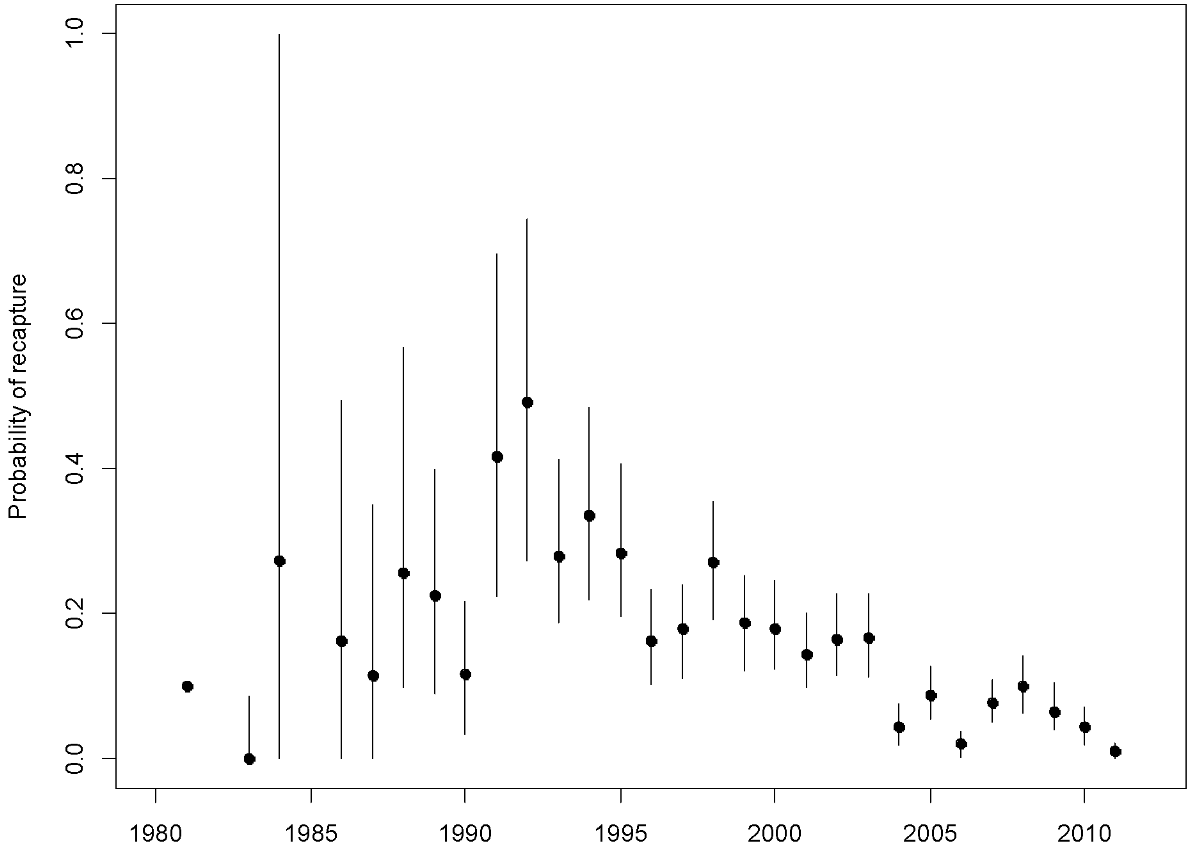

Figure 2.2 Estimates of the annual probability of capture. Error bars represent 95% confidence limits.

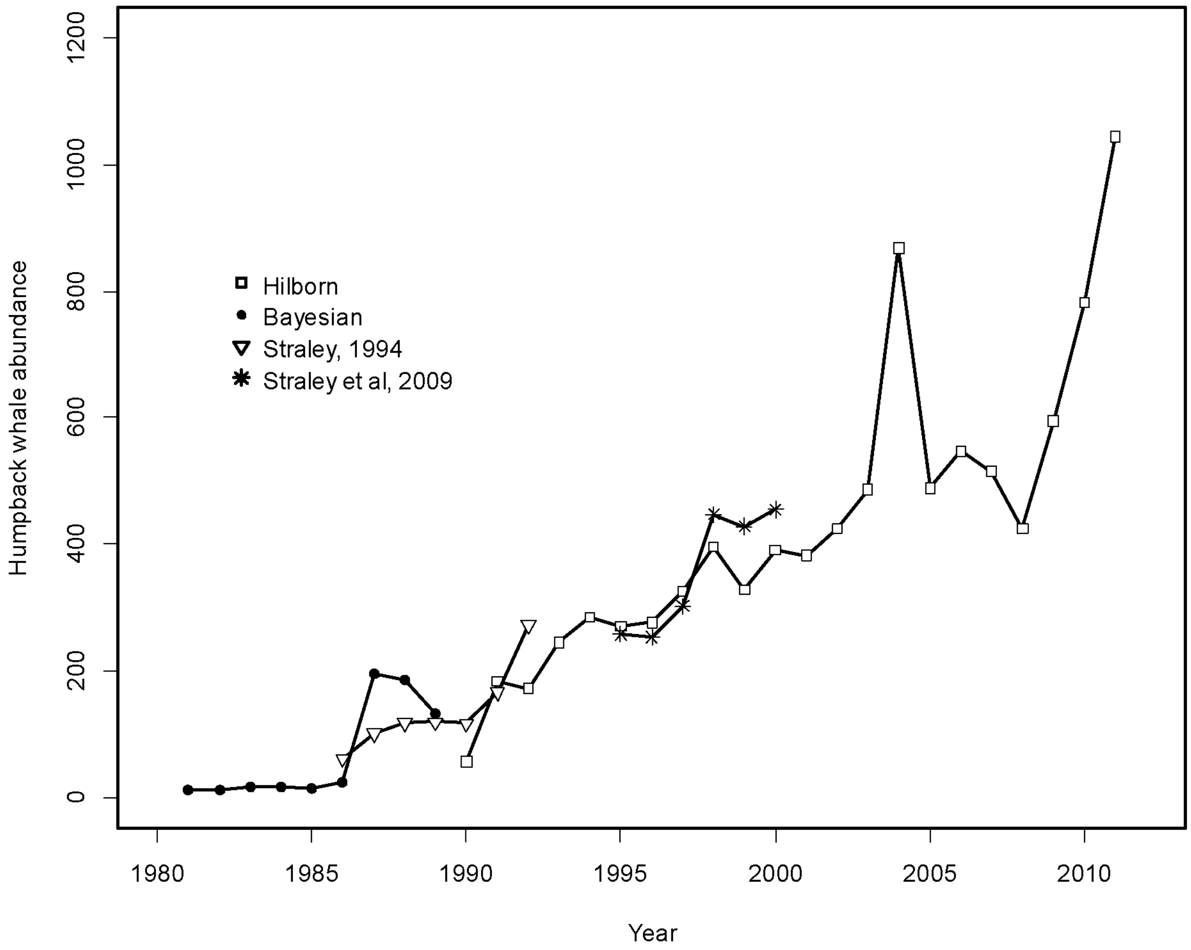

Figure 2.3 Comparison of the various humpback whale abundance estimates. Humpback whale abundance available in Sitka Sound (squares) for 1990-2011 derived from the Hilborn model are compared with Bayesian estimates (dots) for 1981-1989 (Liddle, 2015), Jolly-Seber humpback whale abundance estimates (triangles) for the years 1986-1992 (Straley, 1994), and Hilborn estimates for the years 1995-2000 which account for migration (Straley *et al.*, 2009).

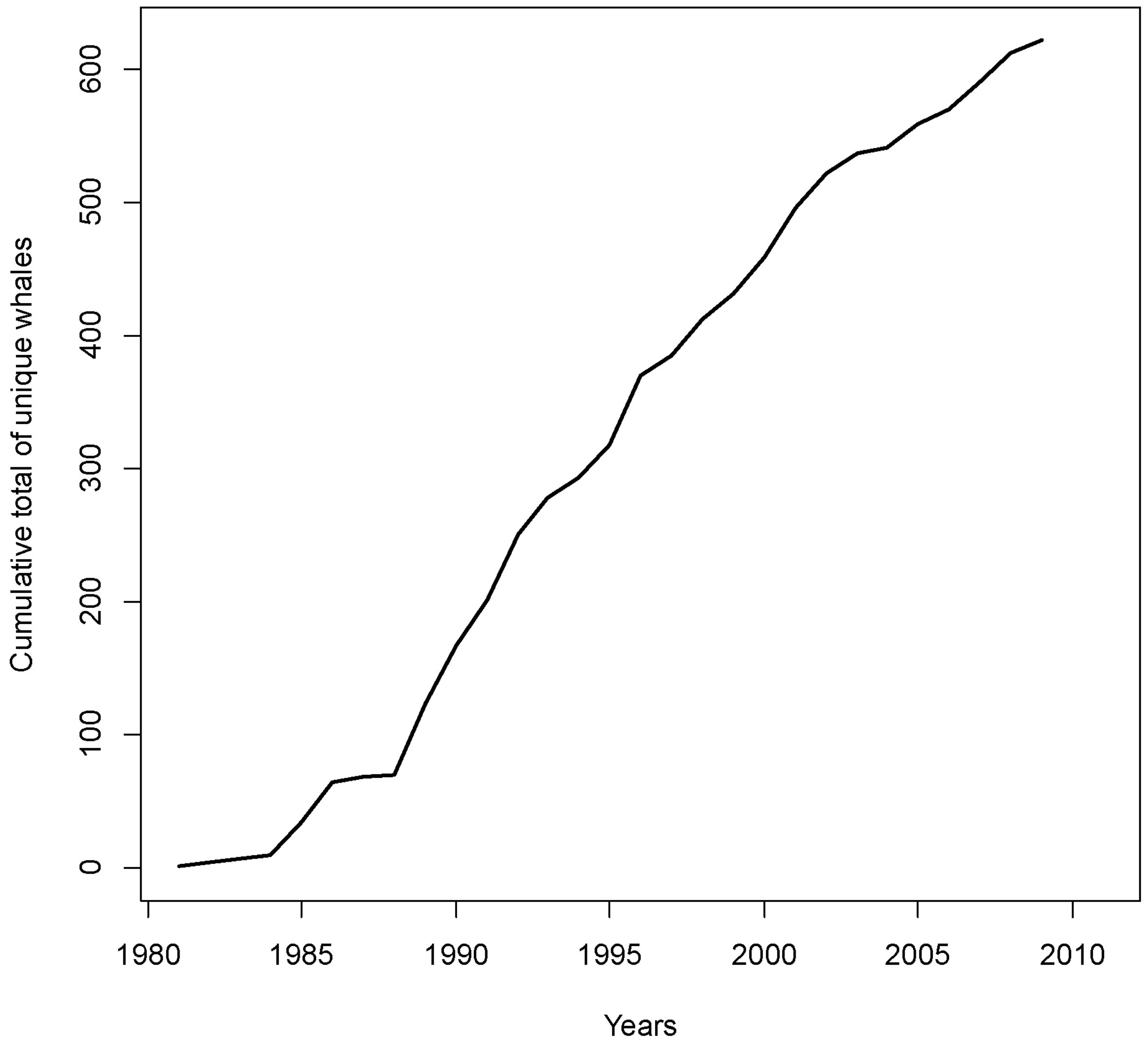

Figure 2.4 Discovery curve for humpback whales in Sitka Sound 1981-2011. The number of newly identified humpback whales is shown over time. These counts are for Sitka Sound from October to April only, corresponding to the herring migration in Sitka Sound.

Table 2.1 Notation

R_t	Release groups
s	Number of sampling periods (years)
n_t	Sample size at year *t*
$\emptyset$	Annual survival of humpback whales in Sitka Sound
$C_{i,t}$	Recaptures of the *i*th release group at time *t*
$\hat{C}_{i,t}$	Expected recaptures of the *i*th release group at time *t*
$M_{i,t}$	Abundance of marked whales of the *i*th release group at time *t*
θ_t	Proportion available for recapture in Sitka Sound at time *t*
p_t	Probability of capture of whales in the sampling area
$N_{t,.}$	Total population abundance associated with Sitka Sound
$N_{t,S}$	Available population abundance of whales in Sitka Sound at time *t*
$N_{t,O}$	Unavailable population abundance of whales at time *t*

Table 2.2 Capture matrix. Release groups (R_t) are on the diagonal with annual re-captures across the rows. Sample sizes (n_t) are shown in the bottom row.

81	83	84	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11
1	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
	3	1	1	1	0	1	0	0	1	0	2	1	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
		3	0	0	0	1	2	0	3	3	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			3	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
				25	7	6	1	8	7	5	5	4	2	2	4	3	2	5	4	3	0	1	0	2	3	2	2	0
					30	3	1	15	11	9	7	13	6	6	8	5	6	7	7	5	1	1	0	3	5	3	1	0
						4	0	3	3	0	1	0	1	1	1	2	2	1	2	0	0	0	0	0	0	0	0	0
							1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
								54	18	12	15	10	4	7	8	6	6	3	1	6	2	1	0	2	3	2	0	1
									44	9	8	8	5	2	7	3	2	2	2	2	1	1	0	3	0	1	1	0
										34	11	6	2	4	6	5	2	0	4	5	0	0	0	0	1	0	2	0
											49	7	3	1	5	3	5	4	2	5	2	1	0	2	1	2	0	0
												28	9	7	11	7	6	4	4	5	2	2	0	1	0	1	0	0
													14	4	5	4	3	1	1	1	0	0	0	0	0	1	0	0
														25	4	3	1	2	1	1	0	1	0	0	0	0	0	0
															52	7	5	1	4	2	1	3	1	2	1	1	0	1
																16	6	4	3	3	1	2	0	0	1	0	0	0
																	27	4	6	6	1	3	2	2	3	2	2	0
																		19	4	3	1	0	1	2	1	2	2	0
																			28	2	0	1	0	1	2	0	0	0
																				36	3	7	1	5	5	2	1	0
																					26	6	1	1	0	0	0	0
																						15	1	0	3	1	0	0
																							5	0	1	1	1	0
																								17	3	1	2	1
																									12	0	0	0
																										20	1	1
																											22	0
																												9
1	3	4	4	26	39	16	7	81	90	73	102	82	48	62	114	66	75	59	75	87	42	46	12	43	45	42	37	13

Table 2.3 Probability of capture and abundance estimates 1981-2011.

Maximum likelihood estimates of probability of capture are denoted p_t. Confidence intervals were estimated with a parametric bootstrap routine. Population abundance estimates for total humpback whales associated with Sitka Sound (2.3) are denoted $N_{t,.}$; humpback whales unavailable in Sitka Sound (2.5) are denoted $N_{t,O}$; and the abundance of humpback whales available in Sitka Sound (2.4) are denoted $N_{t,S}$; and finally the 95% confidence interval for the whales available in Sitka Sound.

Year	$\hat{p}$	95% CI $\hat{p}$	$N_{t,.}$	$N_{t,O}$	$N_{t,S}$	95% CI $N_{t,S}$
1981	0.100	(0.100, 0.100)	10	1	9	(9, 9)
1982	-	-	-	-	-	-
1983	0.001	(0.001, 0.087)	3000	180	2820	(32, 2820)
1984	0.273	(0.001, 0.999)	15	1	14	(4, 3760)
1985	-	-	-	-	-	-
1986	0.163	(0.001, 0.494)	25	1	23	(8, 3760)
1987	0.116	(0.001, 0.350)	224	13	211	(70, 24440)
1988	0.257	(0.098, 0.567)	152	9	142	(65, 373)
1989	0.225	(0.091, 0.399)	71	4	67	(38, 166)
1990	0.118	(0.034, 0.218)	59	4	56	(30, 194)
1991	0.417	(0.223, 0.696)	194	12	183	(109, 342)
1992	0.493	(0.274, 0.745)	182	11	172	(114, 308)
1993	0.280	(0.188, 0.413)	261	16	245	(166, 366)
1994	0.337	(0.220, 0.485)	302	18	284	(198, 435)
1995	0.285	(0.197, 0.408)	288	17	270	(189, 390)
1996	0.163	(0.103, 0.234)	294	18	276	(192, 439)
1997	0.179	(0.111, 0.241)	347	21	326	(242, 527)
1998	0.271	(0.192, 0.356)	421	25	395	(301, 558)
1999	0.189	(0.121, 0.252)	349	21	328	(246, 512)
2000	0.181	(0.124, 0.246)	415	25	391	(286, 570)
2001	0.145	(0.098, 0.201)	407	24	382	(276, 568)
2002	0.166	(0.116, 0.227)	452	27	425	(311, 606)
2003	0.168	(0.113, 0.227)	517	31	486	(360, 726)
2004	0.045	(0.020, 0.076)	923	55	868	(517, 1984)
2005	0.089	(0.056, 0.128)	520	31	489	(339, 770)
2006	0.021	(0.002, 0.039)	582	35	547	(293, 5751)

Table 2.3 (continued)

2007	0.078	(0.050, 0.109)	548	33	515	(371, 804)
2008	0.100	(0.064, 0.143)	451	27	424	(297, 657)
2009	0.066	(0.041, 0.104)	633	38	595	(379, 967)
2010	0.044	(0.019, 0.072)	832	50	782	(480, 1858)
2011	0.012	(0.001, 0.022)	1111	67	1044	(550, 12220)

Table 2.4 Bayesian and Hilborn humpback whale abundance estimates. Annual sample sizes (n_t), recaptures (m_t), 95% Bayesian credible intervals, and 95% bootstrap confidence intervals derived from the Hilborn model are also shown.

Year	n_t	m_t	Bayesian N_t	Bayesian 95% CI	Hilborn N_t	Hilborn 95% CI
1981	1	0	12	(2,258)	9	(9, 9)
1982	0	0	12	(2,258)	NA	NA
1983	3	0	16	(3,436)	2820	(32, 2820)
1984	4	1	16	(5,169)	14	(4, 3760)
1985	0	0	14	(7,264)	NA	NA
1986	4	1	24	(9,172)	23	(8, 3760)
1987	35	1	194	(65,267)	211	(70, 24440)
1988	38	9	186	(117,301)	142	(65, 373)
1989	16	12	131	(103,186)	67	(38, 166)

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Chapter 3

Humpback Whale Predation on Pacific Herring in Sitka Sound, Alaska[3]

3.1 Abstract

The Pacific herring stock of Sitka Sound supports an economically important commercial fishery which for example yielded a harvest of 14,776 tons with a value of $10.6 million in 2009. Humpback whales, a major predator of Pacific herring, use Sitka Sound as a feeding area during the same months when herring arrive to spawn. To investigate the cumulative effect that so many humpback whales have on mortality of Pacific herring, we modified a standard age-structured assessment model (ASA) used by the Alaska Department of Fish and Game to manage the Pacific herring fishery, by expressing mortality as linearly dependent on humpback whale abundance. We found that despite much evidence that whales do consume herring, the mortality effect is not significant within the ASA model. Humpback whales and Pacific herring have trended upwards together, reaching maximum values in 2011. Indeed, for every year after 2002 there were more Pacific herring spawning biomass and more humpback whales than in every other previous year back to 1981. This suggests that some other cause is at work, perhaps improved ecological conditions for both species.

Key words: Humpback whales, Pacific herring, age-structured assessment models, Sitka Sound.

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3.2 Introduction

Pacific herring (*Clupea pallasi*) constitute one of the most valuable fisheries in Alaska (Woodby *et al.*, 2005). Pacific herring are planktivores and therefore are important mid-level consumers in the food chain. Herring are an important prey for a wide variety of fishes, birds and marine mammals, especially humpback whales (Bishop *et al.*, 2015; Pearson *et al.*, 2012; Teerlink, 2011; Thomas and Thorne, 2001; Womble *et al.*, 2009). Herring migrate annually between offshore waters to nearshore waters where they spawn, usually in late March or April in Southeast Alaska (Woodby *et al.*, 2005). Herring reach sexual maturity at three years and continue to spawn each year thereafter (Funk, 2007). The average life span is about 8 years for herring in Southeast Alaska. Female herring lay more than 20,000 eggs annually (Funk, 2007).

Herring fisheries in Alaska are big business, with 864 permit holders catching an average total of 37,500 tons of herring worth more than $12 million between 1998 and 2002 (Woodby *et al.*, 2005). The sac roe herring fisheries in Southeast Alaska caught an average of 9500 tons between 1998 and 2002 (Woodby *et al.*, 2005). In 2009, the sac roe harvest in Sitka Sound was 14,776 tons with an ex-vessel value of $10.6 million (Hebert and Pritchett, 2009).

Herring stocks in Alaska and around the world have collapsed before, wreaking havoc on fishing communities as well as the many predators who prey on herring (Peterson *et al.*, 2003). For example, in 1993 and 1994 the Prince William Sound Pacific herring stock declined precipitously (Pearson *et al.*, 1999). This sharp decline prompted a great deal of concern and the herring fishery was shut down. With the exception of 1998 and 1999, this fishery has remained closed ever since due to concerns about the slow recovery (Botz *et al.*, 2013; Marty *et al.*, 2010;

Peterson *et al.*, 2003; Woodby *et al.*, 2005). Many explanations for this decline have been explored, such as climate change (Litzow *et al.*, 2014), over-fishing (Litzow *et al.*, 2014; McKechnie *et al.*, 2014), parasitic diseases (Marty *et al.*, 2003), predation by juvenile pink salmon (Pearson *et al.*, 2012), predation by Steller sea lions (Thomas and Thorne, 2001), and predation by marine birds (Bishop *et al.*, 2015).

Humpback whales are a large migratory baleen whale which migrates annually from low latitude calving grounds (e.g., Hawaii) to high latitude feeding areas such as Southeast Alaska (Witteveen *et al.*, 2009, 2004; Zimmerman and Karpovich, 2008). The humpback whale feeding areas in Southeast Alaska include Frederick Sound, Glacier Bay, Lynn Canal and Sitka Sound (Liddle, 2015a; Straley *et al.*, 2009). Humpback whales are filter feeders and consume a great deal of plankton and small forage fishes every day while on their feeding grounds in Southeast Alaska (Heintz *et al.*, 2010; Witteveen *et al.*, 2006, 2011). Stomach content data collected in 1937 at the Port Hobron whaling station on Kodiak Island, Alaska, showed that humpback whales can consume more than 338 kg of forage fish per day (Witteveen *et al.*, 2006, 2002), at least some of which were Pacific herring. Humpback whales were found to have a significant effect on the mortality of Pacific herring in Prince William Sound, Alaska (Teerlink, 2011).

Meanwhile, in recent decades humpback whale population abundance in Sitka Sound has rebounded dramatically as it recovers from near extinction from commercial whaling in the 1930's (Baker *et al.*, 1992; Hendrix *et al.*, 2012; Liddle, 2015a; Straley, 1994; Straley *et al.*, 2009). From 1986 to 1992 the Sitka Sound humpback whale population grew to as many as 272 whales (Straley, 1994). Further growth occurred between 1995 and 2000 to as many as 491 (Straley *et al.*, 2009). The population growth of humpback whales has continued since 2000, with the humpback whale abundance estimate for 2011 being 1044 (Liddle, 2015a). In 2008, the entire estimated humpback whale population abundance for all of northern Southeast Alaska including Sitka Sound was 1585, with the population rate of increase estimated as 5.1% (Hendrix *et al.*, 2012). The adult survival rate of humpback whales in Alaska has been estimated variously as 95% (Mizroch *et al.*, 2004), 96% (Straley *et al.*, 2009) and 99% (Hendrix *et al.*, 2012). All of these survival estimates are consistent with a thriving population of a long-lived species.

It is therefore natural to hypothesize that Sitka Sound humpback whales might also consume a significant amount of Pacific herring during the run-up to the spawning season in April. Supposing that 500 such whales consumed entirely herring at the rate of 338 kg per day for the 100 days prior to spawning, the total would be close to 18,000 tons per year. In contrast, the 2009 observed catch of Pacific herring catch in Sitka Sound was approximately 15,000 tons (Hebert and Pritchett, 2009). The similar magnitude of these of these two values, suggests that humpback whales may significantly reduce the herring spawning biomass in Sitka Sound.

In Sitka Sound, mark-recapture sampling of humpback whales has been conducted concurrently with a robust state-managed commercial herring fishery which includes extensive sampling both before and after the annual sac roe fishery. Together these combined data presented an opportunity to evaluate the impact of whale predation upon Pacific herring from 1981 to 2011. The Alaska Department of Fish and Game (ADF&G) uses a standard age-structured assessment model (ASA model) developed for the Pacific Herring population in Sitka Sound (Quinn and Deriso, 1999; Teerlink, 2011). In Prince William Sound a similar ASA model for Pacific Herring has been modified to assess the effects of disease (Marty *et al.*, 2003, 2010; Quinn *et al.*, 2001), and humpback whale predation (Teerlink, 2011). The standard ASA model was modified by including additional data as a covariate which modified the mortality terms. A similar approach was used to conduct investigations into a wide variety of hypotheses for the collapse of the Prince William Sound herring fishery including disease, predation and climate variables (Deriso *et al.*, 2008). Hydroacoustic data were incorporated into the standard ASA model for Prince William Sound with similar modifications (Hulson and Miller, 2008).

We investigated the relationship between Pacific herring and humpback whales in Sitka Sound. The time series for humpback whale abundance from 1981 to 2011 was incorporated into the natural mortality term of the standard ASA model for Sitka Sound as a covariate.

3.3 Methods

3.3.1 Age-structured assessment model for Pacific herring in Sitka Sound

We modified the standard age-structured assessment model (ASA model, Quinn and Deriso, 1999), used to estimate the spawning biomass, recruitment, survival and abundance of Pacific herring in Sitka Sound (Hulson, 2012). The natural mortality term was modified to include humpback whales' predation on herring, following the methodology in Teerlink (2011). This ASA model combined data from the Sitka Sound herring fishery with data from ADF&G surveys including: the observed annual catch in millions of fish by age class, the observed age composition from the spawning survey, the observed weight at age of the spawning population, the observed weight at age of the catch, the estimated eggs from the aerial spawn survey, and the total catch at age in tons. Parameters for abundance, recruitment, spawning biomass and survival were estimated with least squares by comparing the observed data to the model predicted values.

We assumed that natural mortality (M_t) of Pacific herring in Sitka Sound aged 3 years and older was linearly dependent on the humpback whale abundance as follows:

$$M_t = b_0 + b_1 N_t, \tag{3.1}$$

where N_t is the humpback whale abundance during the months October to the April prior to the herring spawn in Sitka Sound in year *t*. Whale abundance, N_t, was a time series spliced together with Bayesian estimates for the years 1981 to 1989 (Liddle, 2015b) and Hilborn estimates for 1990 to 2011 (Liddle, 2015a). The parameters b_0 and b_1 represent the baseline natural mortality and the predation effect of humpback whale abundance, respectively. Annual herring survival can be expressed as an exponential function of natural mortality:

$$S_t = e^{-M_t}. \tag{3.2}$$

The post fishery abundance of herring (*H*) at age *a*+1 and year *t*+1 is estimated as:

$$H_{a+1,t+1} = \left(H_{a,t} - C_{a,t}\right) S_{t+1}, \tag{3.3}$$

where the annual survival is S_{t+1} and $C_{a,t}$ is the observed annual catch of each age class. The recruitment abundance $H_{3,t}$ for each year and the abundances of each age class in the year 1980 are also parameters in the model.

3.3.2 Bootstrap confidence intervals

Bootstrap confidence intervals were computed for herring spawning biomass, the baseline natural mortality, and the humpback whale mortality terms (Efron and Tibshirani, 1986; Manly, 2007). The bootstrap routine, using estimated age compositions from both the seine fishery and spawn surveys, generated multinomial random proportions for each age class from 3 to 8 in order to generate one bootstrap realization of the data by sampling from the residuals. Model parameters were re-estimated for herring spawning biomass for 1981 to 2011, the baseline mortality effect and the humpback whale mortality effect. The humpback whale mortality effect was assessed by noting if the bootstrap confidence interval contained zero or not (Efron and Tibshirani, 1986; Manly, 2007; Teerlink, 2011).

3.4 Results

3.4.1 Age-structured assessment model for Pacific herring in Sitka Sound

The modified ASA model for herring spawning biomass in Sitka Sound showed that humpback whales were not a significant factor in herring mortality. The mortality effect size of humpback whales within the ASA model was estimated as -0.00061 with 95% bootstrap confidence interval (-0.00124, 0.00034). This confidence interval contains zero and therefore indicates that the humpback whale mortality effect is not significantly different than zero. Indeed the proportion of humpback whale mortality bootstrap estimates that were positive was a mere 0.21, which means that the one sided p-value is approximately p=0.79. Baseline natural mortality was 0.430 with 95% bootstrap confidence interval (0.35080, 0.68789). By comparison, the standard ASA model used for stock assessment by ADF&G (without whales) has corresponding natural mortality estimates of 0.55 and 0.25, for before and after 1998, respectively. Herring spawning biomass in Sitka Sound has increased dramatically, especially between 2002 and 2011 (Fig. 3.1).

3.4.2 Trends in Pacific herring biomass and humpback whale abundance

Humpback whale abundance in Sitka Sound exhibited a moderate positive correlation ($r=0.69$, $p< 0.0001$) with the total pre-fishery abundance of Pacific herring in Sitka Sound for the years 1981 to 2011. Humpback whale abundance also exhibited strong positive correlation ($r=0.87$, $p< 0.0001$) with the spawning biomass of Pacific herring. Both the pre-fishery Pacific herring abundance and humpback whale abundance reached maximum values in 2011. Furthermore, after 2000 both the Pacific herring spawning biomass and whale abundance showed a strong increasing trend (Fig. 3.2). Every year from 2002 onward had both humpback whale abundance and herring spawning biomass greater than in every year before that year. The 1980's were characterized by both low humpback whale abundance and herring spawning biomass less than 40,000 tons.

3.5 Discussion

We have assessed the scale of the impact of humpback whales on Pacific herring in Sitka Sound, which supports an important multimillion dollar fishery. We concluded that humpback whales have no significant effect on herring mortality. Simultaneous large upward trends in both populations, makes a significant mortality effect very unlikely. Consequently, alternative models are needed to describe the predator prey relationship between humpback whales and Pacific herring.

An alternative mortality model would be to account for the apparent "regime shift" around 2002 suggested by examination of the scatter plot of whale abundance and herring spawning biomass (Fig. 3.2). There would be different mortality parameters before and after

2002. For example the standard ASA models used by ADF&G fisheries scientists in both Prince William Sound and Sitka Sound, have different mortality parameters for before and after specific years (Hulson, 2012; Teerlink, 2011). Such a model would retain the paradigm that there is a one way interaction between whales and herring such that whales might increase herring mortality, but that whale abundance would not be influenced by herring spawning biomass. However even if the two different lines fitted well, the inevitable estimate of the slope parameters would be negative because of the strong positive correlation (Rice, 1995) between herring biomass and humpback whale abundance throughout the time period of this study (Fig. 3.2).

Meanwhile, the herring spawning biomass as estimated by the ASA model was also reaching its highest levels in the same years as the humpback population, 2009-2011 (Fig. 3.2). The ASA herring model and the humpback whale estimates are based on separate and independent sampling schemes ongoing from 1981 to 2011 (Hulson, 2012; Straley, 1994; Straley *et al.*, 2009). Every point in the upper right corner of this plot is from after 2002 (Fig. 3.2) and every point in the lower left is from the 1980’s. Points in the central area of the plot are all from the 1990’s (Fig. 3.2). It is difficult to escape the impression that these two species are trending upwards together.

Another possibility is that both species are responding to a regime change in the ecosystem. Although temperature itself is not likely to be the direct cause of the trends, sea surface temperature may prove to have some predictive power. Harbor seals have increased in parts of Southeast Alaska and remained stable in other places (Small *et al.*, 2003). Likewise climate change is implicated in changes to geographic ranges of fish stocks (Cheung *et al.*, 2010;

Litzow, 2006; Litzow *et al.*, 2014; Ward *et al.*, 2009). Warmer temperatures might also promote better marine survival for both species. A model might incorporate sea surface temperatures as a covariate in the mortality term in the herring ASA model. Alternatively sea surface temperature data might be put into the Hilborn model for humpback whales.

A multi-species model which included other species might be a better approach (Van Kirk *et al.*, 2010). A multi-species model could include other predators of herring such as sea-lions (Womble *et al.*, 2009). Humpback whales are generalist predators that prey on many other species such as capelin, pollock, and krill (Witteveen *et al.*, 2008, 2011). Although such detailed data isn't always available for every species in an ecosystem, it is possible to simulate a food chain by using data on which species eats which other species (Ainsworth *et al.*, 2011; Christensen and Walters, 2004; Van Kirk *et al.*, 2010). Perhaps there are winners and losers in Sitka Sound in this ongoing multi-species story.

In Prince William Sound, the herring stock is much smaller and humpback whales do have a significant mortality effect on Pacific herring (Teerlink, 2011). Perhaps the whales of Sitka Sound are taking only the surplus production, so that plenty of fish remain to spawn. Simulations might be devised to demonstrate at what relative abundance levels whales start to have a significant effect on herring mortality (Mackinson *et al.*, 2003).

Another possibility for management of a herring stock is to consider humpback whales in the same way as a fishery. Humpback whales are capable of consuming nearly half a ton of forage fish per day (Witteveen *et al.*, 2006). This implies that a hypothetical population of 500 whales would consume as much as 250 tons per day. After 100 days leading up to the spawning season, such a group of whales would consume close to 25,000 tons of herring which is of the same order of magnitude as the annual herring catch in Sitka Sound (Pritchett and Hebert, 2009; Woodby *et al.*, 2005). Thus if fishery managers could get a rough estimate of how many whales are in the area they could then estimate how much herring are being consumed by whales. Managers might then adjust their estimate of how much herring is actually available for commercial fisherman. The problem which would remain is how to go about estimating the number of whales quickly and efficiently in the weeks before the herring opening. Mark-recapture methods for whales involve months and even years of intensive matching of photographs, and would therefore be too slow. The ASA model isn't predictive, so cannot be used to forecast herring or whales.

A bivariate time series model that includes auto-regressive terms as well as cross correlations between the whales and herring time series (Chatfield, 2004) may be useful in forecasting. There are a variety of diagnostic tools which use time series methods to deduce relationships between predator and prey (Berryman, 2001). For example it might be possible to detect top down control where the predator exerts control over the prey population. Or what seems more likely with herring and whales, is that bottom up control would be detected, meaning that herring abundance exerts an influence over whale abundance. With respect to herring, there are several complexities which may be challenging to include in such a multi-variate time series model in particular age and weight composition. Another issue with time series models in general is that the parameters might not have a useful biological interpretation. Such a model might be used to forecast future whale and herring abundance, yet be unable to estimate crucial parameters needed by fisheries managers.

A goal for future research is to design a multi-species model which describes the two way interaction between the two species. A multi-species model could provide accurate predictions of future whale and herring abundance. Parameters of interest include herring survival, herring spawning biomass, amount of herring consumed by whales, whale probability of capture and whale availability in Sitka Sound. Considering the upward trend in Pacific herring and humpback whales, inclusion of climate variables may be needed for a successful multi-species model.

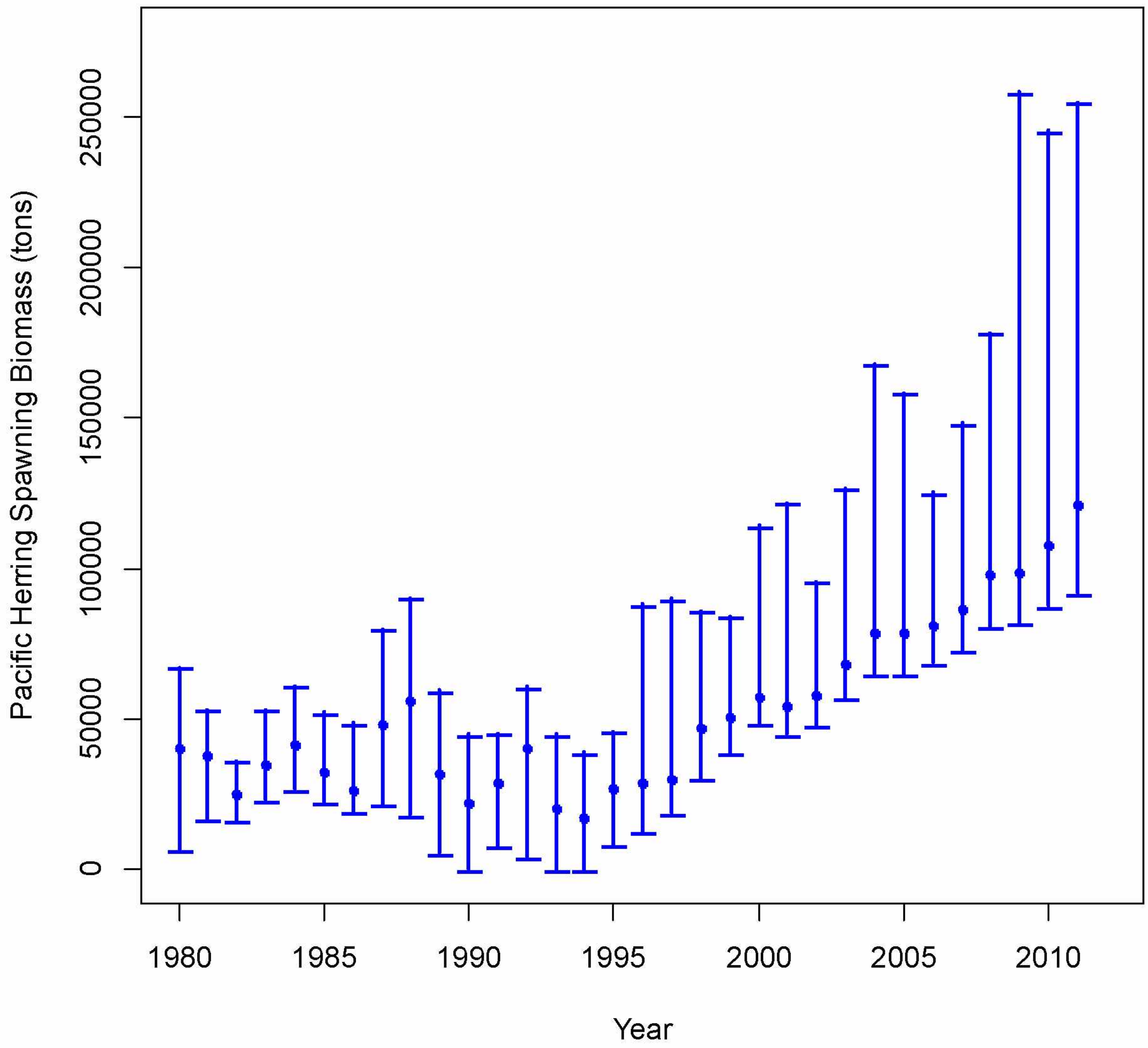

Figure 3.1 Pacific herring spawning biomass in Sitka Sound 1981-2011. Error bars represent 95% bootstrap confidence intervals. Markers are the median bootstrap estimate of the parameter.

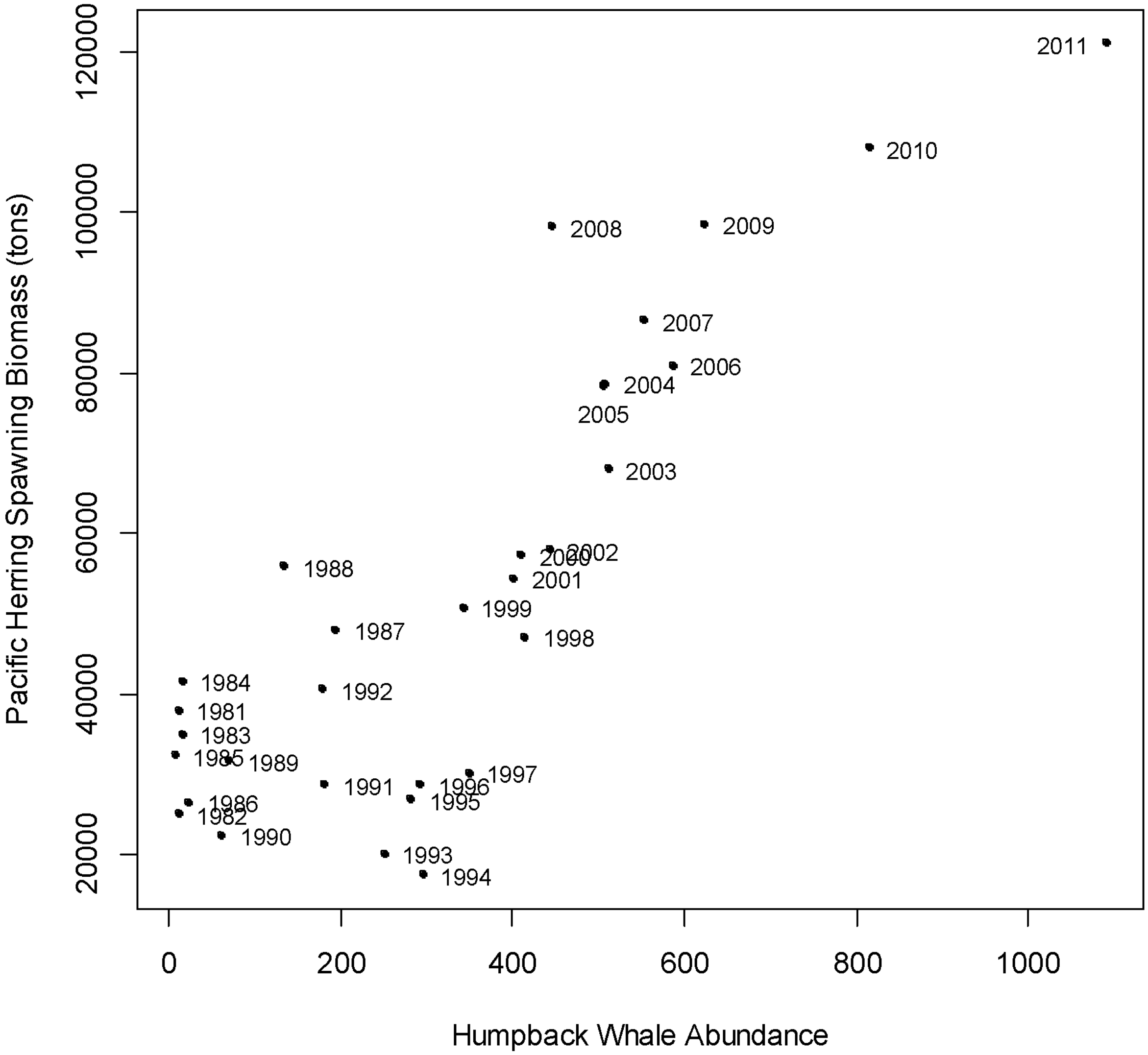

Figure 3.2 Humpback whales and Pacific herring spawning biomass. Correlation is r = 0.87.

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General Conclusion

In this thesis I have explored issues in the modeling of population dynamics of Pacific herring and humpback whales in both single species and multi-species settings. I have considered issues ranging from small sample sizes, missing data, availability of whales in the study area, assumptions which might or might not be valid, and confounding of important parameters. I now propose alternative models which might alleviate these issues.

The Bayesian mark-recapture method in chapter 1 (Liddle, 2015b) takes on the stubborn and difficult issue of small sample sizes. This method proves to be robust in simulation studies on the choice of the prior, and on statistical properties such as bias and the width of the confidence interval. I have shown that the method produces similar estimates as standard methods and outperforms those methods under certain circumstances. There are drawbacks to the Bayesian method, one of which is that if a sample size is really too small, then the prior is just too dominant, as happened in 1981-1983 with humpback whales in Sitka Sound. Meanwhile if the sample size is large enough, then abundance estimates are indistinguishable from those produced by more standard methods as happened in 1988-1989. However, if the number of recaptures is 0 or 1, or if the sample size is 0, then the Bayesian method produces estimates which have a meaningful interpretation, whereas other methods do not. As a rule of thumb, I suggest that when the sample size is less than 5, then the Bayesian method estimates are about the same as what you would get from the prior alone. If the sample size is 30 or more, then the Bayesian method and standard Hilborn method will provide nearly identical results. If there have been 0 recaptures or 1 recapture, regardless of sample size, the Bayesian method will work better.

In Chapter 2, the Hilborn method produced useful estimates of probability of recapture, while accounting for emigration or availability. But I found that this method has probability of recapture, survival, and availability confounded in such a way that is not possible to estimate all thee parameters simultaneously. What this means is, that although the product of these three parameters can be estimated, the values of each parameter cannot be estimated unless one fixes the other two in some way. I used results for survival and availability rates, taken from previous studies (Mizroch *et al.*, 2004; Straley *et al.*, 2009) from the same region and sometimes overlapping data sets to estimate the probability of recapture. An alternative approach would be to fix the probability of capture and estimate the availability rate.

The large increase in whale abundance in 2009-2011 (Liddle, 2015a) suggests that that availability may not be constant over time. If all of the extra whales in Sitka Sound (over 400 from 2009-2011) are due to new arrivals, then it suggests the assumed availability constant must be wrong. On the other hand if the new whales are due to juveniles, then reproductive success must be far greater than previously suspected. Another possibility is that perhaps survival is greater than our assumed value. But even if one assumed that availability was 100% and that survival was 100%, thus removing these parameters from the model, it is still difficult to explain this huge increase in abundance from 2009 to 2011.

In Chapter 3, an ASA model was used to explore the hypothesis that humpback whales might increase the mortality of Pacific herring in a one way interaction. There was not a significant mortality effect attributable to whales. But perhaps this was the wrong question. Maybe whale abundance is responsive to herring abundance but herring abundance is not responsive to whale abundance. In this line of reasoning, humpback whales may have been arriving in Sitka Sound in order to feed on a prolific food source. Meanwhile the herring stock was expanding possibly because of better marine survival due to climate change. Since herring is one of the primary prey items for humpback whales (Witteveen *et al.*, 2011) , this explanation provides a plausible rationale for the spikes in humpback whale abundance in 2004 and 2011, which deserves further exploration.

A bivariate time series model in which whale abundance depends on both the abundance of whales in the previous year, and herring spawning biomass of one or more previous years could shed illumination on the interactions between the two species. The whale lag term N_{t-1} would create an autoregressive time series model (Chatfield, 2004) . The disadvantage of such a time series approach is that parameters are not always interpretable and might not be easily connected to actual biological processes. Furthermore, a time series model would only be useful in a retrospective sense, because mark-recapture data only becomes available two or three years after being collected due to the length of time required for the identification process of comparing photographs. Thus, even if such a model worked, it could not be used to predict whale abundance in 2016 until several years afterwards.

A possibility for management of the herring fishery is to consider humpback whales in the same way as that of a fishery. Humpback whales are capable of consuming nearly half a ton of forage fish per day (Witteveen *et al.*, 2006). This consumption estimate implies that a hypothetical population of 500 whales would consume as much as 250 tons per day. After 100 days leading up to the spawning season, such a group of whales would consume close to 25,000 tons of herring which is of the same order of magnitude as the annual herring catch in Sitka Sound (Hebert and Pritchett, 2009; Woodby *et al.*, 2005) . Thus if fishery managers could get an estimate of how many whales are in the area then they could roughly estimate how much herring are being consumed by whales in the pre-spawning days. Managers might then adjust upwards or downwards their estimate of how much herring spawning biomass is actually available for commercial fisherman.

A classical predator-prey model has an appeal in that it has a long history and a large elaborate literature describing a multitude of models (Berryman, 2001). Such a model can be described as a system of differential equations, so that the rate of change of whales would depend on the abundance of herring, and the rate of change of herring would depend on the abundance of whales. There are plausible rationales for this type of model because it is known that whales do consume as much as half a ton of forage fish per day (Witteveen *et al.*, 2002, 2006). Juvenile humpback survival, especially when nursing, might depend on the amount of feeding which takes place in Sitka Sound.

There are very different scales of measurement used to describe herring and whales. Herring are estimated in the hundreds of millions of fish and tens of thousands of tons, and meanwhile whales are estimated in the hundreds. The traditional predator prey model was about rabbits and foxes (Berryman, 1992), both of which were on numerical scales more similar to whales than to herring. Because of the massive numbers of herring, it is often more convenient to describe their abundance in terms of biomass (tons). This is potentially an issue in a predator-prey model, because such models are set up to describe mortality and reproduction on an individual animal basis (Berryman, 1992).

Age composition and the weight composition are essential to management of the fishery (Hebert and Pritchett, 2009; Woodby *et al.*, 2005). So if a predator-prey model were to ignore the age composition or the weight composition, such models would be almost useless for fishery management. Consequently both age and weight composition data should be included in the multi-species models explicitly for any useful application by fishery management.

The survival of juvenile whales of a given year might depend on herring spawning biomass of the previous two years, rather than the herring spawning biomass of the year in question. Meanwhile the whales arriving in a particular year might be following the migrating herring of the year, or whales might remember the herring of the previous year, or they might be following other humpback whales into Sitka Sound. Each supposition about whale behavior would suggest different terms in the model.

It is also possible that the trend seen for whales and herring might be mirrored by some other species such as sea otters. Or, the same trend might be reversed for another species such as Steller sea-lions. A truly multi-species model might include data on as many of the species of Sitka Sound as possible. Perhaps there are winners and losers in this ongoing story.

Perhaps both whales and herring are responding indirectly to some climate variable such as sea surface temperature (Ainsworth *et al.*, 2011). If this type of influence could be established then it would add to the growing body of scientific research on climate change in Alaska (Beamish *et al.*, 2000; Cheung *et al.*, 2010). Such a model might incorporate sea surface temperatures as a covariate in the mortality term in the herring ASA model. Alternatively sea surface temperature data might be put into the Hilborn model for humpback whales.

I have made strides in modeling for humpback whales in Sitka Sound producing a lengthy time series not previously available. I have also explored a limited question about the effect of humpback whales on herring mortality. What remains to be done is to devise a multi-species model which describes the two way interaction between the two species. Ideally such a model would allow for more accurate prediction of future whale and herring abundance, as well as estimates of key parameters including herring survival, herring spawning biomass, herring consumed by whales, whale probability of capture and whale availability in Sitka Sound.

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