POPULATION ASSESSMENT OF WESTERN NORTH PACIFIC GRAY WHALES (*ESCHRICHTIUS ROBUSTUS*)

AMANDA L. BRADFORD

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

University of Washington

2003

Program Authorized to Offer Degree: School of Aquatic and Fishery Sciences

University of Washington
Graduate School

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Committee Members:

GLENN R. VANBLARICOM

DOUGLAS P. DEMASTER

PAUL R. WADE

Date:

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ABSTRACT

POPULATION ASSESSMENT OF WESTERN NORTH PACIFIC GRAY WHALES (*ESCHRICHTIUS ROBUSTUS*)

AMANDA L. BRADFORD

Chair of the Supervisory Committee:
ASSOCIATE PROFESSOR GLENN R. VANBLARICOM
School of Aquatic and Fishery Sciences

Two geographically and genetically distinct populations of gray whales (*Eschrichtius robustus*) occur in the North Pacific, referred to as the eastern and western populations. Subjected to intensive modern commercial whaling during portions of the 19th and 20th centuries, the western population was proposed to be extinct during the early 1970's. This population presently remains in small numbers and is considered one of the world's most endangered populations of large whales. The need for increased conservation efforts indicates the appropriateness of a quantitative western gray whale population assessment. Since 1997, ongoing studies of western gray whales have resulted in a photographic dataset that can be used for mark-recapture survival estimation. A robust design model was fitted to 116 individual whale encounter histories spanning 22 monthly capture occasions from 1997 to 2002. Constant non-calf and calf (first-year post-weaning) survival and random temporary emigration were assumed. Models incorporating individual heterogeneity in residency patterns and higher temporary emigration probabilities for younger whales provided better fits to the data. Non-calf and calf survival were estimated as 0.952 (SE=0.0151, 95% CI=0.912-0.975) and 0.709 (SE=0.1178, 95% CI=0.443-0.882), respectively. These survival estimates and other life history parameters were utilized in conjunction with the Lotka equation to calculate the 1997-2002 population growth rate of western gray whales. A Monte Carlo simulation method was employed (n=10,000 trials) to account for uncertainty in the life history parameters. A range of possible fecundity values was examined to estimate a *conservative*, *intermediate*, and *liberal* rate of population growth. These growth rates were estimated as 0.026 (SD=0.0190, 5th-95th Percentiles=-0.008-0.054), 0.031 (SD=0.0194, 5th-95th Percentiles=-0.003-0.061), and 0.036 (SD=0.0198, 5th-95th Percentiles=0.001-0.066), respectively. Each calculated growth rate and historical catch data were fitted to the generalized logistic equation in a 20th century back calculation of the western gray whale population. A Bayesian statistical method and the Sample-Importance-Resample algorithm (n_1=2,000,000 initial samples; n_2=5,000 resamples) were used to estimate model parameters and indices of population status. Back calculation results suggest that the western gray whale population is currently growing at its maximum net recruitment rate, the carrying capacity of the population is undefined, the population is currently *at most* between 8-9% of its original size, and the population has been highly depleted for over half of the 20th century. Current threats and low-density population effects could inhibit the recovery of western gray whales, emphasizing the necessity of concerted international protection and conservation planning for this critically endangered population.

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ACKNOWLEDGEMENTS

This work was made possible and accomplished only with the support of an amazing and dedicated group of individuals, who have everlastingly endeared themselves to me. Words will only partially express the extent of my appreciation. Firstly, I would like to recognize my committee members. Glenn VanBlaricom, my committee chair, has been an advisor I have perpetually bragged about to my graduate student friends. He has attentively guided and encouraged my scientific and academic pursuits, while taking the time to intuitively reach out to me during critical moments of both professional and personal struggles. The work of Doug DeMaster on the population dynamics of marine mammals influenced me long before I was a graduate student, and his accomplishments and fair and cheerful professional demeanor inspire me still. During my early tenure as a Master's candidate, a course he taught and his brainstorming ideas served as a foundation for this project. The substance of this effort simply could not have been achieved without the assistance of Paul Wade. He has the incredible gift of quickly, appropriately, and intelligently assessing the whole of a situation, and I greatly relied upon this ability. I'm particularly grateful for his patient support through my venture into 'Bayesian statistics *with* tears.'

The western gray whale project advisors also deserve special recognition and thanks. Their willingness not only to incorporate me into such a difficult study, but to also have faith in my abilities will not be forgotten. Dave Weller has put his heart and soul into the western gray whale project, and has been a long-term friend and mentor. His comprehensive commitment to science and a unique perspective on life have taught me more than he knows. Bob Brownell has been promoting the research and conservation of western gray whales – even when others thought the population was extinct! – for over thirty years. He is truly one-of-a-kind, and I am privileged to have worked in his company. The perseverance and resourcefulness of Alexander 'Sasha' Burdin have been critical to the success of the western gray whale study. He is also one of those rare individuals with true 'joie de vivre' and kept me smiling throughout long days in the field. Bernd Würsig made significant contributions to the western gray whale effort and to my development both as a scientist and a person.

Much appreciation goes to the many participants, both Russian and American, of the western gray whale project. Their involvement has been essential to the study, while their company has made for a more colorful personal experience. Of particular mention are my dear friends Yulia Ivashchenko and Grisha Tsidulko, but thanks go to many others: Stacie Arms, Sergey Blokhin, Galya Fesenko, Bridget Ferriss, Glenn Gailey, Dima and Lena Golovenkov, Toshio Kasuya, Aimee Lang, Yulia Lebedeva, Sergey and Zhana Osokin, Susan 'woman of steel' Reeve-Rickards, Yuri Shvetsov, Olga Sychenko, Karina Tarasyan, Alexey Trukhin, Alexey and Valeriy Vladimirov, Katya Vorobieva, Bridget Watts, Kirill Zcharikov, and Yuri Zhalinsky.

My life has been inexplicably enriched from being able to spend so much time in Russia, working with and amongst some of the most warm and genuine individuals I have yet encountered. They graciously welcomed me into their hearts and homes and humbled me with their kindness. Most of them have been named above, although a few names are written only in my memory. However, to each of them, I offer a heartfelt ‘спасибо большое’ for all they have taught me.

Many individuals within the School of Aquatic and Fishery Sciences offered assistance and camaraderie during my time there. Verna Blackhurst, Dede Garcia, Nichole Byrne Lau, and Lin Murdock provided pleasant and helpful support. Andre Punt and Gavin Fay kindly responded to a ‘likelihood crisis’ and offered invaluable help with the back calculation presented in Chapter 3. Working alongside the members of the VanBlaricom Lab has been delightful. I am especially grateful for the friendship and commiseration of Laura Hoberecht, Josh London, and ‘Captain’ Alex Zerbini over the years. Much needed gabbing has occurred in office 260D with Melinda Chambers and Shannon McCluskey. Michelle Lander, Tony ‘Macaroni’ Orr, Heather Smith, and Susan Wang have brought a new vitality to our group. Carlos Alvarez-Flores, Kristin Laidre, and Robert Suydam have also been fine colleagues.

My family and friends have granted me with unfailing love and encouragement throughout this process. My extended set of ‘parents’ – including my mom Ruth, dad Mike, Bobby, Kay, Shirley, and Larry – and my brother Jason and sister Michelle have stood by me, even though following my dreams has taken me far from home. My friends Kecia Kerr and Kate Willis are my kindred spirits, and have brought vast fulfillment to my life. Jamal Moss, Stephanie Paff, Sarah Pralle, Sarah Stienessen, and Pam Woods have given me much needed on-the-ground friendship here in Seattle, while Gretchen Brown, Scott ‘Skippy’ Edmondson, Brian Knezek, Charles ‘Chubby’ Littnan, Mindy McDonough, John Schivone, Mandy Toperoff, and especially Aili Grasso, Stephanie Cobb, and Gina Johnson – it’s been over 15 years, girls! – have all supported me from afar. My gratitude is limitless.

Funding and support for this work and the western gray whale project were provided by the Washington Cooperative Fish and Wildlife Research Unit, the School of Aquatic and Fishery Sciences at the University of Washington, Texas A&M University, the National Marine Fisheries Service, Sakhalin Energy Investment Company, Exxon Neftegas Limited, the International Fund for Animal Welfare, the National Fish and Wildlife Foundation, the Marine Mammal Commission, and the U.S. Environmental Protection Agency. The western gray whale project (1995-2002) was conducted as part of the Marine Mammal Project under Area V: Protection of Nature and the Organization of Reserves within the U.S.-Russia Agreement on Cooperation in the Field of Environmental Protection.

DEDICATION

At the risk of appearing overly sentimental, I would like to dedicate this work to the western population of gray whales. First and foremost, as a scientist, my hope is that this effort can be used objectively in the formulation of increased protection and conservation measures that are needed to promote the recovery of this critically endangered population. However, a particularly interesting aspect of studying such an extremely small population of recognizable individuals is that I have spent a significant amount of time over the years in the company of known whales. Memories of countless encounters with Pirate, Otter, Svetlana, Ponchik, Tooman, Speedy, Vova, and many other whales are permanently etched in my heart and mind. Out of respect and gratitude for such a privilege, concurrent with my scientific aspirations, I will be anxiously rooting for this population – as a *person*, who sincerely wishes western gray whales the opportunity to thrive in the years to come.

CHAPTER 1

THE WESTERN POPULATION OF GRAY WHALES

INTRODUCTION

The present status of the two extant gray whale populations in the North Pacific Ocean is a study in contrasts. The eastern gray whale population, reduced by commercial harvesting to a few thousand individuals by the end of the 19th century, has rebounded in size to levels most likely approaching carrying capacity. The western population, also depleted by commercial whaling during portions of the 19th and 20th centuries, was suggested to be extinct during the early 1970's. This population currently exists in small numbers and is considered one of the world's most endangered populations of large whales. The present thesis project explores the demography and population dynamics of western gray whales, offering a quantitative description of this population for incorporation into future conservation and management plans.

BACKGROUND

Two populations of gray whales (*Eschrichtius robustus*) occur in the North Pacific, the eastern (California/Chukchi) population and the western (Korean/Okhotsk) population (Rice and Wolman, 1971). The two populations can be differentiated genetically at the population level, and should be considered geographically and genetically distinct population units (LeDuc *et al*., 2002). Historically, gray whales also occurred in the eastern and western North Atlantic, possibly as two populations, but were extinct by the early 18th century (see Lindquist, 2000 for a review). Although the direct cause of their extinction is unknown, it has been linked to human activity (Mitchell, 1973).

Eastern gray whales have long been known to migrate along the western coast of North America from winter breeding grounds off Baja California to summer feeding grounds in the Bering and Chukchi Seas (e.g., Pike, 1962; Rice and Wolman, 1971). Western gray whales, also annual migrators, return to summer feeding grounds in the Okhotsk Sea (Berzin, 1990). Winter breeding grounds for this population are unknown, but are suspected to be along the coast of southern China (Wang, 1984; Omura, 1988; Kato and Kasuya, 2002).

Throughout their range, gray whales typically do not occur outside the shallow waters of the continental shelf. Their coastal distribution made them accessible to both aboriginal and commercial whalers (see Table 1.1 for definitions of whaling terminology used frequently in this text: Aboriginal Whaling, Commercial Whaling, Japanese Hand Harpooning, Japanese Net Whaling, Modern-type Whaling, and Yankee-type Whaling). Both populations were subject to intensive commercial whaling during portions of the 19th and 20th centuries. Yankee-type commercial whaling of eastern gray whales reportedly began in 1846 (Scammon, 1874). Prior to that time, eastern gray whales were taken solely by aborigines, although the extent and duration of the aboriginal whaling is unknown (Mitchell, 1979). By the late 19th century, the eastern population was reduced to levels of commercial 'extinction' (Henderson, 1972, 1984), and was suggested to number anywhere from 2,000 to 10,000 individuals (see Scammon, 1874; Henderson, 1972, 1984; Ohsumi, 1976; Reilly, 1981 for various estimates). After receiving international protection (see below), recovery of the population was observed (Reilly, 1992). Abundance estimates of approximately 26,600 whales in 1997/98 (Hobbs and Rugh, 1999) and 18,800 and 17,400 in 2000/2001 and 2001/02, respectively, (Rugh *et al.*, 2002) suggest that this population is above its pre-commercial exploitation population level (i.e., 1846 population size) and is possibly equilibrating at its current carrying capacity (Reilly, 1992; LeBoeuf *et al.*, 2000; Moore *et al.*, 2001; Rugh *et al.*, 2002).

Before the onset of modern-type commercial whaling in 1891 (Kato and Kasuya, 2002), western gray whales were subject to a long but poorly documented history of takes. Groups of maritime Koryak natives along the northeastern Okhotsk Sea hunted whales, presumably including western gray whales (Krupnik, 1984). In Japan, western gray whales were probably taken by hand harpooners dating back to the late 16th century, and were definitely taken by net whalers beginning in the late 17th century (Omura, 1984). Omura (1984) estimates that Japanese net whalers took 50-60 gray whales annually during the net whaling period (1675-1890). However, Japanese net whalers caught at least 78 western gray whales between 1891 and 1899, concurrent with the spread of modern whaling techniques (Tada, 1978; Omura, 1984; Park, 1987; Kato and Kasuya, 2002). From the middle to the late 19th century, Yankee-type pelagic whalers operating in the Okhotsk Sea also caught western gray whales, taking possibly around 500 individuals during this period (Henderson, 1984).

A Russian whaling company initiated modern-type commercial whaling for western gray whales off the coast of the Korean peninsula in 1891 (Kato and Kasuya, 2002). Russian western gray whaling there lasted until 1904 (Kato and Kasuya, 2002), although Yablokov and Bogoslovskaya (1984) noted that western gray whales were sporadically hunted by Russians near Peter the Great Bay, Russia, during World War II (WWII). Modern whaling began in Japan in 1898 (Omura, 1984), although few western gray whales were caught there (less than 3% of total commercial catches; Appendix A), as they were no longer abundant (Omura, 1984). Instead, Japanese modern whalers began operating off the northeastern and southeastern Korean coasts in 1900, where they worked until the end of WWII in 1945 (Kasahara, 1950; Kato and Kasuya, 2002). The majority of modern commercial western gray whale catches occurred during this operation (Figure 1.1; Appendix A).

Modern western gray whaling off the Korean peninsula was resumed following WWII by the Republic of Korea (South Korea), although the dwindling catch numbers (Figure 1.1) reflect the depleted status of the population (Brownell and Chun, 1977; Kato and Kasuya, 2002). Although western gray whales had previously been taken by the Japanese in the vicinity of the Democratic People's Republic of Korea (North Korea), nothing is known about whaling in these waters subsequent to WWII (Kato and Kasuya, 2002). Little is known about Chinese modern commercial whaling, but records exist of at least 14 takes in the waters adjacent to China (Appendix A; Kasahara, 1950; Mizue, 1951; Wang, 1978, 1984; Omura, 1988; Kato and Kasuya, 2002). Wang (1984) indicated that half of these whales were caught by Japanese whalers. In total, a minimum of 1,868 western gray whales were taken in the 20th century, the period when they were taken predominately by modern commercial whalers (Figure 1.1; Appendix A).

Gray whales were first accorded international protection in 1937 with the International Agreement for the Regulation of Whaling (Committee for Whaling Statistics, 1942; Reeves 1984). At the time, none of the range states of western gray whales (Russia, Japan, North Korea, South Korea, and China) were signatories to this agreement (Committee for Whaling Statistics, 1942; Reeves, 1984). When the International Convention for the Regulation of Whaling was established in 1946, gray whales legally became a protected species exempt from commercial whaling by the International Whaling Commission (IWC) (International Whaling Commission, 1950; Scarff, 1977; Reeves, 1984). Russia was a signatory to this agreement (International Whaling Commission, 1950), and Japan formally adhered by 1951 (International Whaling Commission, 1951). South Korea and China did not join the IWC until 1978 and 1980, respectively (International Whaling Commission, 1980, 1982). North Korea is presently not an IWC member.

Each gray whale population remained an IWC *Protected Stock* until 1978, when eastern gray whales were reclassified as a *Sustained Management Stock* (International Whaling Commission, 1979; Reeves, 1984). Both populations are listed in *Appendix 1* (i.e., most endangered) of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Russia, Japan, South Korea, and China are all CITES member parties. Despite international protection of western gray whales throughout most of their range, at least one direct take occurred between 1980 and the present (Brownell and Kasuya, 1999).

The western gray whale population has failed to exhibit the successful recovery demonstrated by its eastern counterpart (Clapham *et al*., 1999; Weller *et al*., 2002c). Western gray whales were proposed to be extinct during the early 1970's (Bowen, 1974), but they do survive as a remnant population (Brownell and Chun, 1977; Blokhin *et al*., 1985; Weller *et al*., 1999; 2002c). Blokhin (1996) and Vladimirov (1994) reported population estimates of 100 and 250 whales, respectively. However, these estimates were not quantitatively derived. Recent studies indicate that the population may currently consist of approximately 100 individuals (Figure 1.2; Wade *et al*., 2003). The current depleted status of western gray whales is possibly a result of intense harvesting prior to the onset of modern-type whaling (Omura, 1984), a prolonged period of modern commercial whaling (Kato and Kasuya, 2002), a pre-exploitation population level that may never have been very large in size (Yablokov and Bogoslovskaya, 1984), or more likely, a combination of these factors.

In 2000, the World Conservation Union (IUCN) designated western gray whales as *Critically Endangered*, that is, "…facing an extremely high risk of extinction in the wild in the immediate future, as defined by criteria (A to E)" (Hilton-Taylor, 2000). Western gray whales are listed according to *Criterion D*, which states that the "population [is] estimated to number less than 50 mature individuals." Mature is defined as "…capable of reproduction." For western gray whales, the number of mature individuals is approximately 47 (see Weller *et al*., 2002c for details of the estimation). The small population size and low number of mature individuals emphasize the western gray whale's status of one of the world's most endangered populations of large whales (Clapham *et al*., 1999; VanBlaricom *et al*., 2001; Weller *et al*., 2002c).

Whereas eastern gray whales are one of the better-studied baleen whale populations, western gray whales have only recently come under concerted study (Brownell *et al*., 1997; Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*. 1999, 2000). Initiated in 1997, an ongoing study of western gray whales takes place on their only presently known summer feeding ground, located off the northeastern coast of Sakhalin Island, Russia, in the near-shore waters proximate to Piltun Lagoon (Figure 1.3). This research has documented the regular use of the feeding ground by western gray whales of both sexes and multiple age classes, including reproductive females and their weaning calves. The Piltun study is being conducted by Texas A&M University (TAMU) and the National Marine Fisheries Service (NMFS), in collaboration with the Kamchatka Institute of Ecology and Nature Management (KIENM)[1].

PROJECT OBJECTIVES

This thesis project uses available population data and life history information to examine the demography and population dynamics of western gray whales. Specific objectives of the population assessment are: 1) mark-recapture estimation of non-calf and calf survival and associated mark-recapture parameters (Chapter 2); 2) Monte Carlo simulation estimation of current population growth rate (Chapter 3); and 3) Bayesian back calculation of the population to determine the population level prior to concerted

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[1] Over the six years of the TAMU, NMFS, and KIENM study, I have participated in data collection and analysis for five and six years, respectively.

modern commercial whaling (Chapter 3). Given a previous lack of quantitatively based knowledge regarding western gray whale demography and population dynamics, results from the assessment will be a valuable contribution to conservation efforts of this critically endangered population. This project is one component of the aforementioned larger study being carried out by TAMU, NMFS, and KIENM.

Table 1.1. Definitions of terminology used frequently in this text to describe gray whaling. Definitions were adapted from Mitchell and Reeves (1980) unless noted otherwise.

Term(s)	Definition
Aboriginal Whaling	Whaling conducted by endemic local people, for a period generally exceeding their documented history, who consume the products locally.
Commercial Whaling	Whaling conducted by anyone for the primary purpose of selling the products in a cash economy.
Japanese Hand Harpooning	Whaling conducted by Japanese villagers who formed small teams of vessels and took whales using hand harpoons*.
Japanese Net Whaling	Whaling conducted by Japanese villagers who formed large, coordinated fleets and used nets to secure whales for subsequent harpooning*.
Modern-type Whaling (Norwegian-type Whaling, Modern Whaling)	Whaling based on mechanical means of transport (i.e., gas, diesel, or steam-powered vessels) and the use of firearms and explosives to take whales.
Yankee-type Whaling (19th Century Whaling)	Whaling conducted from oar- and/or wind-driven vessels that involved the use of harpoons and lances to take whales.

*Definition adapted from Omura (1984).

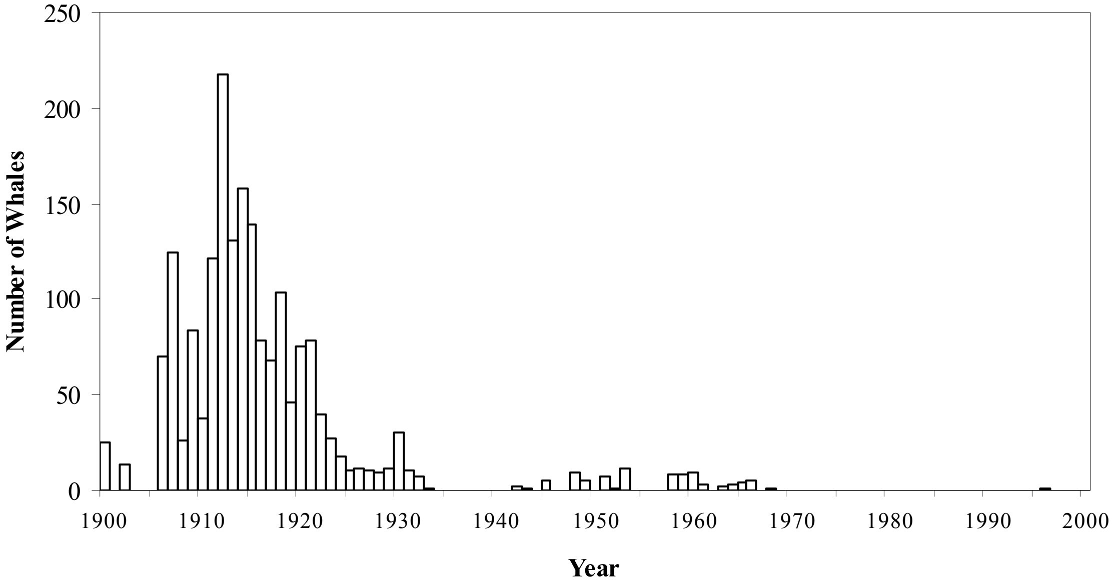

Figure 1.1. Minimum numbers of western gray whales caught during the 20th century, predominantly by modern-type commercial whalers off the Korean peninsula. Catch history compiled from Andrews (1914), Kasahara (1950), Mizue (1951), Nishiwaki and Kasuya (1970), Brownell and Chun (1977), Tada (1978), Wang (1978, 1984), Omura (1984, 1988), Park (1987), Brownell and Kasuya (1999), and Kato and Kasuya (2002). See Appendix A for details of catches.

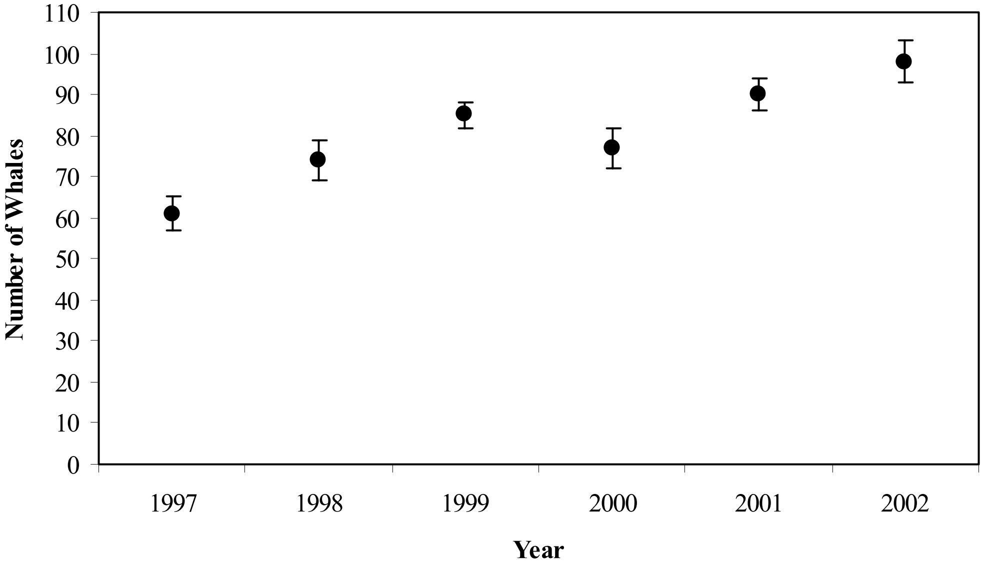

Figure 1.2. Yearly estimates of the number of western gray whales associated with the Piltun study area from 1997 to 2002 determined using closed-capture mark-recapture techniques (Wade *et al.*, 2003). The trend in the estimates is considered to overestimate the present population growth rate, although the 2002 estimate is thought to closely approximate current population size. Circle = point estimate. Bars = standard error.

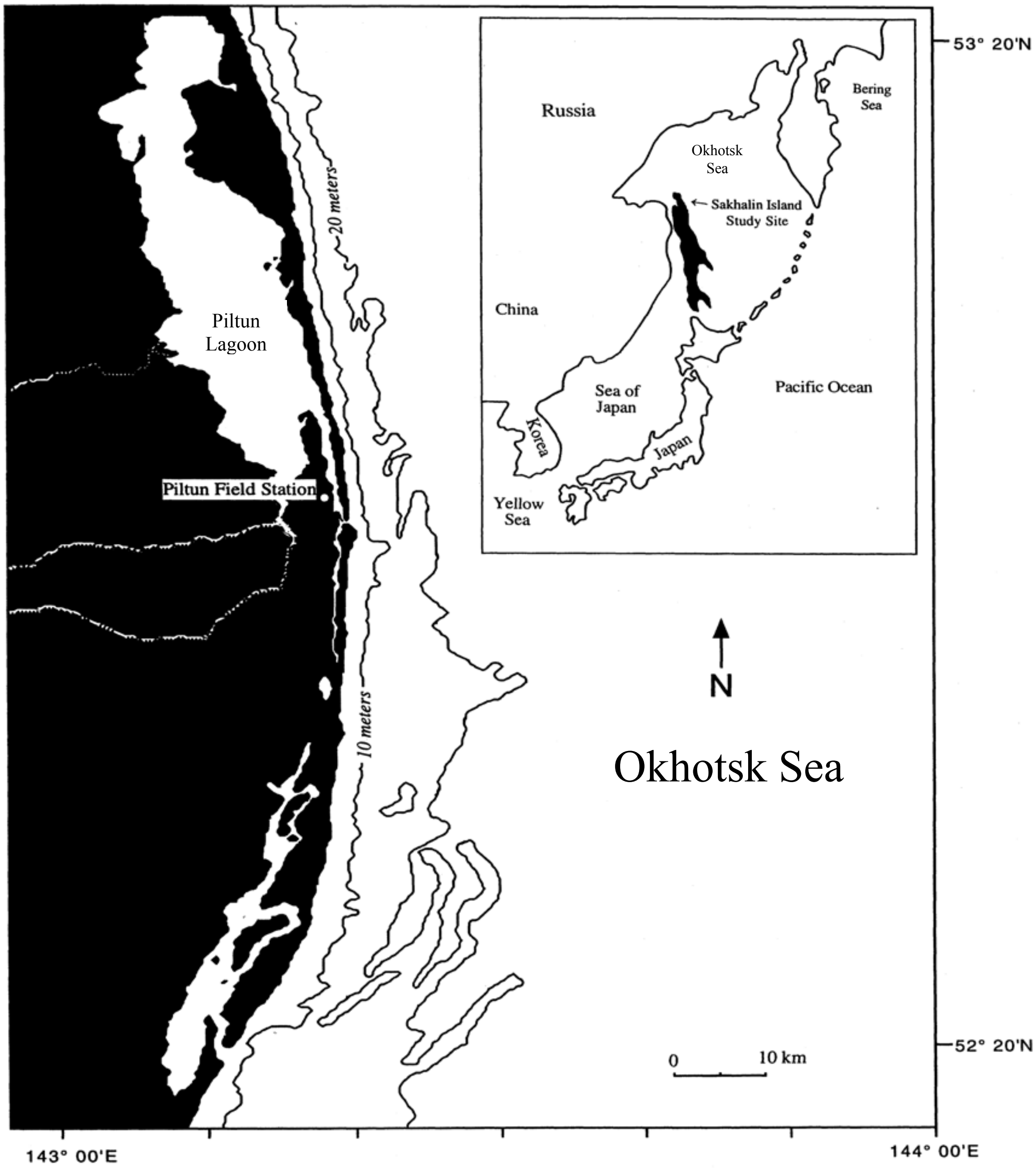

Figure 1.3. Map of the Piltun study area. Inset shows relative location of Sakhalin Island in the Okhotsk Sea.

CHAPTER 2

SURVIVAL ESTIMATES OF WESTERN GRAY WHALES INCORPORATING INDIVIDUAL HETEROGENEITY AND TEMPORARY EMIGRATION[2]

INTRODUCTION

The use of marked individuals and mark-recapture theory in assessing biological populations is well documented (see Pollock, 1991 for review). In many whale populations, individuals can be identified from photographs of their natural markings (e.g., scars and pigmentation patterns) in a method known as photo-identification (see Hammond *et al*., 1990 for overview). In the application of mark-recapture theory to photo-identification methodology, the first photographic sighting of an individual constitutes the *mark* and subsequent sightings the *recaptures*. The complete individual sighting record serves as the *encounter history* (White and Burnham, 1999). Encounter histories are fitted to an appropriate mark-recapture model (see Seber, 1982 for examples) to estimate the population parameter of interest. Mark-recapture photo-identification studies can be used to estimate the abundance (e.g., Hammond, 1986), survival (e.g., Buckland, 1990; Caswell *et al*., 1999), and fecundity (e.g., Barlow and Clapham, 1997) of whale populations. However, for most mark-recapture whale studies, care must be taken to reduce bias in the parameter estimates that can arise from individual heterogeneity in capture probabilities (Buckland, 1990). Individual

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[2] The text of this chapter has been submitted to the Scientific Committee of the IWC with the following citation: A. L. Bradford, P. R. Wade, A. M. Burdin, Y.V. Ivashchenko, G. A. Tsidulko, G. R. VanBlaricom, R. L. Brownell, Jr., and D. W. Weller. 2003. Survival estimates of western gray whales (*Eschrichtius robustus*) incorporating individual heterogeneity and temporary emigration. Paper SC/55/BRG14 submitted to the International Whaling Commission (unpublished).

heterogeneity in capture probability can occur if some whales are more easily identified (e.g., possess distinctive markings or are more approachable) or spend more time in the study area than other whales (Buckland, 1990).

Gray whales (including calves) are individually identifiable by natural pigmentation patterns and in some cases scarring from dead barnacles. Numerous multi-year studies have shown photo-identification to be a reliable and effective research technique for this species (Hatler and Darling, 1974; Darling, 1984; Swartz, 1986; Jones 1990; Weller *et al*., 1999). Photo-identification has been the main research tool of the TAMU, NMFS, and KIENM western gray whale study being conducted off Piltun Lagoon, Sakhalin Island, Russia (Figure 1.3). Photo-identification results have demonstrated that many individuals exhibit a consistent annual return and strong seasonal fidelity to the study area, while other whales are absent for all or part of any given field season. The Piltun study has generated the multi-year (1997-2002) photographic dataset used for the mark-recapture survival estimates presented here.

An unusually low return to the Piltun feeding ground of whales first observed as calves has been continuously noted prior to the 2002 field season (Weller *et al*., 2000, 2001, 2002c, 2003a). Of the 16 calves identified between 1997 and 2000, only six (37.5%) had been resighted subsequent to their year of weaning (Weller *et al*., 2003a). Ensuing mark-recapture estimates of calf survival (0.389, SE=0.1255) suggested that survival of post-weaned calves was extremely low (Bradford *et al*., 2002). With the inclusion of results from 2002, 14 of the 22 (63.6%) calves identified between 1997 and 2001 have currently been resighted post-weaning (Weller *et al*., 2003b). Five of the eight returned whales were yearlings (i.e., weaned in 2001), while the remaining three were initially identified in 1997, 1998, and 2000, respectively. Anecdotally, a whale not seen in the study area since it was first observed as a calf during a 1995 pilot study (Brownell *et al*., 1997) was also resighted in 2002 (Weller *et al*., 2003b). These findings indicate that the low calf survival reported in Bradford *et al*. (2002) can partially be attributed to the temporary emigration of some whales first identified as calves, prompting the testing of additional temporary emigration models in the present survival analysis.

METHODS

Photo-identification

For a detailed description of western gray whale photo-identification data collection and analysis protocols, see Weller *et al*. (1999). From 1997 to 2002, 237 photo-identification surveys collected during 22 months produced the 116 individual whale encounter histories analyzed here (Appendix B; Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*., 1999, 2000).

Survival Estimation

Pollock's robust design model (Pollock, 1982; Kendall and Pollock, 1992; Kendall and Nichols, 1995; Kendall *et al*., 1995, 1997), combining the Cormack-Jolly-Seber open recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965) and Huggins' closed capture estimator (Huggins, 1989, 1991), was fitted to the encounter histories using maximum likelihood parameter estimation. The field seasons in each of the six years of the study (1997-2002) were treated as the open *primary* sampling periods (i.e., mortality is assumed to occur between years). Months within a field season (3, 3, 5, 4, 4, and 3 months in each year, respectively) were treated as the closed *secondary* sampling periods (i.e., mortality is assumed to be zero between months in a year). The following parameters were estimated, although non-calf and calf survival are the primary parameters of interest:

φ_g = survival probability of group g, where g is either non-calf or calf (first-year post-weaning);
γ_{gi} = probability of group g being unavailable for capture in *primary* period i, given being alive during period i (i.e., temporary emigration), where g is either >2-yr-old, <2-yr-old, >3-yr-old, <3-yr-old, >4-yr-old, or <4-yr-old and i = 1998, 1999,…, 2002;
p_{ij} = probability of being captured in *secondary* sample j of *primary* period i, given being alive and in the study area during period i, where j = June, July,…, October, and i = 1997, 1998,…, 2002.

Assumptions of the parameter estimation are: 1) general mark-recapture assumptions for sampling open and closed populations (Seber, 1982); 2) all western gray whales used or passed through the study area during the study period, but not necessarily in each year; 3) constant non-calf and calf survival during the study period; and 4) random temporary emigration (Kendall and Nichols, 1995; Kendall *et al*., 1997) that is either constant, group varying (between whales >2-yr-old and <2-yr-old, >3-yr-old and <3-yr-old, or >4-yr-old and <4-yr-old), time varying, or group and time varying. Thus, one model of survival was tested in conjunction with eight models of temporary emigration:

φ(gc)

where gc = group varying between non-calves and calves;

$\gamma(.)$
$\gamma(g2)$
$\gamma(g3)$
$\gamma(g4)$
$\gamma(t)$
$\gamma(g2+t)$
$\gamma(g3+t)$
$\gamma(g4+t)$

where . = constant (no group or time influence)
g2 = group varying between whales >2-yr-old and <2-yr-old
g3 = group varying between whales >3-yr-old and <3-yr-old
g4 = group varying between whales >4-yr-old and <4-yr-old
t = time varying by *primary* period
\+ = additive model.

The >2-yr-old and <2-yr-old group-varying temporary emigration model was developed to account for some of the low return to the study area and reduced apparent survival of whales first sighted as calves (Bradford *et al*., 2002; Weller *et al*., 2000, 2001, 2003a, 2002c), by allowing the temporary emigration probability of yearlings to differ from older whales. Yet, given the return in 2002 of three whales that had been absent from the study area since their respective weaning year of 1997, 1998, and 2000 (Weller *et al*., 2003b), two more explicit models were constructed. In these models, whales first observed as calves were allowed to temporarily emigrate with a characteristic probability for up to two and three years post-weaning (i.e., <3-yr-old and <4-yr-old temporary emigration, respectively). The aforementioned anecdotal return in 2002 of the whale not seen in the study area since it was initially observed as a calf in 1995 (Brownell *et al.* 1997; Weller *et al*., 2003b) suggests that temporary emigration from the Piltun feeding ground can function in the life history of juvenile whales for up to seven years post-weaning. However, estimating juvenile temporary emigration for up to only three years post-weaning permits the temporary emigration probability of younger whales to differ from older whales, but minimizes potential positive bias to the non-juvenile estimate caused by the incorporation into that probability of young whales not first sighted as calves. Furthermore, few whales would contribute to extending the estimate up to four or five years post-weaning (nine and two, respectively), and a longer interval would exceed the length of the study.

Given the constant survival and variable temporary emigration parameters, the effects of various combinations of time, survey effort, and an individual *residency* covariate were examined in nine models of capture probability:

p(t)
p(T)
p(Eff)
p(Res)
p(t+Res)
p(T+Eff)
p(T+Res)
p(T+Eff+Res)
p(Eff+Res)

where t = time varying by *secondary* period
T = trend over time
Eff = *effort* (time covariate)
Res = *residency* (individual covariate).

Testing for a trend over time in capture probability served to address the hypothesis that capture probability could temporally increase because of improved efficiency in survey ability over the *primary* sampling period. *Effort* is the number of photo-identification surveys conducted each month. *Residency* is defined as the number of days a whale was captured per month divided by the mean number of days all whales were captured that month averaged over all months that the whale was captured. This value acts as an index of the duration of residency of an individual whale in the study area, given the whale is seen once, and should reduce individual heterogeneity in capture probability (Figure 2.1). In other words, *residency* indicates whether an individual whale tends to remain over long periods in the study area, or to stay for shorter amounts of time before leaving the area. *Residency* is based on the daily sighting records because these data were not used in the parameter estimation. Likewise, the calculation is conditioned on the individual being seen in a given month, so the residency index does not repeat information in the encounter history used to estimate model parameters. In calculating *residency*, scaling to the mean of each month allows the duration of residency detected monthly to be relative to sampling effort. A histogram of residency values used to model capture probability is shown in Figure 2.2.

With the one survival model, the eight temporary emigration models, and the nine models of capture probability, a total of 72 models were fitted to the encounter histories. The analysis was conducted using Program MARK (White and Burnham, 1999). Models were selected using Akaike's Information Criterion (Akaike, 1973) corrected for small sample size (AICc) (Hurvich and Tsai, 1989). Non-calf and calf survival estimates were averaged across the best models in order to account for model uncertainty (Burnham and Anderson, 2002).

RESULTS

Incorporating *residency*, time, and *effort* into models of capture probability provided the best fits to the data (Table 2.1). As expected, capture probability was positively correlated with residency time and also varied by *secondary* sampling period (Figure 2.3). That is, the positive correlation between capture probability and residency time was characteristically represented during each *secondary* sample (Figures 2.3-2.4). The pattern of monthly capture probabilities differed by *primary* sampling period, although capture probability tended to increase and decrease at the beginning and end, respectively, of each yearly field season (Figure 2.4).

The influence of temporary emigration on model selection was secondary to the effect of capture probability (Table 2.1). However, for each representation of capture probability, the constant and group-varying temporary emigration models fit the data better than models allowing temporary emigration to vary by time or group and time (Tables 2.1-2.2). Specifically, allowing temporary emigration to differ between whales >4-yr-old and <4-yr-old was primarily selected in every case of capture probability (Table 2.1). Values of all temporary emigration parameters estimated in combination with the highest weighted capture probability model are shown in Table 2.2. For the constant and group-varying models, >4-yr-old, <4-yr-old, all-whale (constant), >3-yr-old, <3-yr-old, >2-yr-old, and <2-yr-old temporary emigration were estimated as 0.147 (SE=0.0274), 0.407 (SE=0.1054), 0.175 (SE=0.0269), 0.162 (SE=0.0279), 0.293 (SE=0.1018), 0.171 (SE=0.0275), and 0.244 (SE=0.1219), respectively (Figure 2.5). The time-varying temporary emigration estimates exhibited a similar relative relationship as the constant and group-varying estimates. For each *primary* sampling period, estimates for younger whales were higher than the corresponding estimates for older whales, while the all-whale estimates were only slightly higher than those of older whales (Figure 2.6). The time-varying temporary emigration estimates varied by *primary* sampling period, and were lowest during the 1999 and 2001 field seasons (Figure 2.6).

Non-calf and calf survival estimates were averaged across the 13 best models and a weighted average point estimate, unconditional standard error, and weighted 95% confidence intervals were obtained. Results of model averaging are shown in Tables 2.3-2.4 for non-calves and calves, respectively. Non-calf and calf survival were estimated as 0.952 (SE=0.0151, 95% CI=0.912-0.975) and 0.709 (SE=0.1178, 95% CI=0.443-0.882), respectively (Figure 2.7).

DISCUSSION

Capture Probability

The individual *residency* covariate was included in the 24 best models, indicating that it helped to explain capture probability (Table 2.1). As anticipated, capture probability was higher for whales with longer residency times (Figures 2.3-2.4). In other words, the more often whales used the study area, the more likely they were to be encountered. By allowing capture probability to vary by *residency*, bias resulting from individual heterogeneity was minimized. The seven best models, which received the majority of the AICc weight (see Burnham and Anderson, 2002 for description), allowed capture probability to vary by time and *residency* (Table 2.1). Thus, capture probability differed between *secondary* sampling periods, but residency pattern was an important factor in determining the capture probability of an individual whale.

During each *primary* sampling period, the monthly capture probabilities tended to increase and then decrease as the field season progressed (Figure 2.4). This pattern could reflect many sources of intra-seasonal variation that similarly affected the monthly capture probabilities of all whales. For instance, weather conditions influenced not only the number of photo-identification surveys conducted each month, but also survey duration and coverage. The typically milder weather conditions during August facilitated more frequent and extensive surveys, which may have contributed to the higher capture probabilities consistently observed during that month. The extremely low June capture probabilities are most likely attributable to the small numbers of completed surveys. However, in this case, the reduced survey effort was probably related more to the late-June arrival of the research team and less to the weather.

Other sources of intra-seasonal variation may have had a more direct effect on the overall distribution and abundance of whales in the study area, resulting in the apparent trend in monthly capture probabilities. For example, prey density and availability in parts of the study area could have declined over each feeding season in response to whale foraging. Alternatively, the preferred prey of whales may have changed during each season, as has been suggested for eastern gray whales off Vancouver Island, British Columbia (Darling *et al*., 1998). In either scenario, whales would have then had to locate, and possibly spend more time looking for, other concentrations of prey. These alternate foraging locations might have been positioned more towards the periphery or outside of the study area, which would have generally lowered capture probabilities as the season progressed. This foraging-based hypothesis was offered to explain a seasonal offshore shift in pod distribution detected by shore-based observations of whales in the study area during some years (Ivashchenko, 1999; Würsig *et al.*, 1999, 2000). The late-season decrease in capture probabilities may also have been attributable to the movement of some whales out of the study area in preparation for or initiation of the southbound migration, particularly during the lengthy 1999 field season.

Finally, the Piltun feeding ground overlaps with two of nine major multinational oil and gas projects situated offshore of Sakhalin Island, and associated industrial activities have potentially influenced the behavior and distribution of whales in the study area (Würsig *et al.*, 1999, 2000; Weller *et al.*, 2002d). For instance, whales appeared to shift their distribution away from a region where geophysical seismic surveys were being conducted during August 2001 (Weller *et al.*, 2002d). This shift concentrated whales in an easily accessible portion of the study area, and may have been a factor in the high capture probability noted during that month. The effects of other industrial activities (e.g., well-drilling, production operations, shipping and aircraft traffic) have not yet been evaluated, but could have played a part in shaping patterns of capture probability.

Temporary Emigration

Although model selection was primarily controlled by capture probability (Table 2.1), temporary emigration demonstrated a characteristic influence within each representation of capture probability (Tables 2.1-2.2). Namely, in every case of capture probability, the constant and group-varying models of temporary emigration provided better fits to the data than the time-varying and additive models. This outcome could indicate that temporary emigration probabilities did not vary by *primary* sampling period. However, given that the latter models required the estimation of more parameters, a more likely interpretation is that the data could not support the additional model complexity. That is, the former models were more parsimonious (Burnham and Anderson, 2002).

Out of the constant and group-varying temporary emigration models, the model allowing temporary emigration to differ between whales >4-yr-old and <4-yr-old was always selected, followed by the models of constant, >3-yr-old and <3-yr-old, and >2-yr-old and <2-yr-old temporary emigration (with the exception of the lowest AICc weighted model of capture probability) (Tables 2.1-2.2). Interestingly, the constant temporary emigration model was repeatedly selected over the latter two group-varying models, when the data otherwise suggested that temporary emigration probability was different for younger whales. However, with the large standard errors associated with the estimates for younger whales (resulting from small sample sizes) and the influence of whales three and two years post-weaning on the samples of the corresponding older whale estimate, the data were most likely not able to detect a clear difference between the temporary emigration probabilities of older and younger whales in those two models. Nonetheless, in each of the three group-varying models tested, temporary emigration probabilities were higher for younger whales, particularly for whales <4-yr-old (Figure 2.5).

The order of the time-varying and additive temporary emigration models closely resembled that of the constant and group-varying models. That is, the model estimating temporary emigration over time for whales >4-yr-old and <4-yr-old was primarily selected, proceeded by the models where estimates were solely time-varying, time-varying between whales >3-yr-old and <3-yr old, and time-varying between whales >2-yr-old and <2-yr-old (Tables 2.1-2.2). Likewise, the relative relationship of the time-varying estimates was analogous to that of the constant and group-varying estimates. Within each *primary* sampling period, the temporary emigration estimates were higher for younger whales than the corresponding estimates for older whales, and the all-whale estimates were somewhat higher than those of older whales (Figure 2.6). All the time-varying estimates of temporary emigration differed between *primary* sampling periods, with the lowest probabilities occurring during the 1999 and 2001 field seasons (Figure 2.6). Potentially, the distribution and density of prey in the study area was higher in those years, resulting in lower temporary emigration probabilities for all whales. Alternatively, industrial activities conducted during those seasons may have influenced the presence of whales in the study area. However, interpretation of this finding is difficult, given the lack of data related to the suggested hypotheses and the aforementioned uncertainty in the time-varying temporary emigration models.

Presumably, the temporary emigration of whales from the study area is related to foraging activity (Weller *et al*., 1999; Burdin *et al*., 2002). The present temporary emigration estimates indicate that higher temporary emigration probabilities may play a significant role in the life history of young whales first sighted as calves for at least up to three-years post-weaning. Age-class segregation of eastern gray whales on their feeding grounds has been noted, with observations ranging from the complete separation of younger whales (Zenkovich, 1937), to a less straightforward division (Bogoslovskaya *et al*., 1981), to a combination of both patterns (Darling *et al*., 1998). However, many juvenile western gray whales initially identified as calves did return to the study area and represented some of the most frequently sighted whales throughout each field season (Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*., 1999, 2000). With the exception of a potential preference for nearshore areas, these young whales did not appear to differ appreciably in overall distribution and habitat use from older whales. Thus, given the constant use of the Piltun feeding ground by juvenile whales and the lack of segregation by age exhibited there, the mechanism prompting relatively high temporary emigration probabilities for younger whales is unclear.

Survival

The survival estimates reported here are the first direct survival estimates for gray whales. The non-calf survival estimate is similar to mark-recapture estimates by Buckland (1990) and Barlow and Clapham (1997) for humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine (0.951, SE=0.010 and 0.960, SE=0.008, respectively). Caswell *et al*. (1999) estimated survival of another highly endangered whale population, the western North Atlantic right whale (*Eubalaena glacialis*), but these time-varying mark-recapture estimates (from about 0.99 to about 0.94) are of crude survival and are not directly comparable to the non-calf survival estimates presented here. Likewise, a mark-recapture estimate of adult western Arctic bowhead whale (*Balaena mysticetus*) survival (0.984) by Zeh *et al*. (2002) and indirect estimates of adult female southern right whale (*Eubalaena australis*) survival off South Africa (0.986) and

Argentina (0.981) by Best *et al*. (2001) and Cooke *et al*. (2001), respectively, are not directly comparable. Finally, the western gray whale non-calf survival point estimate is lower than an indirect estimate of 0.987 by Wade and Perryman (2002) for the eastern gray whale population. However, the level of uncertainty in that estimate makes direct inter-population comparisons premature at this time.

Due to the small size of the western gray whale population, relatively few calves can be produced each year. Thus, the calf survival estimate presented here was expected to be imprecise, as only 22 calves were available in the study area between 1997 and 2001. However, if the estimate is assumed to be accurate, it is markedly lower than a 'reasonable' first-year post-weaning calf survival estimate of 0.875 ($SE \approx 0.047$) suggested by Barlow and Clapham (1997) for Gulf of Maine humpback whales. It is important to note that Barlow and Clapham (1997) were simply attempting to bracket the likely range of calf survival values, and the authors caution that 'little credence' should be placed in their estimate. However, it is the only known direct estimate of first-year post-weaning calf survival available for comparison.

As the data used for the western gray whale survival estimation were collected during the feeding season, the resultant calf survival estimate represents survival of calves during their first year post-weaning. Gabriele *et al*. (2001) estimated the survival rate of central North Pacific humpback whale calves, from the breeding season to the subsequent feeding season, using sighting records of individually identified females with calves. Multiple rates were calculated in order to address the effects of various biases, leading to a minimum and maximum survival estimate of 0.759 and 0.850, respectively

(Gabriele *et al*., 2001). These calf survival estimates characterize survival of humpback whale calves from birth to weaning and are therefore not comparable to the western gray whale calf estimate. Similarly, an indirect estimate by Best *et al*. (2001) of first-year survival (0.913) for southern right whale calves born off South Africa also cannot be compared. The survival rates of western gray whales from birth to weaning and first-year post-birth are currently unknown, but are important for better understanding the dynamics of this population.

The estimate reported here suggests that survival of post-weaned western gray whale calves is considerably low, which could be a result of both natural and anthropogenic factors. Possible sources of natural calf mortality are killer whale predation and insufficient nutritional reserves due to natural changes in prey availability. Potential anthropogenic causes of calf mortality are entanglement in fishing gear within the migratory corridor (see Weller *et al*., 2002c for overview of range), direct catching, and inadequate nutritional reserves because of human-related shifts in prey availability.

Killer whale predation on eastern gray whale calves has been documented (Baldridge, 1972; Goley and Straley, 1994). Although killer whales are frequently sighted in the Piltun study area, aggressive interactions with western gray whales have not been observed. However, Weller *et al*. (2002c) recorded that between 1997 and 1998, at least 33% of the western gray whales identified, including calves, had visible killer whale tooth rakes on their bodies, suggesting that they are threatened by killer whales in some portion of their range (Weller *et al*., 2002c). Heyning and Lewis (1990) summarized the entanglements of eastern gray whales in fishing gear off southern

California from 1980 to 1989. Length measurements were obtained from 16 of the 20 whales found dead after entanglement. Of the 16 measured whales, one was considered a calf (i.e., from 4.4 to 6.0m), 12 were deemed yearlings (i.e., from 6.5 to 8.8m), and three were estimated to be two or three years old (i.e., from 8.9m upwards). These findings suggest that younger whales become entangled in fishing gear more frequently or are less likely to survive entanglement than adults (Heyning and Lewis, 1990). The level of western gray whale entanglement in fishing gear within the migratory corridor is currently unknown. However, Zhou and Wang (1994), Kato (1998), and Kim (2000) have reported incidental catches of other cetaceans in coastal net fisheries off southern China, Japan, and Korea, respectively.

At least one direct take of a western gray whale has occurred in recent years (Brownell and Kasuya, 1999). In 1996, the anterior portion of a gray whale was found floating off Suttsu, Hokkaido, presumably killed by Japanese Dall's porpoise fishermen (Brownell and Kasuya, 1999). Although the Suttsu whale was adult-sized, both non-calves and calves are at risk from an undetermined level of illegal hunting. The discovery of gray whale products in Japanese commercial meat markets in 1999 (Baker *et al*., 2002) further heightens this concern. Unusually thin non-calf western gray whales in the study area have been observed since 1999 (Weller *et al*., 2002b), suggesting possible effects of natural or anthropogenic nutritional deficiencies. The cause of this physical deterioration is unknown (Brownell and Weller, 2001; Weller *et al*., 2002c), but could be having a more severe effect on calves. Furthermore, calves born to thin mothers may be susceptible to reduced survival. Interestingly, although the cause of mortality is unknown, all three western gray whale strandings on the east coast of Japan reported from 1990 to the present were of young whales less than 9.5m in length (see Yamada *et al*., 2002 for review).

As survival probability is only a measure of 'apparent' survival (i.e., the probability a whale remains alive and available for recapture), an alternative explanation for low calf survival is that whales permanently emigrate from the Piltun feeding area after their first year. Yet, as stated previously, some juvenile whales initially sighted as calves have exhibited pronounced seasonal site fidelity to the study area (Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*., 1999, 2000). Additionally, aerial and ship-based surveys of the Okhotsk Sea between 1979 and 1989 found concentrations of gray whales only off the northeastern coast of Sakhalin Island near Piltun Lagoon (Blokhin *et al*., 1985; Berzin *et al*., 1988, 1990, 1991; Berzin, 1990; Blokhin, 1996). The distribution of these sightings encompassed some area outside the boundary of typical photo-identification survey coverage. However, whales in the Piltun study area have been noted to travel more than 50 km in less than 24 hours (Burdin *et al*., 2002). This observation indicates that whales could occur within the distribution documented by previous aerial and ship-based surveys and still be encountered in the study area at some point during any given field season. Furthermore, usable photographic sightings of whales in other parts of the Okhotsk Sea have been matched to whales that regularly use the Piltun feeding ground, and have not yet included any whales first sighted as calves that were not resighted in the study area (Burdin *et al*., 2002; Weller *et al*., 2002a).

Therefore, the study area is regarded as the only known location where western gray whales consistently aggregate to feed (Weller *et al*., 1999).

The present non-calf survival point estimate is somewhat higher than the estimate calculated prior to the 2002 field season (Bradford *et al*., 2002). However, the new estimate is within the 95% confidence interval of the former estimate. Conversely, the current calf point estimate is nearly twice as high, but exceeds the upper limit of the 95% confidence interval of the previous estimate. Contrasting results from the temporal addition of data are not unexpected for a small population of long-lived animals with demographic variation, highlighting the importance of continuing the long-term western gray whale study. Future data will also facilitate the refined estimation and additional hypothesis testing of temporary emigration probabilities for younger and older whales. Such clarification is important, given the strong influence the various models of temporary emigration had on corresponding estimates of survival in the present analysis. That is, within each case of capture probability, the different models of temporary emigration lead to the broad range of resultant survival estimates (Tables 2.3-2.4). Consequently, if higher temporary emigration probabilities are not really a significant part of the life history of younger whales, then calf survival is actually lower than the model-averaged estimate presented here (Table 2.4).

Estimation of survival probability may give one of the best indications of underlying causes of population declines (Eberhardt and Siniff, 1977). Indications are more likely to come from juvenile survival estimates (Eberhardt and Siniff, 1977), as adult survival is less affected by density dependence in large, long-lived animals

(Goodman, 1981). Continued estimation and temporal evaluation of western gray whale calf survival are needed to make inferences about the status of the population. Similarly, more data are needed to further refine the non-calf estimates. In population modeling of long-lived species, population growth rate is most sensitive to non-calf survival (Goodman, 1981; Taylor and DeMaster, 1993), emphasizing the need for an accurate and precise estimate.

While the survival estimates reported here do not quantitatively determine the status of western gray whales (i.e., degree of depletion and whether the population is growing or declining), they can be used in population modeling that is needed for such an assessment (e.g., Chapter 3). Undoubtedly, a complete assessment should be made before drawing conclusions from these estimates. However, the low calf survival estimate in conjunction with the small population size (Wade *et al*., 2003), small number of reproductive females identified (n=17), and the predominance of a three-year calving interval (Chapter 3; Brownell and Weller, 2002; Weller *et al*., 2003b) already raises questions about the potential for western gray whale recovery.

Table 2.1. Model comparisons (*n*=72) from Program MARK. Delta AICc is the difference in the AICc of a model from the minimum AICc model, AICc Weight is the Akaike Weight (see Burnham and Anderson, 2002 for description), and Deviance is the difference in –2log(Likelihood) of the current model and –2log(Likelihood) of the saturated model. See text for details of parameters and model notation.

Model	AICc	Delta AICc	AICc Weight	No. Parameters	Deviance
φ (gc) γ (g4) p (t+Res)	1904.23	0.00	0.85179	32	1837.62
φ (gc) γ (.) p (t+Res)	1909.66	5.43	0.05642	31	1845.21
φ (gc) γ (g3) p (t+Res)	1909.95	5.72	0.04876	32	1843.34
φ (gc) γ (g2) p (t+Res)	1911.42	7.19	0.02334	32	1844.81
φ (gc) γ (g4+t) p (t+Res)	1912.18	7.94	0.01604	36	1836.86
φ (gc) γ (t) p (t+Res)	1917.46	13.23	0.00114	35	1844.33
φ (gc) γ (g3+t) p (t+Res)	1917.83	13.60	0.00095	36	1842.51
φ (gc) γ (g4) p (T+Eff+Res)	1917.92	13.69	0.00091	28	1859.92
φ (gc) γ (g2+t) p (t+Res)	1919.13	14.90	0.00049	36	1843.82
φ (gc) γ (.) p (T+Eff+Res)	1923.38	19.15	0.00006	27	1867.52
φ (gc) γ (g3) p (T+Eff+Res)	1923.65	19.42	0.00005	28	1865.65
φ (gc) γ (g2) p (T+Eff+Res)	1925.12	20.89	0.00002	28	1867.12
φ (gc) γ (g4+t) p (T+Eff+Res)	1925.73	21.50	0.00002	32	1859.12
φ (gc) γ (t) p (T+Eff+Res)	1931.05	26.82	0	31	1866.60
φ (gc) γ (g3+t) p (T+Eff+Res)	1931.39	27.16	0	32	1864.78
φ (gc) γ (g2+t) p (T+Eff+Res)	1932.70	28.47	0	32	1866.09
φ (gc) γ (g4) p (Eff+Res)	1934.75	30.52	0	22	1889.51
φ (gc) γ (.) p (Eff+Res)	1940.00	35.77	0	21	1896.87
φ (gc) γ (g3) p (Eff+Res)	1940.34	36.11	0	22	1895.11
φ (gc) γ (g2) p (Eff+Res)	1941.75	37.52	0	22	1896.52
φ (gc) γ (g4+t) p (Eff+Res)	1942.07	37.84	0	26	1888.34
φ (gc) γ (t) p (Eff+Res)	1947.05	42.82	0	25	1895.45
φ (gc) γ (g3+t) p (Eff+Res)	1947.48	43.25	0	26	1893.76
φ (gc) γ (g2+t) p (Eff+Res)	1948.65	44.42	0	26	1894.92
φ (gc) γ (g4) p (t)	1990.12	85.89	0	26	1936.40
φ (gc) γ (.) p (t)	1993.32	89.09	0	25	1941.73
φ (gc) γ (g3) p (t)	1994.40	90.17	0	26	1940.68
φ (gc) γ (g2) p (t)	1995.32	91.09	0	26	1941.60
φ (gc) γ (g4+t) p (t)	1996.82	92.59	0	30	1934.52
φ (gc) γ (t) p (t)	2000.02	95.79	0	29	1939.87
φ (gc) γ (g3+t) p (t)	2001.15	96.92	0	30	1938.86
φ (gc) γ (g2+t) p (t)	2001.92	97.69	0	30	1939.62
φ (gc) γ (g4) p (T+Eff)	2002.09	97.86	0	22	1956.85
φ (gc) γ (.) p (T+Eff)	2005.30	101.07	0	21	1962.17
φ (gc) γ (g3) p (T+Eff)	2006.37	102.14	0	22	1961.13
φ (gc) γ (g2) p (T+Eff)	2007.28	103.05	0	22	1962.04

Table 2.1. Continued.

Model	AICc	Delta AICc	AICc Weight	No. Parameters	Deviance
φ (gc) γ (g4+t) p (T+Eff)	2008.64	104.41	0	26	1954.92
φ (gc) γ (t) p (T+Eff)	2011.85	107.62	0	25	1960.25
φ (gc) γ (g3+t) p (T+Eff)	2012.97	108.74	0	26	1959.25
φ (gc) γ (g2+t) p (T+Eff)	2013.73	109.49	0	26	1960.00
φ (gc) γ (g4) p (Eff)	2015.09	110.86	0	16	1982.43
φ (gc) γ (.) p (Eff)	2018.37	114.13	0	15	1987.78
φ (gc) γ (g3) p (Eff)	2019.44	115.21	0	16	1986.78
φ (gc) γ (g2) p (Eff)	2020.34	116.11	0	16	1987.68
φ (gc) γ (g4+t) p (Eff)	2021.08	116.85	0	20	1980.06
φ (gc) γ (t) p (Eff)	2024.31	120.08	0	19	1985.38
φ (gc) γ (g3+t) p (Eff)	2025.43	121.20	0	20	1984.41
φ (gc) γ (g2+t) p (Eff)	2026.16	121.93	0	20	1985.13
φ (gc) γ (g4) p (T+Res)	2083.31	179.07	0	22	2038.07
φ (gc) γ (.) p (T+Res)	2088.99	184.76	0	21	2045.86
φ (gc) γ (g3) p (T+Res)	2089.14	184.91	0	22	2043.91
φ (gc) γ (g2) p (T+Res)	2090.67	186.44	0	22	2045.43
φ (gc) γ (g4+t) p (T+Res)	2090.91	186.68	0	26	2037.19
φ (gc) γ (t) p (T+Res)	2096.53	192.30	0	25	2044.94
φ (gc) γ (g3+t) p (T+Res)	2096.74	192.51	0	26	2043.02
φ (gc) γ (g2+t) p (T+Res)	2098.13	193.90	0	26	2044.40
φ (gc) γ (g4) p (T)	2155.65	251.42	0	16	2122.99
φ (gc) γ (.) p (T)	2158.74	254.51	0	15	2128.16
φ (gc) γ (g3) p (T)	2159.82	255.59	0	16	2127.16
φ (gc) γ (g2) p (T)	2160.68	256.45	0	16	2128.02
φ (gc) γ (g4+t) p (T)	2162.20	257.97	0	20	2121.18
φ (gc) γ (t) p (T)	2165.30	261.07	0	19	2126.37
φ (gc) γ (g3+t) p (T)	2166.48	262.25	0	20	2125.45
φ (gc) γ (g2+t) p (T)	2167.16	262.93	0	20	2126.13
φ (gc) γ (g4) p (Res)	2186.35	282.12	0	16	2153.69
φ (gc) γ (g3) p (Res)	2192.35	288.12	0	16	2159.69
φ (gc) γ (.) p (Res)	2192.48	288.25	0	15	2161.90
φ (gc) γ (g2) p (Res)	2194.00	289.77	0	16	2161.34
φ (gc) γ (g4+t) p (Res)	2194.10	289.87	0	20	2153.07
φ (gc) γ (g3+t) p (Res)	2200.25	296.02	0	20	2159.23
φ (gc) γ (t) p (Res)	2200.30	296.07	0	19	2161.38
φ (gc) γ (g2+t) p (Res)	2201.88	297.65	0	20	2160.86

Table 2.2. Temporary emigration (γ) parameters estimated in association with the highest AICc weighted model of capture probability, with resulting estimates and associated standard error.

Model	AICc Weight	Parameter	Estimate	Standard Error
φ (gc) γ (g4) p (t+Res)	0.85179	$\gamma_{>4\text{-yr-old}}$	0.147	0.0274
		$\gamma_{<4\text{-yr-old}}$	0.407	0.1054
φ (gc) γ (.) p (t+Res)	0.05642	$\gamma_{all\text{-}whale}$	0.175	0.0269
φ (gc) γ (g3) p (t+Res)	0.04876	$\gamma_{>3\text{-yr-old}}$	0.162	0.0279
		$\gamma_{<3\text{-yr-old}}$	0.293	0.1018
φ (gc) γ (g2) p (t+Res)	0.02334	$\gamma_{>2\text{-yr-old}}$	0.171	0.0275
		$\gamma_{<2\text{-yr-old}}$	0.244	0.1219
φ (gc) γ (g4+t) p (t+Res)	0.01604	$\gamma_{>4\text{-yr-old},1998}$	0.175	0.0706
		$\gamma_{>4\text{-yr-old},1999}$	0.125	0.0432
		$\gamma_{>4\text{-yr-old},2000}$	0.173	0.0565
		$\gamma_{>4\text{-yr-old},2001}$	0.136	0.0459
		$\gamma_{>4\text{-yr-old},2002}$	0.152	0.0573
		$\gamma_{<4\text{-yr-old},1998}$	0.457	0.1612
		$\gamma_{<4\text{-yr-old},1999}$	0.361	0.1245
		$\gamma_{<4\text{-yr-old},2000}$	0.453	0.1343
		$\gamma_{<4\text{-yr-old},2001}$	0.384	0.1338
		$\gamma_{<4\text{-yr-old},2002}$	0.416	0.1390
φ (gc) γ (t) p (t+Res)	0.00114	$\gamma_{all\text{-}whale,1998}$	0.192	0.0725
		$\gamma_{all\text{-}whale,1999}$	0.152	0.0480
		$\gamma_{all\text{-}whale,2000}$	0.210	0.0593
		$\gamma_{all\text{-}whale,2001}$	0.153	0.0504
		$\gamma_{all\text{-}whale,2002}$	0.183	0.0584
φ (gc) γ (g3+t) p (t+Res)	0.00095	$\gamma_{>3\text{-yr-old},1998}$	0.184	0.0713
		$\gamma_{>3\text{-yr-old},1999}$	0.138	0.0461
		$\gamma_{>3\text{-yr-old},2000}$	0.195	0.0586
		$\gamma_{>3\text{-yr-old},2001}$	0.147	0.0494
		$\gamma_{>3\text{-yr-old},2002}$	0.163	0.0591
		$\gamma_{<3\text{-yr-old},1998}$	0.326	0.1497

Table 2.2. Continued.

Model	AICc Weight	Parameter	Estimate	Standard Error
		$\gamma_{<3\text{-yr-old},1999}$	0.256	0.1104
		$\gamma_{<3\text{-yr-old},2000}$	0.342	0.1326
		$\gamma_{<3\text{-yr-old},2001}$	0.270	0.1254
		$\gamma_{<3\text{-yr-old},2002}$	0.294	0.1220
φ (gc) γ (g2+t) p (t+Res)	0.00049	$\gamma_{>2\text{-yr-old},1998}$	0.187	0.0719
		$\gamma_{>2\text{-yr-old},1999}$	0.146	0.0474
		$\gamma_{>2\text{-yr-old},2000}$	0.210	0.0592
		$\gamma_{>2\text{-yr-old},2001}$	0.150	0.0499
		$\gamma_{>2\text{-yr-old},2002}$	0.173	0.0594
		$\gamma_{<2\text{-yr-old},1998}$	0.280	0.1607
		$\gamma_{<2\text{-yr-old},1999}$	0.223	0.1252
		$\gamma_{<2\text{-yr-old},2000}$	0.309	0.1673
		$\gamma_{<2\text{-yr-old},2001}$	0.229	0.1344
		$\gamma_{<2\text{-yr-old},2002}$	0.261	0.1384

Table 2.3. Model averaging of western gray whale non-calf survival estimates across the best models (*n*=13) showing the weighted average point estimate, unconditional standard error, and weighted 95% confidence intervals (logit transformation).

Model	AICc Weight	Estimate	Standard Error
φ (gc) γ (g4) p (t+Res)	0.85179	0.952	0.0151
φ (gc) γ (.) p (t+Res)	0.05642	0.955	0.0146
φ (gc) γ (g3) p (t+Res)	0.04876	0.953	0.0150
φ (gc) γ (g2) p (t+Res)	0.02334	0.954	0.0148
φ (gc) γ (g4+t) p (t+Res)	0.01604	0.952	0.0160
φ (gc) γ (t) p (t+Res)	0.00114	0.955	0.0152
φ (gc) γ (g3+t) p (t+Res)	0.00095	0.953	0.0158
φ (gc) γ (g4) p (T+Eff+Res)	0.00091	0.952	0.0151
φ (gc) γ (g2+t) p (t+Res)	0.00049	0.954	0.0156
φ (gc) γ (.) p (T+Eff+Res)	0.00006	0.955	0.0146
φ (gc) γ (g3) p (T+Eff+Res)	0.00005	0.953	0.0150
φ (gc) γ (g2) p (T+Eff+Res)	0.00002	0.954	0.0148
φ (gc) γ (g4+t) p (T+Eff+Res)	0.00002	0.953	0.0160
Weighted Average:		0.952	0.0151
Unconditional Standard Error:			0.0151
95% CI for Weighted Average Estimate:		0.912	0.975
Percent of variation attributable to model variation:			0.29%

Table 2.4. Model averaging of western gray whale calf survival estimates across the best models (*n*=13) showing the weighted average point estimate, unconditional standard error, and weighted 95% confidence intervals (logit transformation).

Model	AICc Weight	Estimate	Standard Error
φ (gc) γ (g4) p (t+Res)	0.85179	0.715	0.1181
φ (gc) γ (.) p (t+Res)	0.05642	0.661	0.1060
φ (gc) γ (g3) p (t+Res)	0.04876	0.680	0.1094
φ (gc) γ (g2) p (t+Res)	0.02334	0.669	0.1076
φ (gc) γ (g4+t) p (t+Res)	0.01604	0.716	0.1184
φ (gc) γ (t) p (t+Res)	0.00114	0.661	0.1061
φ (gc) γ (g3+t) p (t+Res)	0.00095	0.680	0.1095
φ (gc) γ (g4) p (T+Eff+Res)	0.00091	0.715	0.1181
φ (gc) γ (g2+t) p (t+Res)	0.00049	0.670	0.1078
φ (gc) γ (.) p (T+Eff+Res)	0.00006	0.661	0.1060
φ (gc) γ (g3) p (T+Eff+Res)	0.00005	0.680	0.1094
φ (gc) γ (g2) p (T+Eff+Res)	0.00002	0.669	0.1076
φ (gc) γ (g4+t) p (T+Eff+Res)	0.00002	0.716	0.1185
Weighted Average:		0.709	0.1167
Unconditional Standard Error:			0.1178
95% CI for Weighted Average Estimate:		0.443	0.882
Percent of variation attributable to model variation:			1.87%

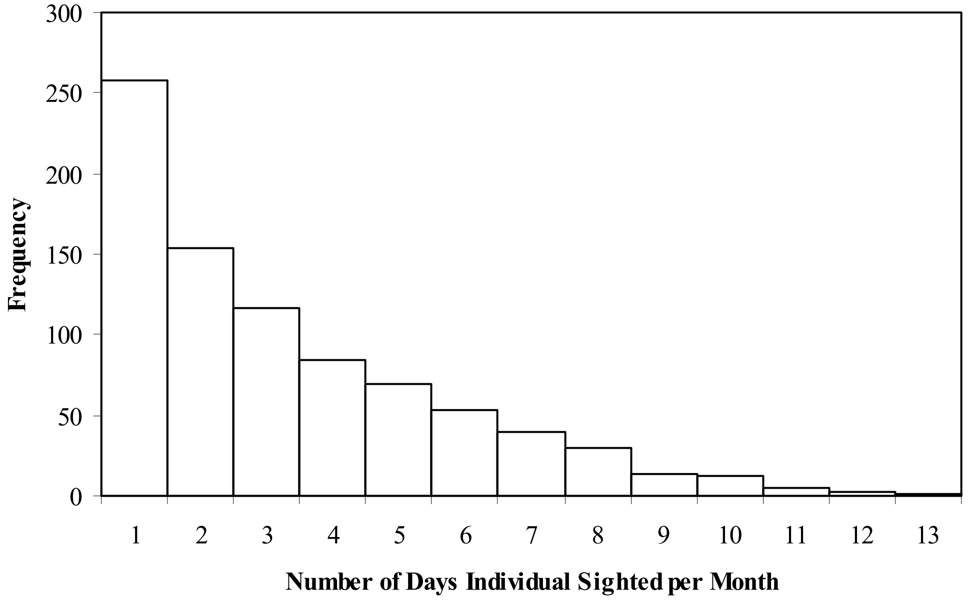

Figure 2.1. Histogram of the number of days an individual was sighted in a month (*n*=841 occurrences of individuals seen 1-13 days in a month) pooled over all *secondary* sampling periods. Note that individual whales are represented in as many months as the individual was seen, and that monthly variation in survey effort is not reflected.

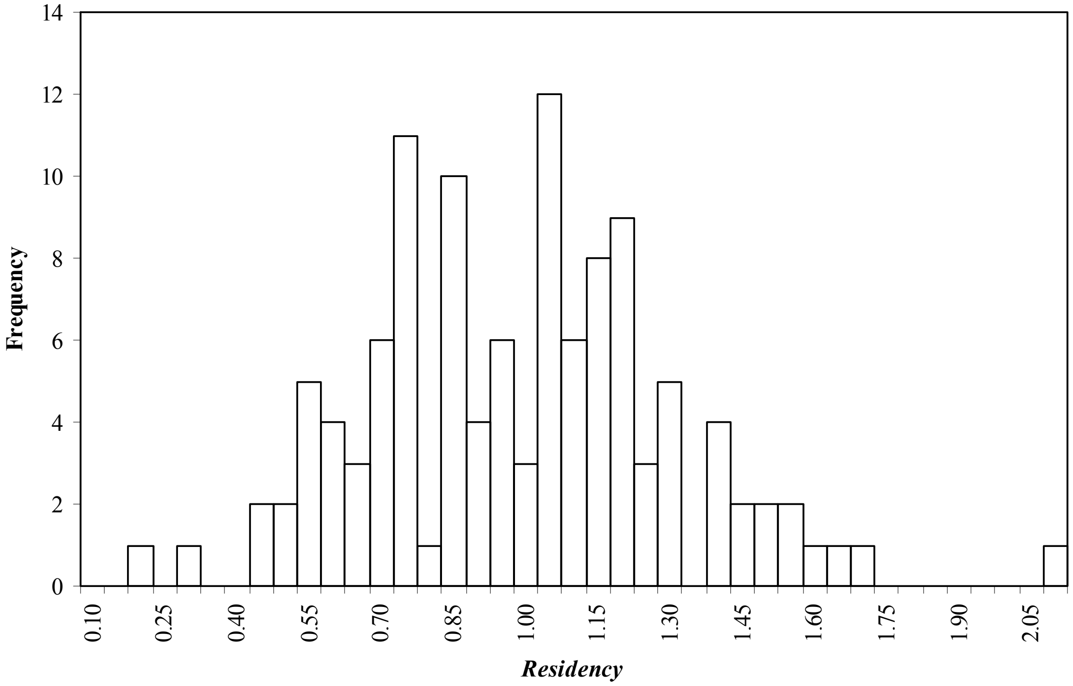

Figure 2.2. Histogram of the individual *residency* covariates (*n*=116) used in models of capture probability.

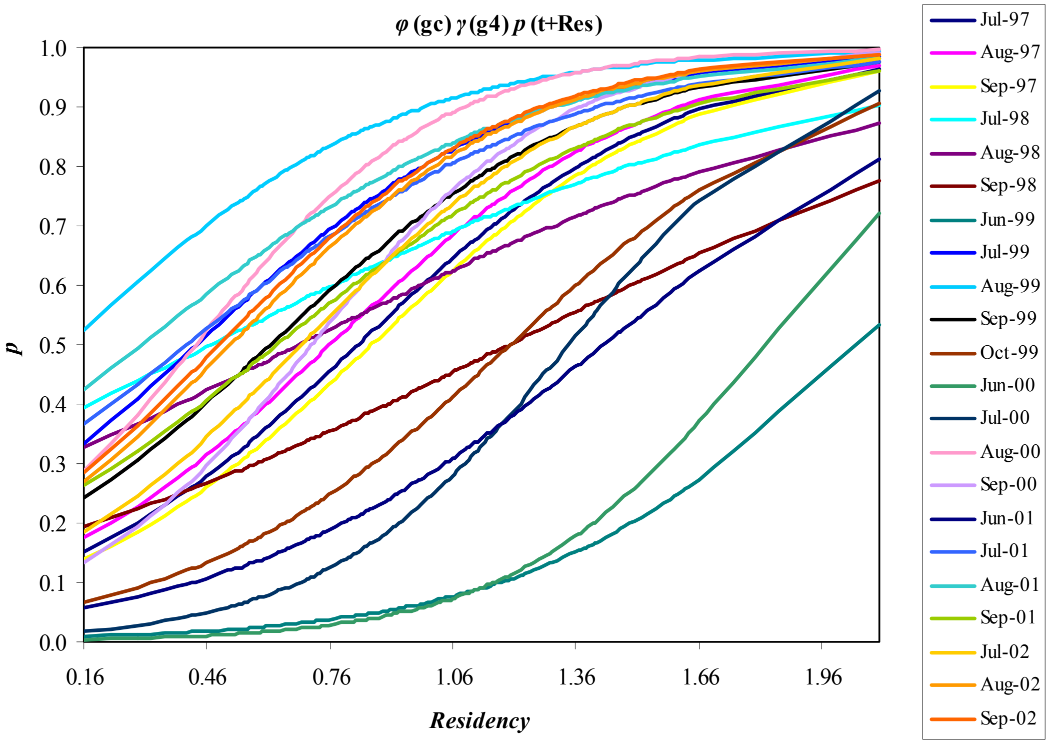

Figure 2.3. Capture probability (*p*) vs. *residency* for each *secondary* sampling period (*n*=22) according to the highest AICc weighted model.

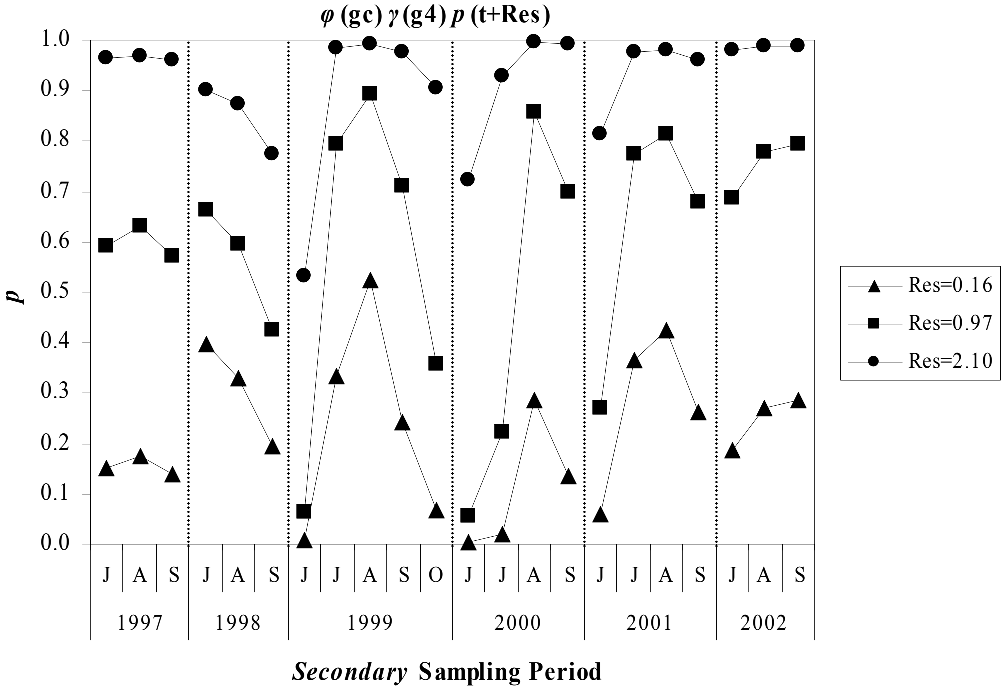

Figure 2.4. Capture probability (*p*) as a function of s*econdary* sampling period (*n*=22) for the whale with the highest (Res=2.10), lowest (Res=0.16), and average (Res=0.97) residency time according to the highest weighted AICc model.

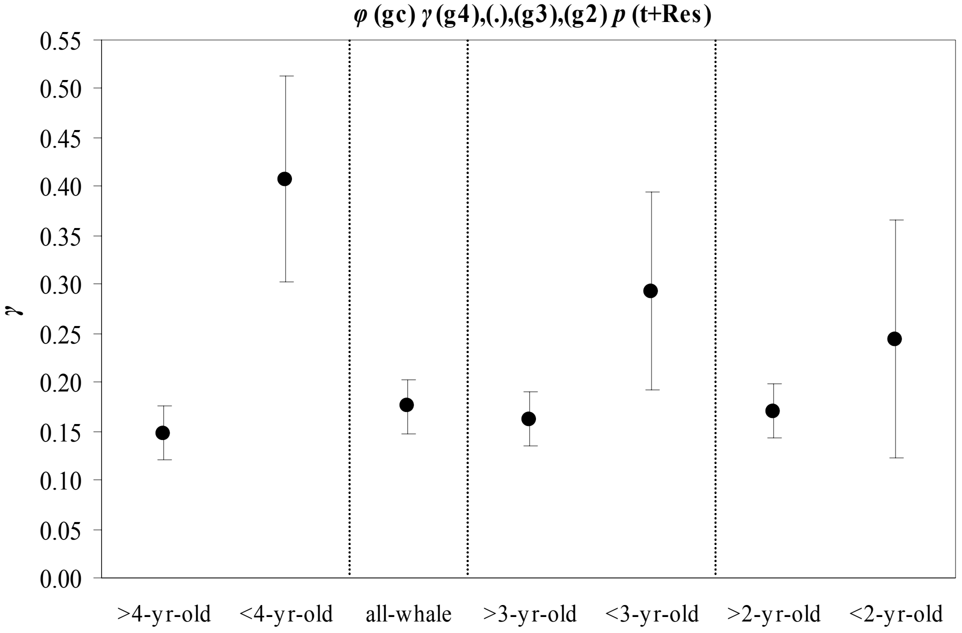

Figure 2.5. Estimates of >4-yr-old, <4-yr-old, all-whale, >3-yr-old, <3-yr-old, >2-yr-old, and <2-yr-old temporary emigration (γ) resulting from four models of temporary emigration in combination with the highest AICc weighted capture probability model. Estimates are presented in the order that their associated model was selected. Circle = the point estimate. Bars = the standard error.

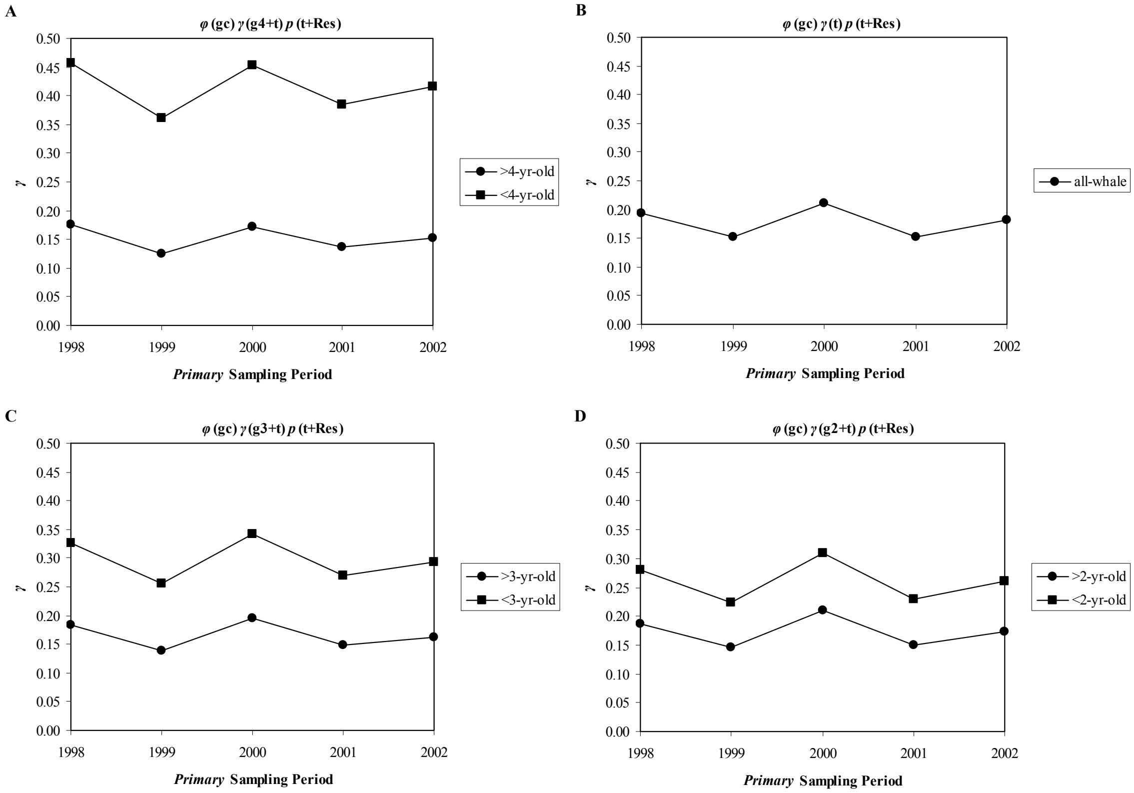

Figure 2.6. Temporary emigration (γ) as a function of *primary* sampling period (n=6) for models considering whales >4-yr-old and <4-yr-old (A), all whales (B), whales >3-yr-old and <3-yr-old (C), and whales >2-yr-old and <2-yr-old (D), according to the highest AICc weighted capture probability model. Note that a temporary emigration probability for the first *primary* sampling period cannot be estimated, as there are no marked individuals outside the study area at that time. Estimates are presented in the order that their associated model was selected.

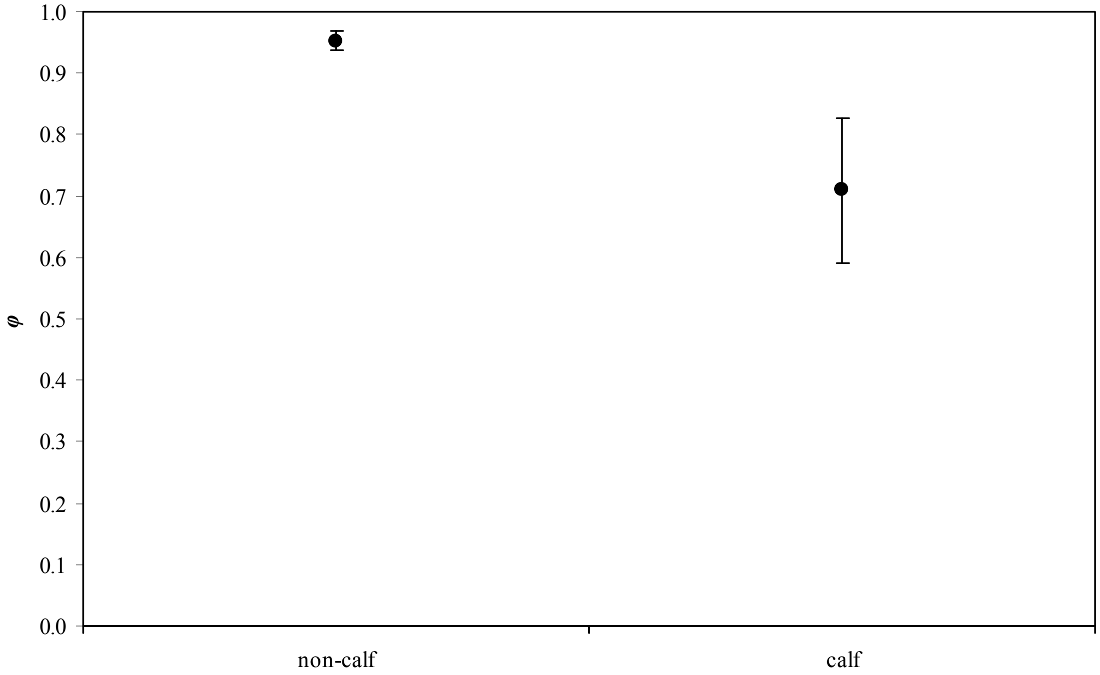

Figure 2.7. Western gray whale non-calf and calf survival (*φ*) estimates. Circle = the weighted average point estimate. Bars = the unconditional standard error.

CHAPTER 3

CURRENT POPULATION GROWTH RATE AND TWENTIETH CENTURY POPULATION DYNAMICS OF WESTERN GRAY WHALES

INTRODUCTION

Similar to other populations of wildlife, determining the status of a whale population requires comparing the current population size with an accepted reference level, usually the current carrying capacity (i.e., equilibrium population size under conditions of no harvest). For whale populations that are presently depleted as a result of historical whaling, current carrying capacity is often unknown and must be estimated. Commonly, historical population levels are used as estimates of current carrying capacity (Fowler and Siniff, 1992), given that the historical population was at equilibrium and that the environment has not changed significantly since that time (Gerrodette and DeMaster, 1990). However, selecting a point in a population's history to reflect carrying capacity can be difficult (e.g., Reilly, 1992). For whale populations with long histories of aboriginal harvests prior to commercial exploitation, the task is confounded by a lack of information on aboriginal harvest levels and by the inherent ambiguity in the definition of carrying capacity (see Hartvigsen, 2001 for a recent overview of the carrying capacity concept). For example, Fowler and Siniff (1992) present carrying capacity as "…the mean naturally occurring population (i.e., in the absence of perturbations by other than aboriginal human activities) level." If aboriginal activity levels varied historically, or if they contrast with present aboriginal use of the population, which historical equilibrium population size, if any, should be regarded as current carrying capacity?

A primary method for estimating carrying capacity of exploited populations is referred to as back calculation (see Gerrodette and DeMaster, 1990 for an overview). Back calculation fits a population dynamics model to a current abundance estimate (or a series of estimates) and historical catch data, back to a point in time before commercial exploitation. That pre-exploitation population size is considered carrying capacity if it meets the aforementioned assumptions described in Gerrodette and DeMaster (1990).

The population dynamics model used in the back calculation can vary, but the model must include the specification of a density-dependent function (Gerrodette and DeMaster, 1990). General forms of commonly used age-independent and age-structured models are referred to as the generalized logistic equation (e.g., Pella and Tomlinson, 1969) and the Leslie matrix (Leslie, 1945, 1948), respectively, although the Leslie matrix should be combined with a density dependent function. Both model forms have been applied to back calculations performed on cetacean populations. Smith (1983) employed the generalized logistic equation to calculate carrying capacity for three dolphin populations in the eastern tropical Pacific. Breiwick *et al*. (1984) used a density-dependent Leslie-type matrix in a back calculation for western Arctic bowhead whales.

In addition to uncertainty involved in the modeling process (e.g., reliability of input parameters; Smith and Polacheck, 1979), problems can arise when interpreting the selected historical reference level (i.e., pre-exploitation population size) as carrying capacity. Most early attempts to back calculate the eastern gray whale population failed to reconcile the available catch records with the degree of observed late 19th century depletion, the current increase in abundance, and standard density-dependent population models (Ohsumi, 1976; Reilly, 1981; Cooke, 1986; Lankester and Beddington, 1986). Punt and Butterworth (2002) more recently confirmed these results. Population projections in these efforts all begin prior to 1846, the onset of commercial eastern gray whaling (Scammon, 1874), when the population was harvested only by aborigines (Mitchell, 1979) and assumed to be at a pre-exploitation equilibrium. Butterworth *et al.* (2002) found that carrying capacity estimates producing reasonable trajectories through the current abundance estimates involved making untestable assumptions regarding the temporal consistency of carrying capacity or about the levels of aboriginal or early commercial catches. In order to avoid these problems, Wade (1997, 2002) relied on the richness of the current abundance data and assessed the population using projections beginning in 1900 and 1967, respectively. These analyses did not make any assumptions about where the starting population levels of the projections were relative to carrying capacity.

Estimating carrying capacity in an assessment of western gray whale status could prove equally, if not more, problematic than attempts for the eastern population. Fewer abundance and vital rate data exist, and a reference population level is not as easily determined. Modern commercial western gray whaling began in 1891 (Kato and Kasuya, 2002), but not all previous harvests were aboriginal (Table 1.1). Further, records of takes prior to the modern commercial whaling period are insufficient. For example, the 200-year history of Japanese net whaling is poorly known (Omura, 1984). Even if adequate records did exist, Gerrodette and DeMaster (1990) caution that back calculation is less useful if the pre-exploitation population level is very far back in time, as the carrying capacity estimate then becomes heavily dependent on the input vital rates. Thus, a variation of the back calculation, such as the method used by Wade (1997) for eastern gray whales, is a more suitable alternative. In that analysis, the initial year of population projections (1900) was after the onset of commercial exploitation, but still far enough back in time to reflect the contrast (i.e., periods of high and low abundance) in the population's history.

The year 1900 is also a suitable year to begin a back calculation of the western gray whale population. The time series of modern whaling catch records begins in this year (Figure 1.1; Appendix A). Moreover, population projections will encompass the concerted Japanese modern whaling operation off the Korean peninsula (Kasahara, 1950; Kato and Kasuya, 2002). Western gray whale population size *circa* 1900 and an apparent estimate of carrying capacity do exist in the scientific literature. Berzin and Vladimirov (1981) suggested that the western gray whale population numbered 1,000-1,500 individuals by 1910, although details of the estimation process were not provided. Yablokov and Bogoslovskaya (1984) speculated that the population might have numbered between 1,500-10,000 whales prior to the onset of the 'whaling industry.' How this range was determined, and to what specific time period it applies, is unclear.

Increased international protection, conservation, and management planning for western gray whales are needed to facilitate the potential recovery of this population. In several predominant national and international contexts, marine mammal conservation currently functions by protecting populations based on the degree to which they are reduced (e.g., Fowler and Siniff, 1992; IWC, 1995; Wade, 1998). Thus, a back calculation adhering to the previously outlined framework was performed to quantitatively demonstrate the degree to which the western gray whale population was depleted during the 20th century, and possibly historically. Along with 20th century catch data (Figure 1.1; Appendix A), mark-recapture estimates of the number of western gray whales associated with the Piltun feeding ground (Figure 1.2; Wade *et al*., 2003) were available for fitting of the population dynamics model. However, as the increase in these estimates only verifies an increase in the number of whales using the Piltun study area, the trend in these values is regarded as an overestimate of the present population growth rate (Wade *et al*., 2003). Thus, fitting the population dynamics model to these estimates would have lead to a biased estimation of model parameters. Therefore, an alternative population characteristic was needed, such as the current population growth rate. Given the survival estimates presented in Chapter 2 and some basic life history information (see below), the current western gray whale population growth rate was estimated accounting for uncertainty in these data. The population dynamics model was then fitted to the calculated growth rate. Results of the growth rate estimation and the ensuing analysis of 20th century western gray whale population dynamics are presented here.

METHODS

Growth Rate Estimation

Population Dynamics Model

According to Lotka's equation of unity (Lotka, 1907; Cole, 1954), any given set of age-specific survival and reproductive parameters can be characterized by a unique population growth rate. The form of the Lotka equation allowing for a discrete time (in this case, annual) life history representation (e.g., Goodman, 1982) was used to estimate the population growth rate of western gray whales from 1997 to 2002:

$$1 = \sum_{x=1}^{w} \lambda^{-x} l_x m_x \qquad \text{(Equation 3.1)}$$

where x = age class
w = maximum age class
λ = finite population growth rate
l_x = survival to age class x
m_x = fecundity of age class x.

When implementing the Lotka equation, the first age class (i.e., age class 1) generally relates to young of the year at the time of birthing (i.e., age 0 individuals), such that l_1=1. As the western gray whale growth rate estimation is based predominantly on information gleaned from the Piltun feeding ground (i.e., between birthing seasons), age class 1 actually corresponds to young of the year (i.e., calves) that are approximately 6-8 months of age (see Weller *et al.*, 1999 for a discussion of likely ages of calves in the Piltun study area relative to eastern gray whale estimates summarized by Rice and Wolman (1971)). The fact that l_1 is technically unknown in this case is offset by the incorporation of apparent fecundity into the growth rate estimate. That is, the measure of fecundity is also based on observations made during the feeding season. Therefore, fecundity estimates will reflect any loss of calves between the breeding and feeding grounds, making l_1=1 an appropriate assumption for the present analysis. The specific life history parameters used in the western gray whale growth rate estimation are detailed below.

The average longevity of western gray whales is unknown, and can only be speculated for eastern gray whales (Rice and Wolman, 1971). However, the maximum age class (w) incorporated into the Lotka equation does not necessarily characterize the longevity of individuals in the population, and can in fact be much larger. When average survival probabilities representing an unknown demographic are used to calculate the l_x schedule, w should be fixed at a value large enough to allow l_w to approach zero. As an average non-calf survival probability was utilized in the western gray whale growth rate estimation (see below and Chapter 2), the maximum age class was set at 150. To illustrate the principle of this concept, summing the Lotka equation to w=1,000 would not have changed the results of the growth rate estimation. Further, in the older scientific literature (e.g., Cole, 1954), w was often alternatively represented by ∞.

The intrinsic growth rate of a population (r) is another measure of population increase often represented in population dynamics modeling. In discrete forms of population dynamics models, the finite population growth rate (λ) estimated by the Lotka equation corresponds to r according to the relationship:

$$\lambda = 1 + r \qquad \text{(Equation 3.2)}$$

As a form of r was a parameter in the back calculation population dynamics model (see below), consistency and comparability of reported growth rates were needed. Therefore, results of the growth rate estimation are described in terms of $\lambda - 1$ when associated with the Lotka equation, and by the r nomenclature when incorporated into the back calculation.

Life History Parameters

Four life history parameters were required for the western gray whale growth rate estimation: 1) calf survival; 2) non-calf survival; 3) calving interval (i.e., time in years between births of consecutive calves); and 4) age at sexual maturity (ASM). The mark-recapture calf and non-calf survival estimates (ϕ) presented in Chapter 2 were utilized to construct the l_x schedule of the Lotka equation for age class 2 (recall that l_1=1) to age class *w*, where:

$$l_x = \phi_{x-1} l_{x-1} \qquad \text{(Equation 3.3)}$$

Thus, the calf survival estimate became ϕ_1, and the non-calf estimate $\phi_{2 \to w-1}$. Calf and non-calf survival values were selected from a beta distribution (i.e., between 0 and 1) with a mean of 0.709 (SE=0.1178) and 0.952 (SE=0.0151), respectively (Chapter 2).

Fecundity (m_x) is the average rate at which female young are produced each year by females, and can be calculated as:

$$m_x = \frac{1}{CI} SR \phi_x \qquad \text{(Equation 3.4)}$$

where CI = calving interval
SR = population sex ratio (assumed to be 0.5).

The western gray whale calving interval was determined from photo-identification records of females with calves on the Piltun feeding ground (Table 3.1; Brownell and Weller, 2002; Weller *et al*., 2003b), following the estimation method of Jones (1990) for eastern gray whales. As in Jones (1990), only females with one or more observed calving intervals contributed to the estimation. In addition to photographic sightings collected by

TAMU, NMFS, and KIENM between 1997 and 2002, photo-identification records from the 1995 pilot study (Brownell *et al*., 1997) were included in the calculation, as these data added one observed calving interval each to the encounter histories of two females (Table 3.1).

Averaging the 10 observed calving intervals (3-year *CI*: *n*=7; 4-year *CI*: *n*=2; 2-year *CI*: *n*=1) highlighted in Table 3.1 would lead to a measure of apparent fecundity. However, this measure could potentially be confounded by the capture probability of one or more of the represented females. That is, a female who might have been associated with a calf during any given feeding season could have been sighted only after her calf was weaned, or potentially not observed at all, such that an observed calving interval might actually represent two separate intervals. In general, such a scenario was assumed atypical given the marked seasonal site fidelity to the study area exhibited by females and their calves (Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*. 1999, 2000), and the infrequency of first sighting calves during a field season after weaning has occurred (*n*=4 of 22 calves identified between 1997 and 2002; Brownell and Weller, 2002; Weller *et al*., 2003b). Further, suggesting that the observed calving interval represents two intervals would have introduced one-year calving intervals in eight of the 10 cases, and annual breeding is considered rare for this species (Jones, 1990).

The remaining two cases are the observed four-year calving intervals of whales No. 005 and No. 015 (Table 3.1). These females both had calves in 1998 and 2002, but it is biologically plausible that one or both of them produced a calf in 2000 that survived until the feeding season. Although whales No. 005 and No. 015 were sighted in 2000, they were first observed on 12 August and 30 July, respectively (Weller *et al*., 2001). Both dates are within the range of known weaning times for western gray whales (Weller *et al*., 1999, 2000, 2001, 2003a, 2003b; Würsig *et al*. 1999, 2000). Further, one of the three calves identified in 2000 was first sighted post-weaning (Weller *et al*., 2001), so its mother was unaccounted for (although planned genetic testing could clarify this issue; Brownell and Weller, 2002). Therefore, suggesting that the observed four-year calving intervals could represent two two-year intervals is not an unreasonable assumption.

The goal of calculating the average western gray whale calving interval is to estimate apparent fecundity, and subsequently the current growth rate. While averaging the 10 observed intervals might underestimate apparent fecundity because of a possible capture probability influence, assuming that the observed four-year calving intervals represent two two-year intervals could overestimate apparent fecundity. That is, if whale No. 005 or whale No. 015 produced a calf in 2000 that did not survive until the feeding season, an overestimate of apparent fecundity (and the violation of the aforementioned l_1=1 assumption) would result. Therefore, the preferred approach was to bracket a likely range of fecundity values, and thus growth rate estimates. Consequently, a low, medium, and high estimate of calving interval was incorporated into a separate fecundity and growth rate estimation. The low calving interval estimate was the average of the 10 observed intervals; the high estimate was the average with both of the observed four-year intervals representing two two-year intervals (n=12). The medium calving interval estimate attributed two two-year calving intervals to either whale No. 005 or whale No. 015 (n=11). The low, medium, and high calving interval values were selected from a normal distribution with a mean of 3.1 (SE=0.18), 2.8 (SE=0.18), and 2.6 (SE=0.15), respectively.

The ASM indicates the first age class with non-zero fecundity in the m_x schedule. As the first age class in the Lotka equation is usually composed of age 0 individuals, m_{ASM+1} is generally the first non-zero value. However, given the previously described 6-8 month offset in the age classes, the first non-zero fecundity value was set at age class ASM. The ASM of western gray whales is unknown, but a median value of 6 years (range 5-9 years) has been estimated for eastern gray whales (see Reilly, 1992 for a summary of eastern gray whale biological parameters). Assuming that eastern and western gray whales share similar reproductive capabilities, values for western gray whale ASM were selected from a discrete uniform distribution of 5-9 years.

According the Equation 3.4, non-zero values of m_x are conditional on the survival of mature females. Given that the ϕ_x used to calculate these values was a non-calf estimate (i.e., based on observations of juvenile and adult whales), and that juvenile survival rates are likely lower than those of adults (Caughley, 1966), there was an inherent negative bias in the fecundity estimates that could not be avoided given the available data. However, population growth rates of long-lived animals are least sensitive to changes in fecundity rates (Goodman, 1981; Taylor and DeMaster, 1993). Hence, the impact of the negatively biased fecundity values on the resulting growth rate estimates was presumed to be minimal.

Statistical Methods

In order to account for the uncertainty of the input life history parameters, the 1997-2002 western gray whale population growth rate was estimated using a Monte Carlo simulation method (e.g., Cox and Baybutt, 1981). Values of the life history parameters were randomly selected from their associated distributions and incorporated into the Lotka equation, and a growth rate specific to that set of parameters was determined. This process was conducted a large number of times (*n*=10,000), producing a growth rate estimate in the form of a distribution. The simulation routine was performed employing the low, medium, and high estimates of calving interval, generating a *conservative*, *intermediate*, and *liberal* growth rate estimate, respectively. Pseudocode for the growth rate estimation procedure is provided in Appendix C.

Back Calculation

Population Dynamics Model

Complex models with more parameters usually provide better fits to data than simpler models. However, simpler models often offer more insight into the modeled system than accurate numerical fits (Hilborn and Mangel, 1997). Thus, the population dynamics model used in the first quantitative western gray whale back calculation was the age-independent generalized logistic equation (e.g., Pella and Tomlinson, 1969), altered for discrete (in this case, year-to-year) growth:

$$N_{t+1} = N_t + N_t r_{MAX}\left[1-\left(\frac{N_t}{K}\right)^z\right] - C_t \qquad \text{(Equation 3.5)}$$

where t = time in integer years from 1900 to 2002

N_{t+1} = population size at time t+1
N_t = population size at time t
r_{MAX} = maximum net recruitment rate
K = carrying capacity
z = shape parameter
C_t = catch at time t.

The shape parameter (z) controls the amount of non-linearity in the density-dependent function, which sets the maximum net productivity level (MNPL) (Taylor and DeMaster, 1993; Wade, 1998), according to the relationship (e.g., Smith, 1983):

$$MNPL = \frac{K}{(1+z)^{1/z}} \qquad \text{(Equation 3.6)}$$

Marine mammal populations are thought to exhibit concave non-linear density dependence, such that MNPL>0.5*K* making z>1.0 (Eberhardt and Siniff, 1977; Taylor and DeMaster, 1993; Fowler, 1994). However, available data make it difficult to estimate MNPL for any marine mammal population. Allowing MNPL>0.5*K* for marine mammals is viewed by Eberhardt and Siniff (1977) as a conservative management policy. Therefore, MNPL was assumed to occur at 0.6*K* (i.e., z=2.39) in the present analysis.

As the projection began in 1900, N_{1900} became an additional parameter in the model. Thus, the set of parameters (θ) specified by the model were r_{MAX}, K, and N_{1900}. Two status indices ($\hat{N}_{2002}/K$ and $\hat{N}_{2002}/N_{1900}$) were also calculated using a model output ($\hat{N}_{2002}$) and two model parameters (N_{1900} and K). Assumptions of the generalized logistic equation are: 1) growth of the population is dependent on population size (i.e., density dependence); 2) the population was initially at a stable age distribution; 3) K is constant; 4) catch values are known, and 5) catch rates are proportional to the size of each age class. Information is sparse regarding both the age-specific selectivity of whalers before and after 1900 and the general uncertainty (e.g., under-reporting and whales struck, but lost) in the post-1900 catch data. Consequently, assumptions 2, 4, and 5 were possibly violated by using this model to characterize western gray whale population dynamics. Examining the validity of model assumptions was not an objective of the present analysis, but should be considered in future assessments.

Realistically, the main status determination objective of the back calculation was to estimate N_{1900}. Although K was technically an estimated parameter, the lack of contrasting observed growth rate estimates (i.e., from periods of both low and high abundance) was expected to provide little information about this parameter. Hilborn and Mangel (1997) illustrate a case where the generalized logistic model was fitted to a series of abundance estimates for Serengeti wildebeest (*Conochaetes taurinus*). Although there was excellent agreement between the model predictions and the observed data, the abundance estimates were uninformative in determining carrying capacity (i.e., K was completely undefined). The abundance estimates merely indicated that K could be any value large enough to account for the increasing population size observed during the study period.

Statistical Methods

A Bayesian statistical method (e.g., Press, 1989; Gelman *et al*., 1995) was used to estimate the model parameters and the status indices. The likelihood function for the parameters calculated the likelihood of the model predicted 1997-2002 growth rate

($r_{1997-2002}^{\text{model}}$) given the observed estimate of 1997-2002 growth rate from the life history data ($r_{1997-2002}^{\text{LH data}}$), where:

$$r_{\text{1997-2002}}^{\text{model}} = \frac{\sum_{t=1997}^{2001}\left(\frac{N_{t+1}}{N_t} - 1\right)}{5} \qquad \text{(Equation 3.7)}$$

Assuming the observed 1997-2002 growth rate estimate was normally distributed with standard deviation (σ_r), the likelihood function was:

$$L(\theta \mid r_{\text{1997-2002}}^{\text{LH data}}, \sigma_r) = \frac{1}{\sqrt{2\pi}\sigma_r} e^{-\frac{1}{2}\left(\frac{r_{\text{1997-2002}}^{\text{LH data}} - r_{\text{1997-2002}}^{\text{model}}}{\sigma_r}\right)^2} \qquad \text{(Equation 3.8)}$$

In order to integrate the product of the prior distributions of the parameters and the likelihood function, the Sample-Importance-Resample (SIR) algorithm (Rubin, 1988; Smith and Gelfand, 1992) was used. SIR requires randomly selecting values of the parameters from their joint prior distributions to form a sample set θ_i, of which the associated likelihood is calculated and stored. The process is repeated until an initial sample of n_1 θ_i s and likelihoods is generated. The n_1 θ_i s are then resampled with replacement n_2 times, with probability equal to weight q_i, where:

$$q_i = \frac{L(\theta_i \mid r_{1997-2002}^{\text{LH data}}, \sigma_r)}{\sum_{j=1}^{n_1} L(\theta_j \mid r_{1997-2002}^{\text{LH data}}, \sigma_r)} \qquad \text{(Equation 3.9)}$$

The resample serves as a random sample of size n_2 from the joint posterior distributions of the parameters (Rubin, 1988).

In the present analysis, a large value of n_1 was established (n_1=2,000,000) to ensure convergence of the integration by avoiding potentially overly influencing the resample with repetitive values. However, to confirm that the initial sample was large enough, the maximum number of times a single θ_i appeared in the resample and the number of unique θ_is in the resample were enumerated. The value of n_2 was set to 5,000 in order to yield sufficiently smooth posterior distributions. The entire back calculation was repeated three times, fitting the population dynamics model to the *conservative*, *intermediate*, and *liberal* 1997-2002 growth rate estimate, respectively. Pseudocode for the back calculation routine is shown in Appendix D.

Prior Distributions

The prior distribution for r_{MAX} was a uniform distribution (U) from 0.00 to 0.10, which was more restrictive than the prior distribution of U(0.01, 0.13) used in the population assessment of eastern gray whales by Wade (2002). However, given the small present population size, the posterior distribution of r_{MAX} was expected to closely approximate the distribution of the specified $r_{1997-2002}^{\text{LH data}}$ and associated standard deviation. The 95th percentiles of the three 1997-2002 growth rate estimates were all well below 0.10 (Table 3.2). Although the 5th percentiles of the *conservative* and *intermediate* 1997-2002 growth rate estimates were both less than 0.00 (Table 3.2), a maximum net recruitment rate below zero was considered biologically implausible.

The prior distribution for K was U(1,500, 20,000). While Yablokov and Bogoslovskaya (1984) hypothesized that the western gray whale population might have previously numbered between 1,500-10,000 whales, there is no quantitative basis for this estimate. Yet, given the over 400-year history of western gray whaling, a value of K less than 1,500 whales was considered highly improbable. Previous speculation (Yablokov and Bogoslovskaya, 1984) and genetic inference (LeDuc *et al*., 2002) suggest that the western gray whale population was never as large as that of the eastern population. Recent point estimates of eastern gray whale carrying capacity range from approximately 25,000 to 32,000 whales (Wade, 2002). Thus, a range of upper bounds for the prior distribution of K between 10,000 and 40,000 was explored for use in the western gray whale back calculation. These preliminary analyses demonstrated that any value within this range could be utilized as an upper prior bound without influencing the general results of the back calculation. Therefore, to avoid potentially increasing the number of initial samples and resamples (which would require more computation time), an upper bound for K of 20,000 was established, with the recognition that this value is somewhat arbitrary. However, to demonstrate the minimal effect a different upper bound for K within the aforementioned range would have on the back calculation results, an additional back calculation was performed. This analysis duplicated the back calculation incorporating the *intermediate* estimate of $r_{1997-2002}^{\text{LH data}}$, with the exception of a prior distribution for K of U(1,500, 10,000).

The prior distribution for N_{1900} was initially set as U(500, 20,000). Given that the population sustained a harvest of at least 1,100 whales between 1900 and 1915 (Figure 1.1; Appendix A), a value of N_{1900} less than 500 whales was regarded as unlikely. For each draw of N_{1900}, the upper bound of the prior was constrained to be less than the value of *K* selected in that sample. However, preliminary analyses revealed that forward projections from most N_{1900} values selected from the upper portion of the prior distribution could not produce a depleted population in 2002. Given that the likelihood function was based on the observed 1997-2002 growth rate, a mechanism to penalize such trajectories was not in place. Thus, the *backwards* method described by Butterworth and Punt (1995) was implemented. In this approach, a current estimate of absolute abundance is treated as a model input along with the other model parameters, with the exception of the projection starting population size parameter. For each sample, these model inputs are selected from their prior distributions, and then used to calculate the initial population level corresponding to those values. That is, the population is projected *backwards* from the current abundance estimate to the starting population level. Therefore, the prior for initial population size is implicitly determined by the priors for the other parameters (Butterworth and Punt, 1995).

The mark-recapture estimate of the number of western gray whales associated with the Piltun study area in 2002, which is considered to closely approximate current population size (Figure 1.2; Wade *et al.*, 2003), was utilized as a model input (N_{2002}) in the western gray whale back calculation. The prior distribution for N_{2002} was normally distributed with mean 98 and standard error 5 (Figure 1.2; Wade *et al.*, 2003). During each initial sample, the randomly selected values from the priors for r_{MAX}, *K*, and N_{2002} were used to calculate a corresponding N_{1900} within the aforementioned prior distribution for this parameter. Specifically, this process was accomplished by using a bisection approach to find the value of N_{1900} between 500 and *K*, given the prior draws of r_{MAX}, *K*, and N_{2002}, that would minimize the difference (i.e., residual) between $\hat{N}_{2002}$ and N_{2002}. That is, N_{1900} was initialized at a value halfway between 500 and *K*, only to become the new upper or lower bound of possible N_{1900} values if the $\hat{N}_{2002}$ and N_{2002} residual was positive or negative, respectively. A value of N_{1900} halfway between the boundaries of the redefined interval was examined, and the bisection routine continued until $\hat{N}_{2002}$ was very close to (arbitrarily defined to mean within five whales of) N_{2002}. At that point, the exact value of N_{1900} was solved for that would minimize the squared residual of $\hat{N}_{2002}$ and N_{2002}, which finally completed the θ_i for that initial sample. Thus, although the resultant N_{1900} was always within the initially designated prior distribution, the actual prior for N_{1900} was a non-uniform distribution dictated by r_{MAX}, *K*, and N_{2002}.

Preliminary analyses revealed that not all combinations of r_{MAX} and *K* (particularly with high values of r_{MAX}) could produce an estimate of $\hat{N}_{2002}$ that closely approximated N_{2002}, regardless of the value of N_{1900} (i.e., the bisection routine could not find an N_{1900} 'solution'). Since the likelihood function was based solely on the observed and predicted 1997-2002 growth rate estimates, a diagnostic was implemented to identify and penalize such parameter sets. That is, before the bisection procedure was initiated with the selected θ_i, N_{1900} was set at both 500 and *K*. If the resulting trajectories did not bracket

N_{2002} (i.e., the $\hat{N}_{2002}$ and N_{2002} residuals were either both positive or both negative), then that θ_i was assigned a likelihood of zero.

As the $r_{1997-2002}^{\text{LH data}}$ utilized in the likelihood function had some basis in the mark-recapture analyses of the western gray whale photographic dataset (i.e., through the survival estimates), concern may be expressed about the lack of independence between $r_{1997-2002}^{\text{LH data}}$ and the mark-recapture estimate used to generate N_{2002}. However, the only data that are shared between these two estimates are the monthly sightings used to estimate capture probability in 2002. Further, a lack of covariance was found between capture probability in 2002 and the non-calf and calf survival estimates. Therefore, the estimates of $r_{1997-2002}^{\text{LH data}}$ and N_{2002} were treated as independent values.

RESULTS

Growth Rate Estimation

Estimates of the *conservative*, *intermediate*, and *liberal* 1997-2002 population growth rates are displayed in Table 3.2. As expected, the sequence of these estimates reflects the incorporation of the low, medium, and high fecundity values, respectively, with higher fecundity estimates resulting in increased growth rates. The growth rate estimates suggest that the western gray whale population was increasing during the observation period (Table 3.2, Figure 3.1). However, in each case, the left tails of the distribution indicate that some combinations of the life history parameters produced a negative growth rate (Figure 3.1).

Back Calculation

The maximum number of times a single θ_i appeared in the resample of each of the three back calculations was two, and the number of unique θ_i s in each of the three resamples was greater than 4,950. Given the small number and reduced extent of repetitive parameter sets in the resample of each version of the back calculations, the size of each initial sample (n_1=2,000,000) was considered adequate for integration convergence. A summary of the back calculation model parameters and status indices according to the *conservative*, *intermediate*, and *liberal* 1997-2002 population growth rate scenarios is shown in Table 3.3.

As expected, the point estimate and posterior distribution for r_{MAX} in each of the three back calculations closely resembled the value and distribution for $r_{1997-2002}^{\text{LH data}}$ used in model fitting (Tables 3.2-3.3, Figures 3.1-3.2). That is, given the model of population dynamics and the small present population size, the western gray whale population is essentially currently growing at its maximum net recruitment rate. However, the left tails of each r_{MAX} posterior distribution (Figure 3.2) and corresponding $r_{1997-2002}^{\text{LH data}}$ distribution (Figure 3.1) differed, as the prior distribution for r_{MAX} prevented negative values of this parameter.

As anticipated, the point estimate and posterior distribution for K in each of the three back calculations reproduced the prior distribution for this parameter (Table 3.3, Figure 3.3). That is, any value of K within the prior distribution could support likely combinations of the other parameters. In other words, the carrying capacity of western gray whales is undefined. The same situation resulted in the additional *intermediate* $r_{1997-2002}^{\text{LH data}}$ scenario back calculation utilizing the prior distribution of U(1,500, 10,000) for *K* (Figure 3.4A). The posterior distributions and point estimates for the other model parameters and status indices in this analysis duplicated those resulting from the initial *intermediate* back calculation (Table 3.3), with the exception of $\hat{N}_{2002} / K$ (see below).

The point estimate and posterior distribution for N_{1900} in each of the three back calculations indicate that only values within the lower range of the investigated prior distribution were able to produce a depleted population in 2002 using the *backwards* method and the likelihood function (Table 3.3, Figure 3.5). The resulting N_{1900} posterior distributions were negatively correlated with the observed 1997-2002 population growth rate estimates incorporated in the back calculations (Figure 3.5). That is, as the value of $r_{1997-2002}^{\text{LH data}}$ increased, the value of N_{1900} that was required to minimize the residual between $\hat{N}_{2002}$ and N_{2002} decreased.

The point estimate and posterior distribution for the status index $\hat{N}_{2002} / K$ were essentially the same between each version of the back calculation (Table 3.3, Figure 3.6), reflecting the similarity between each posterior distribution for *K* (Figure 3.3). Although the back calculation procedure did not define a value of western gray whale carrying capacity, the resulting $\hat{N}_{2002} / K$ suggests that the population is currently less than one percent of its original size (Figure 3.6). However, the posterior distribution for $\hat{N}_{2002} / K$ is the one model output dictated by the selected upper bound of the prior distribution for

K. That is, the $\hat{N}_{2002} / K$ distribution would shift to the left or right if the upper bound was increased or decreased, respectively. A slight rightward shift is evident in the posterior distribution for $\hat{N}_{2002} / K$ resulting from the back calculation using the *intermediate* 1997-2002 growth rate estimate and the prior distribution of U(1,500, 10,000) for K (Figure 3.4B; Median=0.017, 5th-95th Percentiles=0.010-0.049).

Yet, the posterior distribution for $\hat{N}_{2002} / K$ would never shift farther to the right than the posterior distribution for the status index $\hat{N}_{2002} / N_{1900}$, as N_{1900} can only be less than or equal to K in the back calculation (although the over 300-year history of western gray whaling prior to 1900 implies that the population size was already reduced by that year; Omura, 1984). Thus, the resulting $\hat{N}_{2002} / N_{1900}$ values can be interpreted as a maximum estimate of current population size relative to K. The three back calculation point estimates and posterior distributions for $\hat{N}_{2002} / N_{1900}$ suggest that the western gray whale population is currently *at most* between 8-9% of its original size (Table 3.3, Figure 3.7). The $\hat{N}_{2002} / N_{1900}$ posterior distributions were positively correlated with the value of $r_{1997-2002}^{\text{LH data}}$ used in model fitting (Figure 3.7). That is, values of $\hat{N}_{2002} / N_{1900}$ were smaller for the lower estimates of $r_{1997-2002}^{\text{LH data}}$, meaning that the population is most depleted according to the *conservative* back calculation scenario.

Results of the three back calculations reveal that the western gray whale population is presently highly depleted (Figure 3.7). Interestingly, findings from each of the three back calculations also indicate that the population has been highly depleted (i.e., less than 10% of its size in 1900) for over 70 years (Figure 3.8). In other words, the western gray whale population spent over half of the 20^{th} century at extremely low population densities.

DISCUSSION

Growth Rate Estimation

Although variations have been documented, biological and observational data collected when eastern gray whales were recovering have indicated that the population has predominantly adhered to a two-year calving interval (e.g., Rice and Wolman, 1971; Blokhin, 1984; Jones, 1990). Evidence exists that, at least during the late 1980's, pregnancy rates of eastern gray whales have declined (Reilly, 1992). Density dependent mechanisms would suggest that lower pregnancy rates (i.e., increased calving intervals) would be attributed to the population reaching higher densities (e.g., Fowler, 1981). If the reproductive potentials of eastern and western gray whales are comparable, then a maximized reproductive output based on a two-year calving interval would be expected for the low-density western gray whale population. However, the low, medium, and high western gray whale fecundity values used in the growth rate estimation were all based primarily on three-year calving intervals (see Brownell and Weller, 2002 for a potential explanation of the three-year calving interval phenomenon).

Despite the estimates of longer calving interval and reduced calf survival (Chapter 2), the 1997-2002 population growth rate estimates imply that the population was increasing during that time (Table 3.2, Figure 3.1). However, the calculated growth rates are relatively low compared to estimates from other depleted populations of baleen whales. Best (1993) summarized the growth rates of 10 severely depleted baleen whale populations (i.e., estimated to be less than 10% of their original population size at one time), including one bowhead, four right, one gray (eastern), one blue, and three humpback whale populations. These growth rate estimates ranged from 0.031 to 0.144, but were not necessarily measured when the populations were at their lowest levels. Depletion levels were known for five of the 10 populations, and demonstrated that higher growth rates corresponded to more depleted populations (Best, 1993). Yet, the 1997-2002 growth rates calculated for the severely depleted western gray whale population (i.e., at most between 8-9% of its original size; Figures 3.6-3.7) are markedly lower than the growth rate estimates of the three most depleted populations (i.e., ~3-20% of their initial population level during the observation period) discussed in Best (1993). However, drawing conclusions from this contrast is imprudent, as the growth rate values of these three populations (i.e., one right and two humpback whale populations) have large (or unknown) associated errors (Best, 1993).

A potentially more meaningful comparison can be made between the two gray whale populations. The trajectory of abundance estimates for eastern gray whales showed an annual rate of increase of 0.032 (SE=0.0055) during the period when the population doubled from about 10,000 to 20,000 whales, while maintaining an aboriginal harvest averaging approximately 175 whales per year (Reilly, 1992). Thus, estimates of their maximum net recruitment have ranged from 0.05-0.08 in stock assessments (e.g., Wade, 2002; Wade and Perryman, 2002). The small size of the western gray whale population implies that they are likely currently growing at their maximum net recruitment rate. Results of the back calculation support this suggestion (Figure 3.2). Yet, the current western gray whale population growth rate estimates (Figure 3.1) are essentially half in value of the range of maximum net recruitment rates attributed to eastern gray whales. This difference in estimated maximum growth rates between the two populations is likely due to varying natural and anthropogenic influences (e.g., prey availability and human-caused mortality, respectively) on individual life history parameters, although the specific causes are unclear. However, given that the 1997-2002 western gray whale population growth rate estimates do include the effect of possible human-caused mortality (e.g., direct catching, entanglement in fishing gear), these values (and thus estimates of r_{MAX}) may be lower than the actual biological maximum growth rate of the population.

Interestingly, genetic evidence predicted that the rate of population increase of western gray whales could be comparatively low. LeDuc *et al*. (2002) detected the presence of 10 haplotypes in biopsy samples of western gray whales, which was higher than expected. In contrast, only five haplotypes have been identified for western North Atlantic right whales, a population estimated to consist of approximately 300 individuals (Malik *et al*., 2000). A possible explanation for the high retention of haplotypes in western gray whales is that the depleted population has grown much more slowly since 1966 (the last year of reported modern commercial western gray whaling; Brownell and Chun, 1977; Kato and Kasuya, 2002) than recovering eastern gray whales (LeDuc *et al*., 2002). If the population growth rate of western gray whales had been higher than the eastern gray whale rate of 0.032, then the western gray whale populations would have been too low in 1996 to have included enough females to maintain 10 haplotypes (LeDuc *et al*., 2002).

Accounting for uncertainty in the western gray whale life history parameters revealed that some combinations of these values resulted in a negative growth rate (Figure 3.1). A population exhibiting a negative population growth rate is doomed to extinction, unless anthropogenic factors contributing to the population decline (e.g., human-caused mortality, habitat degradation) can be identified and mitigated. Thus, conservation plans for western gray whales should reflect not only the depleted status of the population, but also the possibility that the population is currently declining. Future monitoring will allow for the refined estimation of the life history parameters, which is needed to further investigate the possibility that the population growth rate is not at a replacement level.

Back Calculation

The posterior distributions for r_{MAX} and K resulting from the three western gray whale back calculations were not surprising. As aforementioned, the small population size in conjunction with the model of population dynamics employed was expected to produce a distribution of r_{MAX} similar to the distribution of $r_{1997-2002}^{\text{LH data}}$ used in the likelihood function of each back calculation scenario (Figures 3.1-3.2). Carrying capacity was expected to be undefined, as the data (i.e., $r_{1997-2002}^{\text{LH data}}$) used to fit the population dynamics model were measured only when the population was at low densities. Data characterizing the western gray whale population at higher densities are necessary to make inferences about its carrying capacity. Alternatively, a back calculation in which the initial population size of the projection was assumed to be at a pre-exploitation equilibrium could be attempted. However, for reasons discussed above (e.g., the lack of required historical catch records), this task would currently be unfeasible without making numerous untestable assumptions.

Preliminary analyses exploring the full range of the initial prior distribution for N_{1900} demonstrated that forward projections from higher values could not generate a depleted population in 2002. Increasing the size of the initial samples to ensure that enough reasonable trajectories existed for integration convergence might have mitigated this problem, except that the $r_{1997-2002}$-based likelihood would not have penalized the unrealistic trajectories. Thus, these trajectories could have still appeared in the resample. Instead, allowing r_{MAX}, K, and N_{2002} to implicitly determine the prior distribution of N_{1900} via the *backwards* method (Butterworth and Punt, 1995) was a more appropriate and successful solution. An examination of the posterior distributions for N_{1900} illustrates the utility of the *backwards* method. That is, only a small range of values within the lower portion of the original N_{1900} prior distribution were able to produce a depleted 2002 population in conjunction with the incorporated values of $r_{1997-2002}^{\text{LH data}}$ (Figure 3.5).

The posterior distributions for N_{1900} indicate that the western gray whale population likely numbered around 1,000-1,200 individuals in 1900, when intensive modern commercial whaling for gray whales began (Kasahara, 1950; Kato and Kasuya, 2002). Omura (1984) proposed that the population at this time was already substantially reduced from its original size after sustaining centuries of pre-modern whaling harvests. However, as previously indicated, findings from the back calculations are not able to clarify the degree to which the population in 1900 was depleted from its pre-exploitation level. The estimates of N_{1900} are still important in determining the current status of western gray whales, as associated values of $\hat{N}_{2002} / N_{1900}$ can be regarded as a maximum estimate of current population size relative to *K*. The posterior distributions for $\hat{N}_{2002} / N_{1900}$ imply that the western gray whale is presently *at most* between 8-9% of its initial population size (Figure 3.7). Note that if the 20th century catches were actually higher than the minimum numbers used in the western gray whale back calculations, then a higher and lower value of N_{1900} and $\hat{N}_{2002} / N_{1900}$, respectively, would have been estimated by the analysis. Additionally, the possibility that the population is even further depleted, potentially down to a size below 1% of its original level, should not be disregarded (Figures3.4B and 3.6).

Significance

Perhaps the most significant result of the western gray whale back calculation analysis is the implication that the population spent a majority of the 20th century at extremely low population densities (Figure 3.8). The long-term depleted status of western gray whales raises concerns about the negative effects of the population remaining at low densities. Populations at low densities are subject to increased risk of extinction by threatening factors, such as environmental and anthropogenic catastrophes (Gilpin, 1987).

This extinction risk can be compounded by depensation (i.e., the Allee effect; Allee *et al.*, 1949; Dennis, 1989). In depensation, the population growth rate decreases with decreasing population density (see Fowler and Baker, 1991 for a review of population dynamics at low densities). Severe depensation implies the existence of a critical population density, below which the population will go extinct (Courchamp *et al.*, 1999). Factors such as inbreeding depression, demographic stochasticity (e.g., sex-ratio fluctuations), and reduced cooperative interactions (e.g., reproduction, resulting from the inability to find a mate) can lead to depensation (Fowler and Baker, 1991; Courchamp *et al.*, 1999).

Although empirical evidence supports the occurrence of such negative factors associated with low population densities (see Petersen and Levitan, 2001 for a recent review), little evidence of actual depensation exists in the scientific literature. Further, the role of depensation, if any, in the population dynamics of whales is unknown. However, issues relating to depensation should not be ignored, as the associated low-density effects could be enough to slow the recovery of a population, making it more vulnerable to extinction risk (Petersen and Levitan, 2001). Current threats to western gray whales could also inhibit the recovery of the population, increasing its susceptibility to all of the aforementioned low-density population effects (see Chapter 2 and Weller *et al.*, 2002c for discussions of current threats). Disturbances associated with the intensive multinational oil and gas development off the northeastern shelf of Sakhalin Island are of particular concern (Würsig *et al.*, 1999, 2000; Weller *et al.*, 2002c, 2002d).

Using findings of the back calculations to suggest a magnitude to which the recovery of western gray whales is threatened by current threats and low-density factors would be premature. However, the western gray whale back calculation population dynamics model and resulting parameter estimates could provide a framework for a population viability analysis (PVA) (Gilpin and Soulé, 1986), which could be used to compare estimates of the probability of western gray whale extinction. Results of a PVA could be interpreted through the use of a decision analysis, where probabilities of extinction would be presented relative to both alternative states of nature (e.g., r_{MAX}) and alternative anthropogenic actions (e.g., human-caused mortality).

In conclusion, the western gray whale population is small, highly depleted, and has a low population growth rate. Western gray whales are at risk from factors threatening low-density populations, and current threats could compound these risks. These points highlight the timely need for the increased protection, conservation, and management planning of this critically endangered population.

Table 3.1. Annual records of known reproductive western gray whale females photographically identified in the Piltun study area between 1995 and 2002 (no data were collected in 1996). 1 = photographically identified. XX = photographically identified with a calf. 0 = not photographically identified. *n* = the number of calving intervals (highlighted) observed for each female. Records compiled from Brownell and Weller (2002) and Weller *et al*. (2003b).

Whale ID	1995	1996	1997	1998	1999	2000	2001	2002	*n*
005	0	-	1	XX	1	1	1	XX	1*
007	1	-	1	1	1	1	XX	0	0
009	1	-	1	XX	1	1	XX	1	1
011	0	-	1	1	1	1	1	XX	0
015	0	-	1	XX	1	1	1	XX	1*
018	XX	-	1	XX	1	1	XX	0	2
019	XX	-	XX	1	1	XX	1	1	2
026	0	-	1	1	0	0	0	XX	0
031	0	-	XX	0	0	0	0	0	0
036	0	-	1	XX	1	1	XX	1	1
038	1	-	1	1	XX	0	1	1	0
040	0	-	1	1	XX	0	0	XX	1
043	1	-	0	0	1	1	1	XX	0
055	0	-	0	XX	1	1	XX	1	1
063	0	-	1	XX	0	1	1	1	0
087	0	-	0	0	1	XX	1	0	0
092	0	-	0	0	0	1	XX	1	0

**n* =2 when observed interval was assumed to represent two intervals.

Table 3.2. Summary of 1997-2002 western gray whale population growth rates (λ-1) resulting from a Monte Carlo simulation of 10,000 trials sampling from associated distributions for life history parameters, including a low (*conservative*), medium (*intermediate*), and high (*liberal*) estimate of calving interval (*CI*).

CI	λ-1	Median	Standard Deviation	5th-95th Percentiles
3.1 (SE=0.18)	*conservative*	0.026	0.0190	-0.008-0.054
2.8 (SE=0.18)	*intermediate*	0.031	0.0194	-0.003-0.061
2.6 (SE=0.15)	*liberal*	0.036	0.0198	0.001-0.066

Table 3.3. Summary of model parameters (r_{MAX}, K, and N_{1900}) and status indices ($\hat{N}_{2002}/K$ and $\hat{N}_{2002}/N_{1900}$) resulting from Bayesian back calculations of western gray whales using the SIR algorithm (n_1=2,000,000; n_2=5,000), incorporating the *conservative*, *intermediate*, and *liberal* estimates of 1997-2002 population growth rate ($r_{1997-2002}^{\text{LH data}}$) into the likelihood function.

$r_{1997-2002}^{\text{LH data}}$	Scenario	Parameter	Posterior Median	5th-95th Percentiles
0.026 (SD=0.0190)	*conservative*	r_{MAX}	0.028	0.005-0.058
		K	10,789	2,548-19,093
		N_{1900}	1,216	799-1,769
		$\hat{N}_{2002}/K$	0.009	0.005-0.038
		$\hat{N}_{2002}/N_{1900}$	0.080	0.054-0.123
0.031 (SD=0.0194)	*intermediate*	r_{MAX}	0.033	0.006-0.064
		K	10,919	2,487-19,089
		N_{1900}	1,137	744-1,739
		$\hat{N}_{2002}/K$	0.009	0.005-0.039
		$\hat{N}_{2002}/N_{1900}$	0.086	0.056-0.133
0.036 (SD=0.0198)	*liberal*	r_{MAX}	0.037	0.009-0.069
		K	10,953	2,541-19,031
		N_{1900}	1,071	693-1,666
		$\hat{N}_{2002}/K$	0.009	0.005-0.039
		$\hat{N}_{2002}/N_{1900}$	0.091	0.058-0.142

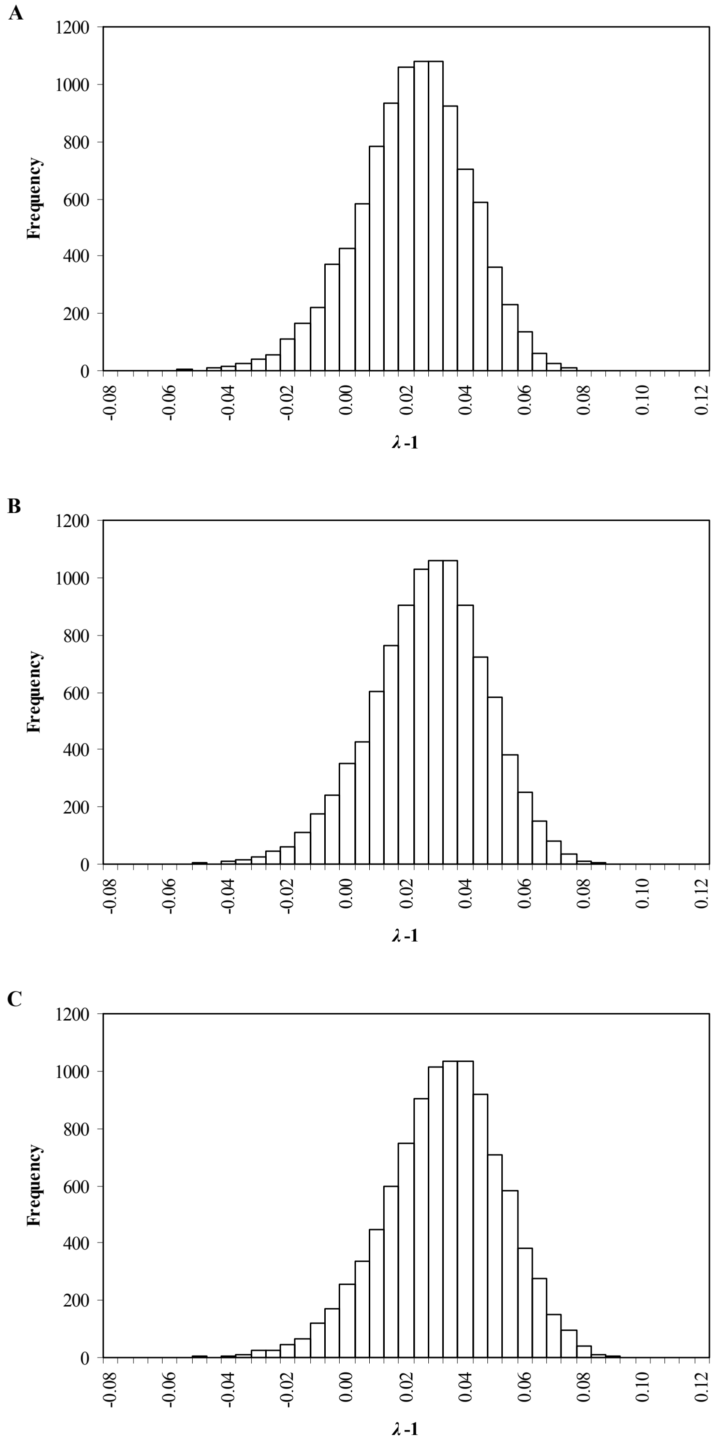

Figure 3.1. Histogram of values for the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate (λ-1).

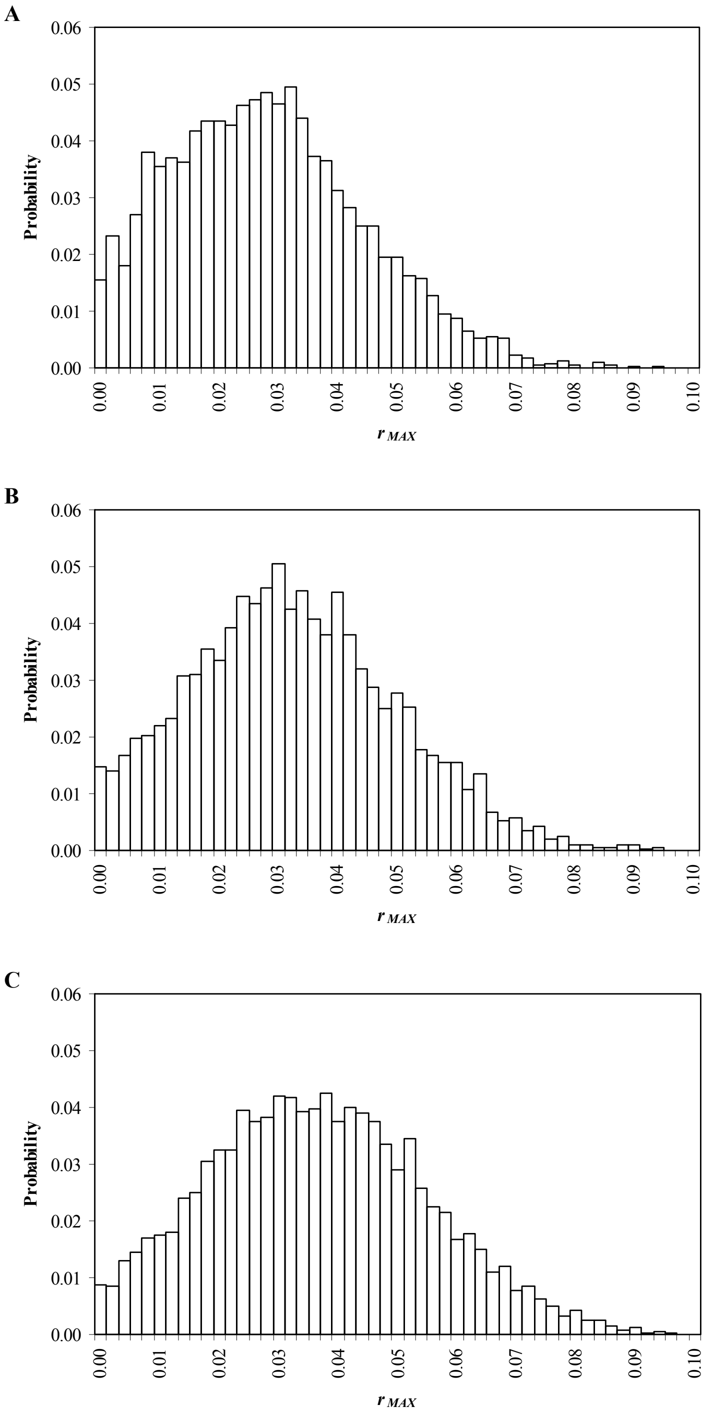

Figure 3.2. Posterior probability distributions for maximum net recruitment rate (r_{MAX}) resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate.

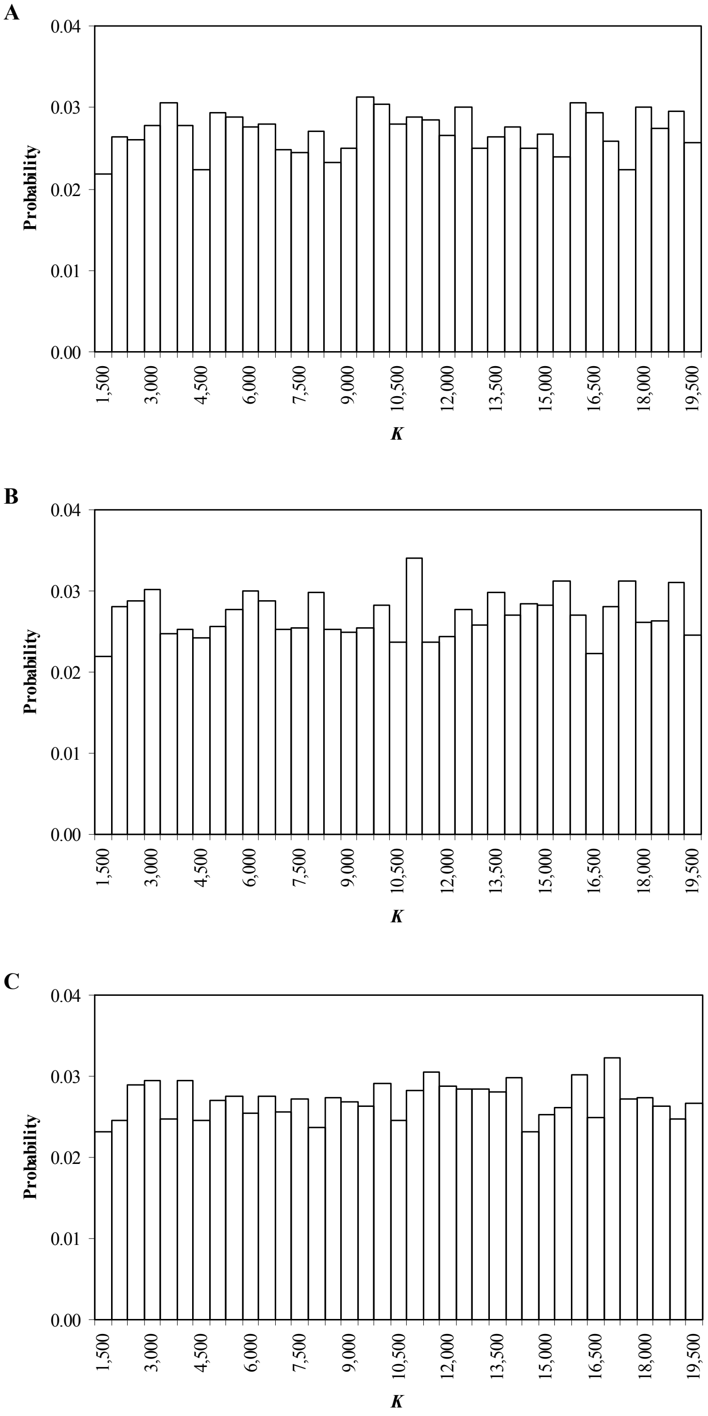

Figure 3.3. Posterior probability distributions for carrying capacity (*K*) resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate.

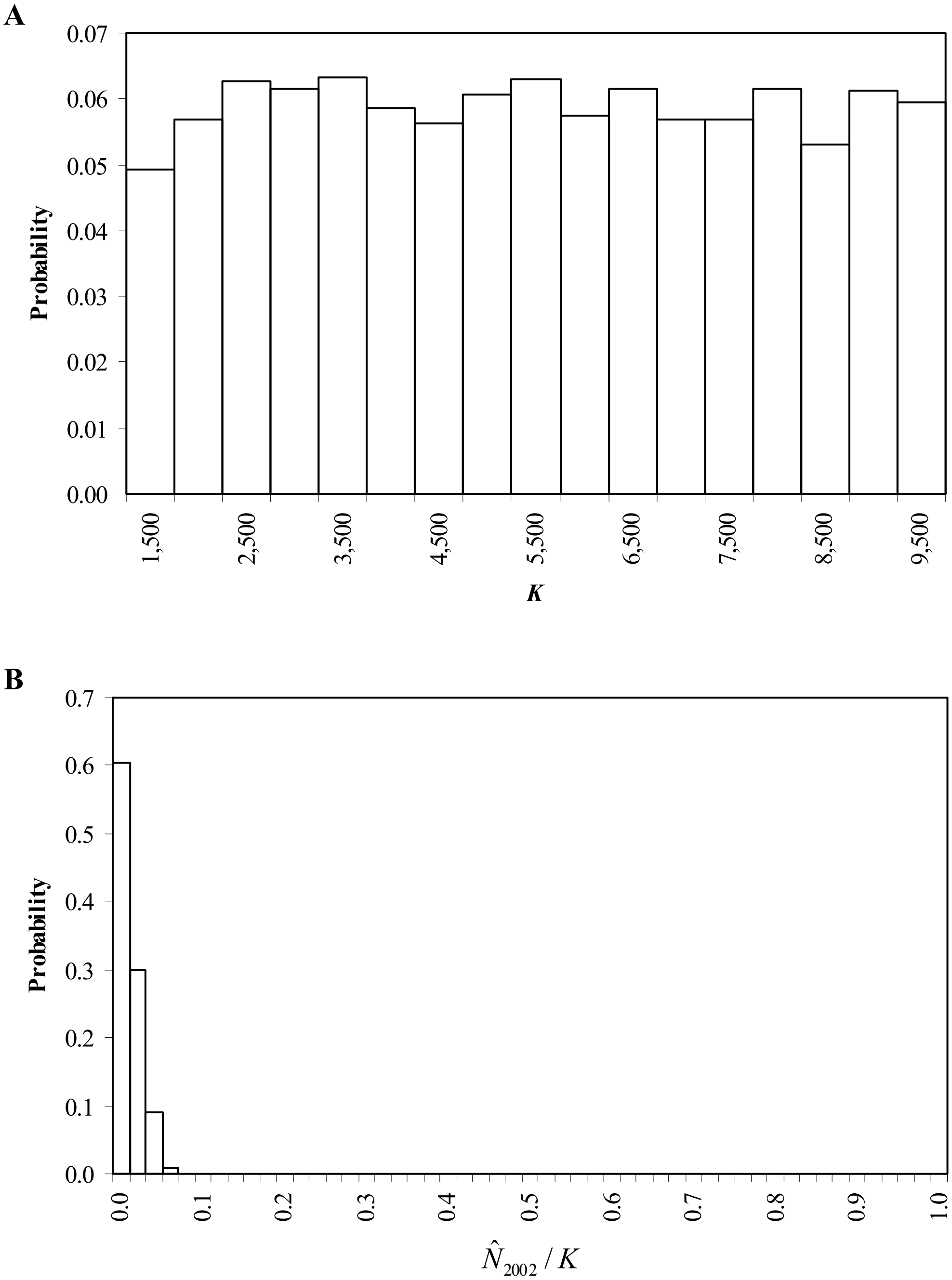

Figure 3.4. Posterior probability distributions for carrying capacity (*K*) (A) and a status index ($\hat{N}_{2002} / K$) (B) resulting from a back calculation using a prior distribution for *K* of U(1,500, 10,000) and the *intermediate* estimate of 1997-2002 population growth rate.

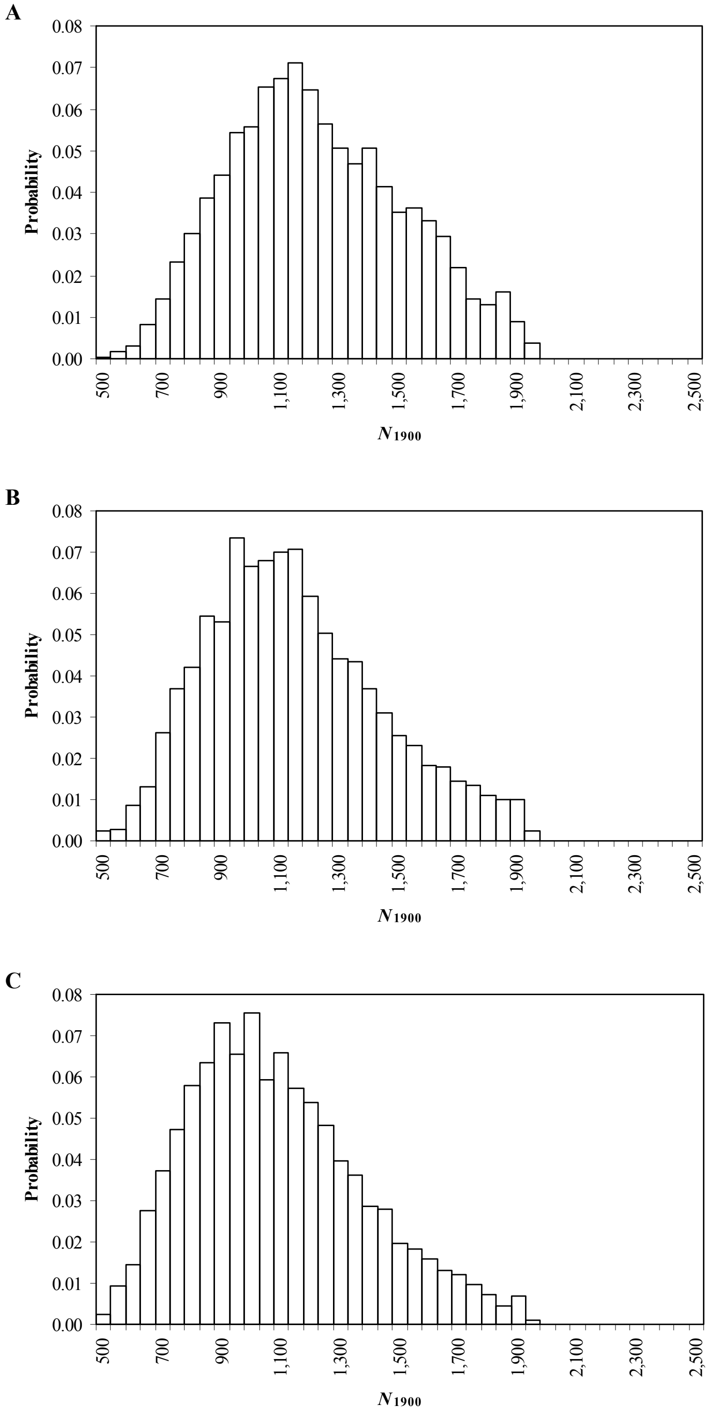

Figure 3.5. Posterior probability distributions for population size in 1900 (N_{1900}) resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate.

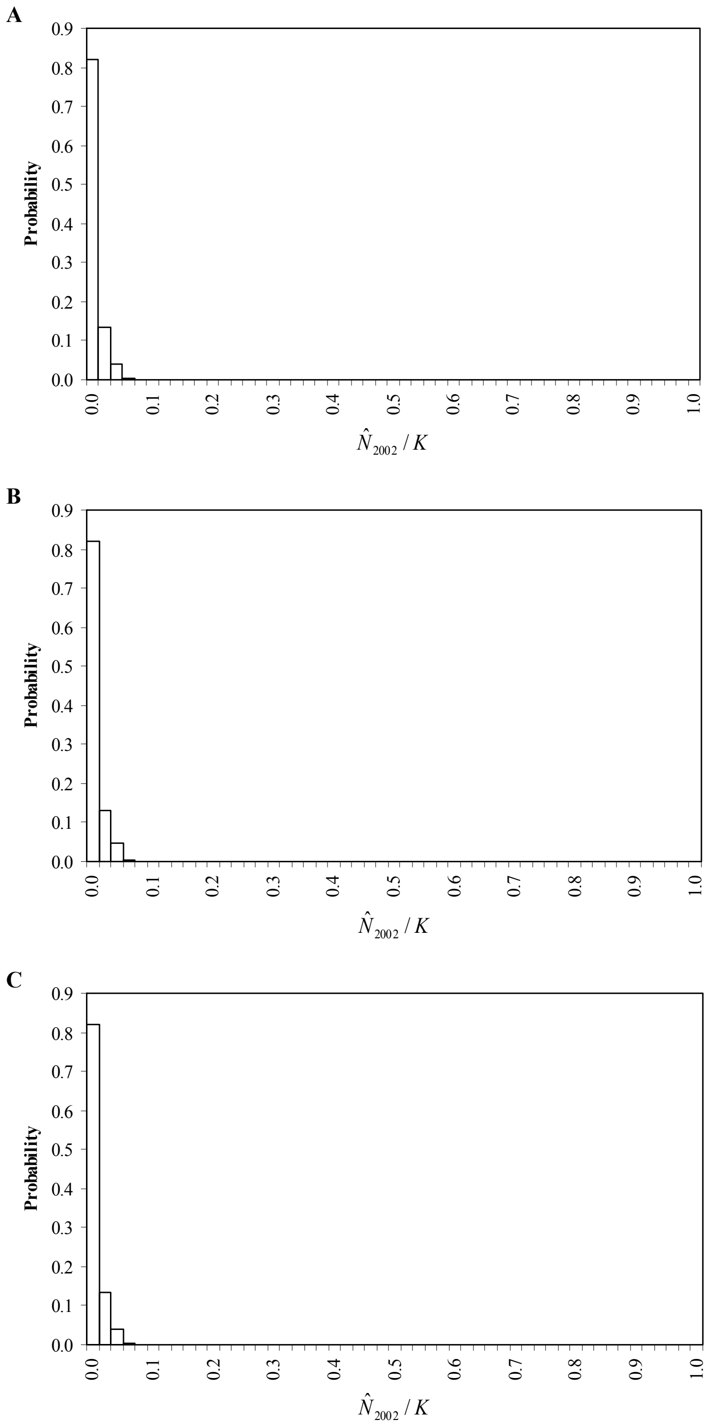

Figure 3.6. Posterior probability distributions for a status index ($\hat{N}_{2002} / K$) resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate.

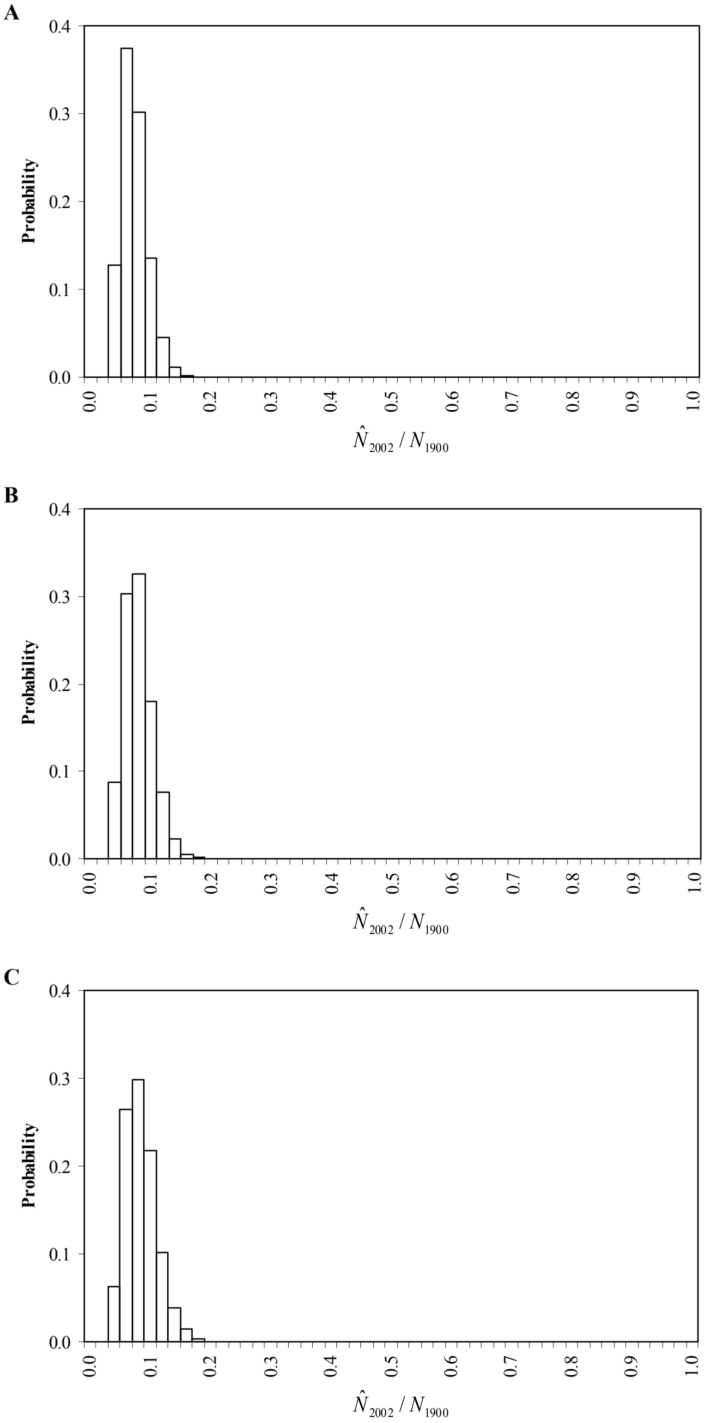

Figure 3.7. Posterior probability distributions for a status index ($\hat{N}_{2002} / N_{1900}$) resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate.

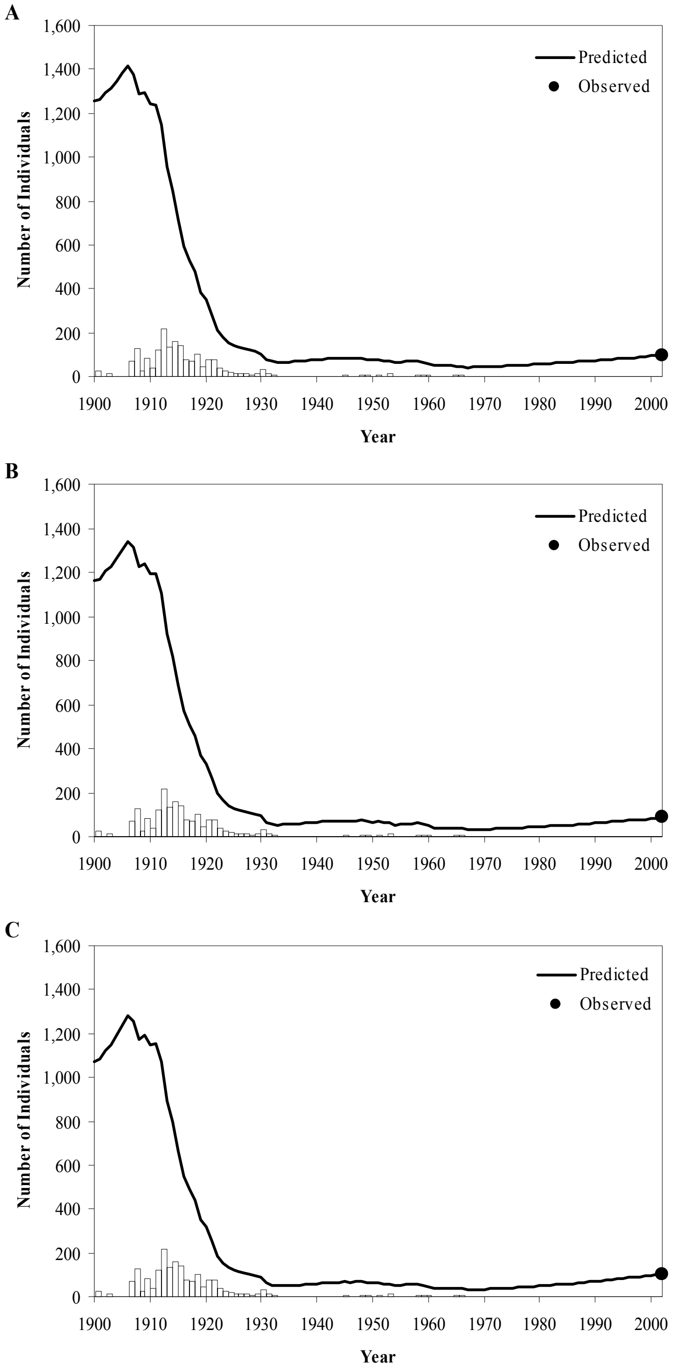

Figure 3.8. Twentieth century population projections resulting from back calculations using the *conservative* (A), *intermediate* (B), and *liberal* (C) estimates of 1997-2002 population growth rate. Predicted = the population dynamics model trajectory with the highest likelihood in the resample. Observed = the 2002 population size used in the *backwards* method. Bars = the minimum numbers of whales caught during the 20th century.

LITERATURE CITED

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, eds. Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia, PA.

ANDREWS, R. C. 1914. Monographs of the Pacific Cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). Memoirs of the American Museum of Natural History 1:227-287.

BALDRIDGE, A. 1972. Killer whales attack and eat a gray whale. Journal of Mammalogy 53:898-900.

BAKER, C. S., M. L. DALEBOUT, AND G. M. LENTO. 2002. Gray whale products sold in commercial markets along the Pacific coast of Japan. Marine Mammal Science 18:295-300.

BARLOW, J., AND P. J. CLAPHAM. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology 78:535-546.

BERZIN, A. A. 1990. Gray whales of the Okhotsk-Korean population in the Sea of Okhotsk. Paper SC/A90/G28 presented to the International Whaling Commission (unpublished).

BERZIN, A. A. AND V. L. VLADIMIROV. 1981. Changes in the abundance of whalebone whales in the Pacific and the Antarctic since the cessation of their exploitation. Report of the International Whaling Commission 31:495-499.

BERZIN, A. A., V. L. VLADIMIROV, AND N. V. DOROSHENKO. 1988. Results of aerial surveys to study the distribution and abundance of cetaceans in the coastal waters of the Sea of Okhotsk in 1986-1987. Pages 18-25 in N. S. Chernysheva, ed. Nauchno-issledovatel'skie ra'boty po morskim mlekopitayushchim severnoi chasti Tikhogo okeana v 1986-1987. All-Union Scientific Research Institute of Fisheries and Oceanography (VNIRO), Moscow. (in Russian).

BERZIN, A. A., V. L. VLADIMIROV, AND N. V. DOROSHENKO. 1990. Aerial surveys to determine the distribution and number of polar gray whales and beluga whales in the Sea of Okhotsk in 1985-1989. Izvestiya Tikhookeanskogo Nauchno-issledovatel'skogo Instituta Rybnogo Khozyaistva I Okeanografii (TINRO) 112:51-60. (in Russian).

BERZIN, A. A., V. L. VLADIMIROV, AND N. V. DOROSHENKO. 1991. Results of aerial surveys to study the distribution and abundance of whales in the Sea of Okhotsk in 1988-1990. Pages 6-17 in L. A. Popov, ed. Nauchno-issledovatel'skie ra'boty po morskim mlekopitayushchim severnoi chasti Tikhogo okeana v 1989-1990. All-Union Scientific Research Institute of Fisheries and Oceanography (VNIRO), Moscow. (in Russian).

BEST, P. B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science 50:169-186.

BEST, P. B., A. BRANDÃO, AND D. S. BUTTERWORTH. 2001. Demographic parameters of southern right whales off South Africa. Journal of Cetacean Research and Management (Special Issue 2):161-169.

BLOKHIN, S. A. 1984. Investigations of gray whales taken in the Chukchi coastal waters, USSR. Pages 487-509 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

BLOKHIN, S. A. 1996. Distribution, abundance and behavior of gray whales (*Eschrichtius robustus*) of American and Asian populations in regions of their summer location nearshore of the Far East. Izvestiya Tikhookeanskogo Nauchno-issledovatel'skogo Rybokhozyaistvennogo Tsentra 121:36-53 (in Russian).

BLOKHIN, S. A., M. K. MAMINOV, AND G. M. KOSYGIN. 1985. On the Korean-Okhotsk population of gray whales. Report of the International Whaling Commission 35:375-376.

BOGOSLOVSKAYA, L. S., L. M. VOTGOGOV, AND T. N. SEMENOVA. 1981. Feeding habits of the gray whale off Chukotka. Report of the International Whaling Commission 31:507-510.

BOWEN, S. L. 1974. Probable extinction of the Korean stock of the gray whale (*Eschrichtius robustus*). Journal of Mammalogy 55:208-209.

BRADFORD, A. L., A. M. BURDIN, P. R. WADE, Y. V. IVASHCHENKO, G. A. TSIDULKO, G. R. VANBLARICOM, AND D. W. WELLER. 2002. Survival estimates of western gray whales (*Eschrichtius robustus*). Paper SC/54/BRG9 submitted to the International Whaling Commission (unpublished).

BREIWICK, J. M., L. L. EBERHARDT, AND H. W. BRAHAM. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Science 41:484-496.

BROWNELL, R. L., JR., AND C. CHUN. 1977. Probable existence of the Korean stock of the gray whale (*Eschrichtius robustus*). Journal of Mammalogy 58:237-239.

BROWNELL, R. L., JR., AND T. KASUYA. 1999. Western gray whale captured off western Hokkaido. Paper SC/51/AS24 submitted to the International Whaling Commission (unpublished).

BROWNELL, R. L., JR., AND D. W. WELLER. 2001. Is the “carrying capacity hypothesis” a plausible explanation for the “skinny” gray whale phenomenon? Paper SC/53/BRG20 submitted to the International Whaling Commission (unpublished).

BROWNELL, R. L., JR., AND D. W. WELLER. 2002. Prolonged calving intervals in western gray whales: Nutritional stress and pregnancy. Paper SC/54/BRG12 submitted to the International Whaling Commission (unpublished).

BROWNELL, R. L., JR., S. A. BLOKHIN, A. M. BURDIN, A. A. BERZIN, R. G. LE DUC, R. L. PITMAN, AND H. MINAKUCHI. 1997. Observations on Okhotsk-Korean gray whales on their feeding grounds off Sakhalin Island. Report of the International Whaling Commission 47:161-162.

BUCKLAND, S. T. 1990. Estimation of survival rates from sightings of individually identifiable whales. Report of the International Whaling Commission (Special Issue 12):149-153.

BURDIN, A. M., G. A. TSIDULKO, Y. V. IVASHCHENKO, A. L. BRADFORD, AND D. W. WELLER. 2002. Photo-identification of western gray whales in coastal and offshore Sakhalin shelf waters. Paper SC/02/WGW4 submitted to the International Whaling Commission (unpublished).

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

BUTTERWORTH, D. S., AND A. E. PUNT. 1995. On the Bayesian approach suggested for the assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. Report of the International Whaling Commission 45:303-311.

BUTTERWORTH, D. S., J. L. KORRÛBEL, AND A. E. PUNT. 2002. What is needed to make a simple density-dependent response population model consistent with data for eastern North Pacific gray whales? Journal of Cetacean Research and Management 4:63-76.

CAUGHLEY, G. 1966. Mortality patterns in mammals. Ecology 47:906-918.

CASWELL, H., M. FUJIWARA, AND S. BRAULT. 1999. Declining survival probability threatens the North Atlantic right whale. Proceedings of the National Academy of Sciences 96:3308-3313.

CLAPHAM, P. J., S. B. YOUNG, AND R. L. BROWNELL, JR. 1999. Baleen whales: Conservation issues and the status of the most endangered populations. Mammal Review 29:35-60.

COLE, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103-137.

COMMITTEE FOR WHALING STATISTICS. 1942. International Agreement for the Regulation of Whaling. International Whaling Statistics 16:58-66.

COOKE, J. G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. Report of the International Whaling Commission 36:363-366.

COOKE, J. G., V. J. ROWNTREE, AND R. PAYNE. 2001. Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina. Journal of Cetacean Research and Management (Special Issue 2):125-132.

CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429-438.

COURCHAMP, F., T. CLUTTON-BROCK, AND B. GRENFELL. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14:405-410.

COX, D. C., AND P. BAYBUTT. 1981. Methods for uncertainty analysis: A comparative survey. Risk Analysis 1:251-258.

DARLING, J. D. 1984. Gray whales off Vancouver Island, British Columbia. Pages 265-280 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

DARLING, J. D., K. E. KEOGH, AND T. E. STEEVES. 1998. Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. Marine Mammal Science 14:692-720.

DENNIS, B. 1989. Allee effects: Population growth, critical density and the chance of extinction. Natural Resource Monitoring 3:481-538.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183-190.

FOWLER, C. W. 1981. Comparative population dynamics in large mammals. Pages 437-455 in C. W. Fowler and T. G. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

FOWLER, C. W. 1994. Further consideration of nonlinearity in density dependence among large mammals. Report of the International Whaling Commission 44:385-391.

FOWLER, C. W., AND J. D. BAKER. 1991. A review of animal population dynamics at extremely reduced population levels. Report of the International Whaling Commission 41:545-554.

FOWLER, C. W., AND D. B. SINIFF. 1992. Determining population status and the use of biological indices in the management of marine mammals. Pages 1025-1037 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Applied Science, New York, NY.

GABRIELE, C. M., J. M. STRALEY, S. A. MIZROCH, C. S. BAKER, A. S. CRAIG, L. M. HERMAN, D. GLOCKNER-FERRARI, M. J. FERRARI, S. CERCHIO, O. VON ZIEGESAR, J. DARLING, D. MCSWEENEY, T. J. QUINN II, AND J. K. JACOBSEN. 2001. Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean. Canadian Journal of Zoology 79:589-600.

GELMAN, A., J. B. CARLIN, H. S. STERN, AND D. B. RUBIN. 1995. Bayesian data analysis. Chapman and Hall, New York, NY.

GERRODETTE, T., AND D. P. DEMASTER. 1990. Quantitative determination of optimum sustainable population level. Marine Mammal Science 6:1-16.

GILPIN, M. E. 1987. Spatial structure and population vulnerability. Pages 125-139 in M. E. Soulé, ed. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

GILPIN, M. E. AND M. E. SOULÉ. 1986. Minimum viable populations: The processes of species extinctions. Pages 13-34 in M. E. Soulé, ed. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

GOLEY, P. D., AND J. M. STRALEY. 1994. Attack on gray whales (*Eschrichtius robustus*) in Monterey Bay, California, by killer whales (*Orcinus orca*) previously identified in Glacier Bay, Alaska. Canadian Journal of Zoology 72:1528-1530.

GOODMAN, D. 1981. Life history analysis of large mammals. Pages 415-436 in C. W. Fowler and T. G. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

GOODMAN, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. The Amercian Naturalist 119:803-823.

HAMMOND, P. S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Report of the International Whaling Commission (Special Issue 8):253-282.

HAMMOND, P. S., S. A. MIZROCH, AND G. P. DONOVAN, EDS. 1990. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission (Special Issue 12).

HARTVIGSEN, G. 2001. Carrying capacity, concept of. Pages 641-649 in S. A. Levin, ed. Encyclopedia of Biodiversity, Volume 1. Academic Press, San Diego, CA.

HATLER, D. F., AND J. D. DARLING. 1974. Recent observations of the gray whale in British Columbia. Canadian Field Naturalist 88:449-459.

HENDERSON, D. A. 1972. Men and whales at Scammon's Lagoon. Dawson's Book Shop, Los Angeles, CA.

HENDERSON, D. A. 1984. Nineteenth century gray whaling: Grounds, catches, and kills, practices and depletion of the whale population. Pages 159-186 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

HEYNING, J. E., AND T. D. LEWIS. 1990. Entanglements of baleen whales in fishing gear off southern California. Report of the International Whaling Commission 40:427-431.

HILBORN, R., AND M. MANGEL. 1997. The ecological detective. Confronting models with data. Princeton University Press, Princeton, NJ.

HILTON-TAYLOR, C. 2000. 2000 IUCN Red List of Threatened Species. IUCN/SSC, Gland, Switzerland and Cambridge, United Kingdom.

HOBBS, R. C., AND D. J. RUGH. 1999. The abundance of gray whales in the 1997/98 southbound migration in the eastern North Pacific. Paper SC/51/AS10 submitted to the International Whaling Commission (unpublished).

HUGGINS, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133-140.

HUGGINS, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725-732.

HURVICH, C. M., AND C.-L. TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.

INTERNATIONAL WHALING COMMISSION. 1950. International Convention for the Regulation of Whaling. Report of the International Whaling Commission 1:9-18.

INTERNATIONAL WHALING COMMISSION. 1951. Report. Report of the International Whaling Commission 2:3-8.

INTERNATIONAL WHALING COMMISSION. 1979. Chairman's report of the 30th annual meeting. Report of the International Whaling Commission 29:21-37.

INTERNATIONAL WHALING COMMISSION. 1980. 31st report of the commission covering the year 1978-1979. Report of the International Whaling Commission 30:10-14.

INTERNATIONAL WHALING COMMISSION. 1982. 33rd report of the commission covering the year 1979-1980. Report of the International Whaling Commission 32:3-7.

INTERNATIONAL WHALING COMMISSION. 1995. Chairman's report of the 46th annual meeting. Report of the International Whaling Commission 45:15-52.

IVASHCHENKO, Y. V. 1999. Distribution, numbers, and behavior of the Okhotsk-Korean gray whale population near the coast of Sakhalin. University Diploma. Yaroslavl State University. 62 pp. (in Russian).

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

JONES, M. L. 1990. The reproductive cycle in gray whales based on photographic resightings of females on the breeding grounds from 1977-82. Report of the International Whaling Commission (Special Issue 12):177-182.

KASAHARA, A. 1950. Whaling in the seas around Japan and its resource. Nihonsuisan K. K. Kenkyujo Hokoku, Tokyo 4:1-103. (in Japanese).

KATO, H. 1998. Japan. Progress report on cetacean research, May 1996 to April 1997. Report of the International Whaling Commission 48:329-337.

Kato, H., and T. Kasuya. 2002. Some analyses on the modern whaling catch history of the western North Pacific stock of gray whales (*Eschrichtius robustus*), with special reference to the Ulsan whaling ground. Journal of Cetacean Research and Management 4:277-282.

Kendall, W. L., and K. H. Pollock. 1992. The robust design in capture-recapture studies: A review and evaluation by Monte Carlo simulation. Pages 31-43 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Applied Science, New York, NY.

Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics 22:751-762.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293-308.

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

Kim, Z. G. 2000. Bycatch of minke whales in Korean waters, 1998. Journal of Cetacean Research and Management 2 (Supplement):103-104.

Krupnik, I. I. 1984. Gray whales and the aborigines of the Pacific Northwest: The history of aboriginal whaling. Pages 103-120 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

Lankester, K., and J. R. Beddington. 1986. An age-structured population model applied to the gray whale (*Eschrichtius robustus*). Report of the International Whaling Commission 36:353-358.

LeBoeuf, B. J., H. Perez-Cortes M., J. Urban R., B. R. Mate, and F. Ollervides U. 2000. High gray whale mortality and low recruitment in 1999: Potential causes and implications. Journal of Cetacean Research and Management 2:85-99.

LEDUC, R. G., D. W. WELLER, J. HYDE, A. M. BURDIN, P. E. ROSEL, R. L. BROWNELL, JR., B. WÜRSIG, AND A. E. DIZON. 2002. Genetic differences between western and eastern gray whales (*Eschrichtius robustus*). Journal of Cetacean Research and Management 4:1-5.

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

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

LINDQUIST, O. 2000. The North Atlantic gray whale (*Escherichtius robustus*): An historical outline based on Icelandic, Danish-Icelandic, English and Swedish sources dating from ca 1000 AD to 1792. Occasional Papers 1. The Centre for Environmental History and Policy, Universities of St. Andrews and Stirling, Scotland. 53 pp.

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

MALIK, S., M. W. BROWN, S. D. KRAUS, AND B. N. WHITE. 2000. Analysis of mitochondrial DNA diversity within and between North and South Atlantic right whales. Marine Mammal Science 16:545-558.

MITCHELL, E. 1973. The status of the world's whales. Nature Canada 2:9-25.

MITCHELL, E. 1979. Comments on the magnitude of early catch of East Pacific gray whales (*Eschrichtius robustus*). Report of the International Whaling Commission 29:307-314.

MITCHELL, E., AND R. R. REEVES. 1980. The Alaska bowhead problem: A commentary. Arctic 33:686-723.

MIZUE, K. 1951. Gray whales in the east sea area of Korea. Scientific Report of the Whales Research Institute 5:71-79.

MOORE, S. E., J. URBAN R., W. L. PERRYMAN, F. GULLAND, H. PEREZ-CORTES M., P. R. WADE, L. ROJAS BRACHO, AND T. ROWLES. 2001. Are gray whales hitting "K" hard? Marine Mammal Science 17:970-974.

NISHIWAKI, M., AND T. KASUYA. 1970. Recent record of gray whale in the adjacent waters of Japan and a consideration on its migration. Scientific Report of the Whales Research Institute 22:29-37.

OMURA, H. 1984. History of gray whales in Japan. Pages 57-77 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The Gray Whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

OMURA, H. 1988. Distribution and migration of the western Pacific stock of the gray whale. Scientific Report of the Whales Research Institute 39:1-9.

OHSUMI, S. 1976. Population assessment of the California gray whale. Report of the International Whaling Commission 26:350-359.

PARK, K. 1987. History of whaling off the coast of the Korean peninsula. Taehwa Press, Pusan.

PELLA, J. J., AND P. K. TOMLINSON. 1969. A generalized stock production model. Bulletin of the Inter-American Tropical Tuna Commission 13:420-496.

PETERSON, C. W., AND D. R. LEVITAN. 2001. The Allee effect: A barrier to recovery by exploited species. Pages 281-300 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, eds. Conservation of exploited species. Cambridge University Press, Cambridge, UK.

PIKE, G. C. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). Journal of the Fisheries Research Board of Canada 19:815-838.

POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752-757.

POLLOCK, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: Past, present, and future. Journal of the American Statistical Association 86:225-238.

PRESS, S. J. 1989. Bayesian statistics: Principles, models, and applications. John Wiley & Sons, New York, NY.

PUNT, A. E., AND D. S. BUTTERWORTH. 2002. An examination of certain of the assumptions made in the Bayesian approach used to assess the eastern North Pacific stock of gray whales (*Eschrichtius robustus*). Journal of Cetacean Research and Management 4:99-110.

REEVES, R. R. 1984. Modern commercial pelagic whaling for gray whales. Pages 187-200 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

REILLY, S. B. 1981. Population assessment and population dynamics of the California gray whale (*Eschrichtius robustus*). Ph.D. dissertation, University of Washington, Seattle, WA. 265 pp.

REILLY, S. B. 1992. Population biology and status of eastern Pacific gray whales: Recent developments. Pages 1062-1074 in D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Applied Science, New York, NY.

RICE, D. W., AND A. A. WOLMAN. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). Special publication of the American Society of Mammalogists 3:1-142.

RUBIN, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. Pages 395-402 in J. M. Bernardo, M. H. Degroot, D. V. Lindley, and A. F. M. Smith, eds. Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1-5, 1987. Clarendon Press, Oxford, UK.

RUGH, D. R., J. M. BREIWICK, R. C. HOBBS, AND J. A. LERCZAK. 2002. A preliminary estimate of abundance of the eastern North Pacific stock of gray whales in 2000/01 and 2001/02. Paper SC/54/BRG6 submitted to the International Whaling Commission (unpublished).

SCAMMON, C. M. 1874. The marine mammals of the north-western coast of North America, described and illustrated: Together with an account of the American whale-fishery. J. H. Carmony and Co., San Francisco, CA.

SCARFF, J. E. 1977. The international management of whales, dolphins, and porpoises: An interdisciplinary assessment. Ecological Law Quarterly 6:323-638.

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

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, NY.

SMITH, A. F. M., AND A. E. GELFAND. 1992. Bayesian statistics without tears: A sampling-resampling perspective. The American Statistician 46:84-88.

SMITH, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin 81:1-13.

SMITH, T. D., AND T. POLACHECK. 1979. Analysis of a simple model for estimating historical population sizes. Fishery Bulletin 76:771-779.

SWARTZ, S. L. 1986. Demography, migrations, and behavior of gray whales *Eschrichtius robustus* (Lilljeborg, 1861) in San Ignacio Lagoon, Baja California, Sur, Mexico and in their winter range. Ph.D. dissertation, University of California, Santa Cruz, CA. 95 pp.

TADA, H. 1978. Studies of whaling history in Yamaguchi Prefecture in Meiji Period. Matsuno Shoten, Tokuyama, Yamaguchi Prefecture. (in Japanese).

TAYLOR, B. L., AND D. P. DEMASTER. 1993. Implications of non-linear density dependence. Marine Mammal Science 9:360-371.

VANBLARICOM, G. R., L. R. GERBER, AND R. L. BROWNELL, JR. 2001. Marine mammals, extinctions of. Pages 37-69 in S. A. Levin, ed. Encyclopedia of Biodiversity, Volume 4. Academic Press, San Diego, CA.

VLADIMIROV, V. L. 1994. Recent distribution and abundance level of whales in Russian Far-Eastern seas. Russian Journal of Marine Biology 20:1-9.

WADE, P, R. 1997. A revised gray whale analysis using both southbound total population counts and northbound calf counts. Paper SC/49/AS24 submitted to the International Whaling Commission (unpublished).

WADE, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14:1-37.

WADE, P. R. 2002. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967-1996. Journal of Cetacean Research and Management 4:85-98.

WADE, P, R., AND W. L. PERRYMAN. 2002. An assessment of the eastern gray whale population in 2002. Paper SC/54/BRG7 submitted to the International Whaling Commission (unpublished).

WADE, P. R., A. M. BURDIN, A. L. BRADFORD, R. L. BROWNELL, JR., AND D. W. WELLER. 2003. Abundance estimates of western gray whales (*Eschrichtius robustus*) off northeastern Sakhalin Island, Russia. Paper SC/55/BRG18 submitted to the International Whaling Commission (unpublished).

WANG, P. 1978. Studies on the baleen whales in the Yellow Sea. Acta Zoologica Sinica 24:269-277. (in Chinese).

WANG, P. 1984. Distribution of the gray whale (*Eschrichtius robustus*) off the coast of China. Acta Theriologica Sinica 4:21-26. (in Chinese).

WELLER, D. W., B. WÜRSIG, A. L. BRADFORD, A. M. BURDIN, S. A. BLOKHIN, H. MINAKUCHI, AND R. L. BROWNELL, JR. 1999. Gray whales (*Eschrichtius robustus*) off Sakhalin Island, Russia: Seasonal and annual patterns of occurrence. Marine Mammal Science 15:1208-1227.

WELLER, D. W., B. WÜRSIG, A. M. BURDIN, S. H. REEVE, AND A. L. BRADFORD. 2000. Gray whales off Sakhalin Island, Russia: June – October 1999. A joint U.S.-Russian scientific investigation. Final contract report to Sakhalin Energy Investment Company (unpublished). 71 pp.

WELLER, D. W., A. M. BURDIN, A. L. BRADFORD, AND B. WÜRSIG. 2001. Gray whales off Sakhalin Island, Russia: June – September 2000. A joint U.S.-Russian scientific investigation. Final contract report to Sakhalin Energy Investment Company (unpublished). 56 pp.

WELLER, D. W., A. L. BRADFORD, A. M. BURDIN, T. MIYASHITA, T. KARIYA, A. M. TRUKHIN, S. A. MACLEAN, V. A. VLADIMIROV, AND N. V. DOROSHENKO. 2002a. Photographic recaptures of western gray whales in the Okhotsk Sea. Paper SC/54/BRG13 submitted to the International Whaling Commission (unpublished).

WELLER, D. W., A. M. BURDIN, A. L. BRADFORD, AND R. L. BROWNELL, JR. 2002b. Observations of skinny whales on the Piltun feeding ground 1999-2002. Paper SC/02/WGW5 submitted to the International Whaling Commission (unpublished).

WELLER, D. W., A. M. BURDIN, B. WÜRSIG, B. L. TAYLOR, AND R. L. BROWNELL, JR. 2002c. The western gray whale: A review of past exploitation, current status, and potential threats. Journal of Cetacean Research and Management 4:7-12.

WELLER, D. W., Y. I. IVASHCHENKO, G. A. TSIDULKO, A. M. BURDIN, AND R. L. BROWNELL, JR. 2002d. Influence of seismic surveys on western gray whales off Sakhalin Island, Russia in 2001. Paper SC/54/BRG14 submitted to the International Whaling Commission (unpublished).

WELLER, D. W., A. M. BURDIN, A. L. BRADFORD, G. A. TSIDULKO, Y. V. IVASHCHENKO, AND R. L. BROWNELL, JR. 2003a. Gray whales off Sakhalin Island, Russia: June – September 2001, a joint U.S.-Russian scientific investigation. Final contract report to Sakhalin Energy Investment Company (unpublished). 68 pp.

WELLER, D. W., A. M. BURDIN, AND R. L. BROWNELL, JR. 2003b. Gray whales off Sakhalin Island, Russia: Interim report of 2002 field studies. Interim contract report to the Marine Mammal Commission (unpublished). 18 pp.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

WÜRSIG, B., D. WELLER, A. BURDIN, S. BLOKHIN, S. REEVE, A. BRADFORD, AND R. BROWNELL, JR. 1999. Gray whales summering off Sakhalin Island, Far East Russia: July-October 1997. A joint U.S.-Russian scientific investigation. Final contract report to Sakhalin Energy Investment Company and Exxon Neftegas (unpublished). 101 pp.

WÜRSIG, B., D. WELLER, A. BURDIN, S. REEVE, A. BRADFORD, AND S. BLOKHIN. 2000. Gray whales summering off Sakhalin Island, Far East Russia: July-September 1998. A joint U.S.-Russian scientific investigation. Final contract report to Sakhalin Energy Investment Company and Exxon Neftegas (unpublished). 133 pp.

YABLOKOV, A. V., AND L. S. BOGOSLOVSKAYA. 1984. A review of Russian research on the biology and commercial whaling of the gray whale. Pages 465-485 in M. L. Jones, S. L. Swartz, and S. Leatherwood, eds. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, FL.

YAMADA, T. K., Y. UNI, AND H. ISHIKAWA. 2002. Recent gray whale strandings and sightings around Japan. Paper SC/02/WGW8 submitted to the International Whaling Commission (unpublished).

ZEH, J., D. POOLE, G. MILLER, W. KOSKI, L. BARAFF, AND D. RUGH. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981-1998 photoidentification data. Biometrics 58:832-840.

ZENKOVICH, B. A. 1937. More on the gray California whale (*Rhachianectes glaucus*, Cope 1864). Vestnik Akademiya Nauk SSSR Dal’nevostochnyi Filiala 23:91-103. (in Russian).

ZHOU, K., AND X. WANG. 1994. Brief review of passive fishing gear and incidental catches of small cetaceans in Chinese waters. Report of the International Whaling Commission (Special Issue 15):347-354.

Appendix A. Minimum numbers and associated details of western gray whales caught during the 20th century. Years are displayed continuously until 1966, the reported end of modern whaling for western gray whales. Highlighted rows represent total yearly minimum catches.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1900	?	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	23	Kato and Kasuya (2002) from Park (1987)
1900	?	Kawajiri, Yamaguchi	Sea of Japan	Japan	Japanese	?	2	Omura (1984) from Tada (1978)
1900							25	
1901							?	Kato and Kasuya (2002) from Park (1987)
1902	?	Jangjeon	Sea of Japan	Korea	Russian	Modern	9	Kato and Kasuya (2002) from Park (1987)
1902	?	Unknown	Unknown	Unknown	Unknown	Modern	5	Kato and Kasuya (2002) from Park (1987)
1902							14	
1903							?	Kato and Kasuya (2002)
1904							?	Kato and Kasuya (2002)
1905							?	Kato and Kasuya (2002)
1906	Nov-Mar	Ulsan	Sea of Japan	Korea	Japanese?	Modern	59	Kato and Kasuya (2002) from Park (1987)
1906	?	Unknown	Unknown	Unknown	Unknown	Modern	11	Kato and Kasuya (2002) from Park (1987)
1906							70	
1907	Nov-Mar	Ulsan	Sea of Japan	Korea	Japanese?	Modern	125	Kato and Kasuya (2002) from Park (1987)
1907							125	
1908	Nov-Mar	Ulsan	Sea of Japan	Korea	Japanese?	Modern	26	Kato and Kasuya (2002) from Park (1987)
1908							26	
1909	Dec	Ulsan	Sea of Japan	Korea	Japanese	Modern	65	Andrews (1914)
1909	Dec	Chan Chien Dogo	Sea of Japan	Korea	Japanese	Modern	18	Andrews (1914)
1909	Dec	Hidokatsu	Sea of Japan?	Korea?	Japanese	Modern	1	Andrews (1914)
1909							84	
1910	Jan	Ulsan	Sea of Japan	Korea	Japanese	Modern	32	Andrews (1914)
1910	Feb	Ulsan	Sea of Japan	Korea	Japanese	Modern	3	Andrews (1914)
1910	Mar	Ulsan	Sea of Japan	Korea	Japanese	Modern	1	Andrews (1914)
1910	Feb	Oshima, Nagasaki	Tsushima Strait	Japan	Japanese	Modern	1	Andrews (1914)
1910	Mar	Chan Chien Dogo	Sea of Japan	Korea	Japanese	Modern	1	Andrews (1914)
1910							38	
1911	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	106	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1911	Nov-Apr	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	13	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1911	?	North Kyushu	Korea Strait?	Japan	Unknown	Modern	2	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1911							121	
1912	Mar	Chan Chien Dogo	Sea of Japan	Korea	Capt. Melsom	Modern	2	Andrews (1914), Mizue (1951)

Appendix A. Continued.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1912	Jan	Ulsan	Sea of Japan	Korea	Japanese	Modern	23	Andrews (1914)
1912	?	Unknown	Unknown	Unknown	Unknown	Modern	193	Kato and Kasuya (2002), Omura (1988) from Kasahara (1950)
1912							218	
1913	?	Unknown	Unknown	Unknown	Unknown	Modern	131	Kato and Kasuya (2002), Omura (1988) from Kasahara (1950)
1913							131	
1914	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	109	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1914	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	30	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1914	Oct?	Ayukawa, Miyagi	Pacific	Japan	Japanese?	Modern	3	Mizue (1951), Brownell and Chun (1977)
1914	Jul?	Nemuro, Hokkaido	Pacific	Japan	Japanese?	Modern	1	Kasahara (1950), Mizue (1951), Brownell and Chun (1977), Kato and Kasuya (2002)
1914	?	North Kyushu	Korea Strait?	Japan	Unknown	Modern	15	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1914							158	
1915	?	Area XII-XIV	Unknown	Unknown	Japanese?	Modern	130	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1915	?	North Kyushu	Korea Strait?	Japan	Unknown	Modern	9	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1915							139	
1916	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	36	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1916	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	41	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1916	?	Area II, III, or IV	Unknown	Japan	Unknown	Modern	1	Kasahara (1950)
1916							78	
1917	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	53	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1917	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	13	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1917	?	Area XIV	Yellow Sea	Korea?	Japanese?	Modern	2	Kasahara (1950), Wang (1984), Omura (1988), Kato and Kasuya (2002)
1917							68	
1918	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	91	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1918	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	10	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1918	?	Area XIV	Yellow Sea	Korea?	Japanese?	Modern	2	Kasahara (1950), Wang (1984), Omura (1988), Kato and Kasuya (2002)
1918	?	"Other"	Unknown	Unknown	Unknown	Modern	1	Kato and Kasuya (2002) from Kasahara (1950)
1918							104	
1919	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	35	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1919	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	11	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1919							46	
1920	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	51	Kasahara (1950), Kato and Kasuya (2002)
1920	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	14	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)

Appendix A. Continued.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1920	?	North Kyushu	Korea Strait?	Japan	Unknown	Modern	10	Kasahara (1950), Kato and Kasuya (2002)
1920							75	
1921	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	23	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1921	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	53	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1921	?	North Kyushu	Korea Strait?	Japan	Unknown	Modern	2	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1921							78	
1922	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	19	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1922	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	19	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1922	May?	Area XIV	Yellow Sea	Korea?	Japanese?	Modern	2	Kasahara (1950), Mizue (1951), Wang (1984), Omura (1988), Kato and Kasuya (2002)
1922							40	
1923	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	4	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1923	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	23	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1923							27	
1924	?	Ulsan	Sea of Japan	Korea	Japanese?	Modern	1	Kato and Kasuya (2002) from Emoto Log
1924	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	13	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1924	?	Unknown	Unknown	Unknown	Unknown	Modern	4	Kato and Kasuya (2002) from Kasahara (1950)
1924							18	
1925	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	10	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1925							10	
1926	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	9	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1926	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	1	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1926	May?	Sakhalin	Sea of Okhotsk	Russia	Unknown	Modern	1	Kasahara (1950), Mizue (1951), Kato and Kasuya (2002)
1926							11	
1927	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	6	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1927	Nov-May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	3	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1927	?	Area III	Sea of Okhotsk	Unknown	Unknown	Modern	1	Kasahara (1950), Kato and Kasuya (2002)
1927							10	
1928	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	9	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1928							9	
1929	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	11	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1929	?	Area XIV	Yellow Sea	Unknown	Japanese?	Modern	1	Kasahara (1950), Wang (1984), Omura (1988), Kato and Kasuya (2002)

Appendix A. Continued.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1929							12	
1930	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	30	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1930							30	
1931	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	10	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1931							10	
1932	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	Modern	7	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1932							7	
1933	Nov-Apr	Ulsan	Sea of Japan	Korea	Japanese?	modern	1	Kasahara (1950), Omura (1988), Kato and Kasuya (2002)
1933							1	
1934							?	Kato and Kasuya (2002) from Kasahara (1950)
1935							?	Kato and Kasuya (2002) from Kasahara (1950)
1936							?	Kato and Kasuya (2002) from Kasahara (1950)
1937							?	Kato and Kasuya (2002) from Kasahara (1950)
1938							?	Kato and Kasuya (2002) from Kasahara (1950)
1939							?	Kato and Kasuya (2002) from Kasahara (1950)
1940							?	Kato and Kasuya (2002) from Kasahara (1950)
1941							?	Kato and Kasuya (2002) from Kasahara (1950)
1942	?	Ulsan	Sea of Japan	Korea	Japanese?	Modern	1	Kato and Kasuya (2002) from Emoto Log
1942	?	Otomae, Kurils	Unknown	Russia	Japanese?	Modern	1	Kasahara (1950), Mizue (1951), Brownell and Chun (1977), Kato and Kasuya (2002)
1942							2	
1943	?	Ulsan	Sea of Japan	Korea	Japanese?	Modern	1	Kato and Kasuya (2002) from Emoto Log
1943							1	Kato and Kasuya (2002) from Emoto Log
1944							?	Kasahara (1950), Kato and Kasuya (2002)
1945	Jan	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	3	Kato and Kasuya (2002) from Emoto Log
1945	May	Jangjeon	Sea of Japan	Korea	Japanese?	Modern	2	Kato and Kasuya (2002) from Emoto Log
1945							5	
1946							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1947							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1948	Jan?	Ulsan	Sea of Japan	Korea	Korean?	Modern	9	Brownell and Chun (1977), Kato and Kasuya (2002) from Park (1987)
1948							9	
1949	?	Ulsan	Sea of Japan	Korea	Korean?	Modern	4	Brownell and Chun (1977), Kato and Kasuya (2002)
1949	Sep	Area XIV	Yellow Sea	China?	Chinese	Modern	1	Kato and Kasuya (2002) from Wang (1978)
1949							5	

Appendix A. Continued.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1950							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1951	?	Ulsan	Sea of Japan	Korea	Korean?	Modern	7	Brownell and Chun (1977), Kato and Kasuya (2002)
1951							7	
1952	?	Ulsan	Sea of Japan	Korea	Korean?	Modern	1	Brownell and Chun (1977), Kato and Kasuya (2002)
1952							1	
1953	?	Ulsan	Sea of Japan	Korea	Korean?	Modern	7	Brownell and Chun (1977), Kato and Kasuya (2002)
1953	Mar-Jun	Wailuo Harbor, Lui Zhou Peninsula	South China Sea?	China	Chinese?	?	4	Wang (1984)
1953							11	
1954							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1955							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1956							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1957							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1958	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	7	Brownell and Chun (1977), Kato and Kasuya (2002)
1958	Jun	Yantai, Shandong	Yellow Sea	China	Chinese	Modern	1	Kato and Kasuya (2002) from Wang (1978)
1958							8	
1959	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	7	Brownell and Chun (1977), Kato and Kasuya (2002)
1959	Jun	Southeast Honshu	Pacific	Japan	Japanese	Modern	1	Nishiwaki and Kasuya (1970), Brownell and Chun (1977)
1959							8	
1960	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	8	Brownell and Chun (1977), Kato and Kasuya (2002)
1960	Apr	Area XIV	Yellow Sea	China?	Chinese	Modern	1	Kato and Kasuya (2002) from Wang (1978)
1960							9	
1961	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	3	Brownell and Chun (1977), Kato and Kasuya (2002)
1961							3	
1962							?	Brownell and Chun (1977), Kato and Kasuya (2002)
1963	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	2	Brownell and Chun (1977), Kato and Kasuya (2002)
1963							2	
1964	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	3	Brownell and Chun (1977), Kato and Kasuya (2002)
1964							3	
1965	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	4	Brownell and Chun (1977), Kato and Kasuya (2002)
1965							4	
1966	Dec-May	Ulsan	Sea of Japan	Korea	Korean?	Modern	5	Brownell and Chun (1977), Kato and Kasuya (2002)
1966							5	

Appendix A. Continued.

Year	Month	Location	Water Body	Country	Whalers	Method	Catch	Source
1968	Feb	Shingu, Wakayama	Seto Inland Sea?	Japan	Japanese	?	1	Nishiwaki and Kasuya (1970), Omura (1984), Brownell and Chun (1977), Kato and Kasuya (2002)
1996	May	Suttu, Hokkaido	Sea of Japan	Japan	Japanese	Hand Harpoon	1	Brownell and Kasuya (1999), Kato and Kasuya (2002)

Appendix B. Monthly encounter histories of western gray whales photographically identified from 1997 to 2002 off Piltun Lagoon, Sakhalin Island, Russia. 1 = photographically identified. 0 = not photographically identified. Whale identification (ID) numbers of whales first identified as calves are italicized. *n* = the number of monthly photo-identification surveys. Encounter histories compiled from Weller *et al*. (1999, 2000, 2001, 2003a, 2003b) and Würsig *et al*. (1999, 2000).

Whale ID number	Jul 97 (*n* =10)	Aug 97 (*n* =8)	Sep 97 (*n* =4)	Jul 98 (*n* =13)	Aug 98 (*n* =9)	Sep 98 (*n* =13)	Jun 99 (*n* =1)	Jul 99 (*n* =18)	Aug 99 (*n* =14)	Sep 99 (*n* =14)	Oct 99 (*n* =9)	Jun 00 (*n* =2)	Jul 00 (*n* =5)	Aug 00 (*n* =22)	Sep 00 (*n* =11)	Jun 01 (*n* =3)	Jul 01 (*n* =14)	Aug 01 (*n* =15)	Sep 01 (*n* =16)	Jul 02 (*n* =12)	Aug 02 (*n* =13)	Sep 02 (*n* =11)
001	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
002	1	1	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	0	0
003	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
004	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
005	1	0	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1
006	1	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	0	0
007	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	0	0	0
008	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
009	1	1	1	1	1	0	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1
010	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	0	1	1	0	1	0	1
011	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	0	0	1	1	0
012	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0
013	1	1	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1
014	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0
015	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	1	1	1
016	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0
017	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
018	1	0	1	1	1	1	0	1	1	1	1	0	0	1	0	0	1	1	0	0	0	0
019	1	1	0	1	0	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	1
020	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
021	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0
022	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
023	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0
024	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	0
025	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
026	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
027	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0
028	1	1	1	1	1	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0
029	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0
030	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0

Appendix B. Continued.

Whale ID number	Jul 97 (*n* =10)	Aug 97 (*n* =8)	Sep 97 (*n* =4)	Jul 98 (*n* =13)	Aug 98 (*n* =9)	Sep 98 (*n* =13)	Jun 99 (*n* =1)	Jul 99 (*n* =18)	Aug 99 (*n* =14)	Sep 99 (*n* =14)	Oct 99 (*n* =9)	Jun 00 (*n* =2)	Jul 00 (*n* =5)	Aug 00 (*n* =22)	Sep 00 (*n* =11)	Jun 01 (*n* =3)	Jul 01 (*n* =14)	Aug 01 (*n* =15)	Sep 01 (*n* =16)	Jul 02 (*n* =12)	Aug 02 (*n* =13)	Sep 02 (*n* =11)
031	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
032	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
033	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1
034	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	1	1	1	0	1
035	1	0	0	1	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1
036	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1
037	0	1	1	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1
038	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1
039	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
040	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1
041	0	0	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	0
042	0	0	1	0	0	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0
043	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1
044	1	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0
045	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
047	0	0	0	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0
048	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1
049	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1
050	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
051	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1	0	0	1
052	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	1	1
053	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0
054	0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	1	0	0	0
055	0	0	0	1	1	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1
056	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1
057	0	0	0	1	1	1	0	0	1	0	1	0	0	1	1	0	1	1	1	1	1	1
058	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0
059	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
060	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
061	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
062	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
063	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1
064	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
065	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix B. Continued.

Whale ID number	Jul 97 (*n* =10)	Aug 97 (*n* =8)	Sep 97 (*n* =4)	Jul 98 (*n* =13)	Aug 98 (*n* =9)	Sep 98 (*n* =13)	Jun 99 (*n* =1)	Jul 99 (*n* =18)	Aug 99 (*n* =14)	Sep 99 (*n* =14)	Oct 99 (*n* =9)	Jun 00 (*n* =2)	Jul 00 (*n* =5)	Aug 00 (*n* =22)	Sep 00 (*n* =11)	Jun 01 (*n* =3)	Jul 01 (*n* =14)	Aug 01 (*n* =15)	Sep 01 (*n* =16)	Jul 02 (*n* =12)	Aug 02 (*n* =13)	Sep 02 (*n* =11)
066	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
067	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0
068	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
069	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0
070	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1
071	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
072	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
073	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
074	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
075	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1
076	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0
077	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
078	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
079	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1
080	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
081	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1	1	1
082	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
083	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	1	0	1	0
084	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1
085	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0
086	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
087	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0
088	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
089	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1
090	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	1
091	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
092	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0
093	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1
094	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
095	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
096	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
097	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
098	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
099	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1

Appendix B. Continued.

Whale ID number	Jul 97 (*n* =10)	Aug 97 (*n* =8)	Sep 97 (*n* =4)	Jul 98 (*n* =13)	Aug 98 (*n* =9)	Sep 98 (*n* =13)	Jun 99 (*n* =1)	Jul 99 (*n* =18)	Aug 99 (*n* =14)	Sep 99 (*n* =14)	Oct 99 (*n* =9)	Jun 00 (*n* =2)	Jul 00 (*n* =5)	Aug 00 (*n* =22)	Sep 00 (*n* =11)	Jun 01 (*n* =3)	Jul 01 (*n* =14)	Aug 01 (*n* =15)	Sep 01 (*n* =16)	Jul 02 (*n* =12)	Aug 02 (*n* =13)	Sep 02 (*n* =11)
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Appendix C. Pseudocode outlining the Monte Carlo simulation procedure used for the western gray whale 1997-2002 population growth rate estimation.

```
1) Specify the distributions for the life history parameters ($\phi_{calf}$, $\phi_{non-calf}$, $CI$, and ASM), the maximum age class ($w$), and the number of samples in the simulation ($n$).
2) Draw values of $\phi_{calf}$ and $\phi_{non-calf}$ from their distributions, and determine the $l_x$ schedule (Equation 3.3).
3) Select values from the distribution of $CI$ and ASM, and compute the $m_x$ schedule (Equation 3.4).
4) Use Equation 3.1 to find the population growth rate ($\lambda$) that characterizes the selected life history parameters.
5) Store the set of life history parameters and the resulting growth rate estimate.
6) Repeat Steps 2-5 until a sample size of $n$ is generated.
```

Appendix D. Pseudocode outlining the Bayesian statistical method used for the 20^{th} century western gray whale back calculation.

```
1) Specify the data ($r_{1997-2002}^{\text{LH data}}$), the prior distributions for the model parameters ($r_{MAX}$, $K$, and $N_{1900}$) and the 2002 abundance estimate ($N_{2002}$), and the number of initial samples ($n_1$) and resamples ($n_2$).
2) Draw a value of $r_{MAX}$, $K$, and, $N_{2002}$ from their joint prior distributions.
3) Given these parameters, determine if a value of $N_{1900}$ exists within its prior distribution that would produce a reasonable $\hat{N}_{2002}$. If so, implement the backwards method by using a bisection approach to find the value of $N_{1900}$ such that $\hat{N}_{2002}$ is as close as possible to $N_{2002}$. If not, penalize the parameter set and proceed to the next sample (Step 2).
4) Use Equation 3.5 to project the population from 1900 to 2002 according to the selected parameters.
5) Estimate $r_{1997-2002}^{\text{model}}$ (Equation 3.7) and the two status indices ($\hat{N}_{2002}/K$ and $\hat{N}_{2002}/N_{1900}$).
6) Calculate the likelihood of the parameters using the likelihood function (Equation 3.8).
7) Store the set of parameters, status indices, and associated likelihood.
8) Repeat Steps 2-7 until an initial sample of size $n_1$ is generated.
9) With probability equal to weight $q_i$, resample the initial sample with replacement $n_2$ times, thus approximating the joint posterior distributions of the parameters and status indices.
```