



Assessment of mark–recapture models to estimate the abundance of a humpback whale feeding aggregation in Southeast Alaska

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ABSTRACT

Aim The aim of this study was to use photographs of the unique pattern on the ventral surface of the flukes to estimate the abundance of humpback whales (*Megaptera novaeangliae*) in a discrete feeding aggregation in northern Southeast Alaska.

Location The study was located in northern Southeast Alaska, USA, in the eastern North Pacific Ocean.

Methods This study evaluated mark–recapture models, ranging from the simpler models (pooled and stratified, closed Petersen estimators) to more complex multi-strata models (closed Darroch and open Hilborn). The Akaike Information Criterion, corrected (AICc) was used as a model comparison statistic.

Results Our best estimate of whale abundance in northern Southeast Alaska in 2000 is 961 whales [95% confidence interval (657, 1076)]. This estimate comes from the Hilborn open, multi-strata approach with constant migration over time, time-dependent capture probabilities by area, and a fixed survival rate of 0.98. The simpler models were problematic owing to several aspects of whale behaviour, including that (1) the whales did not mix randomly throughout the study area, (2) some whales emigrated temporarily outside the study area and were not available for capture, and (3) whales were not equally identifiable because they did not behave in the same way when they showed their flukes upon diving. This led to heterogeneity in capture probability and a bias in the estimates. The more complex models stratified by area, and using migration movements among areas, compensated for some of these issues when estimating population size.

Main conclusions We believe that the Hilborn open, multi-strata model produced the best estimate because: (1) it incorporated the best information about survival, (2) it used detailed information about the various release groups, (3) the analysis provided an integrated environment in which parameters such as migration and capture probabilities are shared, (4) the three strata encompassed a large portion of the areas used by whales, and (5) the Hilborn model selected was superior in terms of model selection criteria and biological realism. These data provide valuable insights into the numbers and movements of humpback whales in three areas of Southeast Alaska.

Keywords

Abundance, capture probability, endangered species, heterogeneity, humpback whales, mark–recapture, monitoring, movement, photo identification, Southeast Alaska.

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INTRODUCTION

Documentation of the recovery of depleted animal populations, in particular of animals that spend their lives in an aquatic environment, poses difficulties for managers. Obtaining realistic, and unbiased, estimates of abundance is necessary to monitor the growth of a population, thus enabling appropriate management decisions. However, it is problematic to estimate accurately abundances for cetacean populations because of the natural behaviour of these animals and their complex life history (Hammond, 1986, 1990). We used the humpback whale [*Megaptera novaeangliae* (Borowski, 1781)] as a case-study species. Our approach is to combine the use of improved statistical analyses and knowledge of whale behaviour to estimate the abundance of humpback whales from a discrete feeding area in Southeast Alaska.

Humpback whales are a cosmopolitan species. They migrate seasonally in winter to warmer, tropical waters for mating and calving from the colder, productive, higher-latitude waters where feeding occurs. They inhabit coastal near-shore waters in all phases of their life history, with the exception of stocks that cross the mid-ocean to reach a feeding or wintering area. This primarily coastal existence makes most humpback whales vulnerable to human activities throughout their range and life cycle, particularly in Southeast Alaska, where these activities (vessel traffic, whale watching, and fishing) directly overlap with the presence of humpback whales.

Historically, humpback whales were commercially exploited during the 1800s and 1900s (Tønneessen & Johnsen, 1982). Monitored stocks have been recovering; some stocks are estimated to have increased 50% since the end of whaling, over three generations ago, in the 1930s (Reeves *et al.*, 2003). The International Whaling Commission protected humpback whales from commercial whaling after the 1965 season. They are classified as vulnerable on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List, and as an endangered species in the United States. Current human impacts include entanglement in fishing gear (see Neilson *et al.*, 2007), collisions with ships, disturbance from anthropogenic noise, and disruption of feeding, mating and calving activities by commercial whale-watching operations.

Humpback whales in the North Pacific are divided into three stocks: western, central, and eastern (Angliss & Lodge, 2002). The whales that feed in the waters of Southeast Alaska belong to the Central North Pacific stock: they winter in the Hawaiian Islands and then migrate to feeding areas in British Columbia and Alaska (Baker *et al.*, 1986). The known feeding areas are used by discrete and genetically distinct populations (Baker *et al.*, 1998; Witteveen *et al.*, 2004). Mothers bring their calves to the feeding areas where they were brought as calves. Their calves, when mature, will return, and, if female, bring their offspring to this same feeding area. The known feeding areas in the North Pacific vary in geographical complexity, from a linear coastline along the western United States to a complex archipelago in Southeast Alaska. The whales that

return to feed in Southeast Alaska are unevenly distributed, with some individual whales showing a strong site fidelity to specific areas (Straley, 1994).

Previous population estimates for humpback whales in Southeast Alaska, using photographs of the flukes of individual whales, range from 393 to 547. Baker *et al.* (1992) estimated the population size for the years 1979–86 to be 547 whales [95% confidence interval (504, 590)], using the Schnabel closed, multi-sample population estimator (Seber, 1982). Straley (1994) recalculated the estimate using the 1979–86 data with the Jolly–Seber open model for multiple capture–recapture data, which resulted in a mean annual population estimate of 393 whales [95% confidence interval (331, 455)]. Using the same Jolly–Seber model with data from 1986 to 1992, collected in the same areas, the estimate was 404 whales [95% confidence interval (350, 458); Straley, 1994].

These simple population models for estimating abundance are problematic as a result of several aspects of whale behaviour (Hammond, 1986, 1990). First, many of the whales showed moderate to high site fidelity, and did not randomly mix throughout Southeast Alaska. Second, some whales temporarily emigrated outside the study areas and were not available for capture every year. Third, all whales were not equally identifiable because they did not behave in the same way when they showed their flukes upon diving. These factors led to heterogeneity in capture probability and, thus, to a negative bias in abundance estimates (Seber, 1982; Pollock *et al.*, 1990).

In recent years, more complex multi-strata models have been developed that can compensate for some of these issues in estimating animal abundance (Lebreton *et al.*, 1992; Burnham, 1993; Barker, 1997; White & Burnham, 1999). These models have resolved some of the biases and model violations that occur in the simpler presence–absence models (Lincoln–Petersen and Jolly–Seber estimators), resulting in improved estimates of population size.

This paper presents a series of mark–recapture models to estimate the abundance of humpback whales, using recent data collected from two studies with similar methods in northern Southeast Alaska. The models range from the simpler presence–absence models to the more complex multi-strata models. The results from these analyses will provide insight into the movements, behaviour, and size of the population of humpback whales that feed in the waters of Southeast Alaska.

METHODS

Study areas and dates

This project used photographs of individually identified whales gathered from three areas in northern Southeast Alaska: (1) Frederick Sound, (2) Glacier Bay, and (3) Sitka Sound (Fig. 1). The designation Frederick Sound included data from Chatham Strait and Stephens Passage; Glacier Bay included Icy Strait; and Sitka Sound included Peril Strait. Survey effort was measured in terms of both days and hours; both measures

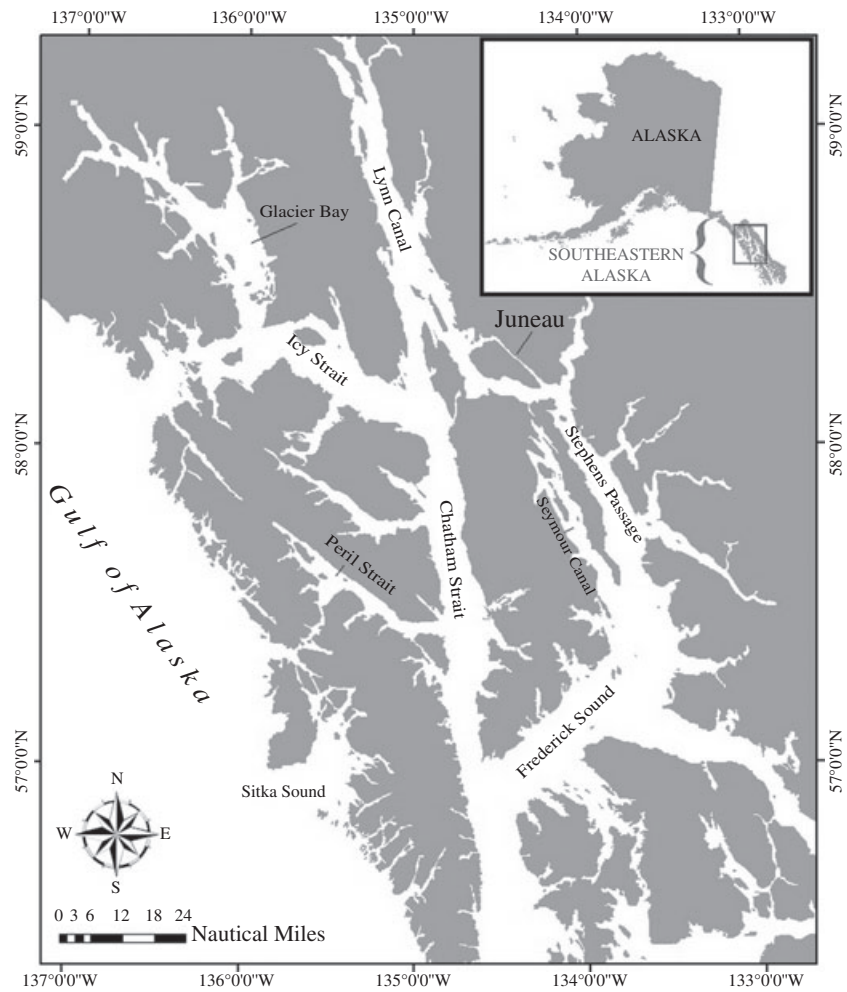


Figure 1 Map of the study area in northern Southeast Alaska.

varied by year and area (Table 1). Glacier Bay and Sitka Sound were surveyed more intensively than Frederick Sound. In particular, Frederick Sound was not surveyed in 1999.

Photographic data collection

We established sighting histories for individual whales using identification photographs of the natural markings on the ventral surfaces of the flukes (Katona *et al.*, 1979). Whales were approached using motorized vessels, and photographs of individual whales were taken with a 35-mm SLR camera equipped with a telephoto lens using black and white high-speed film. Field data were collected on each whale encounter, and included recording the presence or absence of a calf, the number of whales in the group, and the date, time, location and behaviour. Each photograph was graded as good, fair or poor quality using a uniform set of criteria. Only photographs of good or fair quality were used in the analyses. Photographs of calves were excluded because the natural markings on the flukes of some calves can change over time, and hence not all calves were equally available for capture. The recapture data were summarized into individual capture histories; the data set is available from the senior author.

Table 1 Humpback whale (*Megaptera novaeangliae*) survey effort in northern Southeast Alaska in the period 1994 to 2000.

Area	Frederick Sound	Glacier Bay	Sitka Sound	Grand total
1994				
Days	11	48	46	94
Hours	102.0	276.0	141.4	417.4
1995				
Days	11	56	47	103
Hours	102.2	316.3	146.2	462.5
1996				
Days	3	69	43	112
Hours	21.3	421.2	97.5	518.7
1997				
Days	5	76	49	125
Hours	44.9	561.7	121.6	683.3
1998				
Days	6	71	42	113
Hours	39.3	533.3	99.5	632.8
1999				
Days	0	61	50	111
Hours	0.0	435.0	151.2	586.2
2000				
Days	6	70	40	110
Hours	38.9	454.1	108.6	562.7

Multiple counts of individual whales

We developed a decision rule to avoid double-counting whales that were sighted in multiple areas within a year (range 1.0–7.2%, mean 3.8%, SE 0.8%). We gave priority to sightings in Glacier Bay over Sitka Sound and Frederick Sound, and to sightings in Sitka Sound over Frederick Sound. For example, if a whale was sighted in Glacier Bay and Sitka Sound or Frederick Sound, it was counted as occurring in Glacier Bay. If a whale was sighted in Sitka Sound and Frederick Sound, it was counted as occurring in Sitka Sound. This rule was used in multi-strata models.

Estimating abundance

Estimates of abundance were produced using four methods.

1. Minimum number of individually identified whales adjusted for survival

For each of the years 1994 to 2000, the number of new whales not previously identified was determined. The sum of those numbers is the number of unique whales observed during that time period. However, some of those whales have since died. We predicted the number of whales alive in the year 2000 by adjusting the observed numbers by an estimate of the population survival rate. Two values of survival were used: (1) an estimated survival value of humpback whales in the North Pacific of 0.96 (Mizroch *et al.*, 2004), and (2) an intermediate value of 0.98, between the estimate of 0.96 and the value of 1 for a population closed to mortality and emigration. The intermediate value was used because of model selection issues described below. Given that there were N_x new whales in year x , the number of those whales predicted to survive to the year 2000 is

$$N_{x,2000} = N_x \phi^{2000-x}. \quad (1)$$

Summing these predictions across all years produces the predicted number of whales alive in 2000. There is no variance estimate for this prediction.

2. Petersen estimators between two adjacent years

The Petersen estimator is used for mark–recapture experiments with two time periods, one for the release of marked animals and one for recapture. The number of releases is denoted by n_1 , and the number sampled for recaptures by n_2 , of which m_2 turn out to be marked. The Chapman form of the Petersen estimator (Seber, 1982, Chapter 3), namely

$$N^* = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1, \quad (2)$$

is approximately unbiased and has the variance estimator

$$\text{var}(N^*) = v^* = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}.$$

N^* is a traditional symbol of this estimator as found in the highly regarded text by Seber. N^* is used as a nearly unbiased estimator of N rather than a maximum likelihood.

The coefficient of variation (CV), a relative measure of uncertainty, is $CV^* = \sqrt{\text{var}(N^*)}/N^*$. A parametric bootstrap procedure (Efron & Tibshirani, 1993), with the hypergeometric distribution, provided 95% confidence intervals, using the percentile method.

Two approaches were used with the Petersen estimator. First, we pooled the data across areas and obtained a pooled estimate of abundance each year, ignoring geographical information. The rationale for pooling was to obtain larger sample and recapture sizes in order to increase precision. However, if there are consistent differences in capture probabilities among different areas, capture probability is said to be heterogeneous. The effect of this ‘area heterogeneity’ is an underestimate of abundance (Seber, 1982, Chapter 3).

Second, we stratified the data by the three areas, which in essence ignores the interchange of whales among areas. The smaller sample sizes by area generally result in greater uncertainty in estimators, both by individual area and their sum. However, the bias is generally less than that in the pooled approach, because heterogeneity in capture probabilities within areas is smaller than that between areas. When only emigration and/or mortality occurs between the two time periods (no immigration and/or recruitment), the estimator pertains to the time of marking. When immigration and/or recruitment also occurs, the estimator is biased upwards at the times of both marking and recapture. Without additional information, it is not possible to quantify the level of bias.

Because Frederick Sound was not sampled in 1999, it was not possible to obtain an overall estimate of abundance that year. Instead, marked releases from 1998 were related to recaptures in 2000.

3. Darroch estimators with movement

The Darroch estimator pertains to a population closed to mortality but stratified by area and allowing movement between areas: a closed, multi-strata approach. Like the Petersen estimator, it usually involves two time periods (Seber, 1982; Chapter 11; Quinn & Deriso, 1999; Chapter 10; Calambokidis *et al.*, 1997).

The closed-form estimators we used for migration, capture probability and abundance are provided here. Let $a = \{a_i\}$ be the vector of the number of marked releases at time 1 in region i , and $m = \{m_{i \rightarrow j}\}$ be the matrix of the corresponding number of marked recaptures at time 2 in area j . If ρ is the vector of the inverses of the capture probabilities $\{\rho_j = 1/p_j\}$, the maximum likelihood estimators of ρ and the movement matrix Θ are given by

$$\hat{\rho} = m^{-1}a \text{ and } \hat{\Theta} = D_a^{-1}mD_{\hat{\rho}}$$

(Quinn & Deriso, 1999, p. 412), in which D is a diagonal matrix of the elements of the corresponding vector. From the

estimated capture probabilities (\hat{p}_j) by area j , the general law of estimating abundance produces the estimators of abundance as $\hat{N}_j = n_j/\hat{p}_j$, where n_j is the number of animals examined for marks in the second time period in area j .

The Darroch approach has been generalized to three sampling occasions (Seber, 1982, Chapter 12), to any number of sampling occasions (Schwarz & Ganter, 1995), and to an open population subject to mortality (Seber, 1982, Chapter 11). The Hilborn approach used next is a more modern method accomplishing the same goal.

We applied the Darroch method to pairwise, adjacent years in a manner similar to that used for the Petersen approach. In 1996–97, our analysis produced the inadmissible estimate of capture probability for Glacier Bay of 57. We performed a numerical re-analysis with the constraint that capture probability should be no larger than 1, and used the resultant estimates of capture probability, migration, and abundance in place of the original Darroch estimates. This problem did not occur in other years or areas.

4. Hilborn estimators with movement

The Hilborn estimator pertains to a mark–recapture experiment across many years on a population open to mortality, stratified by area, and with movement between areas (Hilborn, 1990; Quinn & Deriso, 1999; Chapter 10; Calambokidis *et al.*, 1997). This approach is an integrated, open, multi-strata approach, similar to that of Brownie *et al.* (1993). For a given release group in a given year stratified by area, a model predicts the matrix of recaptures by area released and area recovered for the years of the experiment. Survival between years is implicit in this method and is denoted by ϕ . The Darroch estimator is a special case of the Hilborn, with two time periods and a closed population [$\phi = 1$]. The formula for the predicted number of marked whales in area j at time $t + 1$ from the number of marked whales $M_{i,t}$ in area i at time t is $M_{i \rightarrow j, t+1} = M_{i,t} \phi \theta_{i \rightarrow j}$, showing the combined processes of survival and movement. Summed over all areas i , the resulting formula $M_{j, t+1} = \sum_i M_{i \rightarrow j, t+1} = \sum_i M_{i,t} \phi \theta_{i \rightarrow j}$ becomes the number of marked whales $M_{j, t+1}$ in area j at time $t + 1$, which is used to continue the recursion process. The predicted number of marked recaptures from area i at time t to area j at time $t + 1$ is then found by multiplying by the capture probability, or $m_{i \rightarrow j, t+1} = M_{i \rightarrow j, t+1} p_j$. This prediction is then compared with the observed number of marked recaptures in a likelihood setting to estimate parameters for capture probability, movement, and possibly survival.

Estimators for migration, capture probability and abundance are obtained numerically by maximizing the likelihood, here assumed to be a product of Poisson distributions. By contrast, the similar Brownie *et al.* (1993) approach uses the multinomial distribution. Once capture probabilities have been estimated (\hat{p}_j) by area j , the general law of estimating abundance produces the estimators of abundance as $\hat{N}_j = n_j/\hat{p}_j$, where n_j is the number of animals examined for marks in the second time period in area j .

The Hilborn approach is a flexible model-building approach that allows migration to be constant or to vary over time. Our examination of marked recaptures revealed results that were similar across areas over time, so we did not find it worthwhile to investigate changes in migration over time. Different modelling scenarios allowed capture probabilities to be constant [$p(\cdot)$], to vary over time [$p(t)$], or to vary as a function of effort [$p(\text{eff})$ or $p(\text{nleff})$]. Model $p(\text{eff})$ assumes that capture probability is proportional to survey effort ($p \propto \text{effort}$). Model $p(\text{nleff})$ assumes that capture probability has a nonlinear, asymptotic relationship with survey effort ($p \propto 1 - \exp(-\text{effort})$). In addition, different scenarios looked at fixing survival at 1 (corresponding to a closed population [$\phi = 1$]), fixing it at some known value [say, $\phi = 0.96$, from Mizroch *et al.*, 2004; or the intermediate value of 0.98, as mentioned above], or estimating it directly [$\hat{\phi}$]. Capture probability for Frederick Sound in 1999 was fixed at 0, and marked recaptures that would have come from there or have been seen there then were treated as missing.

Model selection followed the procedures outlined in Burnham & Anderson (1998), including the use of the AICc (Akaike Information Criterion, corrected, p. 51) as a model comparison statistic: ‘Unless the sample size is large with respect to the number of estimated parameters, use of AICc is recommended [over AIC]’. Central to the AICc is an estimation of the overdispersion parameter c from a χ^2 goodness-of-fit statistic divided by the degrees of freedom, and the calculation of the difference Δ between a given model and the model with the lowest AICc value. For model selection we used the following guidelines developed by Burnham & Anderson (1998).

We might expect $c > 1$ with real data but would not expect c to exceed about 4 if model structure is acceptable and only overdispersion is affecting c ... Substantially larger values of c (say, 6–10) are usually caused partly by a model structure that is inadequate; that is, the fitted model does not actually represent all the explainable variation in the data. (p. 53)

For any model with $\Delta \leq 2$ there is no credible evidence that the model should be ruled out ... For a model with $2 \leq \Delta \leq 4$ there is weak evidence that the model is not the K-L [Kullback-Leibler] best model. If a model has $4 \leq \Delta \leq 7$ there is definite evidence that the model is not the K-L best model, and if $7 \leq \Delta \leq 10$, there is strong evidence that the model is not the K-L best model. Finally, if $\Delta > 10$, there is very strong evidence that the model is not the K-L best model. (p. 128)

We immediately rejected models with $\Delta > 7$. We further pared down models on grounds of biological realism (for example, we know that whales die each year; therefore, a model with no allowed deaths between years is unrealistic).

A parametric bootstrap procedure (Efron & Tibshirani, 1993) provided CVs, and 95% confidence intervals using the percentile method. Marked recaptures were replicated using the overdispersed Poisson distribution, using the predicted mark–recaptures and the estimated overdispersion \hat{c} from the best model. The additional uncertainty in capture sample sizes was accounted for by replicating capture sample sizes from the

binomial distribution, using estimated abundance and capture probability for each area and time.

We also made crude estimates of new whales entering the population (recruitment, immigration) and old whales leaving the population (death, permanent emigration). Recruitment is found from the equation $R_t = N_{t+1} - \phi N_t$ (recruits = abundance – survivors from the previous time). The number of deaths is found from $D_t = (1 - \phi)N_t$ (deaths = those that do not survive). Consequently, it is a tautology that $N_{t+1} = N_t + R_t - D_t$. These estimates are considered crude, because they tend to be highly variable (Seber, 1982).

RESULTS

Minimum count

There were 842 different whales sighted in the study areas in the 1994 to 2000 time period. New whales continued to be photographically ‘discovered’ throughout the study (Fig. 2). Our prediction of the number of those whales that survived to the year 2000 from equation (1) is 721 whales if $\phi = 0.96$, and 778 whales if $\phi = 0.98$.

Petersen estimates

The population estimates that resulted from the Petersen estimators are presented in Tables 2 and 3. The pooled estimates were relatively low (ranging from 407 to 728) but very precise (CV of 6%, Table 2). However, the pooling resulted in heterogeneity in capture probabilities among individuals, because Glacier Bay has much higher capture probabilities than Sitka Sound, which in turn usually has higher capture probabilities than Frederick Sound. Hence these are underestimates of abundance.

The stratified estimates were relatively high (ranging from 778 to 1336) with low precision (CVs above 20% in 4 of 5 years, Table 3). We know there is immigration and recruitment occurring in all areas; hence, the population is overestimated both at the time of marking and at the time of recapture (Seber, 1982, Chapter 3).

Darroch stratified estimate with movement

The data on the number of marks ‘released’ each year and the subsequent mark–recapture matrices of the release groups (see

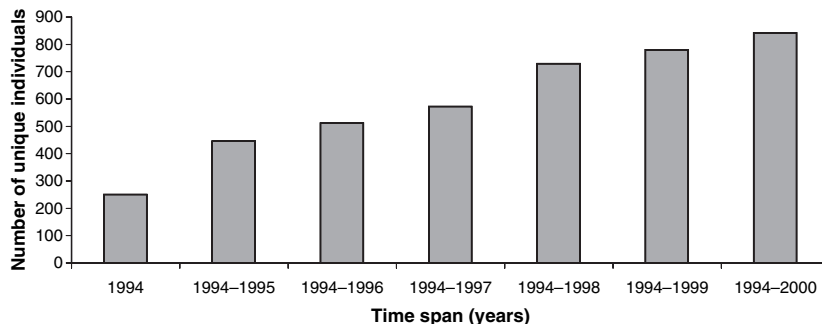


Figure 2 Discovery rate of ‘new’ whales in the period 1994 to 2000.

Table 2 Pooled Petersen estimates for Southeast Alaska humpback whales in the period 1994 to 2000.

Start year	End year	N*	CV* (%)	Lower CI	Upper CI
1994	1995	728	6	646	824
1995	1996	583	6	518	658
1996	1997	433	6	384	490
1997	1998	693	6	616	792
1998	1999	630	6	569	704
1999	2000	407	5	369	444

N*, Chapman estimator of abundance; CV*, coefficient of variation; CI, 95% confidence interval.

Table 3 Stratified Petersen estimates (summed over areas) for Southeast Alaska humpback whales in the period 1994 to 2000.

Start year	End year	N^	CV^ (%)	Lower CI	Upper CI
1994	1995	980	9	827	1159
1995	1996	1264	37	844	2248
1996	1997	778	30	534	1243
1997	1998	1271	28	899	2054
1998	2000	1336	21	984	2022

There were no data collected in Frederick Sound in 1999.

N^, abundance; CV^, coefficient of variation; CI, 95% confidence interval.

Appendix S1 in the Supplementary Material) are used for the Darroch and Hilborn estimators. The marked–recapture matrices for each release group are relatively similar, with most of the marked recaptures found in the same area as releases (as seen along the diagonal of the matrix).

The population estimates from the Darroch model (Table 4) ranged from 774 to 1194 whales. The Darroch method produced highly variable estimates of population parameters in some areas in some years as a result of low sample sizes. Migration rates computed with this model were the most variable parameter, ranging from 0 to 90% (not shown). CVs ranged from 0% to well over 100% (not shown). Capture probabilities were lowest in Frederick Sound and highest in Glacier Bay. As explained in the Methods, there was an inadmissible estimate of capture probability in 1996–97, so the results shown for that pair in Table 4 come from a constrained

Table 4 Darroch estimates for Southeast Alaska humpback whales in the period 1994 to 2000.

Start year	End year	Probability of capture			Abundance at time of recapture			
		FS	GB	SS	FS	GB	SS	Sum
1994	1995	0.40	0.79	0.28	393	69	312	774
1995	1996	0.05	0.84	0.32	851	84	182	1116
1996	1997	0.08	1.00	0.35	433	77	244	753
1997	1998	0.14	0.87	0.46	784	85	325	1194
1998	2000	0.07	0.74	0.36	837	112	239	1188

There were no data collected in Frederick Sound in 1999.
FS, Frederick Sound; GB, Glacier Bay; SS, Sitka Sound.

Table 5 Model fits for Hilborn estimators, based on the probability of capture $p()$ and survival ϕ .

Model	K	-ln L	\hat{c}	AICc	Δ
$p(t), \phi = 1$	23	264.2	1.41	582.0	0.0
$p(t), \phi = 0.98$	23	266.5	1.44	586.4	4.4
$p(t), \phi = 0.96$	23	269.1	1.48	591.7	9.7
$p(n\text{eff}), \phi = 1$	9	288.3	1.59	595.7	13.7
$p(n\text{eff}), \phi = 0.98$	9	289.0	1.61	597.1	15.1
$p(n\text{eff}), \phi = 0.96$	9	290.5	1.63	600.1	18.1
$p(\cdot), \phi = 1$	9	291.6	1.67	602.3	20.3
$p(\text{eff}), \phi = 1$	9	293.2	1.68	605.5	23.5
$p(\cdot), \phi = 0.96$	9	293.7	1.70	606.4	24.4
$p(\text{eff}), \phi = 0.96$	9	296.2	1.72	611.5	29.5

K, number of parameters; -ln L, log likelihood; \hat{c} , overdispersion; AICc, Akaike Information Criterion measuring model fit; Δ , difference between AICc and the lowest AICc. See Methods section for model definitions.

Darroch estimator (essentially obtained as a special case of the Hilborn estimator).

Hilborn estimate with movement

The data used in the Hilborn method are given in Appendix S1. The model comparison statistics (for example -ln L, AICc) for the Hilborn estimator are presented for 10 models in Table 5, chosen to represent a suite of choices for capture probability and survival. The estimates of overdispersion, \hat{c} , were all under 2 (Table 5), suggesting that overdispersion was not a problem. All attempts to estimate survival led to convergence at the boundary value of 1, suggesting that survival is not well determined by these data. The most parsimonious, best-fitting model and the model with maximum likelihood is $[p(t), \phi = 1]$, in which capture probability is a function of time for each area and survival is estimated at 1. The next best-fitting model $[p(t), \phi = 0.98]$ has a fixed survival of 0.98, which is biologically more realistic. For all the models, the estimate of the overdispersion parameter \hat{c} was less than 2, which does not eliminate any models from consider-

Table 6 Migration rates of whales between areas with 95% confidence intervals (in parentheses), from the best Hilborn model.

From area	Migration proportions (%)		
	To: FS	GB	SS
FS	74 (62, 79)	8 (6, 14)	18 (14, 27)
GB	12 (8, 18)	81 (70, 82)	7 (7, 16)
SS	14 (11, 22)	6 (5, 12)	80 (69, 83)

FS, Frederick Sound; GB, Glacier Bay; SS, Sitka Sound.

ation according to Burnham & Anderson’s (1998) standard, mentioned earlier.

We rejected the remaining models, which all had values of $\Delta > 7$, for which capture probabilities were modelled as constant over time, or as functions of sampling effort (from Table 1). This included the models with survival $\phi = 0.96$, suggesting that the current data are not in complete accord with the earlier data examined by Mizroch *et al.* (2004). Furthermore, there is good evidence that capture probabilities change from year to year, and that the changes cannot simply be related to sampling effort. The nonlinear effort model holds some promise for future use in that it fitted better than the linear effort model and the constant capture probability model (Table 1). We then rejected the best-fitting model, because the best-fitting model had an unrealistic survival ϕ of 1. Therefore, we selected the only remaining model $[p(t), \phi = 0.98]$ as our best model, in which capture probability is time-varying and survival is equal to 0.98. The excellent model fit of $[p(t), \phi = 1]$ suggests that estimators that assume closure to death (such as the Petersen and Darroch estimators above and the best-fitting Hilborn model) should produce similar parameter estimates to an open-population Hilborn model if no other problems arise.

Parameter estimates are given only for our selected best model $[p(t), \phi = 0.98]$. Migration rates were assumed to remain constant across all years. Many whales (74%, 80% and 81%, see Table 6) were seen in the same areas each year; however, there was consistent migration among areas. For example, more whales migrate from Glacier Bay to Frederick Sound (12%) than the other way round (8%). However, more whales migrate from Frederick Sound to Sitka Sound (18%) than vice versa (14%). The lowest migration rates occurred between Sitka Sound and Glacier Bay in both directions (6% and 7%). Put another way, we estimate that there is roughly a one in four or five chance that a whale in one area will be in another area the next year. The migration rates were estimated with high precision, as evidenced by the narrow confidence intervals in Table 6.

The population estimates from our best model are presented in Table 7a. The number of whales in Southeast Alaska was estimated to be 961 in 2000, and ranged from 712 to 1008 across all years. The probabilities of capture (Table 8) were highest for Glacier Bay (0.49–0.67), lowest for Frederick Sound (0.00–0.38), and in the mid range for Sitka Sound (0.19–0.35). Confidence intervals for abundance and probability of capture

Year	FS	GB	SS	Total
(a) Estimated abundance				
1995	418 (274, 696)	88 (59, 141)	248 (157, 383)	754 (580, 1070)
1996	484 (232, 938)	104 (69, 157)	264 (159, 427)	852 (565, 1286)
1997	259 (127, 422)	127 (82, 187)	326 (200, 455)	712 (513, 884)
1998	381 (220, 504)	151 (95, 222)	475 (301, 627)	1008 (757, 1129)
1999	NA	170 (102, 235)	419 (252, 547)	NA
2000	346 (157, 491)	169 (97, 229)	446 (243, 595)	961 (657, 1076)
(b) CV of estimated abundance (%)				
1995	24	22	25	15
1996	36	21	27	21
1997	36	23	21	14
1998	21	22	18	10
1998–99	NA	22	20	NA
2000	32	21	21	12
Average	30	22	22	12

There were no data collected in Frederick Sound in 1999. FS, Frederick Sound; GB, Glacier Bay; SS, Sitka Sound.

Table 8 Hilborn estimates of capture probabilities and 95% confidence intervals (in parentheses), using the model $p(t)$, $\phi = 0.98$ for Southeast Alaska humpback whales in the period 1994 to 2000.

Year	Probability of capture		
	FS	GB	SS
1995	0.38 (0.22, 0.55)	0.62 (0.38, 0.88)	0.35 (0.23, 0.52)
1996	0.09 (0.05, 0.16)	0.67 (0.45, 0.96)	0.22 (0.14, 0.34)
1997	0.14 (0.09, 0.23)	0.61 (0.40, 0.89)	0.26 (0.18, 0.38)
1998	0.29 (0.21, 0.45)	0.49 (0.33, 0.74)	0.32 (0.23, 0.46)
1999	0 (NA)	0.58 (0.40, 0.87)	0.22 (0.16, 0.33)
2000	0.16 (0.11, 0.29)	0.49 (0.34, 0.76)	0.19 (0.14, 0.30)

There were no data collected in Frederick Sound in 1999. FS, Frederick Sound; GB, Glacier Bay; SS, Sitka Sound.

were wider than those for migration, showing that it is easier to estimate migration than other parameters. The CVs for the total abundance in Table 7b are about twice as high as those for the pooled Petersen estimate and substantially lower than

Table 9 Crude estimates of recruitment and deaths, derived from the abundance estimates.

Year	Abundance	Recruitment	Deaths
1995	754	114	15
1996	852	-123	17
1997	712	310	14
1998	1008		
1998–99		-6	40
2000	961		
Sum		294	86
Average		59	17

Bold values are totals for the combined 2-year period 1998–99.

Table 7 (a) Hilborn estimates of abundance and 95% confidence intervals (in parentheses), and (b) coefficients of variation (CVs) using the model $p(t)$, $\phi = 0.98$ for Southeast Alaska humpback whales in the period 1994 to 2000.

those for the other estimates. An integrated model with explicit representation of migration and survival, which consequently should be less biased, balances the decrease in precision.

The crude estimates of recruitment are highly variable and even include negative values (Table 9), which often occurs in mark–recapture studies (Seber, 1982). The average recruitment is more precise, resulting in about 59 new recruits (or immigrants from other areas) per year, or 294 new whales from 1995 to 2000. The number of deaths is more consistent, resulting in about 17 deaths per year, or 86 deaths from 1995 to 2000. An important caveat is that these estimates of recruitment and death are highly variable. These values suggest that there has been a net increase of 42 whales per year, although the trend is not statistically significant (test of regression slope, $P = 0.20$).

Figure 3 presents a comparison of the closed Darroch and open Hilborn estimates when $\phi = 1$ (which becomes a closed model when there is no mortality). The estimates for both Glacier Bay and Sitka Sound from the Hilborn model are

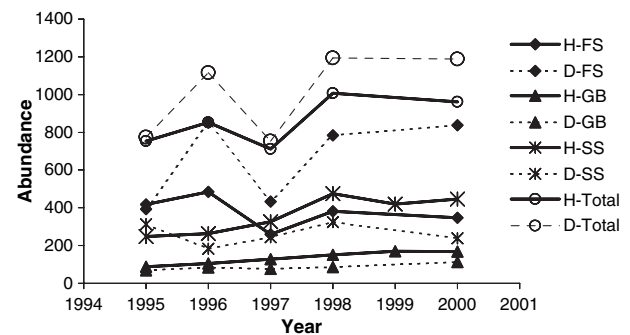


Figure 3 Comparison of abundance estimates from the open Hilborn (H) model with $\phi = 1$ and the closed Darroch (D) model by year and area. FS, Frederick Sound; GB, Glacier Bay; SS, Sitka Sound. There were no data collected in Frederick Sound in 1999.

higher than those from the Darroch model, owing to lower estimated capture probabilities for the most recent times. The Frederick Sound estimates, however, are more variable, reflecting the lack of data in 1999 and low capture probabilities. The estimated capture probabilities are lower for the Darroch model, resulting in a higher abundance estimate for Frederick Sound with the Darroch than with the Hilborn approach. The Hilborn method uses data on all subsequent recaptures from a release group in later years; the Darroch uses only the recaptures from the next year.

DISCUSSION

Our best estimate of whale abundance in northern Southeast Alaska in 2000 is 961 whales. This estimate comes from the Hilborn open, multi-strata approach with constant migration Θ over time, time-dependent capture probabilities $[p(t)]$ by area, and a fixed survival ϕ of 0.98. We believe that this estimate is the best because:

- (1) it uses more detailed information about mark–recaptures from different release groups from 1994 to 2000 than any of the other estimators;
- (2) the analysis is provided in an integrated environment, in which different sets of mark–recaptures share parameters such as migration and capture probabilities, as opposed to performing several pairwise analyses with conflicting parameter estimates;
- (3) the three strata (Frederick Sound, Glacier Bay, Sitka Sound) are utilized regularly by whales and encompass a large portion of the areas commonly used by whales in Southeast Alaska; and
- (4) after exercising various models for capture probability and survival, our best model was superior in terms of model selection criteria and biological realism.

We view our survival estimate of 0.98 to be plausible for humpback whales in Southeast Alaska, although it is higher than the recent survival rate estimate of 0.96 (Mizroch *et al.*, 2004) for this population. First, the 0.96 estimate was derived from a pooled Hawaiian data set that included whales from multiple feeding areas that may have different survival rates from those of Southeast Alaska. Second, use of a Hawaiian data set could result in a lower survival rate because whales in a mating and calving area could be at greater risk than those in feeding areas. Whales, although present in Hawaii, could experience nutritional stress from fasting and are known to engage in strenuous competitive mating activities that could be taxing or fatal (e.g. Pack *et al.*, 1998). Furthermore, predation risks in Hawaii might be higher as a result of the presence of large sharks that are known to attack humpbacks (Mazzuca *et al.*, 1998).

The first approach of determining a minimum estimate of the number of whales adjusted for survival produced estimates ranging from 721 whales, using the Mizroch *et al.* (2004) survival estimate of 0.96, to 778 whales, using the intermediate survival of 0.98. Therefore, our best estimate of 961 is about 200 whales higher than the minimum estimate, suggesting that there

are additional whales yet to be found. The Hilborn estimate improves upon the minimum estimate, in that information is utilized about later recaptures of newly discovered whales. Adopting this minimum approach as a best estimate would presume that there are no longer unmarked whales in Southeast Alaska remaining to be discovered, whereas in reality new whales are discovered each year.

The second approach used pooled and stratified Petersen estimators. As expected, the pooled estimates were relatively low but very precise. We suspect that they are underestimates because of the heterogeneity induced by pooling the data over areas with disparate capture probabilities. The stratified estimates were relatively high but had low precision. We suspect that they are overestimates because the combined occurrence of mortality, emigration, recruitment, and immigration in the Petersen experimental design, results in positive bias (Seber, 1982). The evidence for immigration/recruitment comes from the continued increase in the rate of discovery of new whales (Fig. 2), as opposed to the levelling out that would be expected for a closed population.

The third approach used pairwise annual data with the Darroch estimator in a closed, multi-strata framework. Estimates of migration capture probabilities, and abundance, were variable, especially for Frederick Sound. Low recapture sample sizes could create unintuitive effects on estimates from different areas and inadmissible estimates of probabilities. In one case, we even had to re-estimate parameters using constrained estimation because of these problems. The unrealistic assumption of closure (i.e. no mortality) would be expected to lead to overestimation of abundance. Indeed, the total population estimates were similar to the stratified Petersen estimates, which we considered overestimates.

Ten models were fitted within the integrated Hilborn framework, the fourth approach. Results indicated that there is insufficient information to determine survival unambiguously at the upper end of its range (say from 0.98 to 1). It was clear that probabilities of capture were time-dependent for each area, and that probabilities of capture were highest in Glacier Bay (around 0.5 to 0.7), next highest in Sitka Sound (around 0.2 to 0.4), and lowest in Frederick Sound (usually near 0.1). This result was intuitive, because most survey effort occurred in the areas of Glacier Bay and Sitka Sound. However, the relationship between probability of capture and survey effort was variable. For instance, the lowest amount of effort in Sitka Sound occurred in 1998, but the highest number of whales was found and the second highest capture probability was estimated. Therefore, models that incorporated survey effort or that assumed constant probability of capture over time performed poorly, with the exception of the nonlinear effort model. However, the fit of the nonlinear effort model was poorer than that of the time-varying capture probability models, suggesting that additional information about sighting efficiency is needed.

Among the three best Hilborn models, all of which had a time-dependent probability of capture, the estimates of abundance were fairly constant among years and not highly

variable. The estimated total abundance ranged from about 700 to 1100 across years, which is lower than the Darroch estimate. The lower estimates are first a result of incorporating survival, which would lower estimates. Second, there is a direct effect of different estimates of capture probabilities. Curiously, Hilborn estimates are higher than Darroch estimates for Frederick Sound, and lower for Glacier Bay and Sitka Sound, particularly in the most recent years. There does not seem to be an inherent reason for this difference: theoretically the Darroch and Hilborn approaches should produce comparable estimates when $\phi = 1$, but they do not (Fig. 3). We attribute the difference to sampling variability in the Darroch estimator that is resolved by using multiple release groups across multiple years. Therefore, the year 2000 estimate of 1188 is reduced to 1051 in the $[p(t), \phi = 1]$ model as a result of this sampling variability, and is further reduced to 961 in the $[p(t), \phi = 0.98]$ model by incorporating mortality.

Our estimate of 961 whales for Southeast Alaska in 2000 is considerably higher than previous estimates, which were calculated from data collected from the same areas. The previous estimates are at least a decade older, were derived from simpler models, and violated many of the assumptions of those models. The more complex, multi-strata models used in this report have improved upon some of the assumption violations in the simpler models. Moreover, it is apparent that the population of humpback whales in Southeast Alaska has increased in size.

This estimate is, however, for humpback whales that frequent only northern Southeast Alaska. Although our data were collected from three major areas where large concentrations of whales occur, this estimate does not reflect other areas where whales have been sighted. These unsurveyed areas are: (1) just off shore in the Gulf of Alaska, (2) the upper Lynn Canal, and (3) southern Southeast Alaska, in particular the west coast of Prince of Wales Island. Furthermore, Frederick Sound, an area where seasonally there are large numbers of whales, was poorly sampled. Therefore, the estimate of 961 whales in Southeast Alaska should be considered conservative.

The estimates of the overdispersion parameter c from the various models were around 1.5 (Table 5), not much larger than 1. This is an indication that overdispersion was fairly minor for our data and models. In contrast, Mizroch *et al.* (2004) estimated a much larger overdispersion parameter when using data only from Southeast Alaska. Therefore, our treatment of the data on a finer spatial scale resolved much of the heterogeneity issues found in that analysis. This result is not surprising, given that capture probabilities are highly variable in Frederick Sound and to some extent in the other two areas. Nevertheless, additional removal of heterogeneity may occur by an integrated analysis of Alaskan and Hawaiian sightings, as was done by Mizroch *et al.* (2004).

There are several improvements to methodology that could be attempted.

1. Bayesian methods. In our analysis, we attempted to use auxiliary information about survival ($\phi = 0.96$) (Mizroch *et al.*, 2004), but our data suggested that survival was higher.

We decided to use an intermediate value ($\phi = 0.98$), because the estimated survival of 1 was biologically unrealistic. In a Bayesian framework, both the point estimate and its uncertainty could be used as a prior distribution, avoiding the need for model selection related to survival. This approach would be particularly appropriate for this situation, because Mizroch *et al.*'s data sources came from 1979 to 1996, mostly prior to the time period of interest here, namely 1994 to 2000. Such an approach is likely to require a different likelihood framework, because the overdispersed Poisson distribution is not directly used in the estimation. Rather, the Poisson distribution is used for model fitting; the estimate of overdispersion \hat{c} is derived from a χ^2 statistic; and \hat{c} is used to adjust model selection criteria. It is not clear which distribution would be appropriate for the Bayesian approach. It would be worthwhile to explore different distributions, such as the Poisson and multinomial, to see if estimates are sensitive to the choice of distribution.

2. Time-dependent migration. We assumed that migration does not vary over time. It is possible to use a model with time-dependent migration, and such a model is available in the program MARK (White & Burnham, 1999). Our inspection of the mark-recapture data (Appendix S1) did not reveal gross violations of the constancy assumption, but formal analytical treatment would be useful. We do not believe that total abundance would be greatly altered, because it is affected more by survival, but there could be improvements in population estimates by area.

3. Temporary emigration. Because Southeast Alaskan humpback whales are mobile, it is possible that some of them spend time in areas that have not been studied. They could even be spending time in other areas of Southeast Alaska. New models are able to account for temporary emigration (e.g. Barker, 1997) and are available in the program MARK.

4. Include Hawaiian sightings. Mizroch *et al.* (2004) showed that heterogeneity (as evidenced by overdispersion) could be reduced by including sightings of whales in Hawaii along with Alaskan sightings. Although heterogeneity was not as large here ($\hat{c} = 1.4$) as it was in Mizroch *et al.*'s analysis (\hat{c} ranged from 1.9 to 6.1 for models involving whales from Southeast Alaska), improved estimates of abundance and particularly survival could be possible.

5. Joint modelling of recaptures, deaths, and opportunistic sightings. Some of the new methods available (Barker, 1997; Schwarz & Seber, 1999) analyse not only the mark-recapture data, but also opportunistic data on deaths of individual animals and on sightings of individual whales outside research surveys. If the latter two data sources could be compiled, then improved estimation of abundance, emigration from the study area, migration within the study area, survival, and recruitment might be possible.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Numbers of releases (marked), marked–recaptures, and recapture sample size (n) used in the Hilborn and Darroch analyses.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2008.01906>. (This link will take you to the article abstract).

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