DETERMINING ABUNDANCE AND STOCK STRUCTURE FOR A WIDESPREAD MIGRATORY ANIMAL: THE CASE OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN BRITISH COLUMBIA, CANADA

by

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Abstract

Developing appropriate management plans for species at risk requires information about their population structure and abundance. For most cetacean populations, few reliable population estimates are available and even fewer distributions have been mapped. Accurate abundance estimates can be determined from capture-recapture data if assumptions are met, however this can be difficult when the animal in question demonstrates both strong site fidelity and large-scale migrations, and different models can result in dramatically different results.

I explored these issues by examining a 15-year dataset (1992-2006) of photo-identifications of humpback whales (*Megaptera novaeangliae*) in British Columbia (BC), Canada. I used multiple capture-recapture models to compare how the definition of population and variation in effort affected estimates of population size, and I explored means to correct for these biases. I also considered stock structure by examining individual breeding ground destinations, movement, and localized site-fidelity within BC.

Across the six models considered, the BC humpback whale abundance in 2006 ranged between 1,428 and 3,856 individuals. The Lincoln-Petersen estimate (1,428-1,892) likely best described the number of humpback whales in BC during summer 2006. The effort-standardized Jolly-Seber model (1,970-2,331) is more representative of the larger population of humpback whales that uses or passes through BC over multiple years. Ultimately, selecting the best estimation model requires defining the 'population' of interest and accounting for spatial and temporal distribution of sampling effort.

British Columbia provides feeding habitat and a potential migratory corridor for whales that breed in the northeastern Pacific Ocean. Forty-four percent of the 1,986 humpback whales considered were sighted in BC in more than one year. Identifications were highest from May to October, with a peak in September, but humpback whales were present in BC in all months of

the year. Whales showed strong site fidelity with a median re-sighting distance of 75 km between years, and a maximum re-sighting distance that ranged from 0.41 km to 842 km. Matching rate within BC decreased as a function of north-south distance, though no clear north-south boundary could be established. Stock structure of humpback whales in British Columbia is complex and should be considered in managing this population.

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Dedication

To Susanne Pokotylo

For helping me find the courage to lose sight of the shore

Co-authorship Statement

This thesis was prepared using data collected by Fisheries and Oceans Canada's Cetacean Research Program under the design and direction of Dr. John K.B. Ford. All data analyses and manuscript preparation is the work of Andrea L. Rambeau. Editorial and supervisory assistance was provided by Dr. Andrew W. Trites.

1 General introduction: The history of humpback whales in the North Pacific and specifically, the population that resides in British Columbia, Canada.

1.1. INTRODUCTION

Over the past century, anthropogenic actions have resulted in many species suffering dramatic declines in population size (e.g., Ricciardi and Rasmussen 1999, Ceballos and Ehrlich 2002, Pounds *et al.* 2006). Whether or not a species can recover after severe depletion is a key question not only in terms of conservation efforts, but also in regards to how this process will affect ecosystem function over time (Ferson and Burgman 2000). Tracking population numbers over time can suggest whether the population is able to return to historic levels, or if the ecosystem has changed sufficiently to support a stable but different population density (Holling 1973). However, understanding the ecological factors involved in species' recovery first requires a comprehensive understanding of the population at stake, its life history parameters, and the factors that affect these (e.g., Hilborn and Mangel 1997, Krebs 2001).

For many cetacean populations, few reliable population estimates have been obtained, mostly due to the numerous logistical difficulties in censusing marine mammals (Thompson and Mayer 1996), as many species are fast-swimming, wide-ranging, and spend much of their time underwater (Mann 1999). My study aims to fill some of the critical knowledge gaps concerning the population of humpback whales (*Megaptera novaeangliae*) that utilize British Columbia (BC) waters for summer feeding.

1.2. BACKGROUND

Commercial whaling in the early 1900s depleted many of the world's cetacean populations, several of which are now listed as threatened or endangered (Perry *et al.* 1999). In BC, this

source of mortality ended in 1967 due to local stock depletion and a reduced market for whale oil because of increased commercial competition from vegetable oil (Gregr *et al.* 2000). After 41 years of hunting reprieve, there is some evidence of population growth in certain species (e.g., humpback whales, Calambokidis *et al.* 2008), while others are still viewed as being at severe risk of extinction (e.g., North Pacific right whales, COSEWIC 2004). Although hunting is no longer considered a threat, ship strikes and new marine activities associated with future oil and gas exploration may pose a risk to many whale species (e.g., Aplin and Elliott 2007).

Humpback whales are medium-sized baleen whales that display a cosmopolitan distribution, inhabiting all of the world's major ocean basins (Johnson and Wolman 1984). As with many whale species, they have a history of commercial and subsistence hunting throughout the world. Their pre-exploitation global population may have numbered over 120,000 whales (Johnson and Wolman 1984). Between 1904 and 1938, approximately 71,000 humpback whales were killed in the Southern Ocean alone (Chittleborough 1965, Perry *et al*. 1999). The International Whaling Commission (IWC) banned commercial hunting of humpback whales in the North Atlantic in 1955, in the Southern Hemisphere in 1964, and in the North Pacific in 1966 (Best 1993). By that time, global abundance was reduced by as much as 90-95% (Johnson and Wolman 1984).

Considerable uncertainty exists concerning the current global abundance estimate for humpback whales. Estimates for the 1980s and early 1990s suggest a minimum global abundance of roughly 38,000 individuals divided across the North Atlantic (10,600, Smith *et al*. 1999), Southern Hemisphere (20,000 south of 30°S, Butterworth *et al*. 1993) and North Pacific (6,000 – 8,000, Calambokidis *et al*. 1997). However, even considering only those stocks which have been assessed in some detail, summing up the 1990s estimates provided by the IWC (2007), produces conservative minimum global estimates that are closer to 54,000-75,000. Furthermore, many populations seem to be increasing, and the most recent (2004-2006)

abundance estimate for humpback whales in the North Pacific has risen considerably, to 18,302 individuals (Calambokidis *et al.* 2008).

Prior to the start of modern commercial whaling in 1905, the humpback whale population in the North Pacific was estimated as stable and near carrying capacity with 15,000 individuals (Rice 1978), although this estimate was based on whaling data which may have been inaccurate. During the span of industrial exploitation, from 1905 to 1965, about 28,000 humpback whales were killed in the eastern North Pacific (Rice 1978). This depleted the population to roughly 1,000 - 1,600 individuals (Gambell 1976, Rice 1978, Johnson and Wolman 1984), although the estimation methods used are also considered uncertain and of questionable reliability (Calambokidis and Barlow 2004).

There are two distinct populations recognized in Canada, the western North Atlantic population off the east coast, and the North Pacific population off the west (Baird 2003). The range of the Canadian North Pacific population spans inshore coastal inlets, continental shelf, and offshore waters off the west coast of British Columbia, from Washington to Alaska. As seen in other feeding areas, humpback whales in BC are distributed in unstable, highly-aggregated groups, which likely reflects both the patchy, mobile distribution and abundance of their prey (Whitehead and Carscadden 1985, Piatt *et al.* 1989, Payne *et al.* 1990), as well as the absence of predation (Clapham 1996). Those humpbacks sighted in Canada make up only part of the larger North Pacific population of humpback whales, though little is currently known about crossover with United States waters to the north (Alaska) or south (Washington).

Gregr *et al.* (2000) analyzed BC's coastal whaling records from 1908 to 1967, providing the following insights into the historical distribution and seasonality of humpback whales in this region. The humpback whales' coastal distribution (Johnson and Wolman 1984) made them the easiest targets for coastal whaling stations, and BC whaling stations killed at least 5,638 humpback whales between 1908 and 1967. Catches were very high in the early years (1905-

1913), peaking in 1911 with 1,022 animals killed. The majority of humpback whales were taken by whaling stations off the west side of Vancouver Island, but catch numbers dropped precipitously by 1917, after which humpback whales never again made a large contribution to total BC whaling catch. Distance between the nearest coastline and the point of capture increased significantly between 1948 and 1967, suggesting a disappearance from nearshore waters by the end of commercial whaling. Seasonally, the number of humpback whales killed increased from spring to summer, peaked in August, and then decreased into fall. BC catches dropped off earlier than subsequent depletions in California and western Alaska, which suggests that BC may have been home to a distinct "subpopulation" reaching to at least 54°N, though whether its range extended into southeastern Alaska remains unknown. Humpback whales also inhabited the Strait of Georgia and Barkley Sound (Webb 1988) though animals in these areas were extirpated early in the 1900s.

Sightings of humpback whales off BC were rare in the 1980s (Whitehead 1987), but in recent decades, they appear to be recovering. Williams and Thomas (2007) estimated a 2004-2005 abundance of 1,310 (755-2,280) humpback whales in BC's inshore waters, and the most recent combined estimate (2004-2005) for southeastern Alaska, BC, and Washington is 3,200-5,400 (Calambokidis *et al.* 2008). Humpback whales in Pacific Canadian waters have yet to repopulate all of their former BC range (Baird 2003) and as a result they are currently listed as threatened on Schedule 1 of Canada's Species at Risk Act (SARA) (Species at Risk 2003). No formal assessment of abundance has been done for BC's humpback whale population.

Although there are many feeding sites in the North Pacific, photo-identification studies and mitochondrial DNA analyses have shown that whales have strong feeding site fidelity (Darling and McSweeney 1985, Baker *et al.* 1986) and that there is little interchange between whales from different feeding grounds (Calambokidis *et al.* 1996). The American component of the North Pacific population has already been subdivided into separate "stocks" based on feeding

site fidelity (Angliss and Outlaw 2005). Only minor attempts have been made to match small collections of whales in BC (<93), with those seen in either Washington or Alaskan waters (Darling and McSweeney 1985, Calambokidis *et al.* 1996, Calambokidis *et al.* 1997) and very little interchange was observed. However, no formal attempt has been made to determine the current BC population stock structure, and a large-scale comparison of the existing catalogues for these regions has yet to be performed.

If the population of humpbacks using BC waters is indeed composed of smaller-scale "feeding stocks", as seen in other parts of the North Pacific, this would suggest that protecting and monitoring only certain known feeding areas may be insufficient for this population's long-term recovery. Understanding the fine-scale movement patterns of humpback whales within BC waters, and formally identifying whale critical habitat under the SARA, will aid in developing future management plans and may be integral to the recovery of cetaceans along the BC coast.

1.3. METHODOLOGY

Whale behaviour and distribution are often associated with complex coastal topography; as such, traditional census methods such as line-transect surveys become increasingly difficult for coastal cetacean species (Williams and Thomas 2007). Photo-identification of individual whales from natural markings is a widely used and unobtrusive means of performing 'capture-recapture' analyses, where photography is used as the method of tagging and re-sighting individuals. This technique is applied to humpback whales by examining the distinctive markings on the ventral surface of their tail flukes and the uniquely scalloped pattern of the trailing edge (Katona *et al.* 1979, Katona and Whitehead 1981). Statistical analysis of these 'tagging' programs can then be used to determine population abundance, seasonal distribution, migratory destinations, site fidelity, and other essential baseline biological data.

Photo-identification studies have been used in Canada and across the globe to document and analyze the abundance and distributions of cetacean populations (e.g., Darling 1984, Katona and Beard 1990); however, they rely on certain assumptions being met. One of the material challenges of applying traditional capture-recapture analyses is dealing with data that violate one or more of these assumptions. Most surveys are designed to focus on geographic regions that have been identified in previous years as 'hotspots' for humpback whales. This is done primarily for practical reasons, as it allows 'maximal sighting potential' while at sea, which is often limited by financial constraints. Unfortunately, it violates one of the primary assumptions of capture-recapture calculations - equal probability of capture. If not all areas are surveyed equally, whales that show strong site fidelity to the sampled areas have a higher chance of being captured than whales found elsewhere. This artificially inflates recaptures and thus negatively biases abundance estimates. Photo-ID studies are often more practical than other methods of estimating cetacean abundance, but are rarely sufficiently rigorous in meeting statistical assumptions. There is therefore a need to develop models that function under the financial and temporal limitations of most modern study efforts.

1.4. OVERVIEW

The goals of my thesis were to: 1) contrast capture-recapture techniques to select which method provides the most reasonable estimate of the number of humpback whales that utilize BC waters for summer feeding; 2) attempt to improve current population abundance models by reducing the biases introduced by heterogeneous non-random sampling effort; and 3) outline the stock structure (if any), localized site-fidelity, and small-scale movement patterns of humpback whales in BC.

My thesis is partitioned into two main chapters. Chapter 2 contrasts three models used to estimate the abundance of humpback whales in BC and explores ways to reduce the bias inherent

in many cetacean sampling programs. Chapter 3 evaluates humpback whale feeding site fidelity and distribution within BC in an attempt to define stock structure for the population in Pacific Canada. Each chapter has been written as a manuscript, with the intent of publication in the primary literature. As both chapters were based on the same population and dataset, there is by necessity some redundancy between them.

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2 Implications of model choice for estimating the abundance of cetaceans based on photographic identifications: comparing multiple population estimates for humpback whales in British Columbia, Canada[1]

2.1. INTRODUCTION

Estimating population abundance is integral to applied ecology, conservation biology, and wildlife management (Hilborn and Mangel 1997, Krebs 2001). Assessing population size is a key component of determining population status, monitoring abundance changes over time, and evaluating potential impacts of management actions (Williams *et al.* 2002). Furthermore, a substantial change in management actions may be required when a population shifts from one status level to another (e.g., threatened to endangered) and determining current population levels is vital. A wide variety of techniques exists for ascertaining population size and suitable methodology depends upon survey design.

Population enumeration methods fall into two major categories: complete counts and partial counts. Complete counts or censuses involve enumerating every individual within a sampling area. Although this method is rarely feasible for most animal populations, some examples are known, including wildebeest, buffalo, deer, and killer whales (e.g., Sinclair 1973, Stewart 1976, Kufeld *et al.* 1980, Ford *et al.* 1994). When it is not possible to detect all animals, the common alternative is to make partial counts. Partial counts estimate abundance by expanding the number of individuals observed by some detection probability. This involves developing either index methods or methods to correct for incomplete detectability. Index methods include both presence-absence surveys, and indicators of relative abundance such as harvest data (Elton and Nicholson 1942, Cattadori *et al.* 2003) or frequency of occurrence of tracks (Linhart and Knowlton 1975, Van Dyke *et al.* 1986), scat (Taylor *et al.* 1935, Bennett *et*

[1] A version of this chapter will be submitted for publication. Authors will include: A.L.Rambeau, J.K.B. Ford, A.W. Trites, and others to be determined. The Recovery of Humpback Whales (*Megaptera novaeangliae*) in British Columbia, Canada [working title].

al. 1940), or vocalizations (Harrington and Mech 1982). Methods that adjust for detectability include distance sampling (Burnham *et al.* 1980, Buckland *et al.* 2001, Buckland *et al.* 2004), mark-recapture (Seber 1982, Amstrup *et al.* 2005), sightability models (Samuel *et al.* 1987, Bodie *et al.* 1995), double-sampling (Thompson 1992, Bart and Earnst 2002), and line-intercept sampling (Kaiser 1983, Becker 1991, Thompson 1992). Which enumeration technique is applied depends on the biology of the species, details surrounding the particular population of interest, and practical issues such as time and funding constraints.

Determining the population size of cetaceans is logistically difficult, because the animals spend most of their time underwater, are often migratory, and frequently display aggregated distributions related to social or feeding behaviours. The two most common forms of cetacean estimation are distance sampling (Buckland *et al.* 2001, Buckland *et al.* 2004) and mark-recapture (Amstrup *et al.* 2005). Mark-recapture (or capture-recapture) is a widespread technique for estimating population abundance based on individual identifications. Studies involving cetaceans use photographs of unique individual markings such as dorsal fin variation in killer whales, fin whales, and dolphins, or tail flukes in humpback, blue, and sperm whales (e.g., Katona and Beard 1990, Wilson *et al.* 1999). The ratio of 'marked' to 'unmarked' animals is used to estimate detection probability and ultimately population size.

There have been many mark-recapture studies on humpback whales in the eastern North Pacific, though none has focused specifically on the population that summers in British Columbia (for a broad summary, see Table 2.1). Within mark-recapture methodology, a wide selection of models exists. These range from commonly applied models such as the Lincoln-Petersen (closed population) and the Jolly Seber (open) through to the more complex geographically-stratified models such as the Hilborn and the Darroch, or Pollock's Robust Design.

Regardless of which estimation technique is selected, producing accurate, unbiased abundance estimates depends on data meeting inherent statistical assumptions. Meeting such assumptions when animals occur over large areas, display strong site fidelity, and undergo large-scale migrations is a challenge, and any sampling design is likely to violate some of the required assumptions. Therefore, different assessment methods may produce dramatically different population estimates.

The following applies a variety of capture-recapture models to a long-term photo-identification dataset of humpback whales (*Megaptera novaeangliae*), collected by Fisheries and Oceans Canada (DFO) in British Columbia (BC), to explore potential biases in estimates of abundance that can result from the method used. I consider the pros and cons of each mark-recapture method, and ways in which some of the biases resulting from violating statistical assumptions can be offset. I also show that the definition of population can change depending on the method used. Understanding how sampling design may violate method assumptions and affect population estimates is critical when assessing widespread migratory species. Furthermore, my analysis provides the first comprehensive assessment of humpback whale abundance within the waters of British Columbia, and contributes to future cetacean management plans in this region.

Table 2.1. Previous mark-recapture abundance estimation studies of humpback whales in the eastern North Pacific.

Region	Time Period	Model(s) Used	Reference
southeastern Alaska	1979-1986	2 models: Bailey form of Petersen, Schnabel	(Baker *et al.* 1992)
North Pacific basin	1991-1993	3 models: Hilborn, Darroch, and Chapman form of Petersen	(Calambokidis *et al.* 1997)
southeastern Alaska	1994-2000	3 models: Chapman form of Petersen, Darroch, Hilborn	(Straley *et al.* 2002)
west coast of U.S. and Mexico (Washington, Oregon, California, Baja California)	1991-1997	3 models: Chapman form of Petersen, Pooled Petersen, and Jolly-Seber	(Calambokidis and Barlow 2004)
northern Washington coast	1989-2002	Chapman form of Petersen	(Calambokidis *et al.* 2004)
Shumagin Islands, Gulf of Alaska	1999-2002	Cormack-Jolly-Seber	(Witteveen *et al.* 2004)

2.2. METHODS

2.2.1. Humpback whale database

In 1984, DFO established a photo-identification program to develop a catalogue of individual humpback whales sighted in BC waters, similar to what was developed for killer whales in this region (Ford *et al.* 1994). Photographs were compiled by three general methods: 1) opportunistically collected photographs contributed by individuals and external research groups (1984-2006), 2) photographs collected by DFO during multi-purpose/multi-species cetacean surveys (2002-2006), and 3) humpback-targeted DFO photo-ID surveys (2004-2005).

The resulting photographic database consisted of 8,900 records of humpback whale sightings in BC between 1984 and 2006. As effort in the early years was modest and scattered, I removed data collected between 1984 and 1991 (34 records), and only considered records from 1992 onwards. Humpback whales are migratory, and although individuals can be seen in BC in all months of the year, most whales spend the winter months in tropical waters, and are only in BC to feed during the summer. For my analyses, I therefore further restricted data to those for

the months of May to October (8,653 records), during which both sampling effort and whale identifications were highest.

Survey design was neither random nor uniform in either its geographical coverage or invested temporal effort, both of which increased exponentially over the 15 years of surveying (Figs. 2.1 and 2.2). This was partly because survey effort was often focused primarily in regions that had demonstrated high whale density during previous surveys, or had been identified as humpback "hotspots" from commercial whaling records. Budget considerations and availability of ship time also allowed for more intensive sampling in later years. Photographs were collected primarily in an opportunistic fashion up until 2002, after which dedicated cetacean surveys were conducted. Although survey track-lines and sighting logs were available for 2002 onward, to make use of the entire dataset, I developed a rough proxy for effort by tallying the number of days that photographs were taken per year. Although such an index does not account for hours spent searching per day, nor for effort invested in 'whale-free' regions, a reasonable relative index of overall 'effort days' annually is achieved.

2.2.2. Photo-identification analyses

Individual humpback whales were identified using a standardized method for analyzing the natural markings found on the ventral surface of the whales' flukes (Katona *et al.* 1979). The technique of photographic comparison is well documented (e.g., Katona and Beard 1990, Calambokidis and Barlow 2004). In the early years of the program, black

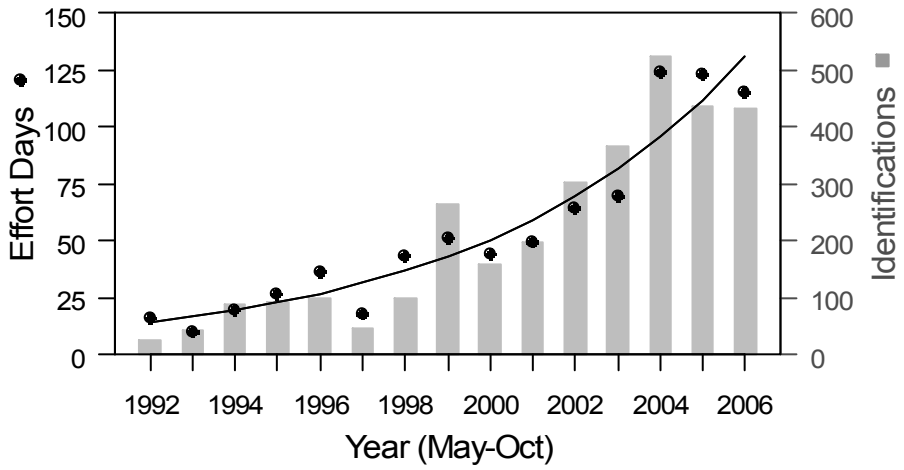

Figure 2.1. Exponential increase in number of days identification photographs were taken and number of humpback whales identified in British Columbia, Canada from 1992 to 2006. Effort days (points) are the number of days an ID photograph was taken between May and October that year. Identifications (grey bars) represent the total number of unique individual humpback whales photographed in British Columbia between May and October that year. An exponential regression was fit to the effort days' data to show how it increased over 15 years ($Effort$=12.5e$^{0.08years}$)

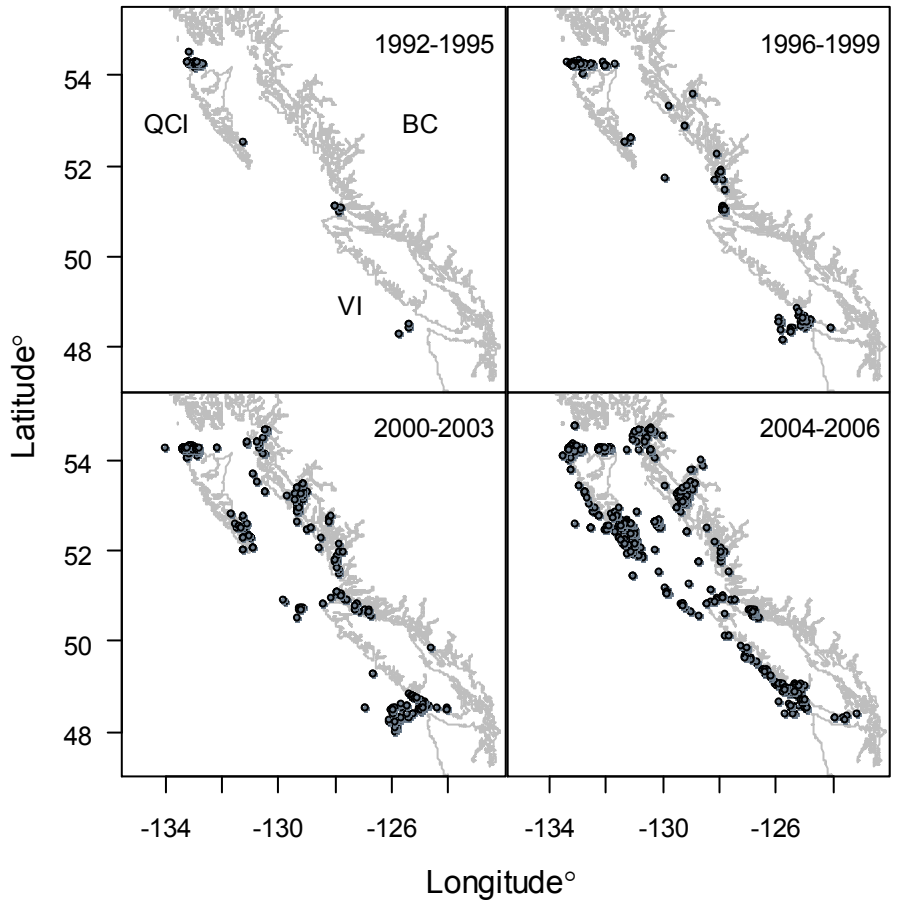

Figure 2.2. Locations of photo-identified humpback whales, showing variation in spatial effort from 1992 to 2006 in British Columbia (BC), Canada. Years are pooled for ease of viewing only. QCI = Queen Charlotte Islands, VI = Vancouver Island

and white film was used to photograph flukes, and contact sheets were examined with a loupe for inter-matches within a season. The best quality full-fluke photographs were printed and added to the catalogue. In later years, digital photographs were taken and matched on-screen with a digitally scanned catalogue. All photographs were inter-matched across years by two independent and experienced matchers, thereby confirming all identified whales and reducing the chance that identifications were missed.

2.2.3. Model assumptions for estimating cetacean abundance

Capture-recapture models can produce accurate abundance estimates, but only if model assumptions are satisfied. This requires careful selection of the model, as different models can produce highly different results. Here, I consider three models, and variations thereof. To be valid and provide unbiased parameters, the first two models, the Lincoln-Petersen and the Jolly-Seber, both require the following assumptions to be met (Seber 1982):

1. All animals have equal probability of capture.
2. All animals have equal probability of surviving from one sample to the next.
3. Marks are not lost or overlooked, and do not affect an animal's catchability.

In photo-identification studies, the assumption of equal catchability is potentially violated due to heterogeneity in the ease of identifying individuals, as distinctively marked animals have a lower chance of being misidentified. If this occurs, the effect on the model is an artificial increase to the abundance estimate (Friday *et al.* 2008). However, due to the strict double-matching protocol applied, I consider the overall effects of this bias to be negligible for my study.

Lincoln-Petersen Model. The Lincoln-Petersen method is a closed two-sample model that assumes the population does not change during the sampling interval (no birth, death, immigration, or emigration). I used the Chapman form of the Lincoln-Petersen estimator (Seber 1982) to predict population abundance across British Columbia between adjacent survey years in

2005 and 2006 (model Petersen 05/06). I followed this with a parametric bootstrap procedure based on a hypergeometric distribution to reduce bias and to determine 95% confidence intervals. Since the degree of geographic closure cannot always be rigorously quantified for some populations, I also considered an open model – the Jolly-Seber.

Jolly-Seber Model. Unlike the Lincoln-Petersen model, the Jolly-Seber is an open model (incorporates birth, death, immigration, and emigration into its estimates), allowing the population to change over time. In addition to the aforementioned three assumptions, the Jolly-Seber further assumes that sampling time is negligible in relation to the intervals between samples. This is because if sampling times are extensive, animals captured near the end of the sampling period have to survive less time to the next sampling period than animals that were captured near the beginning, and the Jolly-Seber is unable to take this change in survival rates into consideration (Amstrup *et al.* 2005). Sampling times in the humpback whale dataset generally extended over the length of the summer, which is a long sampling period compared to many capture-recapture studies. However, given the long lifespan of whales (humpback whale, >48 years, Chittleborough 1965), the effects of this violation are assumed to be minor, and Jolly-Seber models are frequently used in estimating cetacean populations (e.g., Calambokidis and Barlow 2004, Witteveen *et al.* 2004).

Using a traditional Jolly-Seber model (Seber 1982), mean and 95% credible intervals for the 2006 population size, population growth rate and survival were estimated using Sampling Importance Resampling (SIR) assuming a Poisson likelihood. A multivariate *t*-distribution (LearnBayes package for R statistical software, R Core Development Team 2006) was used as the sampling distribution, and posterior distributions were generated from 100,000 resamples of the initial 1,000,000 samples. Survival rate was constrained to $\leq$ 1.0, and "growth rate" represented net population change (which did not separate out immigration and emigration).

Accumulation Model. The third model I examined, an accumulation model, is a completely separate technique most often used to estimate species richness and diversity. However, adjustments can be made to this model to make it applicable for estimating a species' population size (Krebs 1999). In order for accumulation models to be valid, the following assumptions must be met:

1. Sampling methods must be the same for all samples taken.
2. All samples must come from the same habitat.
3. All individuals within the population are randomly and evenly dispersed.

Accumulation models take into account that the capture rate for unmarked whales will decrease as the number of marked whales increases. The rate of accumulation of "new" whales decreases exponentially until all whales in the population have been captured, producing an estimate of total population size.

Eggert *et al*. (2003) found that the following exponential accumulation curve delivered the most reliable estimates of population size:

$$E(x) = a(1 - e^{bx}) \qquad \text{Equation 2.1}$$

Where, x is the total number of samples (whale sightings) over time, $E(x)$ is the cumulative number of unique individuals found in x sightings, a is the function's asymptote and therefore the estimated population size, and b determines the rate at which the discovery of unique individuals declines as total sample size increases. Mean and 95% credible intervals for a and b were calculated from posterior distributions obtained assuming a normal likelihood and uniform priors. Estimates of the posterior densities were obtained from 100,000 samples using the Metropolis-Hastings algorithm available in the MCMCpack library for R 2.3.1.

2.2.4. Modifications made to the models

In the Petersen 05/06 model, 14 years of historical information was discarded. However, since humpback whales have high longevity and low adult mortality, these earlier data might reasonably be incorporated, and thus better describe the long-term population usage of this area. I therefore performed another Lincoln-Petersen estimate (henceforth referred to as Petersen 92-05/06), but modified it by pooling the first 14 years of data. All whales seen before 2006 thereby made up the 'marked' group, and re-captures comprised all whales marked between 1992 and 2005 that were also seen in 2006. A second pooled calculation was performed using only data from 2002-2005 against 2006 (Petersen 02-05/06).

I also recognized that spatial and temporal effort varied through time. I therefore modified the Jolly-Seber model to account for some of the bias introduced by both temporal and geographic increases in effort. Although the traditional Jolly-Seber evaluates population estimates every year, parameter estimates are based on the maximum likelihood of annual capture probability, which is positively biased with increased time spent searching. To correct for this, I standardized capture probabilities in my modified Jolly-Seber by assuming a constant per unit effort probability of capture, and multiplying this by an effort proxy. The effort proxy was calculated as days spent photographing annually.

Accumulation models are used when communities are sampled with different intensities or success, as well as when different sample sizes are taken (Hilt *et al.* 2006). Thus, differences in sampling effort can be accounted for in population estimates (Bellemain *et al.* 2005) and no modifications were needed for the accumulation model.

2.3. RESULTS

The final dataset consisted of 807 sampling effort days over 15 years (1992-2006), and contained 4,683 photo-identifications of 1,779 individual whales. The 2006 abundance estimates presented below display a range of 1,428 to 3,856 humpback whales, a more than two-fold difference.

Lincoln-Petersen Estimates. The Chapman-modified Lincoln-Petersen estimate for 2005/2006 (Petersen 05/06) was 1,660 whales (95% CI; 1,428-1,892). Pooling data taken between 1992 and 2005 (Petersen 92-05/06), resulted in a large increase in the 2006 estimate to 2,659 whales (2,457-2,861). Pooling only data from 2002-2005 (Petersen 02-05/06), yielded an intermediate 2006 value of 2,115 whales (1,942-2,288). Note that none of the confidence limits of these estimates overlaps (Fig. 2.3).

Jolly-Seber Estimates. The posterior mean 2006 abundance estimate predicted by the SIR Jolly-Seber model was 2,739 individuals (95% credibility set; 2,496-2,965), with a survival rate of 98.6 (97.0-99.9) and a growth rate of 1.15 (1.13-1.16). After correcting for variation in temporal effort, these estimates decreased to 2,145 whales (95% credibility set; 1,970-2,331), with a survival rate of 97.6 (96.0-99.2) and a growth rate of 1.04 (1.03-1.05) (Fig. 2.3).

Accumulation Model Estimates. The accumulation model predicts that as the number of samples increases, the component of the population that is marked will increase until it reaches a theoretical limit where all whales (except new recruits) are marked. This limit (the asymptote a) represents the posterior mean estimated population size, and was 3,346 individuals (95% credibility set; 2,954-3,856) (Fig. 2.3).

2.4. DISCUSSION

Selecting an appropriate model for evaluating species abundance is complicated by the nature of the available data and the complexity of the population. It is not always possible to meet the

necessary statistical assumptions given inevitable logistical restrictions in how sampling programs are conducted. Assessing species that are migratory, widespread, and have home ranges that potentially extend outside the range of a study area may further obscure the appropriate method that should be used to estimate abundance. For many cetacean species, the ability to sample the entirety of their distribution is simply not feasible. Random sampling is often impractical as many species show highly aggregated and clumped distributions associated with feeding patterns or social structure. Yet, focusing sampling on high-density regions may bias capture probabilities in species that show strong site fidelity. Management of species is quite often regional in nature, and therefore the population in question might be more of a political designation than a biological one. Furthermore, funding may vary from year to year, affecting the possible distribution of survey effort. All of these issues are of serious concern for cetacean researchers and managers.

2.4.1. Effects of spatial and temporal variation in effort on abundance estimates

Many cetacean surveys are somewhat opportunistic in nature, as time and money are limited. Systematic coverage of large coastal areas limits the potential time available to photograph the animals once they are located, and is often cost-prohibitive. In some instances, sampling (photographing) may be purely opportunistic. In others, vessels travel primarily to whale 'hotspots', which are frequently determined based on historical knowledge (such as whaling data) and previous survey experiences.

Focused sampling on 'hotspots', or areas of high whale density, contributes to potential bias in population estimates. Humpback whales show strong site fidelity to summer feeding grounds (Craig and Herman 1997). Because of this, it is safe to assume that uniform mixing of the population does not occur; however, mark-recapture models such as the Lincoln-Petersen and the Jolly-Seber assume that every animal has the same probability of capture (Seber 1982).

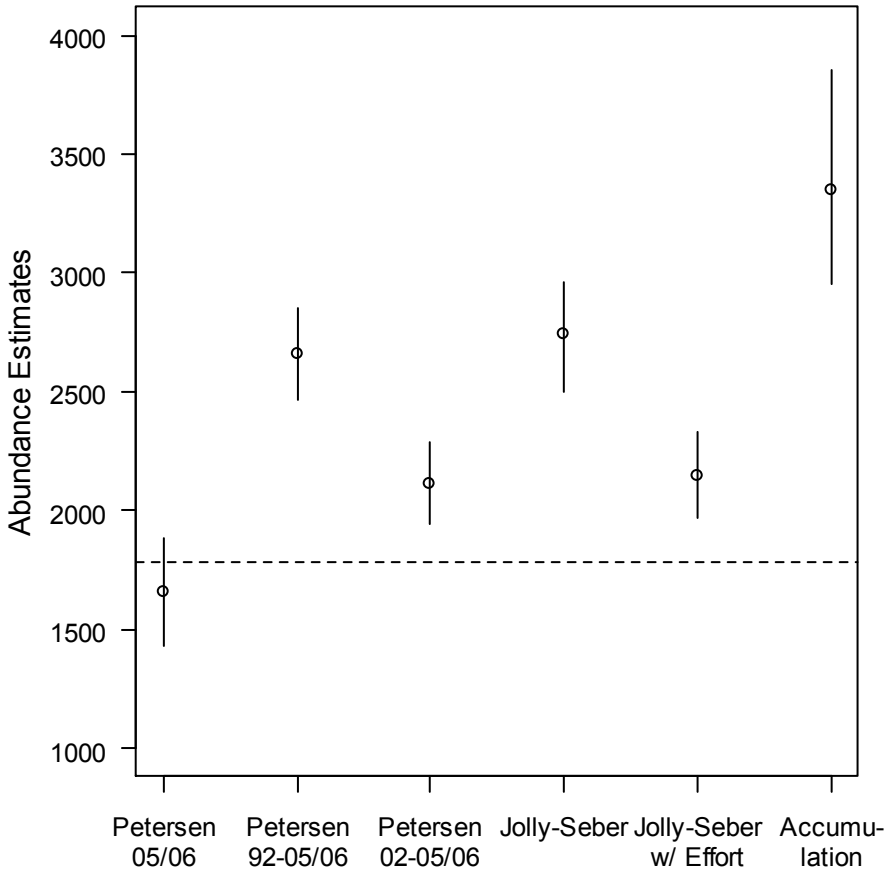

Figure 2.3. Abundance estimates derived from six models, for humpback whale abundance in British Columbia, Canada in 2006. The horizontal line represents the number of individual humpback whales in the DFO catalogue (1992-2006). Values are means and 95% confidence interval for the three Petersen models, posterior means and 95% credibility sets for the Jolly-Seber and accumulation models. Note that the confidence intervals are calculated assuming that the models' assumptions are fully met. Precision appears high because of the large sample sizes, but the true confidence intervals are likely much wider than are those represented here for all but the accumulation model.

Selective sampling of certain locations means that whales with strong site fidelity to the sampled areas have a higher probability of capture than whales found elsewhere. This results in artificially inflated recaptures and thus negatively biases abundance estimates. Conversely, whales that show fidelity to areas that are not sampled have zero capture probability, which negatively biases abundance estimates and also violates the base assumption of mark-recapture models.

For surveys that span numerous years, changes in funding may also lead to changes in available survey time. An increase in temporal effort can produce a correlated increase in the number of 'new captures' per year, which makes it appear as though the population was growing

at a higher rate than it likely was. The artificially inflated growth rate then leads to a larger population estimate than what the model would have predicted otherwise.

2.4.2. Selecting the appropriate model

As expected, the three models I explored produced a range of abundance estimates, due to the different assumptions and methods associated with each model. The DFO catalogue of humpback whales in BC between 1992 and 2006 consists of 1,779 individual whales, which I used as a baseline to evaluate the various estimated abundances. Some of these whales would have died during this time interval. However, the total number of whales in the catalogue represents only the marked population, and unmarked whales continue to be sighted at a high rate. Therefore assuming the effects of mortality are small, the true abundance might be reasonably expected to be higher than 1,779 humpback whales.

2.4.3. Open versus closed models

The first model I chose to examine, the Chapman-modified Lincoln-Petersen, is a closed, two-sample model, and thus assumes demographic and geographic population closure. Across the one-year time interval considered in these estimates, demographic processes can reasonably be considered negligible because humpback whales are long-lived (at least 48 years, Chittleborough 1965), have high adult survival rates (93-97% in the Gulf of Maine, Buckland 1990, Barlow and Clapham 1997, 94.3-99.5% in the Central North Pacific, Mizroch *et al.* 2004), and calves are generally excluded from photo-identification analyses. Meeting the assumption of geographic closure is somewhat more questionable. Humpback whales migrate to low-latitude breeding grounds in the winter (Chittleborough 1965, Baker *et al.* 1986, Katona and Beard 1990) and, therefore, most whales leave the BC study area between summer sampling periods. However, it is likely that a large percentage of these whales return to the sampling region the following summer, given the high fidelity humpback whales show to feeding sites. Closed models may

therefore still be capable of providing realistic estimates over short time frames, and have been used to estimate humpback whale abundance off the west coast of the US (Calambokidis and Barlow 2004, Calambokidis *et al.* 2004) and in southeastern Alaska (Straley *et al.* 2002).

The other mark-recapture model I examined, the Jolly-Seber, is an open model. The benefit of the Jolly-Seber model is that it allows estimation of survival and apparent population growth, allowing the population to change over time, and it is a better descriptor for migrating populations over longer time frames. The concern in using the Jolly-Seber is that time-catchability interaction has a greater effect on models with multiple recapture sessions, and bias due to such an effect will be multiplied (Seber 1982). Witteveen *et al.* (2004) used the Cormack-Jolly-Seber to estimate abundance of humpback whales in the Shumagin Islands (Gulf of Alaska). The fact that this population was determined to be a demographically and genetically segregated feeding population may have helped reduce the degree of variation in catchability. Even so, Witteveen *et al.* (2004) recommended that future models allow for variable re-sighting probability and migration.

Although I explored other models, I have not presented the details here. Of the other models I considered, I found those that geographically stratify a population (Darroch 1961, Hilborn 1990) were a potentially good option because they estimate sub-populations that move between areas and are sampled at different times. Calambokidis *et al.* (1997) used a Darroch model to estimate humpback whale abundance on North Pacific breeding grounds, but found it to be less accurate on the more complex summer feeding grounds, due to heterogeneous capture probabilities and geographic sampling bias. They also considered the Hilborn (1990) model for feeding ground estimates, but could not calculate abundance estimates in areas where capture probability was zero, and in the end concluded that abundance estimates based solely on the breeding grounds were superior. In order to make use of stratified models in BC, survey strata

must be designed in advance, so that sampling areas are representative, effort is comparable between sampling occasions, and sufficient sample sizes are collected.

I also considered and tested Pollock's robust design (Pollock 1982), which incorporates both Lincoln-Petersen and Jolly-Seber models, and which I believe shows high promise for future application to geographically stratified populations such as those in British Columbia. Unfortunately, the complexity of Pollock's robust design, which potentially allows it to better capture uncertainty, also requires a more strict survey design than the existing data collection methods allowed for in post-hoc analysis. Sub-division of the dataset into smaller sampling sessions (months) frequently resulted in capture probabilities of zero. This prevented calculation of abundance estimates across many of the sub-samples, and preliminary results therefore proved unrealistically low.

2.4.4. Defining the population of interest

The Petersen 05/06 abundance estimate is the lowest of all the estimates and falls below the value of catalogued individuals (Fig. 2.3). Temporal and spatial effort was reasonably consistent between 2005 and 2006 (Fig. 2.1) and roughly the same "hotspots" were targeted between the two years. Heterogeneity in capture probabilities might still account for some degree of negative bias, however if we ignore for the moment questions of bias, the Petersen 05/06 estimate may still be plausible depending on the definition of 'population' used.

For management purposes, there may be a substantial difference between assigned abundance estimates depending on how the population of interest is defined. The term 'population of BC humpback whales' might be interpreted in multiple ways. It could for example refer to the number of 'resident-type' humpback whales that regularly return to BC waters as their primary feeding ground. Alternatively, it might be the number present at any point in time, or over the course of a particular summer season. Finally, it could refer to the

much larger pool of North Pacific humpback whales, which might potentially transit through the region, and may or may not be present from year to year.

2.4.5. Offsetting common violations and putting the numbers in context

I applied the pooled Lincoln-Petersen method as a means to incorporate all information available in the dataset. Pooling the 14 years also allows for more equally distributed spatial coverage in the first sample, making it more spatially comparable to the broad surveying of 2006. In using only the data from the last two years of the study (Petersen 05/06), I excluded sightings of 1,024 marked whales. However, adding this information back in via pooling increased the population estimate by almost 1,000 whales (Fig. 2.3 – Petersen 92-05/06). The pooled value might better represent the larger population of whales that have used BC waters over the entire 15 years. It would overestimate the 'annual population' by violating the assumption of demographic closure, but it is potentially more accurate at representing BC's importance as humpback whale summer habitat. The intermediate model (Fig. 2.3 – Petersen 02-05/06) pooled 2002-2005 and acted as a compromise between the various violations. It reduced the timeline so that the value might better represent a 2006 estimate while still supplying good spatial coverage and incorporating historical information.

As in the Petersen model, I wanted to correct the Jolly-Seber model estimates for the large increase in effort. To force the model's growth rate to approximate the population growth rate, and not include a 'discovery rate', I standardized my model by temporal effort. This resulted in a reduction of the 2006 Jolly-Seber estimate by almost 600 whales. The high survival rates predicted were only slightly affected by the effort standardization (96.0-99.2 with effort, 97.0-99.9 without) and are fairly consistent with estimates made by previous studies (85-102% in SE Alaska, Straley 1994, 94.3-99.5% for Central North Pacific, Mizroch *et al.* 2004).

In their study of humpback whales in the Gulf of Maine, Barlow and Clapham (1997) estimated a population growth rate of 6.5% per year, which is less than half of that predicted by my original Jolly-Seber model (increase of 13-15%). Reducing the effect of the 'discovery rate' by incorporating an effort proxy appears to significantly increase the accuracy of my population growth rate estimate, reducing it to 3.4-5.4%, and explaining the large difference in resultant abundance estimates. The effort-standardized model is also much closer to the most recent estimates for the North Pacific humpback population annual rate of increase, which range from 4.9 to 6.8%, depending on the method used and the timeline considered (Calambokidis *et al.* 2008).

Finally, I evaluated the accumulation model because it considers effort, does not require equal sample sizes, and does not assume that sampling time is negligible. As a result, the biases that violate and generate error in the Lincoln-Petersen and Jolly-Seber models' estimates were eliminated (Krebs 1999). My estimate of the 2006 population under the accumulation model was the highest of all the estimates. This discrepancy may be explained by the models' different assumptions and the population they described. Accumulation assumes that all members of the sampled population are randomly and evenly distributed (Krebs 1999). As previously discussed, humpback whales show high feeding site fidelity, which gives them a non-random, clumped distribution (Fig. 2.2).

Fager (1972) used computer simulations to test the effects of clumped populations on accumulation estimates, and found that they overestimated the size of the populations. In fact, the more clumped a population, the higher the overestimation that occurs (Fager 1972). Given that humpback whales characteristically display aggregated distributions, applying an accumulation model to the data will predictably overestimate the true population size, which begins to explain the large contrast against the much lower estimates of the effort-standardized Jolly-Seber and the Petersen 02-05/06 models. Furthermore, if British Columbia provides not

only feeding habitat, but also a migratory corridor to other populations such as southeastern Alaska, it may be important habitat for a much larger pool of whales.

The accumulation model considers this larger number because it accounts for the 'accumulation' of individuals over time. Thus, it may be correct to say that there were on the order of 1500 to 2000 whales within the BC borders in the summer of 2006, but considered over a longer time period, it is likely that a much larger population of humpback whales used this region. The biggest problem with applying the accumulation model over a long period is that it does not account for new recruits. If the population truly increased at 3.4-5.4% per year over the 15 years, the addition of 'new' unmarked whales will confound the rate at which discovery of unique individuals declines (parameter *b* in Equation 2.1). This will also overinflate the abundance estimate. Therefore, the accumulation model is not a good choice for estimating actual abundance; however, it does provide a maximum cap, or upper bound, within which the other estimates can be framed.

2.4.6. Conclusions and recommendations

Cetaceans are difficult animals to study because they spend most of their lives underwater, often live in remote or hard to survey areas, and can have home ranges that span oceans. Overcoming these obstacles is necessary to develop management plans and recovery strategies for endangered cetacean species. One way to accurately assess widely migrating marine species such as cetaceans is to undertake coordinated ocean-basin wide surveys. More challenging is assessing the portion of a wide-ranging population that resides within smaller areas.

No model is perfect, and all have advantages and disadvantages. The two most important factors in selecting a model are clarity concerning the research question being asked and a detailed understanding of the population being considered. The Lincoln-Petersen is best applied in determining the immediate population of a closed discrete area. If there is movement into and

out of the area, or the population changes over time, the Jolly-Seber is a better model to apply. However, each of these two models requires variations in spatial and temporal variation in sampling effort to be considered. Accumulation models are not affected by heterogeneous effort, but will overestimate spatially aggregated or increasing populations. The conservative approach may thus mean sacrificing precision and using multiple models to provide a range of values. Providing estimates that both under- and over-estimate the expected population should yield confidence that the true value correctly lies within these bounds, while still providing information that is useful for management decisions.

I applied models that both under- and over-estimate abundance to the population of humpback whales in BC to consider the actual numerical effect that sampling effort and model selection has on estimates of abundance. BC's complex and extensive coastline, in combination with the migratory nature of these animals, makes efficient unbiased surveying of this particular management population challenging. The most recent (2004-2006) population estimate for humpback whales in the North Pacific was 18,302 individuals, with a combined estimate for southeastern Alaska, BC, and Washington of 3,200-5,400 (Calambokidis *et al.* 2008). Williams and Thomas (2007) used line transects to estimate a 2004-2005 abundance of 1,310 (755-2,280) humpback whales in BC's inshore waters. Looking across all the models I examined provides a rough range for the 2006 population of humpback whales in BC alone at somewhere between 1,428 and 3,856 individuals. Given that the lower bound is expected to be negatively biased, and that the upper is certainly an overestimate, the best estimate likely lies within these bounds. Furthermore, since there may be much variation in the definition of population applied, considering the results of a range of models may better reflect the variation in the number of individuals that both feed in and/or transit through BC over time. An extended analysis that includes inter-matching of BC whales to southeastern Alaska and Washington/Oregon is a necessary next step in understanding the dynamics of this particular population. Until then, my

analysis provides the first comprehensive assessment of humpback whales within the waters of British Columbia.

2.5. SUMMARY

Establishing accurate means to estimate fundamental baseline parameters such as population abundance, under financial and time constraints that are common in cetacean research, is essential to any conservation management plan for cetaceans. As a case study to explore the effect of model selection on abundance estimates, I used three estimation models (the Lincoln-Petersen method, the Jolly-Seber method, and an accumulation model) as well as two modifications thereof, to analyze capture-recapture data of humpback whales (*Megaptera novaeangliae*) in British Columbian waters from 1992-2006. The six models provided an abundance range of 1,428 to 3,856 individuals in 2006. I also compared how the definition of population, and variation in spatial and temporal effort, affected estimates of population size. The Lincoln-Petersen provided the lowest estimate (1,428-1,892) and likely best described the numbers present in British Columbia in 2006. The effort-standardized Jolly-Seber model (1,970-2,331) was likely more representative of the larger pool of humpback whales that made use of these waters over the 15-year period. Spatial and temporal effort had a large influence on the individual estimates and must be accounted for when estimating the abundance of similar populations. In general, it can be difficult to obtain regional abundance estimates using photo-identification of whales because the sampling designs used to collect the mark-recapture data often fail to meet the assumptions of the estimation models. As such, the best approach is to conservatively use both upper and lower bounds as the best estimates of population size when model assumptions cannot be met.

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3 Site-fidelity and small-scale movement of humpback whales in British Columbia, Canada[2]

3.1. INTRODUCTION

Previous studies have examined the current population structure of humpback whales (*Megaptera novaeangliae*) in various parts of the North Pacific Ocean (Rice 1978, Baker *et al.* 1986, Calambokidis *et al.* 1996, Calambokidis *et al.* 1997, Calambokidis *et al.* 2000, Calambokidis *et al.* 2001, Calambokidis *et al.* 2008). They have also investigated interchange, site fidelity, and seasonal migration patterns. However, no study has yet examined the complex small-scale structure and site fidelity of those that feed in coastal waters off British Columbia (BC), Canada. Strong site fidelity to feeding grounds has been observed in humpback whales in both the North Atlantic (Clapham *et al.* 1993) and the North Pacific (Darling and McSweeney 1985, Baker *et al.* 1986, Craig and Herman 1997, Mizroch *et al.* 2004). This is thought to be a learned maternally-directed behaviour, with whales returning to the feeding areas they first visited as calves with their mothers (Martin *et al.* 1984, Baker *et al.* 1987, Clapham and Mayo 1987).

Baker *et al*. (1986) proposed that humpback whales in the eastern and central North Pacific comprise a single "structured stock", composed of geographically-isolated 'feeding herds' that merge on one or more breeding grounds. Commercial whaling data in the North Pacific suggest that humpback whales in BC may comprise such a 'feeding herd', as whales in BC were depleted earlier than whales in California and western Alaska (Gregr *et al.* 2000). A photo-identification analysis by Calambokidis *et al.* (1996) further supports this idea, suggesting that a demographic boundary exists between the humpback whales that feed in Washington, Oregon,

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[2] A version of this chapter will be submitted for publication. Authors will include: A.L. Rambeau, J.K.B. Ford, A.W. Trites, and others to be determined.. Site-fidelity and small-scale movement of humpback whales (*Megaptera novaeangliaea*) in British Columbia, Canada.

and California, and those that feed further to the north in BC and Alaska. Furthermore, only low rates of interchange have been observed between BC and southeastern Alaska (Darling and McSweeney 1985, Calambokidis *et al.* 2008).

Humpback whales migrate tens of thousands of kilometers between high-latitude temperate feeding grounds and low-latitude tropical breeding areas (Chittleborough 1965, Baker *et al.* 1986, Katona and Beard 1990). The United States (US) recognizes three humpback whale stocks (relatively separate populations) within the US Exclusive Economic Zone of the North Pacific (Calambokidis *et al.* 1997, Baker *et al.* 1998, Angliss and Outlaw 2005). The eastern North Pacific stock consists of whales that feed along the coast of California to southern BC in the summer and fall, and which migrate to coastal Central America and Mexico in the winter and spring (Steiger *et al.* 1991, Calambokidis *et al.* 1996, Angliss and Outlaw 2005). The central North Pacific stock spends summer and fall in northern BC, southeastern Alaska, and Prince William Sound west to Unimak Pass, and migrates to the Hawaiian Islands for the winter and spring (Baker *et al.* 1990, Perry *et al.* 1990, Calambokidis *et al.* 1997, Calambokidis *et al.* 2001, Angliss and Outlaw 2005). The western North Pacific stock includes winter populations in Japan, which likely migrate to the Bering Sea and Aleutian Islands in the summer and fall (Nishiwaki 1966).

Cetacean population structure is most commonly examined using genetic analyses (Amos *et al.* 1993, Baker *et al.* 1994, O'Corry-Crowe *et al.* 1997), while patterns of movement and site fidelity are perhaps best-analyzed using satellite tracking (Mate *et al.* 1998, Heide-Jørgensen *et al.* 2003, Elwen *et al.* 2006). Genetic samples have been collected as part of the SPLASH study (Structure of Populations, Levels of Abundance, and Status of Humpbacks) (Calambokidis *et al.* 2008), and analysis of these, once complete, may help to elucidate genetic relationships within BC and throughout the North Pacific. However, long-term photo-identification studies can still reveal much about population structure and movement patterns (Calambokidis *et al.* 1997,

Whitehead 2001). Whales that feed in BC during the summer months have been re-sighted in Hawaii, Mexico, and Japan during the winter (Darling and McSweeney 1985, Calambokidis *et al.* 2001) and for management purposes, Pacific Canada's humpback whale population is currently treated as a single population (Baird 2003). There is some question, however, as to whether BC is best described as a single distinct feeding population, as two distinct populations, or as extensions of the central, and eastern North Pacific stocks, although it is not known where and to what degree this 'stock' division might occur.

Support for a north-south divide within BC could be obtained by photo-identification data in three ways: 1) If within BC, there was a tendency for northern whales to show greater fidelity to the north than the south, and vice versa, 2) if whales in the north and south of BC displayed different breeding ground preferences, and 3) if there was a high degree of interchange observed between northern BC and southeastern Alaska, and between southern BC and northern Washington, with lesser interchange within BC. With this in mind, I analyzed the inter-annual site-fidelity, within BC population structure, and breeding-ground preference for humpback whales identified across British Columbia, to evaluate whether a north-south divide exists within the BC population.

3.2. METHODS

I quantified the site-fidelity and small-scale movement of the British Columbia population of humpback whales, by analyzing 16 years of records (1992-2007) that were part of a photographic-identification database collected by Fisheries and Oceans Canada (DFO). I used this long-term dataset to examine seasonality, maximum distances between sightings (site-fidelity), and small-scale movement within BC waters, as well as connections to breeding ground destinations. This information was then used to assess whether this 'population' is best described

as a separate singular 'feeding population', as two distinct populations, or as two populations that belong to the central and eastern North Pacific stocks to the north and south, respectively.

3.2.1. Photo-identification dataset

Photo-identification is a common technique for identifying individual animals and is often used in mark-recapture (i.e., capture-recapture) studies (Katona and Beard 1990, Wilson *et al.* 1999). However, it can also be used to glean information about distribution, stock structure, and movement (Whitehead 2001). For humpback whales, photo-identification involves a standardized method for analyzing the uniquely identifiable natural markings found on the ventral surface of the whales' flukes (Katona *et al.* 1979). Between 1992 and 2007, humpback whale identification photographs were taken on 1,006 days throughout BC coastal waters. The 9,749 photographically recorded sightings of humpback whales resulted in identifying 1,986 unique individuals. Geographic locations of 1,929 of these whales (8,782 sightings) are shown in Fig. 3.1. Methods for photographic comparison are as documented by others (Katona and Beard 1990, Calambokidis and Barlow 2004).

3.2.2. Seasonality

I determined the primary months for humpback whale presence in BC by considering the total number of individual whale identifications made on a monthly basis over the 16-year study period. Any one whale might be counted multiple times if it was observed in either more than one month of the same year (e.g., if it was seen in May and September of 2005) or in the same month in multiple years (e.g., June in 1997 and 2003). Multiple sightings in the same month of any given year were not included. Effort days were calculated as the total number of days that a photographic identification was made each month, summed over the 16 years.

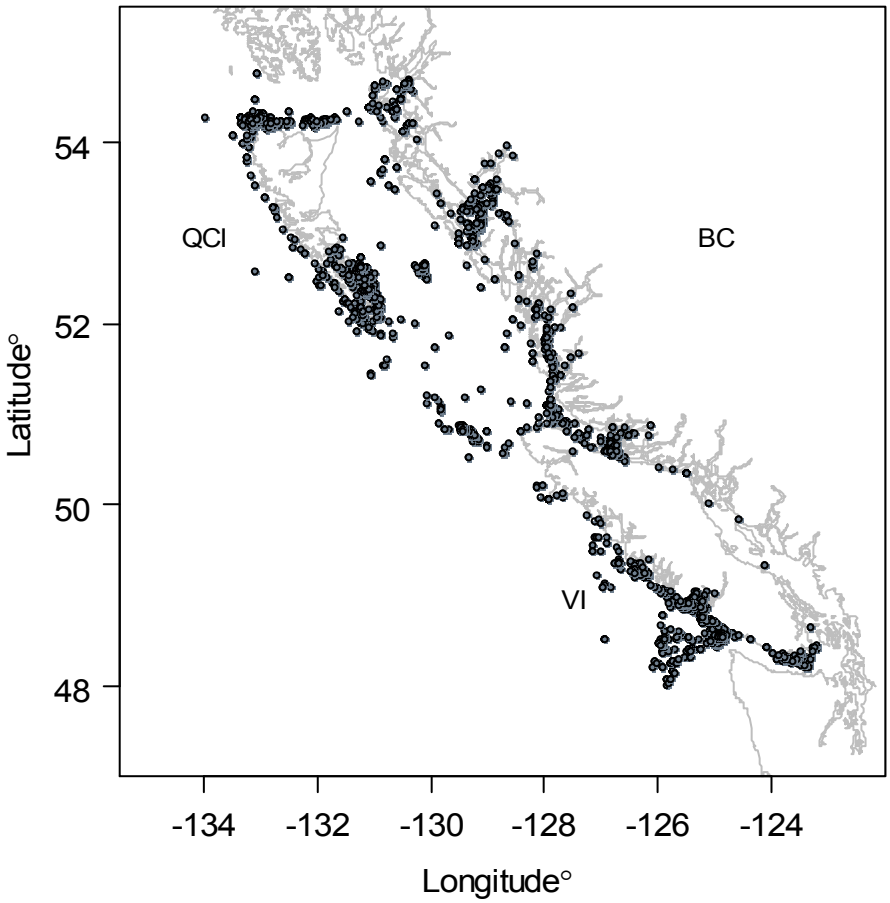

Figure 3.1. Geographic location of humpback whales photographically-identified in British Columbia (BC), Canada between 1992 and 2007. VI = Vancouver Island, QCI = Queen Charlotte Islands

3.2.3. Inter-annual site-fidelity

I determined the inter-annual patterns of summer feeding site fidelity in BC by only considering whales that were identified between May and October in more than one year, and for which GPS sighting coordinates were available (585 whales). Only the first sighting location was assigned (2,448 sightings) for whales that were seen on more than one occasion in any one year. I then calculated the Great Circle Distance (minimum distance between any two points on the surface of the Earth) (Bowditch 1995) between all possible year pairings of each individual whale. Distances did not represent swimming distances, but instead maximum distance was the furthest distance between any two re-sightings of an individual whale across the 16 years of data. Mean values were the mean distance across all years. I also fit negative exponential and inverse power functions to the frequency distribution as suggested by Stevick *et al.* (2006).

3.2.4. Within BC population structure

I examined intra-BC population structure using all daily sighting locations within and across years for every whale between May and October 1992-2007. Nominal locations were assigned for whales without exact GPS locations, but with sufficient descriptions to identify the region within BC. All whale sightings fell within Pacific Canada's international borders, and none was recorded north of 55° or south of 48°. The resulting dataset consisted of 1,880 whales and 8,497 sightings.

I examined how much small-scale mixing and movement there was north-south within the province by setting all whales observed north of 54° as a northern 'sub-population'. I then compared these to all whales south of 54°, by observing if and how matching rate fell away to the south in 0.5° latitudinal bins. For comparison, I also determined the proportion of whales re-sighted north of 54° in multiple years.

3.2.5. Breeding ground migrations

Only the 853 whales photographed in BC in 2004 and 2005 have yet been inter-matched to breeding grounds, and of these, 217 matches were made. I used all BC sightings (1992-2007) of these 217 individuals to determine whether whales seen in different BC sub-areas travel to different breeding areas. I first grouped the sighted whales into five subcategories: Queen Charlotte Islands (QCI), North Coast (North), Central Coast (Central), northwest Vancouver Island (NWVI), and southwest Vancouver Island (SWVI) (Fig. 3.2) . I then cross-referenced these whales against whales that were photo-identified in North Pacific breeding grounds during the international SPLASH project in 2004-2006 (Calambokidis *et al.* 2008). The breeding grounds considered in the SPLASH study were: the Philippines, Japan, Hawaii (HI), Central America (Cent Am), and Mexico (Mainland (MX-Main), Baja California (MX-Baja), Revillagigedo (MX-Rev)).

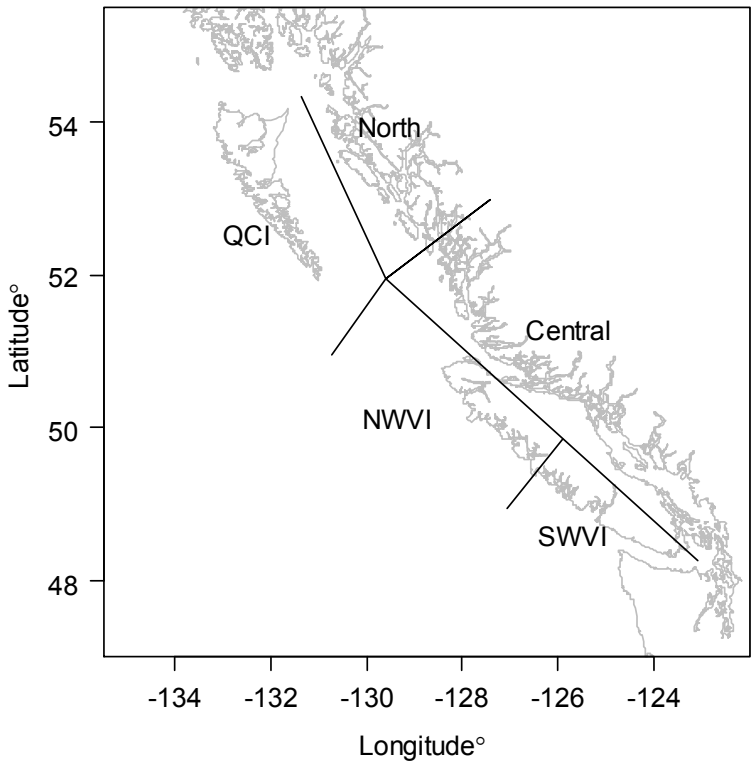

Figure 3.2. Division of BC into five subcategories for breakdown of breeding ground destinations. Queen Charlotte Islands (QCI), North Coast (North), Central Coast (Central), northwest Vancouver Island (NWVI), and southwest Vancouver Island (SWVI)

3.3. RESULTS

3.3.1. Sighting frequency

Of the 1,986 humpback whales identified in BC, 1,114 (56.1%) were observed only in a single year, and another 644 (32.4%) were observed in 2 or 3 years. The remaining 228 whales (11.5%) were seen over 4 to 10 years (Fig. 3.3).

3.3.2. Seasonality

Humpback whales were observed in BC predominantly during the months of May to October (Fig. 3.4). There was a minimal presence throughout the winter as well, with at least one whale seen in every month; however, effort during the winter months was also limited. Identification per unit effort may appear artificially high in December and January, since the effort proxy applied considered only days that photographs were successfully taken, and could not factor in number of days in a month where effort was invested but where no whales were observed.

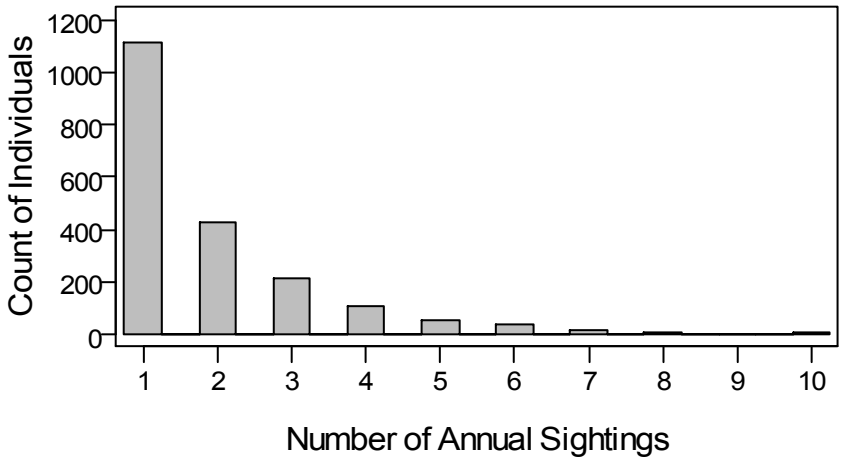

Figure 3.3. Number of years that individual humpback whales were identified between 1992 and 2007, out of 1,986 uniquely photo-identified individuals in British Columbia, Canada. Each animal was included in only one sighting category (e.g., animals seen in four different years were recorded exclusively in the four category).

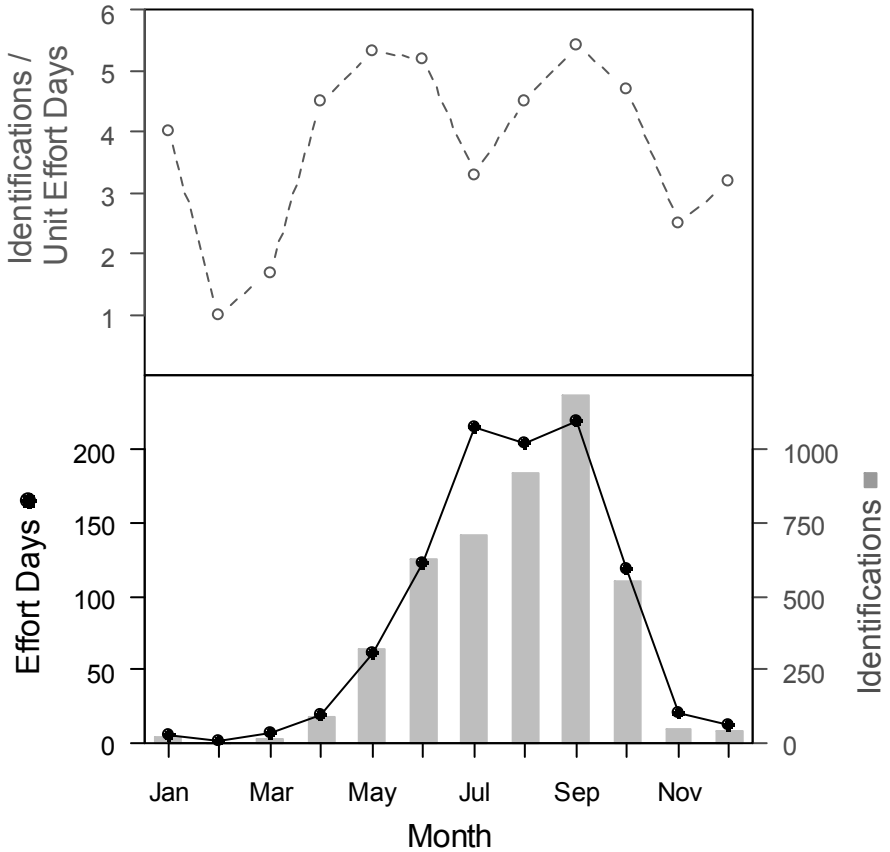

Figure 3.4. Seasonal representation of number of days where an identification photograph was taken (effort days), cumulative number of individual humpback whale identifications obtained in British Columbia, Canada between 1992 and 2007 in each month, and identifications per unit effort.

3.3.3. Inter-annual site-fidelity

Of the 585 whales considered, 25% (149) were seen a maximum distance of less than 25km from where they were seen in a previous year, with 57% (331) seen within 100km (Fig. 3.5). The minimum distance observed between inter-annual sightings was 0.41km, with 41 whales (7%) seen within <5 km from previous sightings. Only thirteen whales (2%) were identified at maximum distances >600km, with the single maximum distance at 842km (the distance between southwest Vancouver Island and the northwest corner of the Queen Charlotte Islands). Frequency (F) of re-sighting distances (D) was best modeled by an inverse power function ($F=4086.55D^{-1.0185}$, SSE=2510.6), which was better than the negative exponential ($F=200.41e^{-0.015D}$, SSE=4217.5) at describing over-dispersed data. There was no seasonal pattern associated with whales seen on the tail end of the re-sighting distribution (i.e., for whales re-sighted at distances of > 500km).

3.3.4. Within BC population structure

Inter-matching of whales within BC decreased as a function of increasing north-south distance (Fig. 3.6). Thirty-two percent of the whales seen above 54° were re-sighted above 54° in later years, yet matching rate decreased linearly, the further away from 54° that the comparison was made ($y = -2.6x + 35, R^2 = 0.836, F = 50.849, df = (1,10), p < 0.001$).

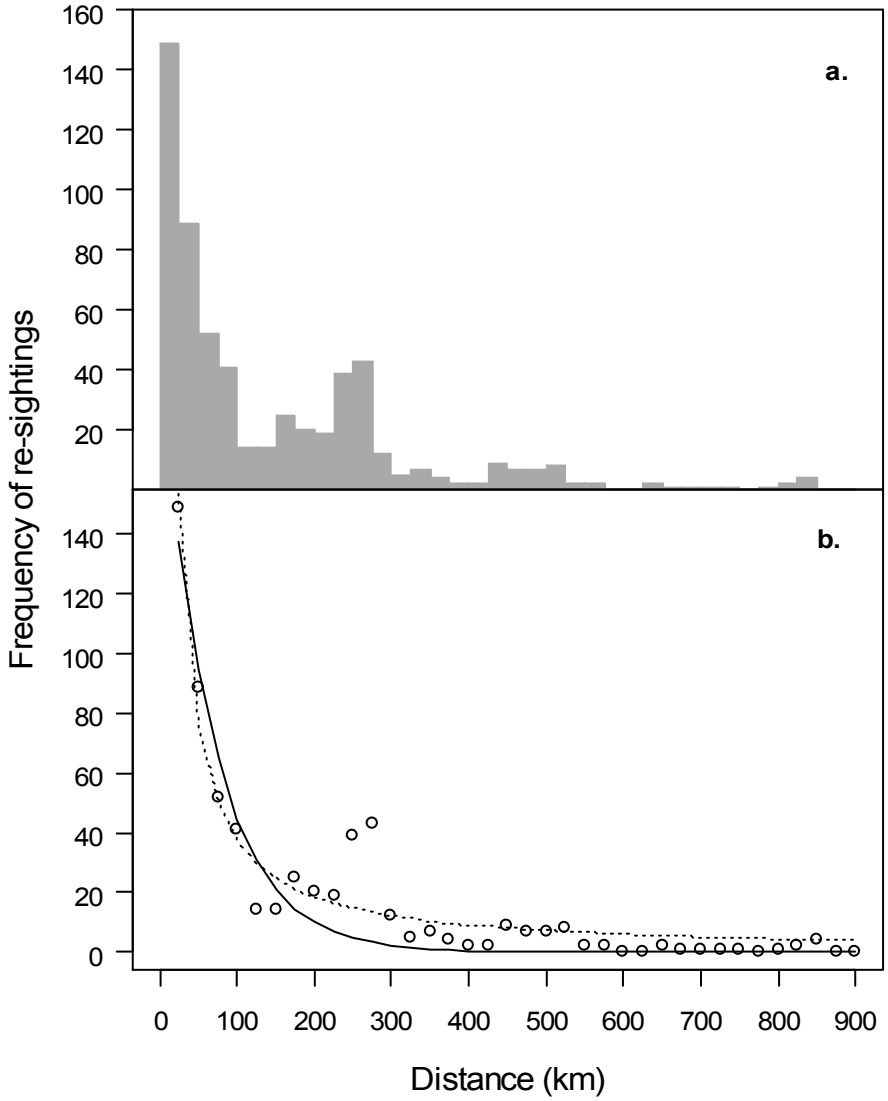

Figure 3.5. Maximum distances recorded between inter-annual re-sightings of humpback whales in British Columbia, Canada between 1992 and 2007. a. Frequency of maximum distances observed between all possible pairings of inter-annual sightings for 585 humpback whales photo-identified in British Columbia between 1992 and 2007. b. The inverse power function (dotted line) showed a better fit to the frequency distribution (F=4086.55$D^{-1.0185}$, SSE=2510.6), than did the negative exponential (solid line) (F=200.41$e^{-0.015D}$, SSE=4217.5) SSE = Error Sum of Squares.

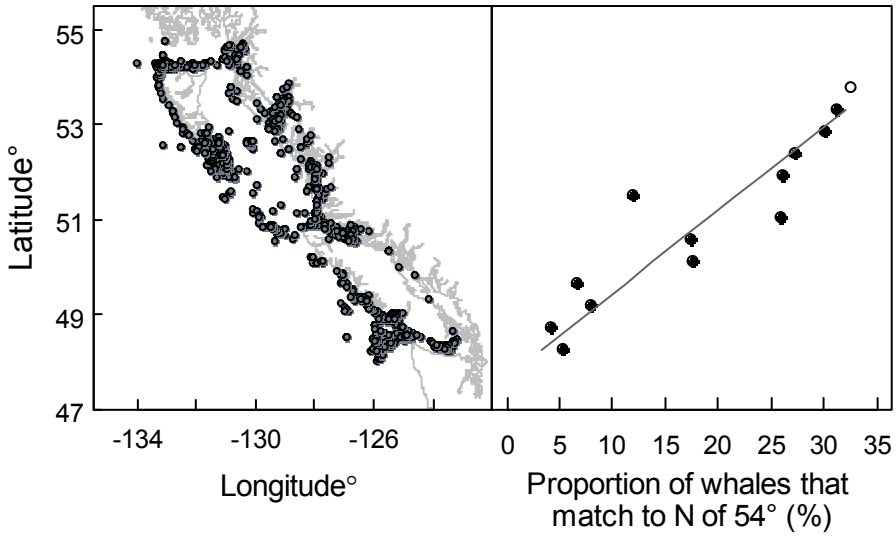

Figure 3.6. Proportion of humpback whales observed in 0.5° bins below specified latitude that match to whales observed above 54° in British Columbia, Canada between 1992 and 2007. The independent categorical variable (latitude) is plotted on the y –axis here for ease of viewing against regional map only. Open circle is proportion of whales sighted above 54° that were re-sighted in multiple years. Line = linear regression $(y = -2.6x + 35, R^2 = 0.836, F = 50.849, df = (1,10), p < 0.001)$

3.4. DISCUSSION

3.4.1. Inter-annual site-fidelity and population structure within BC

Humpback whales in BC display extremely strong site fidelity to very localized feeding grounds; as is seen in other parts of the North Pacific (Darling and McSweeney 1985, Baker *et al.* 1986, Craig and Herman 1997, Mizroch *et al.* 2004). Almost half of the 1,986 humpback whales identified in BC (43.9%) were known to have returned to BC in subsequent years, and this may be an underestimate as more were likely missed during sampling. Although some individuals appeared to stay throughout the winter, the majority were present between May and October (Fig. 3.4), before departing to breeding grounds in the lower latitudes. More than half (57%) of the returning whales observed, were seen within 100km of their sighting location from previous years. Some individuals appeared to return to almost the exact same location within BC (0.41km separation).

Table 3.1. Humpback whale matches made between sightings in British Columbia, Canada feeding areas from 1992-2007 (columns) and North Pacific breeding areas from 2004-2006 (rows). Italicized numbers are total number of whales per breeding area that were successfully matched to a feeding area, and vice versa. Acronyms defined in text.

		QCI	North	Central	NWVI	SWVI
Total IDs (*217*)		*82*	*58*	*29*	*13*	*35*
Hawaii	*175*	69 (84%)	53 (91%)	25 (86%)	11 (85%)	17 (49%)
MX-Main	*15*	4 (5%)	0 (0%)	1 (3%)	0 (0%)	10 (29%)
MX-Baja	*14*	4 (5%)	4 (7%)	0 (0%)	1 (8%)	5 (14%)
MX-Rev	*11*	5 (6%)	1 (2%)	3 (10%)	1 (8%)	1 (3%)
Cent Am	*2*	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (6%)

As noted by Stevick *et al.* (2006) in their analysis of humpback whale population spatial structuring in the North Atlantic, the frequency of inter-annual re-sightings was best described by an inverse-power function (Fig. 3.5b). The inverse-power function better described the over-dispersion seen in these data, where strong site fidelity was combined with occasional long distance movements (Hill *et al.* 1996, Baguette *et al.* 2000, Stevick *et al.* 2006). This has important implications for management, as localized processes and anthropogenic actions could have very large effects on whales that return to these small feeding localities.

Due to strong site fidelity, most whales were more likely to be seen nearest to their previous sighting than anywhere else, and thus no clear demographic boundary was apparent within BC. Matching proportion however, did decrease significantly (Fig. 3.6) as the north-south distance grew, suggesting that although there may be no clear demarcation between northern and southern whales within BC, a general partiality between the two areas may exist.

3.4.2. Breeding ground differential in northern and southern BC

Whales photographed in the northern four BC sub-areas (QCI, North, Central, NWVI) showed a higher match rate to Hawaii (87%) than to Mexico or Central America. In contrast, whales sighted off SWVI were more equally distributed between Hawaii (49%) and Mexico, and in two cases were seen as far south as Central America. Although not observed over the course of my study, others have linked BC and Japan (Darling *et al.* 1996, Calambokidis *et al.* 1997). This

picture of interconnection between geographic regions could be further elucidated by matching the remaining 1,133 whales identified in BC outside the 2004-2005 season to the catalogues developed for all of the North Pacific breeding areas. In the interim, it appears that BC provides important feeding habitat for whales that breed in all of the eastern North Pacific breeding areas, and that there may exist a difference in preferred breeding habitat, between whales that feed in northern BC, and those in the south.

3.4.3. Connections with feeding grounds to the north and south

Due to the somewhat variable nature of the geographical and temporal effort invested in collecting photo-identifications, within any given year, there were unquestionably whales that were present in BC that were not photographed. Some whales photographed early in the program, will undoubtedly also have died during the course of the study. However, as a relatively large percentage (56.1% of the 1,986) were photographed in only a single year over a 16 year period, it seems highly feasible that at least some of these whales were potentially also summering outside of BC. This is further supported by the small percentage of whales (12% of 585) seen at maximum distances of >300km and the rapid decrease of re-sighting frequency with distance (Fig. 3.5). These distant sightings may represent whales that do not return specifically to BC for summer feeding, but transit through BC waters en route to other North Pacific feeding grounds, such as southeastern Alaska or the Canadian-US borders.

Calambokidis *et al*. (2008) found low rates of within-season interchange between northern BC and southeastern Alaska, and even identified one northern BC whale in the northern Gulf of Alaska. They considered whales in Washington and whales in southern BC together, and these showed very little interchange with whales in northern BC. Unfortunately, a comprehensive inter-matching of these regions has not yet been performed despite the large identification catalogues of whales that exist for BC, Washington and southeastern Alaska. Incorporating this

step in future analyses may provide further support for the theory that northern BC is the southern limit of the US central North Pacific stock and that southern BC is the northern limit of the eastern North Pacific stock.

3.4.4. Conclusions

Overall, humpback whales in BC showed a strong pattern of high site fidelity to small, localized areas with occasional longer distance movements. Although there is not enough weight of evidence to support a strong north-south divide, my results highlight important information about stock structure within BC. Notably, the humpback whales in BC show strong site fidelity from year to year as seen in the Atlantic and other areas of the North Pacific. In addition, the data show that BC is feeding habitat for whales that breed in all of the eastern North Pacific breeding areas, and that BC may be a migratory corridor for whales that feed in other areas further north. There may not be an absolute dividing line or boundary separating humpback whales in northern and southern BC; however, the data do support the idea that BC may be comprised of two loosely distinct populations, and do not yet refute the possibility that these make up extensions of the central or eastern North Pacific stocks. Further insights into the population structure within BC will require additional inter-matching of the BC, southeastern Alaska, and Washington catalogues, as well as genetic analysis and the tracking of individuals using satellite tags.

3.5. SUMMARY

British Columbia provides important feeding habitat and a potential migratory corridor for whales that breed in all of the breeding areas of the northeastern Pacific Ocean. I examined site-fidelity and population spatial structuring of humpback whales (*Megaptera novaeangliae*) in British Columbia, Canada, using a 16-year dataset (1992-2007) of 8,785 photographic sightings containing 1,986 individuals identifiable by natural markings. Forty-four percent of the

identified whales (872) were seen in BC in more than one year. Humpback whales were seen in BC in all months of the year, but identifications were highest from May to October, and peaked in September. Matching rate within British Columbia decreased as a function of north-south distance. Maximum distances between sightings of the same individual across years ranged from 0.41 km to 842 km, and showed strong site fidelity with a median distance of 75 km. Despite the fact that there may not be an absolute demarcation or boundary for humpback whales within BC, the data provide support to the hypothesis that BC may be comprised of two loosely distinct populations to the north and south, and do not yet refute the hypothesis that these make up extensions of the central or eastern North Pacific stocks. Future genetic work could help elucidate this picture. Stock structure of humpback whales in British Columbia is highly complex and site fidelity in particular should be considered in future management of this population.

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4 General conclusions

The goal of my thesis was to fill critical knowledge gaps concerning the population of humpback whales in British Columbia. In order to do this, I set out to determine the most appropriate capture-recapture techniques for estimating abundance, and to improve these estimates by correcting for biases inherent to the sampling methodology. I also attempted to define stock structure in BC based on localized site-fidelity, small-scale regional movement, and breeding ground migration patterns.

4.1. ABUNDANCE MODELS

My study demonstrated the substantial effects that variation in spatial and temporal effort can have on population abundance estimates. The results shown in Chapter 2 suggest that multiple models should be used to estimate the abundance of spatially aggregated, migrating species. The conservative approach to estimating abundance, when biases in the data cannot be corrected for, is to apply models known to under- and over-estimate abundance, and in so doing provide realistically bounded ranges.

4.2. BRITISH COLUMBIA STOCK STRUCTURE

Humpback whale stock structure in BC was evaluated using 16 years of photo-identification data. Whales were seen in all months of the year, but presence was highest between May and October, and peaked in September. Almost half of the whales seen returned in multiple years, and showed extremely high site-fidelity to localized areas within BC. This has important implications for management of this particular population, as localized anthropogenic processes could have substantial effects on whales returning to these small feeding localities. There may not be a well-demarcated divide between humpback whales in northern and southern BC, however, matching rate of humpback whales was shown to decrease linearly with increasing

north-south distance. Furthermore, whales in northern BC were more likely to breed in Hawaii, while those in southern BC migrated to either Hawaii or Mexico. As such, the data provide some support for the existence of two loosely distinct populations of humpback whales to the north and south of BC.

4.3. STRENGTHS AND WEAKNESSES

Photo-identification studies are a non-invasive, highly effective tool for cataloguing and keeping long-term track of individuals in a population. In order to be applied for mark-recapture analyses however, study designs must carefully consider and attempt to meet all assumptions of the chosen model. Conventional mark recapture analyses are currently not adequate to deal with the dynamic realities of complex populations, particularly those that are widespread, and show a combination of both high site fidelity and transience. Although my analysis shows a few of the options available for analyzing capture-recapture data given current methodologies and attempts to offset some of the common violations, I am not able to provide a better methodology, and can only recommend that the effects of effort and of violating assumptions be considered when working with such complex populations.

It is also important to remember that the conclusions shown in my thesis are based on "snapshots in time" and cannot be assumed to provide a complete behavioural picture. For example, analyses such as the maximum distance observed between sightings represent only this, and cannot account for the amount or pattern of movement that occurred between sightings.

Despite the challenges described, my research is the first to provide an abundance estimate specifically for the population of humpback whales in Pacific Canada, and to examine the stock structure and site-fidelity of humpback whales in this region. I have also provided support to the hypothesis that British Columbia may be comprised of two loosely distinct populations of

humpback whales, and I have considered potentially new ways for dealing with and offsetting the biases commonly associated with cetacean photo-ID studies over large areas.

4.4. FUTURE STUDIES AND CONCLUSIONS

Future research of the population structure in BC would benefit from the use of satellite tags and genetic analysis. Satellite tagging would allow for a more complete picture of how humpback whales use summer feeding grounds, and whether their fidelity to small, localized areas is truly as high as suggested by my research. Analysis of genetic samples collected during the SPLASH project (Structure of Populations, Levels of Abundance, and Status of Humpbacks) (Calambokidis *et al.* 2008) will also help to place BC within the context of the North Pacific population.

Much photo-identification data have yet to be analyzed. Although long-term identification catalogues exist for southeastern Alaska and Washington, there has yet to be a dedicated matching of these to the BC catalogue. If BC whales regularly occur in US waters, and vice versa, cooperative international management plans would be a more suitable strategy. Matching individuals between the existing catalogues is therefore an important next step. There is also little understanding of the migratory corridors used by this species. This too could benefit from tracking individuals using satellite tagging and from the further matching of the BC catalogue to breeding ground catalogues.

As attempts are made to balance expanding human resource needs with diminishing wildlife habitat, governments are asked to manage the growing number of species that are listed as threatened or endangered. Yet for many of these populations, basic life history parameters that would allow for 'progress-checking' and effective implementation of adaptive management plans are lacking. Attaining this knowledge is essential to formulating informed and enforceable population management decisions. One of the major tenets of adaptive management is the ability

to assess changes in populations, and in the case of species at risk, evaluate the efficacy of implemented recovery strategies. With the recent implementation of the Canadian Species at Risk Act (2003), determining cetacean life history parameters and management concerns, such as 'critical habitat', are more important than ever. Conducting thorough photo-identification surveys can provide this information, assuming models can be developed that use data realistically, acknowledging the practical limitations of data collection. My study has provided information on abundance, distribution, movements, and population structure, allowing ecologically pertinent questions to be answered about the population of humpback whales in British Columbia.

4.5. BIBLIOGRAPHY

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