INDIVIDUAL-BASED POPULATION ASSESSMENT FOR CETACEANS: USING PHOTOGRAPHS TO INFER ABUNDANCE, DEMOGRAPHY AND INDIVIDUAL QUALITY

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THESIS CONTENTS

Author’s Declaration

I declare that I composed all of the work presented in this thesis, and no part of this work has been accepted in any previous application for a degree. All sources of information have been specifically acknowledged and all quotations have been distinguished by quotation marks. All of the work presented in this thesis is my own and all assistance from others has been acknowledged in the preface and text.

Holly Fearnbach, 2012

Summary

Population assessments are required to inform management and conservation of wildlife. These require estimates of abundance and trends, but analysis of demographics is also key to understanding the drivers of population dynamics. However, there are great challenges when studying cetaceans in their marine environment, which can constrain our ability to fully evaluate abundance and demographics, or understand their relationship with environmental covariates.

This thesis highlights the utility of using photographic data, combined with robust statistical analyses, to make inference about the abundance, demography and population dynamics of three cetacean populations: the abundant “resident” type fish-eating killer whales (*Orcinus orca*) in Alaskan coastal waters of the far North Pacific, the endangered “southern resident” population of fish-eating killer whales in the eastern North Pacific coastal waters of Canada and the USA., and an “island” population of bottlenose dolphins (*Tursiops truncatus*) in the shallow waters of Little Bahama Bank, Bahamas. These populations inhabit a diverse range of environments and habitats, ranging from the tropics to the subarctic, and from relatively urban to very remote. In combination, these case studies allowed inference about variability in abundance and demography, and their key covariates, over both time and space.

These case studies are linked by a common methodological approach that builds on established techniques of photo-identification and photographic mark-recapture for cetaceans. Notably, I also adopt alternative photographic and photogrammetric methods for inferring demography and population status by assessing individual attributes, including comparisons across populations. These provide a complementary and alternative approach when suitable time series are not available, and demonstrate how population assessments can incorporate data on individual quality as well as quantity.

Preface

The data chapters in this thesis present results of long-term and large-scale field studies, which were only possible due to the collaborative involvement of multiple researchers over many years. I was integrally involved in data collection for each of these case studies, and took a leading role in data processing, data analysis and inference for the aspects of these studies that are presented here. However, I would also like to acknowledge the contributions of my key collaborators, who are also listed as coauthors on the chapters.

Photo-identification of bottlenose dolphins on Little Bahama Bank. Chapters 2 and 3

Chapters 2 and 3 are based on photo-identifications of bottlenose dolphins from Little Bahama Bank that were collected as part of a long-term project of the Bahamas Marine Mammal Research Organization (BMMRO; www.bahamaswhales.org). This project was initiated by Diane Claridge, the director of BMMRO, and Diane has provided logistic support for the duration of this project. BMMRO personnel Diane Claridge (1992-1996) and Kim Parsons (1994-2000) undertook key data collection during the early part of the time series, and John Durban has played a central role in data collection and project steering throughout the majority of the study (1995-2010). I have been personally involved in collecting all photo-identifications from 2006-2010, I analyzed all images taken from 2003-2010 for individual recognition, and reviewed the entire dataset for documentation of shark-bite wounds and neonate dolphins. I undertook all databasing and statistical analyses of the full dataset using statistical models developed by John Durban. Papers based on chapters 2 and 3 have now been published in peer-reviewed journals *Marine Mammal Science* and *Ecological Applications*, respectively.

Photogrammetry of southern resident killer whales. Chapter 4

Chapter 4 is based on aerial photogrammetry images collected from southern resident killer whales in the San Juan Islands, WA, during 2008. This was a research project led by the Center for Whale Research (CWR; www.whaleresearch.com), drawing on a 30+ year photo-identification database of individuals collected by CWR director Ken Balcomb to link photogrammetric measurements to individual whales of known age and life history. John Durban (working jointly with CWR and NOAA) conceived of this project, obtained funding, and supervised the field work. Dave Ellifrit (CWR) led boat-based operations to guide the photogrammetry helicopter to specific individual whales, and matched the aerial images to photographs taken simultaneously from the boat platform and to the Center for Whale Research photo-identification catalog to determine individual identity. I participated in all data collection and specifically took all the photogrammetry images from a helicopter platform. Furthermore, I processed and databased all aerial images, and performed all the photogrammetric measuring. I conducted all analyses myself, with the guidance of John Durban on database queries for measurement summaries. A paper based on chapter 4 has now been published in *Endangered Species Research*.

Population assessment of resident killer whales in the far North Pacific. Chapters 5 and 6

Chapters 5 and 6 use photo-identification data on killer whales encountered in the coastal waters of the western Gulf of Alaska, Aleutian Islands and Bering Sea between 2001 and 2010. These data primarily resulted from ship-based sightings surveys conducted by the National Marine Mammal Laboratory of the NOAA Alaska Fisheries Science Center, led by Paul Wade and John Durban. I participated in these annual surveys between 2005 and 2010, leading shipboard collection and processing of photo-identification data. Additional photo-identifications were contributed by Craig Matkin (North Gulf Oceanic Society) from surveys conducted in a coastal study site in the eastern Aleutian Islands. Jay Barlow from the NOAA Southwest Fisheries Science Center provided killer whale photo-identifications collected during a research survey in 2004 that covered the full extent of the survey area, extending effort into offshore waters; I was involved in the collection and processing of photo-identification data on this survey. Megan Peterson collected photo-identifications of killer whales that were observed depredating research long-line surveys for sablefish, led by Chris Lunsford of the NOAA Alaska Fisheries Science Center.

These surveys generated a huge quantity of photo-identification data (~80,000 images). To make inference from this large dataset, I led a team employed/contracted by NOAA Alaska Fisheries Science Center to organize and analyze these data, adopting a database structure and process designed by John Durban. Although I performed the bulk of this analysis, including all databasing, I was assisted in photographic processing by Dave Ellifrit and Janice Waite. Myself and Janice selected the best photograph of each whale from each group of killer whales encountered, and digitized the images when black and white film was used (2001-2005). We assessed the photographs from each encounter for ecotype determination, to focus on the “resident” type, and then initial identification numbers were assigned to each whale. Dave Ellifrit then confirmed these identifications against a “Western Resident” photo-identification catalog, and assigned quality grades to all identifications for consistency. I then imported all photo-identifications and their assigned metadata data into a relational database and conducted all data summaries and statistical analyses. John Durban provided code for statistical modeling approaches for social network analysis (Chapter 5) and mark-recapture analysis (Chapter 6), but I performed all the model fitting and inference.

Chapter 6 also uses laser-photogrammetry images collected from killer whales around the Aleutian Islands (2005-2010) to estimate morphometrics. I collected all laser-metric images and conducted all of the morphometric measurements. Serving as reference populations, laser-photogrammetry images were also collected during boat based photo-identification surveys of southern resident (SR) and Gulf of Alaska resident (GOA) killer whales collected by John Durban, working collaboratively with Ken Balcomb from the Center for Whale Research (SR) and Craig Matkin from the North Gulf Oceanic Society (GOA). However, I conducted all analysis and measurements from these images; integrating the results with those from the Aleutian population. Chapter 6 also makes use of remote biopsy samples, collected by John Durban and Bob Pitman (NOAA Southwest Fisheries Science Center), to estimate ages of biopsied whales from blubber fatty acid composition, using a technique developed by David Herman (NOAA Northwest Fisheries Science Center). I integrated these age data into assessments of age distributions and size-at age comparisons. A paper based on chapter 5 is under review in the peer-reviewed journal *Marine Ecology Progress Series.*

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This thesis would not have been possible without the support and encouragement of so many people. First and foremost, I would like to thank my family and friends for their love and support during this adventure. I would not have made it without you! To John, you are my inspiration and guide in life. You have been so truly patient and supportive of me. I would never have made it this far without the support and love from my sister, mother and father. You have always been there for me- I know it has not been easy!

I am grateful for the supervision of Paul Thompson at the University of Aberdeen and John Durban and Paul Wade at the National Marine Mammal Laboratory in Seattle, WA (USA). Thank you for the opportunity to work on this project, your financial support and patience over the years. Thanks to Dave Ellifrit and Janice Waite for your tireless work on the photo analysis. Funding for fieldwork in Alaska, data processing and analysis was provided by National Marine Fisheries Service and conducted under permits 545-1488-03, 782-1510, 932-1489-05, and 782-1719 issued by the National Marine Fisheries Service. Aerial and boat-based fieldwork conducted on the southern resident killer whale population in 2008 was funded by NMFS and conducted under permit 532-1822. I would like to thank Ken Balcomb and the Center for Whale Research staff for their logistic support and assistance with this project.

I would like to thank Diane Claridge for the opportunity to work on the bottlenose dolphin project in the Bahamas and for support through the Bahamas Marine Mammal Research Organization (BMMRO). I would also like to thank Friends of the Environment and the Abaco community for valued support in recent years. Cha Boyce and the Boyce family, the Haestad family and Brenda Claridge provided accommodation, friendship and entertainment!

CHAPTER ONE

GENERAL INTRODUCTION

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Background

Population assessments are required to inform management and conservation of wildlife. For example, in the United States, population viability analyses are used to inform listing decisions under the Endangered Species Act (Morris *et al*. 2002) and assessments of depletion levels are required to assess status under the Marine Mammal Protection Act (Wade 1998; Read and Wade 2000). Within the European Union (EU), where wildlife populations are protected under the EU Habitats Directive, member states are required to report the condition of a population of interest as either favorable or unfavorable, and if unfavorable, determine whether it is declining, recovering, or showing no change (Council of European Communities, 1982; Baxter 2001). Furthermore, in the current context of multi-species management, assessments are required to provide key input into ecosystem models (e.g. Guénette *et al*. 2006).

Central to these assessments are estimates of abundance and trends (Thompson *et al*. 2000), and this has driven the development of methodologies for abundance estimation (Schwarz and Seber 1999; Buckland *et al*. 2000). Notably, approaches have been developed for estimating abundance by sampling defined areas using line transect and point transect surveys (Buckland *et al*. 1993a; Buckland *et al.* 2001) or by using mark-recapture methods for sampling individuals (Otis *et al*. 1978; Greenwood 1996; Pollock 2000). For migratory species, abundance estimation has been based on migration counts (Buckland *et al*. 1993b), perhaps combined with estimates of residency times (Routledge *et al*. 1999), representing elements of both the approaches of sampling space and sampling individuals. However, in addition to monitoring abundance, understanding the causes of population trends is required for a fuller understanding of population ecology and is pivotal to effective management (Clutton-Brock and Sheldon 2010). As such, analysis of demographics and demographic changes are also key components of status assessments (Norris 2004), particularly when demographic variance can be linked to environmental covariates (Beamish and Boullion 1993; Tufto *et al.* 1996; Beamish *et al*. 1997; Milner *et al*. 1999; Post *et al*. 1999; Saether *et al*. 2000; Post and Forchhammer 2001; Thompson and Ollason 2001; Jenouvrier *et al.* 2003, 2005a, b; Ford *et al*. 2010). Understanding the link between environmental changes and demography is therefore essential for informing the conservation and management of wildlife populations in this period of unprecedented environmental change.

Complete longitudinal records of the demography and life history of individuals have been realized for several well-studied populations of terrestrial mammals (Clutton-Brock *et al*. 1991; Gaillard *et al*. 1998; Loison *et al*. 1999; Coulson *et al*. 2001; Clutton-Brock and Coulson 2002), and even for accessible populations of marine mammals (Oleisuk *et al*. 1990, 2005; Ford *et al*. 2010). However, typically such complete observations are rarely possible for cryptic or mobile species and populations that occur in remote environments, where year-round and full-time monitoring is not feasible (e.g. forest elephants, Eggert *et al*. 2003; high latitude killer whales, Durban *et al.* 2010). Such difficulties constrain the ability to fully evaluate the demographics of populations and understand their relationship with environmental covariates. However, mark-recapture sampling of individuals can be used to make inference about demography in these cases (Pollock 1991; Lebreton *et al.* 1992; Pollock 2000). Conventionally, marking or tagging is used to identify individual animals caught as samples of a population, and the mark-recapture approach uses information on the recapture of individuals, or not, in successive samples, to estimate population parameters. More recently, the mark-recapture approach has been extended to include non-standard applications including individual genotypes (Kohn *et al*. 1995; Palsboll *et al*. 1997; Eggert *et al*. 2003) and photo-identifications (e.g. camera trap studies; Karanth and Nichols 1998; Gardner *et al*. 2010), greatly increasing the utility of the approach.

The photographic documentation of individuals has been particularly important in advancing individual-based studies of marine mammals (Hammond *et al*. 1990). It was first discovered in the 1970's that individuals within cetacean populations can be distinguished by naturally occurring marks and individual photo-identification was first applied to killer whales in the eastern North Pacific (Balcomb and Goebel 1976; Bigg 1982; Balcomb and Bigg 1986). Since then it has become the standard technique for sampling individuals for a variety of cetacean species (Katona and Whitehead 1981; Wells *et al.* 1987; Dufault and Whitehead 1995; Ford *et al*. 2000; Gowans and Whitehead 2001; McSweeney *et al*. 2007), as well as seals (Forcada and Aguilar 2000; Harting *et al*. 2004; Karlsson *et al*. 2005; Forcada and Robinson 2006; Mackey *et al*. 2008) and sirenians (Reid *et al*. 1991). These photographic re-sightings of individuals can be treated as "captures" and "recaptures" to which analytical mark-recapture models can be fit to estimate population parameters (Hammond 1990a), including abundance (Wilson *et al*. 1999; Calambokidis and Barlow 2004; Durban *et al*. 2005; Durban *et al.* 2010), survival (Slooten *et al*. 1992; Caswell *et al*. 1999; Mizroch *et al*. 2004; Bradford *et al*. 2006; Mackey *et al.* 2008; Silva *et al*. 2009), reproductive parameters (Barlow and Clapham 1997; Ward *et al*. 2010), life history (Olesiuk *et al*. 1990; 2005), population structure (Urian *et al*. 2009; Durban *et al*. 2010), and social structure (Lusseau *et al*. 2006; Parsons *et al*. 2009).

However, despite an increasing number of growing photo-identification studies, inference about demographic changes and population dynamics has only been possible in a limited number of cases (Whitehead *et al*. 1997; Cameron *et al*. 1999; Caswell *et al*. 1999; Fujiwara and Caswell 2001; Mizroch *et al*. 2004; Leaper *et al*. 2006; Corkery *et al*. 2008).

Making inference about the status of cetacean populations using mark-recapture has been constrained in many cases by problems adhering to the assumptions inherent in the mark-recapture approach, particularly those of defining the population and sampling with homogeneous probabilities of capture (Hammond 1990a). The wide ranging patterns of individuals (Rasmussen *et al*. 2007; Durban and Pitman 2011), coupled with logistical constraints to the size of workable study areas, results in problems of population definition (Hammond 1990b; Whitehead *et al*. 1997) and can require an explicit treatment of spatial mark-recapture sampling (Durban *et al*. 2005). Furthermore, social structuring within populations (Lusseau *et al*. 2006; Parsons *et al*. 2009) can lead to heterogeneity in capture probabilities and differential site fidelity to local study areas (Conn *et al*. 2011), requiring the use of non-standard and tailored models for capture probability (Durban *et al*. 2010). Even when these assumptions can be met or relaxed through modeling approaches, the logistical challenges of working in marine study sites has limited the compilation of multi-year time series that are sufficiently long enough to detect changes in populations of slowly-reproducing cetaceans with generation times that can span decades (Olesiuk *et al.* 1990; 2005).

In this thesis I combine robust mark-recapture methods for estimation of abundance and demographics of cetaceans with alternative photographic and photogrammetric methods for inferring demography and population status; these provide a complementary and alternative approach when suitable time series are not available. This approach builds on the established method of photo-identification to glean further data about individual life history and population demographics from photographs. Studies of terrestrial mammals have shown how the assessment of demographic trends, and the task of relating these to environmental changes, can be greatly facilitated by assessments of individual attributes (Gaillard *et al*. 2000). In particular, demographics and life history signals can be inferred from photogrammetric studies of individual size and population size structure (Croze 1972; Milner *et al*. 1999): individual size can be used to infer long-term changes in the environment that have been integrated into an individual pattern of growth (Choquenot 1991; Catchpole *et al*. 2000; Trites and Donelly 2003) and size structure can serve as a proxy for age structure, reflecting long-term demographic changes (Croze 1972), even if animals have not been monitored their whole life.

There are a growing number of examples of the use of photographs to assess individual attributes for cetaceans, such as phenotypic differences (Pitman and Ensor 2003) and body condition (Pettis *et al*. 2004; Bradford *et al*. 2008; Miller *et al*. 2012). I extend this approach to show how photographic documentation of wounds can be used to infer predation risk, and photographic assessment of age class can be used to infer the timing of key life history events, specifically calving, and assess the demographic composition of populations. I also adopt photogrammetric tools to estimate quantitative morphometric attributes. Photogrammetry is a growing tool for assessing scaled measures of size and body condition of cetaceans (Perryman and Lynn 1993; Perryman and Westlake 1998; Durban and Parsons 2006; Jaquet 2006; Pitman *et al*. 2007; Webster *et al*. 2010), providing data to address fundamental questions with respect to conservation and management, such as taxonomy (Perryman and Lynn 1993; Perryman and Westlake 1998; Pitman *et al*. 2007), health assessment (Perryman and Lynn 2002; Trites and Donnelly 2003), estimation of energetic requirements (Williams *et al*. 2004; Noren 2011), and identification of key life-history and demographic events (Koski *et al*. 1992; Perryman and Lynn 1993; Read *et al*. 1993; Flamm *et al*. 2000; Durban and Parsons 2006). I combine individual photo-identification with photogrammetry to link size and growth to individual age, in order to assess temporal changes in individual quality related to possible environmental covariates. I also compare individual size and demographic composition across populations with contrasting population dynamics to assess key differences in individual quality.

Case studies

This thesis is written as a series of distinct papers, demonstrating the utility of employing photographic data to make inference about the abundance, demography and population dynamics of three cetacean populations: the Aleutian population (AI) of “resident” type fish-eating killer whales (*Orcinus orca*) that occurs in waters ranging from the northern Gulf of Alaska along the Aleutian chain and up the Bering Sea shelf edge (USA), the “southern resident” (SR) fish-eating killer whale population that mostly occurs in the waters off British Columbia, Canada and Washington, USA, and an “island” population of bottlenose dolphins (*Tursiops truncatus*) that occurs in the shallow waters of Little Bahama Bank (Bahamas). In addition to a common methodological approach building through the chapters, there are also consistent themes, with these case studies allowing inference about variability in abundance and demography, and their covariates over *Time*: a 19-year dataset on the bottlenose dolphins from Little Bahama Bank and a 30+ year photo-id dataset on the SR killer whales from the eastern North Pacific, with coverage across seasons and over years; and *Space*: photo-id datasets from killer whales in the eastern and far North Pacific, particularly from a study area spanning several thousands of kilometers along the Aleutian Islands. Additionally, I have collected and analyzed photogrammetry data from three killer whale (SR and Aleutian populations, in addition the reference population in the northern Gulf of Alaska [GOA]) to make inference about individual sizes, and use this information on individual quality to infer long-term trends in demography and environmental conditions determining food availability. These photogrammetric approaches demonstrate that population assessments can incorporate data on individual quality as well as quantity.

Abaco dolphins: An "island" population of bottlenose dolphins in the Bahamas

Bottlenose dolphins are an example of a marine predator with a cosmopolitan distribution (Leatherwood and Reeves 1990). They are among most frequently studied cetacean species due to their common occurrence and accessibility in nearshore waters, with the most notable long-term, individual-based study dating back to the early 1980s (Wells *et al*. 1987; Wells and Scott 1990). Individual photo-identification has enabled researchers to monitor individuals and assess abundance and demographics of bottlenose dolphins (Williams *et al*. 1993; Urian *et al*. 1996; Wilson *et al*. 1999; Read *et al*. 2003; Durban *et al*. 2005; Corkery *et al*. 2008; Urian *et al*. 2009; Silva *et al*. 2009; Conn *et al*. 2011; Cheney *et al*. 2012), but inference about population dynamics has been limited (Corkery *et al*. 2008). This is because the range of bottlenose dolphins can be wide (Defran *et al*. 1999; Durban *et al.* 2005; Cheney *et al.* 2012), and may change over time (Wells *et al.* 1990; Wilson *et al.* 2004), despite apparent high fidelity in coastal study areas (Durban *et al.* 2000). Furthermore, social structuring within populations (Lusseau *et al*. 2006; Urian *et al.* 2009) can lead to heterogeneity in capture probabilities and differential site fidelity to local study areas (Conn *et al*. 2011). In combination, these present problems for population definition and consistent population coverage over time using photo-identification surveys, which has prevented effective population monitoring and understanding of population dynamics in most cases.

Two of my thesis chapters focus on a population of bottlenose dolphins using Little Bahama Bank in the NE Bahamas. Little Bahama Bank is a shallow sandbank system, approximately 17000 km^2 in size, surrounded by deep oceanic waters on all sides. It has been estimated that approximately 1000 bottlenose dolphins occur in these waters (Durban 2002) and represent an isolated population (Parsons *et al*. 2006). The Bahamas Marine Mammal Research Organisation (BMMRO) has been monitoring a small portion (~160 km^2) of Little Bahama Bank, off the east side of Great Abaco Island, since 1992, resulting in almost 800 encounters with bottlenose dolphins over two decades and across different seasons. Re-sightings of individuals over multiple years (e.g. Durban 2002; Parsons *et al*. 2003; Parsons *et al*. 2006) indicate the utility of a mark-recapture approach for assessing population status. Such an assessment is required to inform conservation and management decisions under the newly established Marine Mammal Protection Act of the Bahamas (2005), but more generally, this defined island population offers a unique opportunity to investigate the factors affecting population dynamics. Nonetheless, this is not without challenges, and my first two data chapters address these challenges when making inference about this population from photographs. In particular, I quantify seasonal and inter-annual trends in demography and abundance, and evaluate these relative to key environmental variation, notably the incidence and intensity of hurricanes.

Chapter 2 "***Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank***". This chapter uses photographs to assess calving seasonality and predation risk of bottlenose dolphins on Little Bahama Bank, and correlates these to the observed seasonality of tropical cyclones. Photographs from 1992-2007 are evaluated for the presence of fresh shark scar wounds (proxy for predation risk) and fetal folds (proxy of neonatal or newborn status) to make inference on the timing of calving and shark scar wound acquisition. This chapter forms the basis of a paper published in *Marine Mammal Science* in June 2011 (Fearnbach *et al*. 2011a).

Chapter 3 "***Photographic mark-recapture analysis of local dynamics within an open population of dolphins*.** This chapter applies mark-recapture analysis to 19 years of photo-identification data (1992-2010) to assess population dynamics through inter-annual trends in abundance, survival and recruitment. A novel Bayesian mark-recapture approach is used to identify a cluster of dolphins with relatively high capture probabilities in our local study area, therefore overcoming the problems of population definition caused by heterogeneous movement beyond the boundaries of the study site. This approach enables key changes in the dynamics of this "resident" sub-population to be identified, with significant reductions in survival probability and abundance coinciding a particularly active period of tropical cyclone activity. This chapter forms the basis of a paper published in *Ecological Applications* in 2012 (Fearnbach *et al*. 2012).

Killer whales of the North Pacific

Killer whales are another example of a top marine predator that occurs throughout the world's oceans (Dalheim and Heyning 1999; Forney and Wade 2006). They have high caloric requirements and are therefore anticipated to have considerable trophic impacts (Williams *et al.* 2004) and demands (Noren 2011) within marine systems. As such, they are of increasing management concern due to their predatory impacts on protected and endangered marine mammals (Springer *et al*. 2003) and due to their vulnerability as top predators to food shortages (Ford *et al.* 2010) and reduced food quality through contaminants (Ross *et al*. 2000; Hickie *et al*. 2007; Krahn *et al*. 2007b).

Killer whales are best known from the eastern North Pacific, where coastal populations have been studied since the early 1970's using photo-identification methods to assess population size (Bigg 1982; Balcomb 1982; Ford and Ellis 1999; Ford *et al*. 2000), life history (Olesiuk *et al*. 1990, 2005; Ford *et al*. 2000), social structure (Bigg *et al*. 1990; Baird and Whitehead 2000; Parsons *et al*. 2009) and population dynamics (Olesiuk *et al*. 1990, 2005; Brault and Caswell 1993; Ford *et al*. 2010; Ward *et al*. 2009, 2010). Notably, three sympatric lineages exist that display differences in genetic composition (Stevens *et al.* 1989, Hoelzel and Dover 1990; Hoelzel *et al*. 1998; Barrett-Lennard 2000; Hoelzel *et al*. 2002; Morin *et al*. 2010), morphology (Baird and Stacey 1988; Ford *et al*. 2000), vocalizations (Ford 1989; Barrett-Lennard *et al*. 1996; Deecke *et al.* 2005) and social structure (Bigg *et al.*

1990; Baird and Whitehead 2000). These lineages have distinct prey specializations (Ford *et al*. 1998; Saulitis *et al.* 2000), with “transients” feeding on marine mammals, “residents” feeding on fish, notably salmon in some areas (Ford and Ellis 2006) and “offshores” thought to specialize on higher trophic level fish (Herman *et al*. 2005; Krahn *et al*. 2007a), notably sharks in recent observations (Ford *et al*. 2011). Consequently, these lineages are often referred to as “ecotypes” (Ford *et al*. 2000).

It is the fish-eating residents that have been most studied, particularly the “southern” residents that return to the coastal waters of Washington State (USA) and British Columbia (Canada) each summer to feed on returning runs of Pacific salmon (Ford *et al*. 2000; Krahn *et al*. 2004; Ford and Ellis 2006; Ford *et al*. 2010). As a result of their coastal habitat, these accessible whales are among the best studied mammalian populations, with population size, individual life histories and demographics having been monitored through an annual photo-identification census of individuals dating back to the early 1970s (Bigg *et al*. 1990; Olesiuk *et al*. 1990; Ford *et al*. 2000). This monitoring has revealed prolonged periods of population decline (Parsons *et al*. 2009) which have formed the basis for listing as “endangered” under the Species at Risk Act in Canada and the Endangered Species Act in the USA.

Long-term prey-habit studies of southern resident killer whales have shown distinct prey specialization on Chinook salmon (*Oncorynchus tshawytscha*) during the summer months (Ford and Ellis 2006), and recent analysis of long-term demographic data has shown this population to be food-limited, with declines in survival (Ford *et al*. 2010), fecundity (Ward *et al*. 2009) and social cohesion (Parsons *et al*. 2009) during years with low Chinook salmon availability.

Chapter 4 “***Size and long-term growth trends of endangered fish-eating killer whales***”. This chapter presents the results of an aerial photogrammetry study to assess size and growth trends of the southern resident population of killer whales. The aim was to collect size data to better inform energetic calculations of food requirements for this population, and to compare size-at-age data to make inference about long-term growth trends. Notably, a long term decrease in the adult size of whales is consistent with a decrease in food availability (salmon abundance) in recent decades. This chapter forms the basis of a paper published in *Endangered Species Research* in March 2011 (Fearnbach *et al*. 2011b).

This chapter illustrates how detailed data on individual life history (ages) can be combined with photogrammetry data to make inference about changes in individual quality, possibly related to environmental covariates, and used to complement and add to our understanding of long term trends in abundance and demographics. The level of detail and precision possible for estimates of population parameters for southern residents is unique for cetaceans, and as such, data on southern residents can serve as a benchmark reference for a resource-limited population that can be used to evaluate the status of other killer whale populations in comparative analyses (see Chapter 6 below).

In contrast to southern residents, “resident” type fish-eating killer whales in the coastal waters of the northern Gulf of Alaska (GOA, Matkin *et al*. 1999) have been increasing steadily in recent decades and show no signs of resource limitation. Photo-identification data collected annually since 1984 in the coastal waters of Prince William Sound and the adjacent Kenai Fjords have documented the GOA population increasing at an average rate of 3.2% in recent decades (1984-2008; Matkin *et al.* 2008), excluding the contribution of a single social unit (AB pod) that is thought to have suffered the prolonged effects of exposure to an oil spill in 1989. Therefore, this GOA population can serve as another reference benchmark, but this time for an increasing population (used in Chapter 6 below).

Although killer whale populations in the coastal waters of the eastern North Pacific have been monitored for several decades, relatively few data exist for the more remote waters of the far North Pacific, where killer whales are known to be found in particularly high abundance (Dahlheim *et al.* 1997; Forney and Wade 2006). Recent interest has focused on the role of killer whales within the remote marine ecosystems of the western Gulf of Alaska, Aleutian islands and Bering sea (GOA/AI/BS), primarily because predation by “transient” type mammal-eating killer whales has been implicated in the decline of several marine mammal species, notably endangered Steller sea lions (*Eumetopias jubatus*) and sea otters (*Enhydra lutris*) (Estes *et al*.1998; Springer *et al.* 2003; Williams *et al*. 2004). Sightings surveys conducted by the National Marine Mammal Laboratory (NMML) of the U.S. National Marine Fisheries Service in the GOA/AI/BS region from 2001-2010 have documented that all three lineages occur sympatrically in these waters, and analysis of blubber biopsies have shown that their consistent dietary specializations also persist in this study area (Herman *et al.* 2005; Krahn *et al.* 2007a). However, the ecotypes do vary in abundance in this region. Line transect analyses indicate that the abundance of residents in coastal waters between the Kenai Fjords, in south-central Alaska, and Tanaga Pass, in the central Aleutians (991, 95% CI 379-2585) is approximately 4 times the abundance of transients (251, 95% CI 97-644) during the summer months (Zerbini *et al.* 2007). A recent individual-based mark-recapture analyses of the mammal-eating transients estimated approximately 350 whales in the coastal waters from the western Gulf of Alaska to the central Aleutian Islands (Durban *et al*. 2010), but no precise estimates have been made for “resident” type fish-eating killer whales that occur in this region.

This high density of fish-eating residents overlaps in distribution with the most lucrative commercial fisheries in U.S. waters, resulting in direct and indirect competition with fisheries. Killer whale depredation on long-lines is commonly reported (Yano and Dahlheim 1995; Lunsford and Rutecki 2010), and killer whales have also been observed to feed on the discards of trawlers. Incidence of depredation has been increasing in recent years

(Lunsford and Rutecki 2010) and estimates of the spatial distribution and abundance of the resident type killer whales in the GOA/AI/BS region will assist in determining the spatial variability in fisheries interactions and potential trophic impact of this large killer whale population within the marine ecosystem (e.g. Guénette *et al*. 2006). In this thesis I analyze photo-identification data collected over 10 years in a study area spanning a longitudinal range of more than 4000 km to describe population structure and distribution through an analysis of social and spatial connectivity, estimate area-specific abundance and evaluate population status of “resident” type fish-eating killer whales that occur in the western GOA/AI/BS.

Although “resident” type killer whales in this region are currently managed as a single “Eastern North Pacific Alaska Resident” stock (Allen and Angliss 2012), existing information suggests the possibility of population structure. This study area is comprised of a varied physical environment, ranging from continental shelf waters in the east to deep pelagic waters around the western Aleutian Islands, including highly productive passes between the Aleutian Islands (Hunt and Stabeno 2005; Ladd *et al*. 2005). Hunt and Stabeno (2005) reported a strong discontinuity in the composition of the marine ecosystem between the eastern and central Aleutian Islands, near Seguam Pass, where organisms ranging from corals to marine mammals showed a “step change in species composition” and diets. Krahn *et al*. (2007a) reported that this biophysical gradient was reflected by an east-to west gradient in the stable isotope ratios found in skin biopsy samples collected from “resident” killer whales, indicating spatial trends in diet, likely the result of spatial structuring of whales to different feeding areas.

Chapter 5 “***Social and spatial connectivity of fish-eating killer whales in the far North Pacific***”. This chapter investigates spatial patterns of distribution and population structuring by describing individual movements and social affiliations from photo-identification data (2001-2010) collected from “resident” type fish-eating killer whales that occur in the western GOA, AI and BS. Social network analysis is used to reveal a social basis to movement patterns, with distinct social and spatial clustering that may represent population divisions. A large connected network ranging from the central Aleutian Islands to the western Gulf of Alaska overlaps with the spatial occurrence of longline depredation by killer whales, suggesting a possible social mechanism for cultural transmission of this behavior. This chapter forms the basis of a paper that is in review (as of August 2012) by *Marine Ecology Progress Series*.

Chapter 6 "***Abundance and demographic status of resident-type killer whales around the Aleutian Islands***". Due to this evidence of population structuring, this chapter adopts photographic mark-recapture analysis to produce estimates of resident killer whale abundance within the range of this large connected network, in an area that was consistently surveyed in the coastal waters of the eastern and central Aleutian Islands, and the Bering Sea shelf edge to the north. A spatially explicit mark-recapture model is used to describe spatial population clustering, and estimate a remarkably high abundance of resident killer whales using these waters. In the absence of a longer time series, I assess demographic status by comparing the composition of adult males in the photographic sample from the Aleutian population to well-studied SR and GOA "reference" populations of "resident" type fish-eating killer whales in the eastern North Pacific with contrasting population dynamics. Adult males are a class known to suffer high mortality during periods of food shortages and population limitation (Olesiuk *et al*. 2005; Ward *et al.* 2010), and a high proportion of adult males in the Aleutian population are suggestive of a good feeding history leading to population expansion. Estimates of age from blubber biopsies (Herman *et al*. 2008) support this, with typically older males in the Aleutians, and initial comparisons of measurements obtained from boat-based laser photogrammetry efforts on the SR population (Durban and Parsons 2006) suggests that the Aleutian population is comprised of larger adult males with particularly large dorsal fins. I discuss how the high abundance and high proportion of large males reflects high caloric requirements, which are likely to have a significant impact on the marine system around the Aleutian Islands, likely leading to competition with commercial fisheries and other protected marine mammal populations. This chapter will be submitted to *Marine Biology* in fall 2012.

This final data chapter is a fitting culmination to this thesis, as it represents components of the methodological approaches and results introduced in the previous chapters: identification of age classes from photographs (e.g. Chapter 2); photographic mark-recapture accounting for heterogeneous sightings probabilities (e.g. Chapter 3), as a result of spatial population structure (e.g. Chapter 5); and estimates of quantitative individual morphometrics from photogrammetry data (e.g. Chapter 4). I show how individual attributes can be related to individual age, to estimate the timing of key life history events (e.g. Chapter 4), and infer the demographic consequences. In the absence of a useable time series from the target population, I show how useful inference on population status can be made using a comparative approach, using results from longer-term "benchmark" reference studies.

As such, the chapters of this thesis are related and build upon each other, together representing a complementary presentation of transferrable methods that can be applied to evaluate abundance, demography and trends in a variety of animal populations, not just cetaceans. Specifically, these methods have been developed out of a requirement to monitor populations of animals that are highly mobile and therefore cryptic, exhibit heterogeneity in space use, and are difficult to catch or sample. We are in a period of unprecedented environmental change and conservation management of wildlife requires us to monitor and understand how animal populations respond (Walther *et al*. 2002; Clutton-Brock and Sheldon 2010). The results presented in this thesis describe the response of cetacean populations to key environmental variability, in both high and low latitude systems, and therefore represent important contributions to population assessment in these case studies. Equally, the approaches presented in this thesis should provide tools for future monitoring to assess how and if populations are adapting to ongoing changes in resource availability and distribution in their environment.

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CHAPTER TWO

SEASONALITY OF CALVING AND PREDATION RISK IN BOTTLENOSE DOLPHINS ON LITTLE BAHAMA BANK

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CHAPTER TWO

Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank

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Abstract

Seasonal reproduction in odontocetes has primarily been linked to bottom-up forcing through changes in the physical environment and/or prey availability, with little consideration of top-down selection through seasonal changes in predation pressure. Here we report on a distinct seasonal peak in calving for bottlenose dolphins (*Tursiops truncatus*) using Little Bahama Bank, despite its tropical latitude, and describe an inverse seasonal peak in the risk of predation by sharks, inferred by the incidence of fresh shark-bite wounds. Analysis of photo-identification data from 1992-2007 revealed that all (16/16) neonates were documented during a six month "winter" period (Nov-Apr), whereas 13/16 of all fresh shark-bite wounds were documented during the contrasting six month "summer" period (May-Oct). Notably, the timing of wound acquisitions coincided with the season for intense tropical cyclones in the NW Atlantic, and 11/16 of the fresh wounds were documented immediately after three intense hurricanes passed directly over the study site, likely forcing dolphins into deeper waters with higher risk of predation by sharks. We suggest that calving seasonality may be at least in part a response to the selective disadvantage of rearing a young calf during the potentially dangerous summer.

Introduction

Environmental variability has been found to have marked effects on vertebrate demography in numerous ecological systems (e.g. Tufto *et al.*1996; Owen-Smith 1990; Beamish and Boullion 1993; Beamish *et al.*1997; Saether *et al.*2000; Miller *et al*. 2010), and recent studies have highlighted the importance of environmental trends for long-lived predators (e.g. Thompson and Ollason 2001; Jenouvrier *et al.*2003, 2005*a,b*; Lusseau *et al.* 2004; Ford *et al.* 2010). Reproduction is a key component of population demographics, particularly for large-bodied and long-lived species for which environmental effects on survival might be buffered (Clapham 1996; Gaillard *et al.*1998). To maximize reproductive success, the timing of births is selected to occur at times of favorable environmental conditions, particularly at times of increased food availability to support the rearing of dependent young (Bronson 1985; Rutberg 1987; Owen-Smith 1990; Boyd 1996; Hill *et al*. 2000; Weimerskirch *et al.* 2003), or when physical conditions are not too demanding for mothers or neonates (Dunbar 1980; Ohsawa and Dunbar 1984; Bronson 1985; Dunbar 1990; Boyd *et al*. 1996; Clapham 1996, 2001; Hill *et al*. 2000; Rasmussen *et al*. 2007). Less commonly reported is the influence of predation risk on the timing of reproduction, but this can also be an important selective force (Rutberg 1987; Lycett *et al.*1998; Corkeron and Conner 1999).

In the marine environment, calving seasonality is well known for some migratory large whale species which give birth in low latitude calving areas with warmer water temperatures, where neonate calves are less thermally challenged (*e.g.* Clapham 1996; Calamokidis *et al.* 2000; Rasmussen *et al.* 2007). However, the influence of seasonal environmental change on the reproduction of odontocete species, which are typically non-migratory, but can still range widely across different environments, is less clear. Nonetheless, calving seasonality has been reported for odontocetes in a number of study areas (Barlow 1984; Wells *et al.*1987; Urian *et al.*1996; Read 1990; Mann *et al*. 2000; Whitehead and Mann 2000; Haase and Schneier 2001; Thayer *et al*. 2003; Westgate and Read 2007; Mcquire and Aliaga-Rossel 2007). More diffuse reproductive periods have been reported in low latitudes, with births occurring during most months of the year, with slight to moderate single or bimodeal peaks for some study areas (Barlow 1984; Wells *et al*. 1987; Cockcroft and Ross 1990; Urian *et al.* 1996; Mann *et al*. 2000; McQuire and Aliaga-Rossel 2007). In contrast, synchronous and strongly seasonal reproductive periods have been reported in higher latitudes (Wursig 1978; Read 1990; Haase and Schneider 2001; Thayer *et al*. 2003; Westgate and Read 2007), reflecting the more pronounced seasonal variability in environmental conditions and prey availability.

However, most studies on seasonal reproduction in odontocetes have considered bottom-up forcing through changes in the physical environment and/or prey availability, with little consideration of top-down selection through seasonal changes in predation pressure. Predation pressure by sharks has been shown to affect delphinid habitat use and group size (Norris and Doh1 1980; Wells *et al.*1987; Heithaus 2001; Heithaus and Dill 2002), but the influence of predation pressure on reproductive patterns of delphinid populations has rarely been assessed. Here we report on a distinct seasonal peak in calving for bottlenose dolphins (*Tursiops truncatus*) using Little Bahama Bank, despite its tropical latitude and describe an inverse seasonal peak in the risk of predation by sharks, inferred by the incidence of fresh shark-bite wounds (Heithaus 2001). We suggest seasonal changes in the environment that might mediate increased predation risk and hypothesize that this may be a selective force for calving seasonality.

Methods

Study site

Little Bahama Bank (~ 26^{o}N, ~ 077^{o}W) comprises part of the northern Bahamas, and encompasses the two main islands of Great Abaco and Grand Bahama (Figure 1). This carbonate bank is approximately 17000 km^{2} in size (approximately 65% covered by water), characterized by shallow waters (average <7m deep) and chains of small islands bounded on all sides by the deep (>500m) waters of the sub-tropical NW Atlantic Ocean. Seasonal variability in surface water temperature on Little Bahama Bank is limited, but temperatures are moderately elevated in summer compared to winter (Table 1). This increase in summer temperatures is coincident with tropical cyclones in the NW Atlantic (Vecchi and Soden 2007), which typically occur between June and October (Landsea 1993). Little Bahama Bank is inhabited by approximately 1000 bottlenose dolphins (Durban 2002) and part of this population has been monitored annually since 1992 through boat-based photo-identification surveys in a 160km^{2} study site on the east side of Abaco Island (~ 26^{o}33’N, ~ 077^{o}04’W). Photo-identification monitoring has shown that around 100 dolphins use the east Abaco study area each year (Claridge 1994; Durban 2002), with a high re-sighting rate of some individuals (Durban *et al.* 2000; Parsons *et al.* 2003; Parsons *et al*. 2006). Individuals in this inshore population have not been sighted in the surrounding pelagic waters, despite extensive survey effort over more than 16 years, and therefore, this population appears to be restricted to this shallow water bank system (Parsons *et al*. 2006).

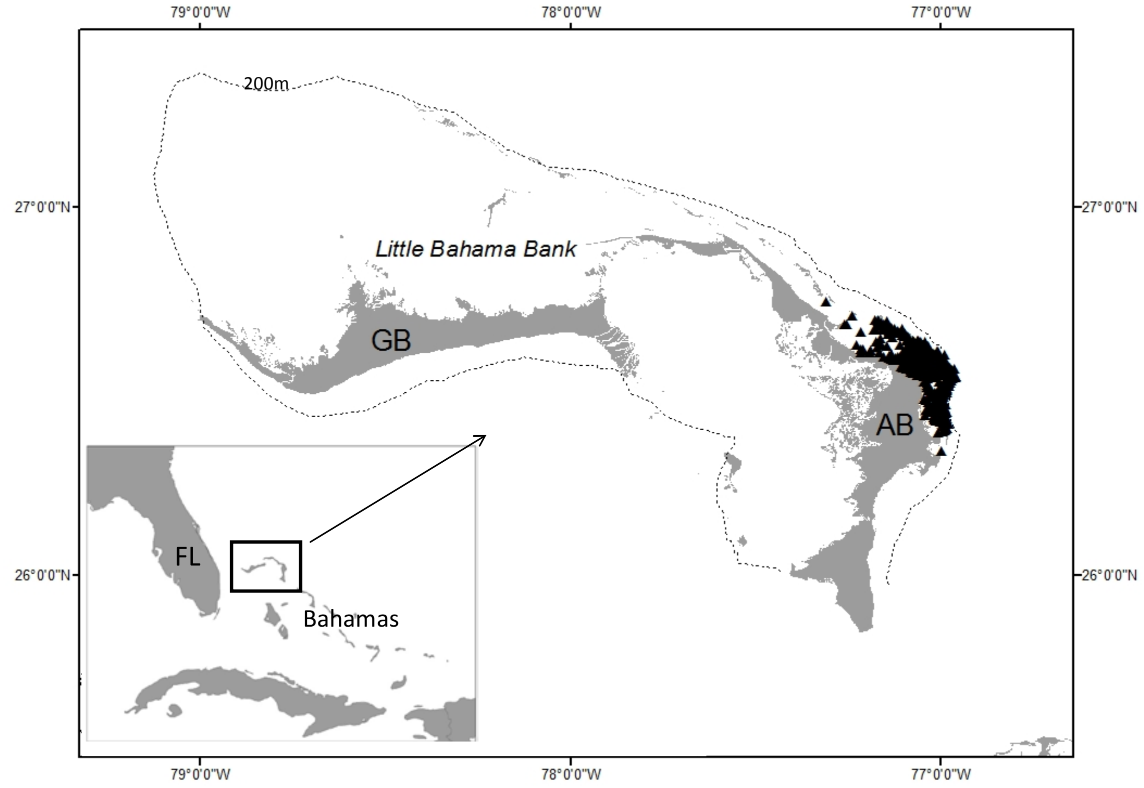

Figure 1: Map of Little Bahama Bank, around Abaco (AB) and Grand Bahama (GB) Islands. The bank is surrounded by the deep waters of the NW Atlantic Ocean, with the 200 m depth contour represented by a broken line. Locations of 788 dolphin encounters between 1992 and 2007 are represented by solid triangles off the east side of Abaco Island where surveys were conducted. The insert shows the position of the study area in the northern Bahamas off the east coast of Florida (FL).

Survey methods

Small (~5m), rigid-hulled inflatable boats have been used to survey in a primarily opportunistic fashion: either in response to reported dolphin sightings, shore-based observations or by visiting areas where dolphins had been previously seen. As a result, survey effort was not uniformly distributed throughout the study area, but rather was focused on areas of high dolphin occurrence to maximize the population coverage through photographic samples. Additionally, randomized line-transect surveys were conducted during five years (1997-2000 and 2007) to ensure that the full extent of the study area was surveyed. Whenever dolphins were encountered, dorsal fin photographs were taken of as many individuals as possible. Between 1992 and 2003, Ilford HP5 black and white film was shot using Nikon 35mm cameras. The film was later push processed to enhance contrast, and reveal markings on the photographed dorsal fins. Between 2004 and 2007 Nikon Digital SLR cameras were used to shoot high resolution images of at least 6MP. Water temperature was recorded during encounters, when possible, using either a hull-mounted or hand-held temperature transducer.

Each identification image was examined on either a light table for black and white negatives or on a high-resolution computer monitor for digital images. Photographs were assigned a quality grade (Q value ranging from 0 to 3) based on the image size, focus, lighting, angle of the fin, and exposure of the photograph. Only high quality ($Q \geq 2$) photos were used for individual recognition. Individual dolphins were identified based on either the pattern of naturally-acquired nicks in the dorsal fin or distinctive fin profiles. These features have been demonstrated to provide reliable individual identification of bottlenose dolphins over time periods of at least several years (Wells *et al.*1987; Scott *et al.*1990; Smolker *et al.*1992; Wilson *et al.* 1999; Connor 2000). Individual identity was assigned by comparing photographs with a photo-identification catalog comprised of distinct individuals documented during the duration of the study. If matched, the photograph was linked to the existing identification number. If not matched, it was given a new number and added to the catalog. The best photograph of each dolphin from each group encountered was selected and databased.

All photographs were examined to detect newborn dolphins. Neonates were easily distinguished based on small body size (typically <1/3 the size of the mother), dark coloration, and floppy dorsal fin, and were often observed surfacing in echelon position next to an attendant adult. However, to standardize for age in this analysis we designated a calf to be a neonate only when there was clear evidence of changes in pigment around linear “folds” oriented dorso-ventrally on the body, resulting from folding of the fetus in utero (Figure 2). All encounter photographs were also examined to document fresh shark-bite wounds on individuals. Fresh wounds do not, of course, inform us of mortality events as a result of predation, but we assume that they provide an indicator of predation pressure. Wounds were classified as shark bites based on a semi-circular shape matching a shark’s jaw and marks resembling teeth marks were observed in association with most large wounds (Figure 3). Additionally, fresh wounds were identified based on a dark tone (black and white images) or red color (digital images) from exposed blood or muscle (Corkeron *et al*. 1987*a*,*b*; Orams and Deakin 1997; Heithaus 2001).

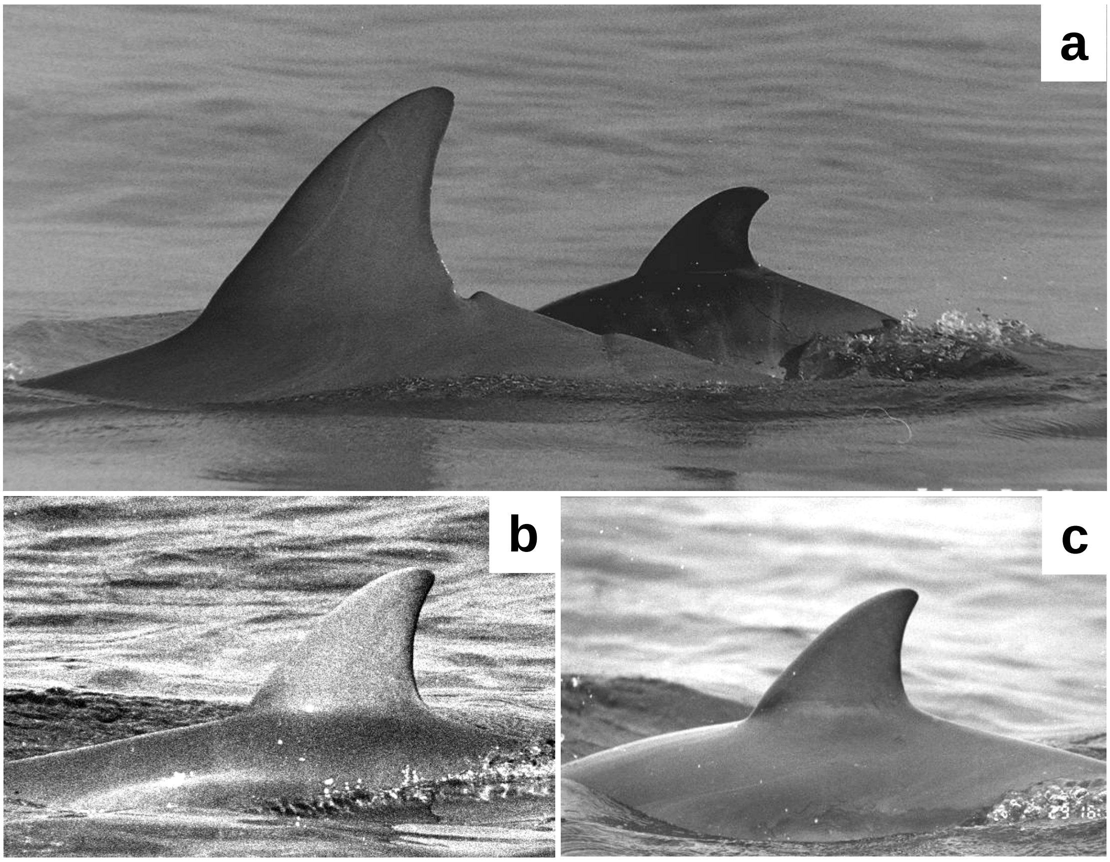

Figure 2. a) Photograph displaying a neonate calf in echelon position next to adult mother, illustrating prominent fetal folds on the calf's small body and darker coloration of the calf. Repeat photographs of a neonate (Tt164, Table 2), first seen on 25th February 1995 (b) and then a month later on 29th March 1995 (c), showing the disappearance of noticeable fetal folds.

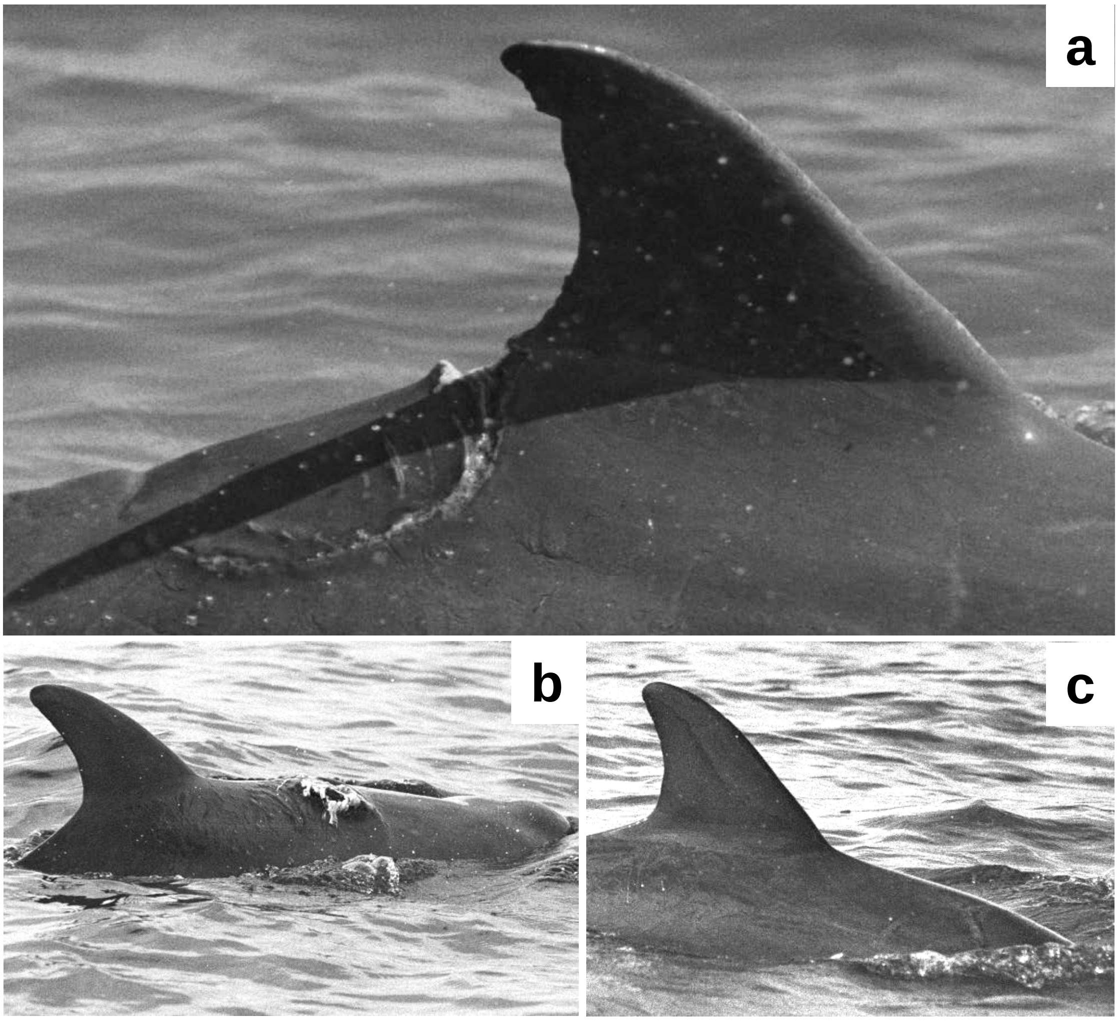

Figure 3. a) Photograph of a fresh shark bite wound just posterior to the dorsal fin of an adult bottlenose dolphin, displaying a semi-circular bite shape with penetration into both blubber and muscle layers, surrounded by teeth marks. Repeat photographs of an individual observed with a prominent, fresh shark bite wound on 23rd August 1996 (b), but only faint healed scars were noticeable when later encountered on 26 November 1996 (c).

Data analysis

To assess monthly variability in both calving and shark bite wounding rates, data across 16 years (1992-2007) were pooled into 12 calendar months to count both the number of neonates and individuals with fresh shark-bite wounds in each monthly interval. To control for survey effort, and the degree to which the population was sampled, the number of neonates/newly wounded individuals was represented as a proportion of the total number of individuals identified in each month, pooled across all years. Because the sample sizes of both neonates and newly wounded dolphins were low, and the total number of identifications varied across the months, point estimates of proportions will vary in how well they represent the true proportion of calves/newly wounded dolphins in the population. To account for inherent uncertainty in these estimates of proportions, we adopted a Bayesian model for the estimation of the proportions, to represent uncertainty in the form of probability distributions.

The Bayesian approach bases inference on full ‘posterior’ probability distributions for parameters of interest (Gelman *et al*. 1995), rather than for point estimates with associated standard errors. Bayesian methods have been repeatedly advocated and used for the analysis and communication of uncertainty in ecological data analysis (Ellison 1996; Durban *et al*. 2000; Wade 2000; Link *et al*. 2002). In our case, the number of neonates/individuals with fresh wounds in each month was modeled as binomially distributed from the total number of individuals identified in that month. This allowed the binomial proportions to represent an estimate of the proportion of individuals that were neonates/newly wounded. The Bayesian approach to estimation first requires prior probability distributions to be assigned to each parameter, and these prior probability distributions are then updated to posterior distributions by conditioning the observed data (Gelman *et al.*1995). Each monthly binomial proportion was initially assigned a flat Beta(1,1) prior, where Beta(a, b) indicates a distribution with mean, $c = a/(a+b)$, and variance, $v = c(1\text{-c})/(a+b+1)$, which was updated conditional on the data to estimate the posterior distribution for each monthly proportion. We used the freely available WinBUGS software (Lunn *et al*. 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to simulate sequences of values from the posterior distributions conditional on the observed data. The sampled values were then used to construct box plots of the posterior distributions for parameters of interest and estimate summary statistics for the posterior distributions.

To examine seasonal differences in the study area, we defined two distinct seasons: a 6-month “summer” period (May – October), characterized by increased water temperatures and encompassing the entire season of tropical cyclones in the NW Atlantic and a contrasting “winter” period (November – April), characterized by cooler water temperatures and a complete absence of cyclonic activity (Table 1). We modified our Bayesian model to have a separate probability distribution underlying the proportions of calves/individuals with new wounds in both winter and summer. In particular, instead of a separate Beta (1,1) prior distribution for each month, we adopted a separate Beta(1,1) prior probability distribution for each season. When the estimates for the two seasonal distributions were made in the same MCMC run, we calculated the proportion of the MCMC sampled values where the winter proportion of calves/wounds exceeded that from the summer (or vice versa) providing an estimate of the probability that the proportions were higher in one season than the other, while accounting for the variability in each seasonal distribution.

Results

A total of 251 individual dolphins were identified from 788 different dolphin groups encountered between 1992 and 2007. Although surveys were not conducted year-round in every year of the study, the population was surveyed in every month, when pooled across years (Table 1). The median number of individual dolphins encountered each month, pooled over all years, was 77 (min 31; max 107) (Table 1). The level of coverage was consistent across seasons, with 185 different individuals documented in “summer” (from 1665 dolphin identifications) and 175 in winter (1236 identifications).

Table 1. Total number of dolphins and neonates identified and the number of individuals with fresh shark-bite wounds for each month pooled over all years (1992-2007). Also presented are the total number of dolphin groups encountered in each month, and the number of years in which each month was surveyed. Water temperature data is also presented by month for March 2007 to February 2008, recorded at a coastal mangrove creek monitoring site (Craig Layman, unpublished data [1]), along with the average surface water temperature during dolphin encounters (1992-2007), where available. Tropical cyclone seasonality is indicated (***), based on long-term records reported in Landsea (1993), along with named storms whose centers passed within 60nm of the study site during the 1992-2007 study period (www.hurricanecity.com/city/abacoisland.htm).

Month	**Years surveyed**	**Groups encountered**	**Total IDs**	**Neonates**	**Fresh wounds**	**Water temperature °C (at dolphins)**	**Cyclone season (Abaco storms)**
January	10	43	67	3	0	22.5 (NA)	-
February	8	58	76	4	1	24.4 (23.6)	-
March	9	63	95	1	0	23.1 (22.3)	-
April	8	39	77	0	0	25.1 (22.8)	-
May	5	27	31	0	0	26.5 (NA)	-
June	9	85	85	0	0	28.6 (27.4)	***
July	7	56	76	0	2	31.1 (29.2)	*** (Bertha 1996)
August	6	65	76	0	4	31.0 (28.2)	*** (Erin 1995[2]); (Dennis 1999)
September	2	123	83	0	4	29.8 (28.4)	***(Floyd 99); (Frances 04[2]);(Jeanne 04[2])
October	9	138	107	0	3	28.0 (27.2)	***
November	8	54	79	3	0	24.3 (26.2)	-
December	5	48	55	5	2	24.3 (NA)	-

[1] Craig Layman, Florida International University, 3000 NE 151st St., North Miami, FL 33181.

[2] No field effort was conducted in the two months directly following each of these hurricanes.

Sixteen neonates were identified during the 17 year study, and seven of these neonates were repeatedly identified throughout the year following first sighting. Photographic analysis revealed that fetal folds were typically only evident for approximately one month in this warm-water environment (Table 2), compared to a period of several months and even years in bottlenose dolphins from more temperate habitats (Grellier 2000). Despite uncertainty due to sample sizes (see error bars), there were clear differences across months in the proportion of individuals that were new calves (Figure 4), with neonates only identified during the "winter" months. The calving rate peaked in December, with a posterior median for the proportion of individuals that were neonates of 0.10 (95% Probability Interval (PI) = 0.04 – 0.19), and was lowest in Oct (posterior median = 0.01, 95% PI = 0.00 - 0.03) (Figure 4). Notably, almost all calves (15/16 or 94%) were born during four months (Nov - Feb) of the winter period. As a result, there was marked difference in the monthly average calf proportion between seasons. The calf proportion in winter (posterior median = 0.09, 95% PI = 0.06 - 0.14) was significantly greater than that in the summer period (posterior median = 0.003, 95% PI = 0.00 - 0.02), with no overlap of the posterior distributions and therefore a high probability (p =1) that the summer and winter calf proportions were different.

Table 2. Dolphin calves first seen as neonate with fetal folds that were subsequently re-photographed within a year; with indication of whether the fetal folds were still visible at time of re-sighting. Only photographs of sufficient quality ($Q \geq 2$) to see folds, should they exist, were used.

Dolphin ID	**First seen with folds**	**Next Seen**	**Folds still visible?**
Tt15	15-Jan-92	21-Mar-92	No
Tt74	13-Dec-92	18-Jan-93	Yes
Tt127	04-Dec-93	06-Mar-94	No
Tt164	25-Feb-95	29-Mar-95	No
Tt166	25-Feb-95	12-Jul-95	No
Tt176	13-Dec-95	09-Mar-96	No
Tt178	13-Dec-95	24-Apr-96	No

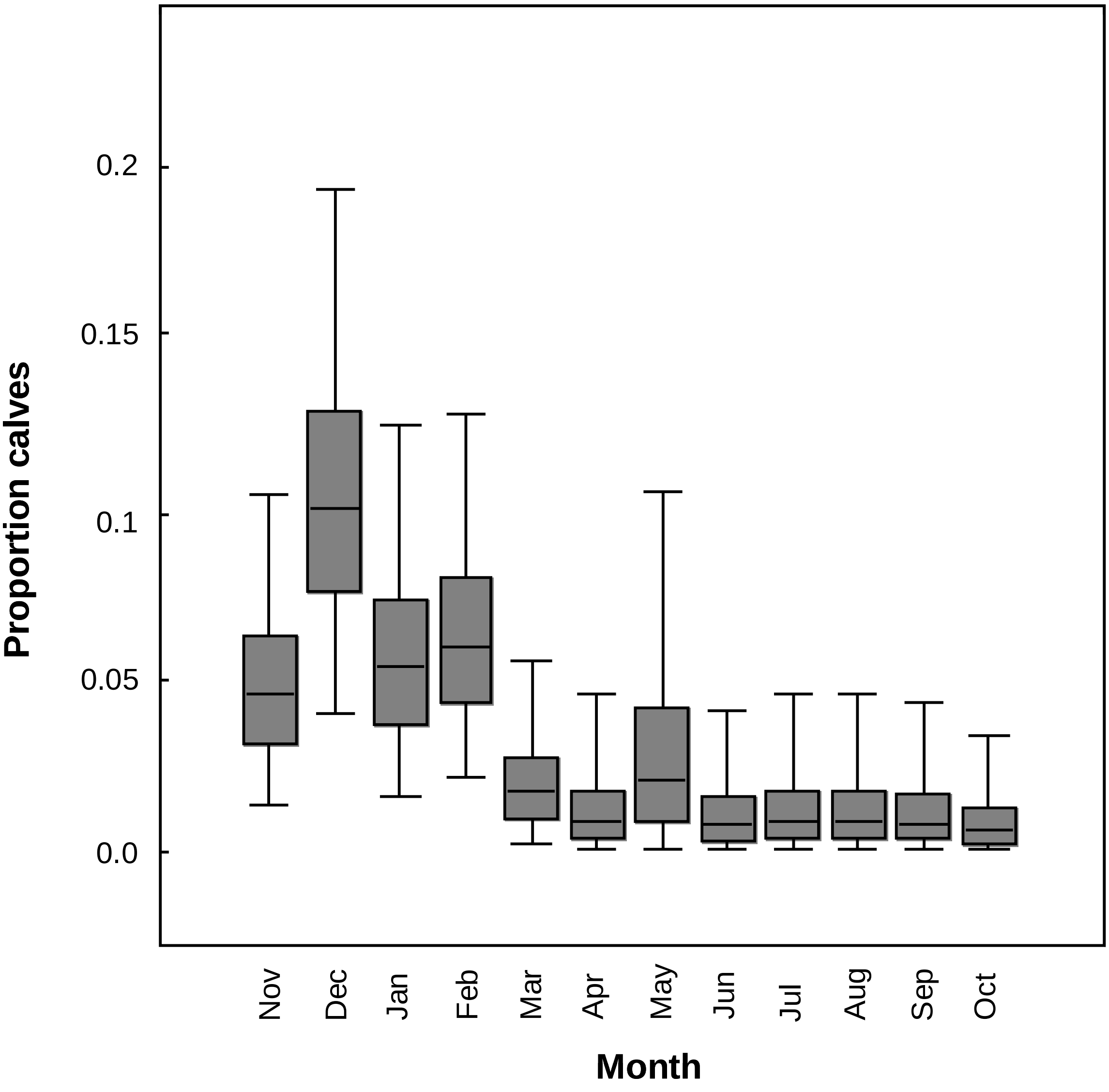

Figure 4. Box plot of the number of neonates as a proportion of the total number of individuals identified in each month. Vertical lines represent the intervals encompassing 95% of the distribution, the boxes represent the central 75% inter-quartile range and horizontal lines represent the posterior medians.

Sixteen fresh shark bite wounds were identified in total, comprising adult males (2), adult females (3), adults of unknown gender (3), subadults (2), and juveniles (6). Analysis of within-year re-sightings, possible for nine of these dolphins, documented that these wounds only appear fresh (red or dark) for typically around a month (Table 3; Figure 3), and therefore we consider fresh wounds to be a sensitive indicator of the timing of shark attacks. Similar healing rates were reported in another warm-water study area off Australia (Corkeron *et al*. 1987*a*; Orams and Deakin 1997), where the complete closure of a fresh shark bite wound was observed to occur within 30 days, and all that remained after 45 days was “an obvious indented white un-pigmented scar” (Orams and Deakin 1997). Wounds from skin and blubber biopsies from dolphins in our Abaco study site were also reported to be “closed” (covered by epidermal tissue) after 30 days (Parsons *et al.* 2003). Most (13/16, 81%) of the shark-bite wounds we observed were acquired during a four month period (Jul - Oct) within the summer season for tropical cyclones and increased water temperatures. The wounded proportion was highest in both August and September, with a posterior median for the proportion of individuals that possessed fresh wounds of 0.06 (95% PI = 0.02 – 0.13 and 0.02 - 0.12, respectively), and was lowest in March (posterior median = 0.01, 95% PI = 0.00 - 0.04) (Figure 5). The wounded proportion was significantly higher in summer (posterior median = 0.07, 95% PI = 0.04 – 0.12) compared to winter (posterior median = 0.02, 95% PI =0.01 – 0.05). There was some overlap in the ranges of posterior distributions for these two estimates, but little overlap in the regions of highest probability density, and therefore a very high probability ($p = 0.99$) that the summer and winter average wound proportions were different. Notably, the majority (11/16) of the documented wounds were observed immediately following either the direct passage of hurricane Bertha over Little Bahama Bank in July 1996 or the joint impact of direct hits from Hurricanes Dennis and Floyd in late August and September 1999.

Table 3. Dolphins first seen with a fresh shark bite wound that were subsequently re-photographed within a year; with indication of whether the wound was still fresh (e.g. dark or red) at time of re-sighting. Only photographs of sufficient quality (Q ≥ 2) to see the wound site in good clarity were used.

Dolphin ID	**Fresh wound first seen**	**Re-sighted**	**Wound still fresh?**
Tt70	06-Dec-92	29-Jan-93	No
Tt42	08-Dec-93	16-Jan-94	No
Tt32	31-Jul-96	21-Aug-96	No
Tt55	23-Aug-96	26-Nov-96	No
Tt17	27-Aug-97	27-Apr-98	No
Tt276	30-Sep-99	06-Oct-99	Yes
Tt247	30-Sep-99	19-Oct-99	Yes
Tt62	24-Sep-99	19-Oct-99	Yes
Tt287	05-Oct-02	19-Feb-03	No

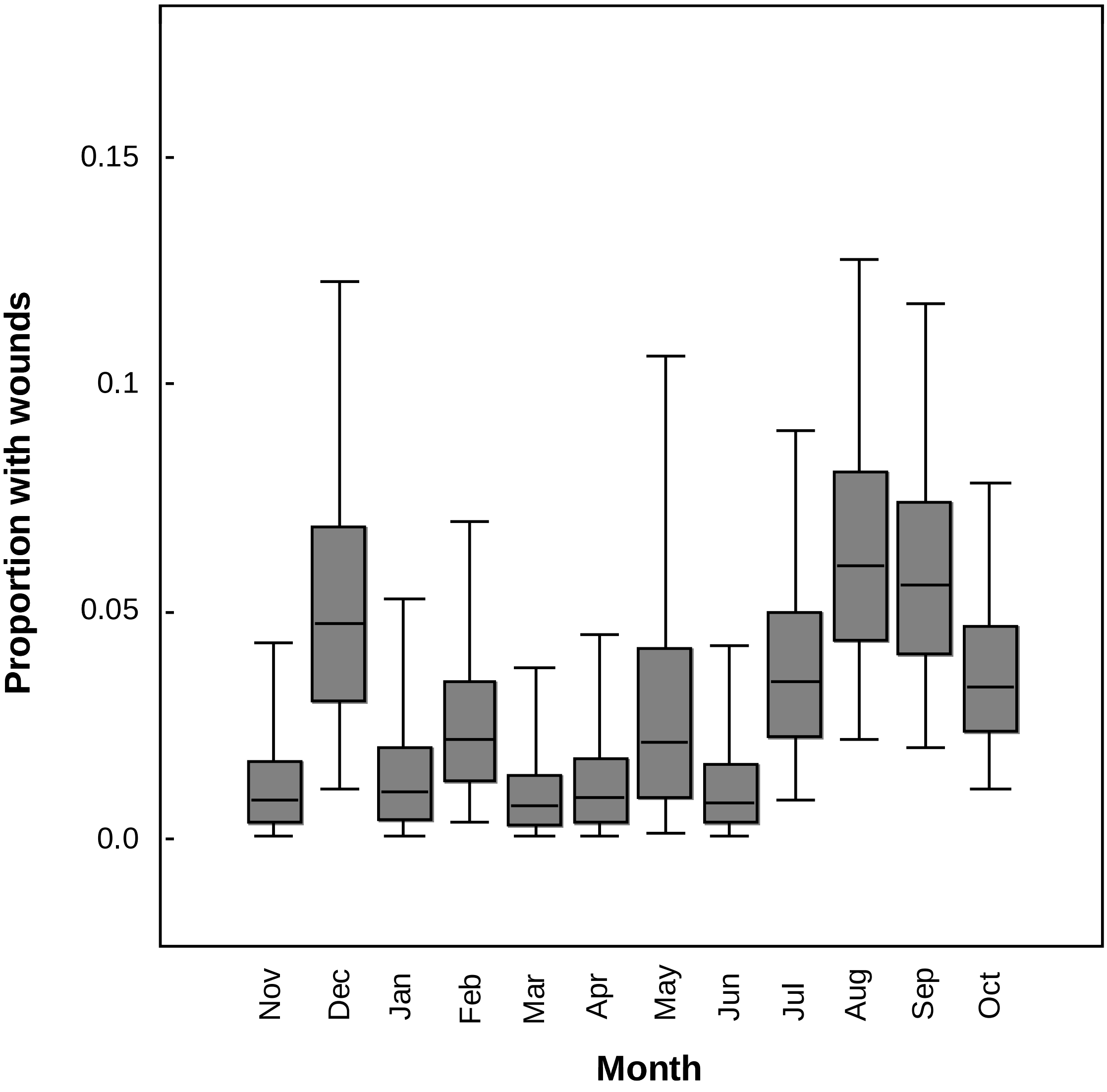

Figure 5. Box plot of the number of individuals with fresh shark bite wounds as a proportion of the total number of individuals identified in each month. Vertical lines represent the intervals encompassing 95% of the distribution, the boxes represent the central 75% inter-quartile range and horizontal lines represent the posterior medians.

Discussion

These data describe distinct calving seasonality for dolphins on Little Bahama Bank, with all neonates documented during the winter months, and none during the seven months with the highest water temperatures. This is similar to findings from higher latitude study sites, where distinct calving seasonality of odontocetes has been suggested to be linked to seasonal changes in water temperature and/or changes in prey (Read 1990; Urian *et al.* 1996; Haase and Schneider 2001; Thayer *et al.* 2003; Westgate and Read 2007; McGuire and Aliaga-Rossel 2007). However, there are notable contrasts with these studies, as calving in our study is inversely related to summer increases in water temperature, and the temperature variability on Little Bahama Bank is relatively minor compared to higher latitudes.

We cannot rule out the possibility of calving in response to a seasonal shift in prey availability as we do not have detailed data on feeding habits, but known dolphin prey species are observed throughout the year. It is also possible that even small increases in water temperature in this shallow water system create an environment that is too physiologically demanding in summer. High costs of maintaining a stable body temperature, when confronted with suboptimal ambient temperatures (high or low), have been shown lead to changes in reproduction and survival of several mammalian populations (Dunbar 1980; Ohsawa and Dunbar 1984; Rutberg 1987; Dunbar 1990; Boyd 1996; Hill *et al.* 2000). However, an inverse correlation between calving seasonality and the acquisition of fresh shark-bite wounds suggest that seasonal changes in the environment may have also selected indirectly for calving seasonality by driving shifts in distribution and habitat use of dolphins and/or predatory sharks that lead to increased predation risk for dolphins. Although constrained by small sample sizes, we documented a relatively high proportion of juveniles with fresh shark-bite wounds, and all three adult females observed with fresh wounds had dependent calves at the time; this might imply the targeting of young animals by predatory sharks.

Unfortunately, data on shark movements is lacking from our study area, and equal-area coverage surveys for dolphins have not been conducted year round to provide a robust assessment of seasonal changes in dolphin distribution. Nonetheless, 13 of the 16 fresh shark-bite wounds on dolphins were documented in the summer months, indicating a seasonal change in dolphin and shark interactions. We suggest that dolphins seeking cooler oceanic waters, or alternate prey sources, may spend more time in summer close to the deeper, exposed waters at the edge of the bank, which in turn may expose them to increased predation risk from oceanic sharks, particularly tiger sharks, that are known to prey on dolphins (Norris and Dohl 1980; Wells *et al*. 1987; Corkeron *et al*. 1987*a,b*; Cockcroft *et al*. 1989; Cockcroft 1991; Oram and Deakin 1997; Heithaus 2001). There may also be seasonal inshore movements of sharks, but although predatory sharks are common in the deep waters surrounding Little Bahama Bank, they are rarely sighted in the shallow, protected waters on the bank (BMMRO unpublished data).

The selective disadvantage of calving in summer may be accentuated by acute weather events, specifically the incidence of hurricanes. Hurricanes are a key feature of climatic and seasonal variability in the environment of the NW Atlantic (Landsea 1993; Webster *et al.*2005; Vecchi and Soden 2007). These storms have been shown to have significant impact on both marine and terrestrial ecosystems (Spiller *et al.*1998; Walther *et al*. 2002; Harley *et al.* 2006) and have been implicated in the mass-stranding of cetaceans (Mignucci-Giannoni *et al*. 2000). The wind-driven wave heights and storm surge during intense hurricanes easily exceed the shallow water depth on Little Bahama Bank, making the shallow waters uninhabitable to dolphins. Although we have one anecdotal report of dolphins in a protected creek during Hurricane Bertha in 1996, we suspect that the primary survival response is to seek this deeper water habitat at the edge of the bank, which in turn exposes them to increased predation risk from oceanic sharks. Most (11/16) of the fresh shark-bite wounds were documented immediately following either the direct passage of hurricane Bertha over Little Bahama Bank in July 1996 or the joint impact of direct hits from Hurricanes Dennis and Floyd in late August and September 1999.

Unfortunately, photo-identification effort was limited in the months immediately following hurricanes in recent years. Nonetheless, these data suggest that predation risk is increased by these acute weather events. Notably, all neonates documented during this study were seen outside of the hurricane season for the NW Atlantic (June – Oct, Landsea 1993), and only two calves were documented in the three calendar months prior to the onset of hurricane season. We suggest that this may be a response to the selective disadvantage of rearing a young calf during this potentially dangerous time (Miller *et al.* 2000).

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CHAPTER THREE

PHOTOGRAPHIC MARK-RECAPTURE ANALYSIS OF LOCAL DYNAMICS WITHIN AN OPEN POPULATION OF DOLPHINS

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Ecological Applications **22(5),** 1689-1700

CHAPTER THREE

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Abstract

Identifying demographic changes is important for understanding population dynamics. However, this requires long-term studies of definable populations of distinct individuals, which can be particularly challenging when studying mobile cetaceans in the marine environment. We collected photo-identification data from 19 years (1992-2010) to assess the dynamics of a population of bottlenose dolphins (*Tursiops truncatus*) restricted to the shallow (<7m) waters of Little Bahama Bank. This population was known to range beyond our study area, so we adopted a Bayesian mixture modeling approach to mark-recapture to identify clusters of individuals that used the area to different extents, and specifically estimated trends in survival, recruitment and abundance of a "resident" population with high probabilities of identification. There was a high probability (p = 0.97) of a long-term decrease in the size of this resident population from a maximum of 47 dolphins (95% Highest Posterior Density Intervals, HPDI = 29-61) in 1996, to a minimum of just 24 dolphins (95% HPDI = 14 - 37) in 2009; a decline of 49% (95% HPDI = -5% to -75%). This was driven by low per-capita recruitment (average ~ 0.02) that could not compensate for relatively low apparent survival rates (average ~ 0.94). Notably, there was a significant increase in apparent mortality (~5 apparent mortalities vs. ~2 on average) in 1999 when two intense hurricanes passed over the study area, with a high probability (p = 0.83) of a drop below the average survival probability (~0.91 in 1999; ~0.94 on average). As such, our mark-recapture approach enabled useful inference about local dynamics within an open

population of bottlenose dolphins; this should be applicable to other studies challenged by sampling highly mobile individuals with heterogeneous space-use.

Introduction

Identifying demographic changes is key to understanding population dynamics (e.g. Chapron *et al.* 2009). However, this requires long-term studies of definable populations of distinct individuals, which can be particularly challenging when studying mobile cetaceans in the marine environment. In exceptional circumstances, cetaceans can be monitored through complete annual censuses of individuals (e.g. Ford *et al.* 2010), but in most cases demographic analyses rely on following the fates of individually marked animals using mark-recapture sampling (Lebreton *et al.* 1992). Specifically, photo-identification of natural markings has allowed individual cetaceans to be monitored in photographic “capture” and “recapture” samples (Hammond 1990a; Hammond *et al.* 1990), and in a limited number of cases this approach has been used to make inference about demographic changes and population dynamics (Whitehead *et al.* 1997; Cameron *et al.* 1999; Caswell *et al.* 1999; Fujiwara and Caswell 2001; Mizroch *et al.* 2004; Leaper *et al.* 2006; Corkery *et al.* 2008).

However, despite a growing number of long-term photo-identification studies of dolphins, inference about demographic changes has been constrained by the large-scale movements of individuals relative to the small coastal study sites that are logistically feasible (Durban *et al.* 2005). This mobility results in uncertainty over population definition, heterogeneity in ranging patterns (e.g. Lusseau *et al.* 2006), temporary emigration beyond the study area (Whitehead 1990), and the presence of “transient” individuals among local or “resident” populations (Pradel *et al.* 1997; Conn *et al.* 2011): all violate assumptions of traditional mark-recapture approaches and constrain inferences about demographic parameters.

Although modern mark-recapture approaches provide tools to separate the effects of movement from survival estimates (e.g. Whitehead 1990; Pradel *et al.* 1997; Cameron *et al.* 1999; Silva *et al.* 2009), these approaches require sampling designs that are often impractical for wide-ranging dolphins, or have unrealistic assumptions about movements. Specifically, it is generally impossible to obtain an adequate sample from “secondary” periods within each year that are sufficiently short to guarantee an absence of movement beyond the study area (e.g. Durban *et al.* 2000), and therefore provide unbiased estimation of detection probability using the “robust design” (Pollock *et al.* 1990). Furthermore, assumptions of constant or random temporary emigration between “primary” annual periods (Whitehead 1990; Kendall and Nichols 2002) are unlikely to be met in populations with heterogeneous ranging patterns (e.g. Lusseau *et al.* 2006). Similarly, within-year movements between study areas (e.g. Durban *et al.* 2005) violate assumptions of a multi-state mark-recapture approach (Cameron *et al.* 1999). Furthermore, sparse data samples and low detection probabilities can lead to uncertainty in distinguishing “resident” and “transient” individuals based on recapture histories alone (Pradel *et al.* 1997).

To overcome these issues, we applied a new parameterization of the established Jolly-Seber model (Royle and Dorazio 2008; Gardner *et al.* 2010) to photographic identification records to make inference about the population dynamics of bottlenose dolphins (*Tursiops truncatus*) occurring in a coastal study area in the northern Bahamas. Long-term re-identifications over a 19-year period allowed us to monitor the “superpopulation” using the area, even though the entire population was not always present, through imputation of out-of-sample identification data. In contrast to existing estimators for open populations (Schwartz and Arnason 1996), this new parameterization adopted an individual-specific factorization that was amenable to modeling individual effects, which allowed us to identify distinct population clusters (e.g. Durban *et al.* 2010), that used the study area to different extents (Whitehead and Wimmer 2005). Specifically we used hierarchical Bayesian mixture modeling to identify a “resident” cluster, or population, of individuals with relatively high probabilities of identification, allowing us to reduce the influence of “transient” individuals (e.g. Pradel *et al.* 1997), providing increased power for estimating trends in survival, recruitment and abundance. We discuss between-year changes in demographic parameters and abundance in relation to key environmental covariates, notably the incidence and intensity of hurricanes, highlighting the utility of this approach.

Methods

Population definition and field sampling

Annual surveys were conducted in each of 19 years between 1992 and 2010 in a 160km^2 study site on the east side of Abaco Island (~ 26^{o}33’N, ~ 077^{o}04’W); part of Little Bahama Bank in the northern Bahamas (Figure 1). Dolphins in this area are part of a larger population of approximately 1100 individuals (Durban 2002) that are restricted to the shallow waters (generally <7m) of Little Bahama Bank by the deep surrounding waters of the NW Atlantic Ocean (Parsons *et al.* 2006). Although only a fraction of this overall population uses the east Abaco study area (Chapter 2), there is a high re-sighting rate of individuals within the study area (Claridge 1994; Durban *et al.* 2000; Parsons *et al.* 2003, Parsons *et al.* 2006; Chapter 2), implying site fidelity of at least some of the individuals over the two decades of study.

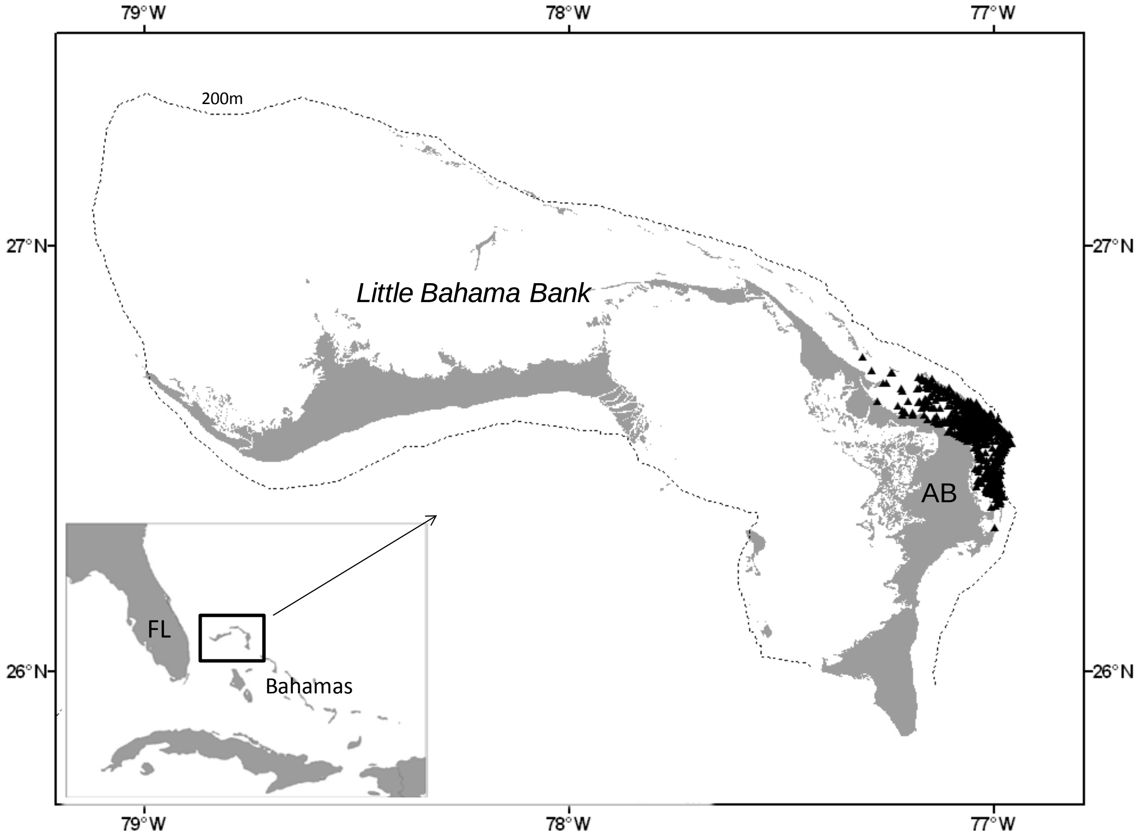

Figure 1. Map of the study area east of Abaco Island (AB) on Little Bahama Bank, off the coast of Florida (FL). Solid triangles show locations of 881 encounters with bottlenose dolphins between 1992 and 2010, from which photo-identification data were collected.

Small (~5m), rigid-hulled inflatable boats were used to survey in a primarily opportunistic fashion: either in response to reported dolphin sightings and shore-based observations or by visiting areas where dolphins had been previously seen. As a result, survey effort was not uniformly distributed throughout the study area, but rather was focused on areas of high dolphin occurrence to maximize the population coverage through photographic samples. Additionally, randomized line-transect surveys were conducted during seven years (1997-2000, 2007-2009) to ensure that the full extent of the study area was surveyed. When dolphins were encountered, dorsal fin photographs were taken of as many individuals as possible. Between 1992 and 2003, Ilford HP5 black and white film was shot using Nikon 35mm cameras. The film was later push processed to enhance contrast, and reveal markings on the photographed dorsal fins. Between 2004 and 2010 Nikon digital SLR cameras were used to shoot high resolution images of at least 6MP.

The timing and number of surveys each year varied due to weather, logistic support and personnel availability. We therefore defined an annual census period between January and October, overlapping with the majority of dolphin encounters. In addition to mark-recapture analyses of data from each year we also compared sighting frequencies for the month of October in six “index” years between 1998 and 2010. These index months were chosen because of high and comparable survey effort.

Photographic mark-recapture

Each identification image was examined on either a light table (black and white negatives) or on a high-resolution computer monitor (digital images). Photographs were assigned a quality grade (Q value ranging from 1 to 3) based on the image size, focus, lighting, angle of the fin, and exposure of the photograph (Durban *et al.* 2000). Only high quality ($Q \geq 2$) photos were used for individual recognition. Individual dolphins were identified based on either the pattern of naturally-acquired nicks in the dorsal fin or distinctive fin profiles. These features have been demonstrated to provide reliable individual identification of bottlenose dolphins over time periods of at least several years (Scott *et al.*1990; Wilson *et al.* 1999). Individual identity was assigned by comparing photographs with a photo-identification catalog comprising distinct individuals identified during the duration of the study. If matched, the photograph was linked to the existing identification number. If no match was found, it was given a new number and added to the catalog. The best photograph of each dolphin from each group encountered was selected and added to the database.

We treated these photographic identifications and re-identifications of individuals as “captures” and “recaptures” to which analytical mark-recapture techniques could be applied. Specifically, we pooled all identifications into binary identification histories for each dolphin in each annual period, and constructed a matrix of identification histories with elements h_{ij} taking the values 1 or 0 to indicate whether or not each observed individual $i = 1,\ldots, n$ was identified during each of the $t = 1,\ldots, T = 19$ annual sampling periods. To make inference about population dynamics, we adopted a new parameterization of the Jolly-Seber mark-recapture model that allowed for estimation of both survival and recruitment (Royle and Dorazio 2008; Gardner *et al.* 2010). Because the size of the “superpopulation” available to be identified was not fixed, but unknown, we augmented the list of individuals observed with a large number (M=50) of all zero identifications histories to represent the pool of unidentified individuals available for recruitment.

For each identification history h_i there was a corresponding population history given by x_i, a vector of binary state variables describing whether or not individual i was alive or not. Estimation of these population states was accomplished through a model for the demographic processes of survival and recruitment (Royle and Dorazio 2008):

$$x_{i,t+1} \sim \text{Bern}\left\{\phi_{it} x_{it} + \gamma_{it+1}\left\{\prod_{k=1}^{t}(1 - x_{ik})\right\}\right\}$$

with the initial state given by $x_{i1} \sim \text{Bern}(\gamma_{i1})$. Thus, if an individual was alive at time t (i.e. $x_{it} = 1$) then its status at time $t + 1$ was modeled as the outcome of a Bernoulli random variable with parameter φ_{it}, the probability of surviving from time interval t to $t + 1$. If an individual was not alive during the previous time intervals 1,.., t (i.e. $x_{it} = 0$), then the outcome was a Bernoulli trial with parameter γ_{it+1}, the probability of entry into the population between intervals t and $t +1$.

Known deaths were incorporated by inputting values of 0 for x following the recovery of a carcass of a known individual: this occurred once during the study. Similarly, values of 1 were inputted for x in years when any dolphin was not identified ($h = 0$) between years of repeated identifications ($h = 1$), and similar imputation was based on identifications in the out-of-sample months (November and December) subsequent to annual sampling intervals when a dolphin was not seen, but was previously known to be alive. Where the status was unknown following the interval of last identification or before first identification, and for all unobserved augmented individuals, we treated x_{ij} as a missing value about which inference may be made. Annual estimates of population abundance, N_t were therefore simply derived as a function of the latent state variable x_{it}, indicating how many individuals were alive in each year:

$$N_t = \sum_{i=1}^{n+M} x_{it}$$

Similarly, contributions to changes in the abundance were assessed by monitoring changes in the latent state variable x_{it} to derive the number of deaths D_{t+1} and recruits R_{t+1} occurring between each consecutive pair of years t: $t + 1$:

$$R_{t+1} = \sum_{i=1}^{n+M} (1 - x_{it}) x_{it+1} \qquad D_{t+1} = \sum_{i=1}^{n+M} x_{it} (1 - x_{it+1})$$

Per capita recruitment, b_t, was then derived as a simple ratio of the number of recruits to abundance in each year R_t / N_t.

The parameters and missing data of the population process were estimated from the observed data through an observation model for the identification histories h_{it}. Conditional on the partly observed population process x, the binary observations were modeled as independent random variables:

$$h_{it} \sim \mathrm{Bern}(p_{it}\, x_{it})$$

The model for the observed identification histories h therefore reflected the fact that an animal could only be identified if it is alive. If $x_{it} = 0$ (individual i has either died, or has not yet recruited) then $h_{it} = 0$ with probability 1, otherwise h_{it} was a Bernoulli trial with parameter p_{it} describing the identification probability. Not all individuals that were known or estimated to be alive necessarily used the study area in each year, so this identification probability inherently encompassed the combined process of temporary emigration away from the area and detection probability when in the area (e.g. Whitehead 1990). This alleviated the requirement to impose unrealistic assumptions about random or constant temporary emigration (Whitehead 1990; Kendall and Nichols 2002), and allowed for temporary emigration beyond the study area to vary across time and across individuals in response to both individual movement and effort-dependent changes in the effective size of the study area. As a consequence, the population size N_t referred to the size of the sample population that used the study area, despite the realization that all these individuals are not necessarily present in the study area in each year.

Temporal and individual variation in identification probabilities were specified by modeling p as a function of a mean (μ) and time-varying individual random effects terms (ε):

$$\text{logit}(p_{it}) = \text{logit}(\mu^{p}) + \varepsilon_{z[i]=c,t}{}^{p}$$
$$\varepsilon_{ct}{}^{p} \sim \text{N}(0, \sigma^{p})$$

where logit(a) = log(a/(1-a). Instead of a separate effect for each individual in each year, we adopted a mixture formulation where each annual random effect was drawn from a specific cluster, c , with assignment of individuals to clusters through estimation of the indicator variable $z_i = c$. For a ceiling of $C = 10$ potential clusters, we used a Dirichlet process to draw a set of C values of $\varepsilon_{ct}{}^{p}$ for each year t from a baseline distribution with mean 0 and standard deviation σ^{p}, and estimated which value $z_i = c=1,\ldots,C$ was appropriate for each individual (following Durban *et al.* 2010). The model therefore identified clusters of dolphins with similar vectors of capture probabilities across years. We used a similar stratification of survival (φ) and recruitment (γ) probabilities, with annual random effects terms drawn from a distribution stratified by the cluster indicators that were estimated from the capture probabilities:

$$\text{logit}(\varphi_{it}, \gamma_{it}) = \text{logit}(\mu^{\varphi,\, \gamma}) + \varepsilon_{c,t}{}^{\varphi\, \gamma}$$
$$\varepsilon_{ct}{}^{\varphi,\, \lambda} \sim \text{N}(0, \sigma^{\varphi,\, \lambda})$$

Therefore the model did not estimate clusters of dolphins with similar survival or recruitment histories, but rather estimated survival and recruitment for the clusters with similar capture probabilities.

Bayesian Inference

The Bayesian approach is well suited to conveying uncertainty due to small sample sizes, as inference is based on full probability distributions (Gelman *et al.* 1995; Wade 2000). This approach required prior distributions to be specified for all model parameters, and we adopted similar priors for the mean and standard deviation of each parameter set: Uniform (0,1) prior distributions were placed on each of the mean probabilities $\mu^{\varphi,\gamma,p}$ and a Uniform (0,10) was adopted for the standard deviations $\sigma^{\varphi,\gamma,p}$ to allow annual differences from the means to emerge. This hierarchical prior allowed years in the set with relatively informative data to contribute largely towards the mean, and estimates from sparse data years were drawn towards the overall mean. This had the effect of smoothing estimates across each set so that notable variability from the mean was detected, but there was “borrowing strength” across each set to allow for more precise estimates in sparse data years. Note that we set $p_1 = p_2$ and $p_T = p_{T-1}$ to ensure parameter identifiability (Link and Barker 2005), and therefore we only present estimates for $t = 2,\ldots,T\text{-}1$.

Once these priors had been assigned, the model described a series of probability distributions for the unknown parameters and missing data components conditional on the observed data. Missing data were thus treated the same as the other unknown parameters, and updated based on the observed data. We used the WinBUGS software (Lunn *et al.* 2000) to implement Markov Chain Monte Carlo (MCMC) sampling to make repeated draws from the conditional distributions and estimate the posterior distribution for each parameter. We based inference on 30,000 MCMC iterations after discarding a “burn-in” of 10,000 iterations prior to convergence of three different chains (Brooks and Gelman 1998). With repeated iterations, the modal cluster allocation z_i attaching to individual i was taken over the candidate values assigned at each iteration of the chain, and variability in the sampled values represented uncertainty about cluster membership. Simultaneous MCMC sampling from the multiple parameters in the model enabled this uncertainty to be propagated into uncertainty about the cluster-specific parameters. Similarly, by simultaneously monitoring estimates of parameter values across MCMC iterations we were able to make probabilistic statements about hypotheses, for example the probability that a specific annual survival probability was less than the average that was estimated from the proportion of iterations for which $\varepsilon_{c,t}^{\varphi}<0$.

We employed the same MCMC simulation approach to generate predictive observations to compare the fit of the competing models using a posterior predictive criterion (Gelfand and Ghosh 1998). In order to assess the utility of allowing for clustered heterogeneity, we tested the fit of this Jolly-Seber model with clustered time-varying individual effects (JS$_{tc}$) to a model with just time-varying random effects (JS$_{t}$):

$$\text{logit}(p_{it}, \varphi_{it}, \gamma_{it}) = \text{logit}(\mu^{p, \varphi, \gamma}) + \varepsilon_t^{p, \varphi, \gamma}$$
$$\varepsilon_t^{p, \varphi, \gamma} \sim \text{N}(0, \sigma^{p, \varphi, \gamma})$$

For each model, we predicted a new set of data of the same dimensions as the observed data (i in 1,…,n and t in 1,..,T) by generating samples directly from the posterior distributions of the fitted model parameters. We then calculated a loss function that measured the discrepancy between the observed data, H, and the predicted data, H^{new}. As a loss function, we used the sum of the predicted errors (PE):

$$PE = \sum_{i=1}^{n} \sum_{t=1}^{T} \left[h_{it}^{new} - h_{it}\right]^2$$

As with other model selection methods, the predictive criterion achieves a compromise between the goodness-of-fit and a penalty for the number of free parameters in the model (Gelfand and Ghosh 1998). The model with the smallest criterion value was estimated to be the model that would best predict a replicate dataset of the same structure as that currently observed.

However, the predictive model selection criterion did not reveal whether the selected model was a plausible fit for the observed data. We therefore also adopted a posterior predictive approach for goodness-of-fit checking (Gelman *et al.* 1996), by drawing predicted data from the posterior distributions of model parameters for each selected cluster, *c*, and calculating a discrepancy measure, D_c, for both the predicted H^{new} and observed data H (e.g. Durban *et al.* 2010):

$$D(H)_c = \sum_{i=1}^{n} \sum_{t=1}^{T} \left| h_{z[i]=c,t} - p_{z[i]=c,t} \right|$$

$$D(H^{new})_c = \sum_{i=1}^{n} \sum_{t=1}^{T} \left| h^{new}_{z[i]=c,t} - p_{z[i]=c,t} \right|$$

Because the discrepancy measures themselves both had posterior distributions, they were compared by estimating the exceeding tail area probability, termed the posterior predictive p-value, as the percentage of MCMC draws for which $D(H^{new})_c$ exceeded $D(H)_c$. Values close to 0.5 indicated that the realized discrepancy of the data was very similar to what one might expect from replications under the model and values close to zero or one implied a poor fit (Gelman *et al.* 1996).

Results

Mark-recapture sample

Photographs were taken during 881 encounters with dolphins (Figure 1), resulting in 3558 individual identifications. Most (779 encounters, 3121 identifications) occurred within the January-October sampling interval, comprising 284 individual dolphins. After constraints for photographic quality and individual distinctiveness were applied, the mark-recapture sample was restricted to 237 individuals, representing 820 non-zero entries in the identification matrix (*h*). There were 52 additional identifications of these same individuals that were used as out-of-sample re-sightings, and 513 additional annual records that were imputed as "alive" (x_{it} =1) for years when dolphins were not identified between years of repeated identifications. The number of these individuals identified in each annual sample varied across years (median = 36, range = 4 - 90), reflecting variability in the number of encounters (Table 1). Individuals were identified in an average of two different years (median = 2, range = 1 - 15), but there was evidence of some bimodality to the frequency of identification, and 18 dolphins were seen in 10 or more years (Figure 2). The cumulative number of distinct individuals increased throughout the study period (Figure 3), suggesting an open population with regular recruitment of new animals to the study area.

Table 1. The number of encounters with dolphins and number of distinct individuals identified from high quality photographs in the annual January-October sampling intervals (Nov-Dec out of sample encounters, and additional individuals, shown in parentheses).

Year	**Number of Encounters**	**Number of Individuals**
1992	31 (25)	35 (14)
1993	32 (24)	46 (12)
1994	31 (13)	45 (6)
1995	72 (15)	67 (7)
1996	135 (11)	81 (8)
1997	31 (0)	32 (0)
1998	194 (9)	86 (14)
1999	78 (0)	90 (0)
2000	35 (2)	35 (0)
2001	3 (0)	5 (0)
2002	3 (0)	13 (0)
2003	11 (0)	49 (0)
2004	2 (0)	4 (0)
2005	9 (0)	36 (0)
2006	4 (0)	13 (0)
2007	20 (0)	33 (0)
2008	25 (3)	50 (0)
2009	21 (0)	32 (0)
2010	42 (0)	68 (0)

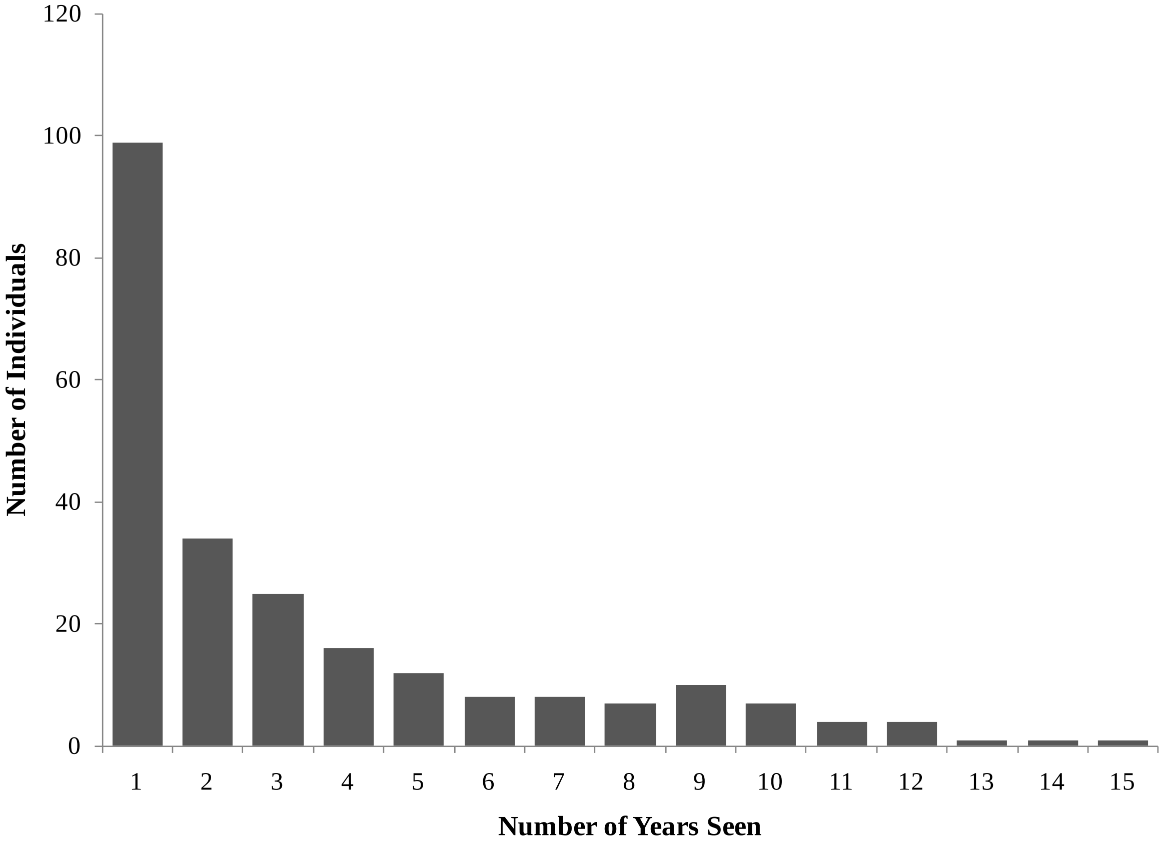

Figure 2. Number of years in which distinctly marked individual dolphins were documented from high quality photographs.

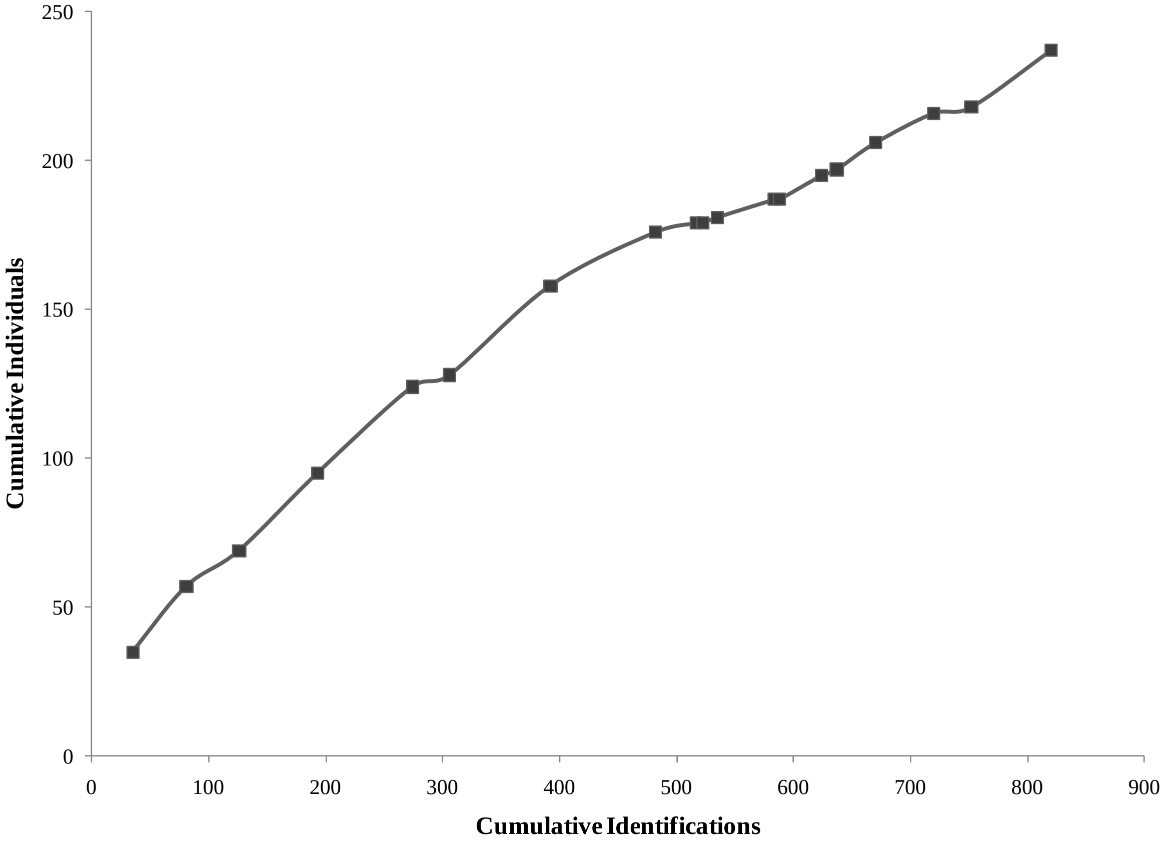

Figure 3. Discovery curve of the total number of distinctly marked individual dolphins identified from the growing number of cumulative identifications made in each year between 1992 and 2010.

Model fitting

There were notable differences in the estimates produced using the Jolly-Seber model with clustered time-varying individual effects (JS_{tc}) compared to the standard model with only time-varying parameters (JS_t) (Table 2). The incorporation of heterogeneous individual effects into the model had the effect of lowering the estimated average probability of identification, therefore raising the average size of the estimated “superpopulation” using the area. Estimates of the average survival and recruitment probabilities were comparable under both models, but both were higher for the JS_{tc}. Model selection supported the incorporation of clustered individual effects, with predicted values from the JS_{tc} model displaying closer agreement to the observed identification histories than the JS_t model, with 648 predicted errors over the 4503 binary observations, compared to 669 (Table 2). Further inference was therefore based solely on the JS_{tc} model, which had the smallest predictive error (Gelfand and Ghosh 1998).

Table 2. A comparison of two mark-recapture models fit to the photo-identification data: a Jolly-Seber formulation with time-varying parameters (JS_t) and a model with heterogeneity incorporated through clustered time-varying individual effects (JS_{tc}). Best fit was determined by the sum of the predicted errors (PE) from each model across the 4503 binary observations. Posterior median values (with 95% highest probability density intervals in parentheses) are shown for the average annual probability of identification, survival, and per-capita recruitment, and size of the superpopulation using the study area. For the JS_{tc} model, the number of clusters to which individuals could be assigned with the majority of their probability density ($p_{z_i=c}$>0.50) is shown, from a ceiling of 10 potential clusters.

	PE	**Probability of Identification** μ_p	**Probability of Survival** μ_φ	**Probability of Recruitment** mean(b_t)	**Superpop** $\hat{N}$	**Clusters** C
JS_t	699	0.42 (0.28 – 0.59)	0.92 (0.87 – 0.96)	0.07 (0.02 – 0.17)	95 (79 – 113)	-
JS_{tc}	648	0.29 (0.14 - 0.48)	0.95 (0.92 - 0.97)	0.04 (0 – 0.10)	142 (96 – 187)	2

Up to nine different clusters were sampled during the MCMC iterations from the JS_{tc} model, reflecting uncertainty about the number of clusters and cluster allocation of individuals. However, dolphins were only assigned with maximum probability to two distinct clusters of approximate sizes of 68 and 153 (Table 3). Most of these individuals could be assigned to a specific cluster with high probability, with 50 and 111 dolphins having the majority of their allocation density ($p_{z_i=c} > 0.50$) associating them with clusters 1 and 2 respectively. Notably, individuals in cluster 2 had a relatively low average identification probability, whereas individuals in cluster 1 had an average identification probability more than three times as high (Table 3), indicating higher site fidelity to the study area. Indeed, dolphins assigned with high probability ($p_{z_i=c} > 0.50$) to this "resident" cluster were identified in more years (median = 2, range = 2 – 15), compared to the "transient" cluster (median = 1, range = 1 – 5). The identification probability of dolphins within the "resident" cluster varied between years, with posterior medians ranging from 0.07 to 0.90 reflecting the degree of survey effort (Figure 4; Table 1), and was close to one in years with high photo-identification coverage. This relatively high probability of identification provided more power for monitoring demographic changes, because estimates of survival and recruitment parameters were more precise compared to the "transient" cluster (Table 3). There was good agreement between the posterior predictive distribution of $D(H^{new})_c$ and the posterior distribution of $D(H)_c$ for the resident cluster 1. The posterior predictive p-value equaled 0.46, indicating that the discrepancy of the data was similar (close to 0.5) to what one might expect from replications under the model (Gelman *et al.* 1996), supporting that the model was a plausible fit to the data. The posterior predictive p-value for the transient cluster 2 was only 0.23, implying the limited utility of the model for making inference about the infrequently seen transient individuals. We therefore focused assessment of demographic trends on this "resident" cluster, which could be thought of as a local population.

Table 3. Estimates of parameters from the Jolly-Seber model with clustered time-varying individual effects (JS_{tc}) for two clusters to which individuals could be assigned with the majority of their probability density ($p_{z_i=c}$>0.50). Posterior median values (with 95% highest probability density intervals in parentheses) are shown for the average annual probability of identification, survival, and per-capita recruitment for each cluster. The size of the cluster reflects the number of dolphins that were assigned with majority probability to each cluster over the full time series, not necessarily alive in each year.

Cluster	**Probability of Identification** *mean($p_{z=c,t}$)*	**Probability of Survival** *mean($\varphi_{z=c,t}$)*	**Probability of Recruitment** *mean($b_{z=c,t}$)*	**Cluster Size**
c=1, “residents”	0.56 (0.39 – 0.73)	0.94 (0.82 – 0.99)	0.02 (0 – 0.09)	68
c=2, “transients”	0.17 (0.01 - 0.79)	0.94 (0.77 - 0.99)	0.02 (0 – 0.13)	153

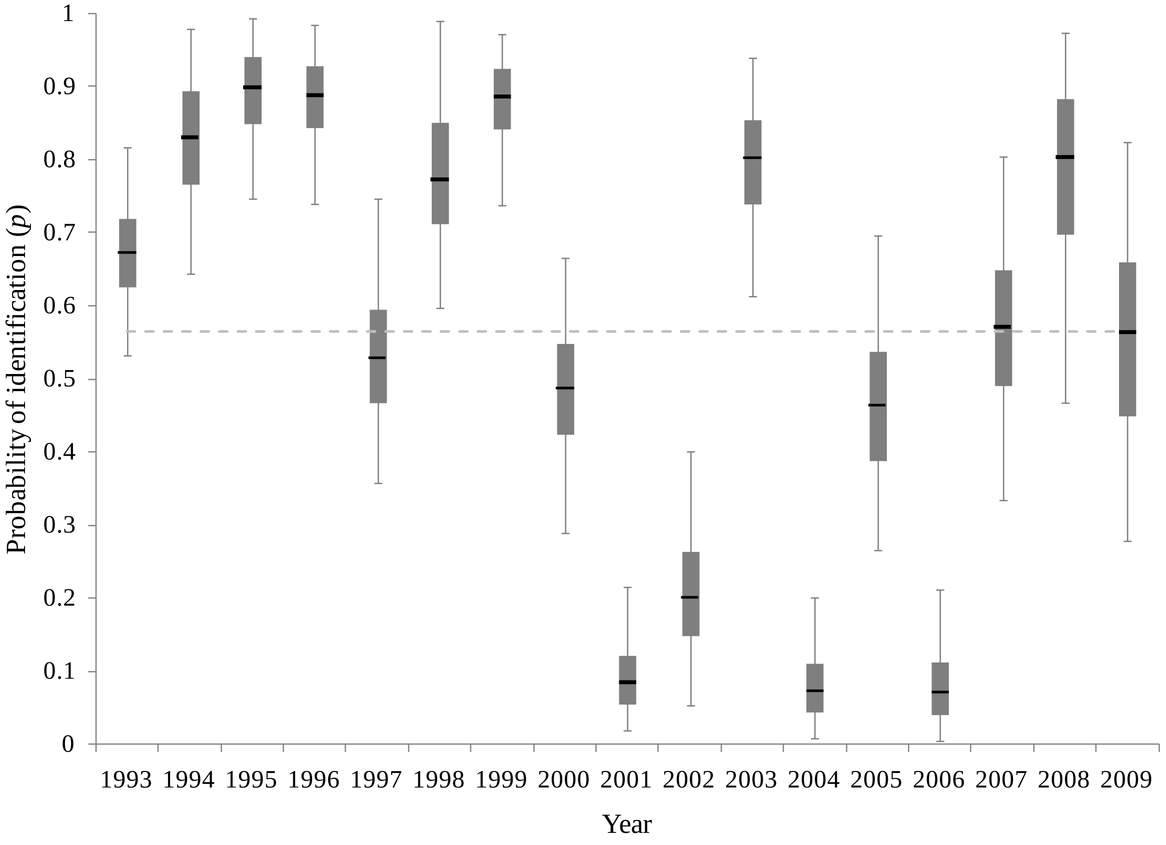

Figure 4. Annual estimates of identification probability for the “resident” cluster of dolphins. Estimates are presented as posterior medians (horizontal solid lines), with 75% (gray bars) and 95% (vertical lines) highest posterior density intervals, and the average annual probability of identification ($p_{z=1,t}$= 0.56) is represented by the horizontal dashed line.

There was a high probability (p = 0.97) of a long-term decrease in the size of this resident population from a high of 47 dolphins (95% Highest Posterior Density Intervals, HPDI = 29-61) in 1996, to a low of just 24 dolphins (95% HPDI = 14 - 37) at the end of the time series in 2009 (Figure 5); a decline of 49% (95% HPDI = -5% to -75%). This decline was based on low per-capita recruitment that could not compensate for high apparent mortalities. Estimates of per capita recruitment rate were low on average (mean($b_{z=1,t}$)

posterior median = 0.02; 95% HPDI = 0 – 0.09), corresponding to an average of 1 recruit per year (95% HPDI = 0 - 5),with relatively low estimates of survival rate ($\varphi_{z=1,t}$) posterior median= 0.94, 95% HPDI = 0.82 – 0.99) equating to a comparatively high average of 2 deaths per year (95% HPDI = 0 – 7). Therefore the apparent mortalities were estimated to be twice as high as the recruitments on average and mortalities exceeded recruitment in all years following the peak abundance in 1996 (Figure 6).

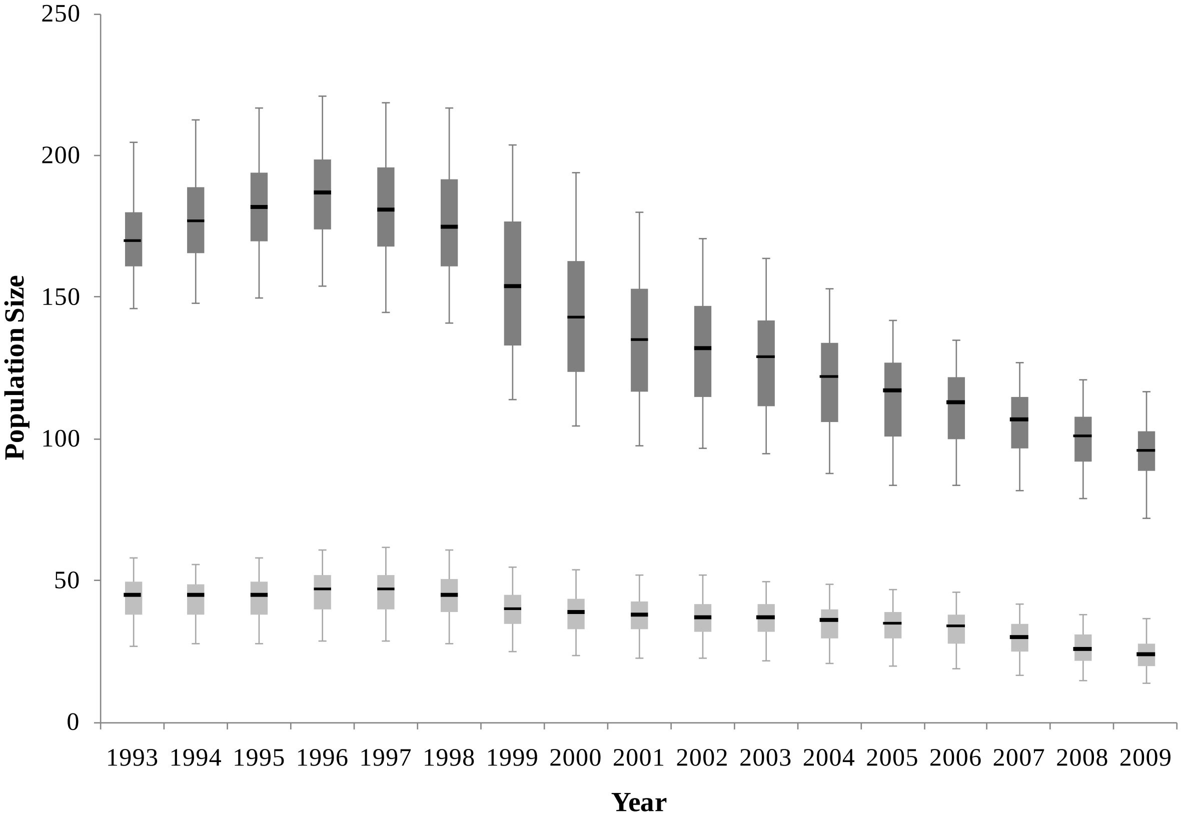

Figure 5. Annual estimates of abundance of the “superpopulation” using the study area during the study period (1993-2009) (top) and the “resident” population (bottom). Estimates are presented as posterior medians (horizontal line), with 75% (gray bars) and 95% (vertical lines) highest posterior density intervals.

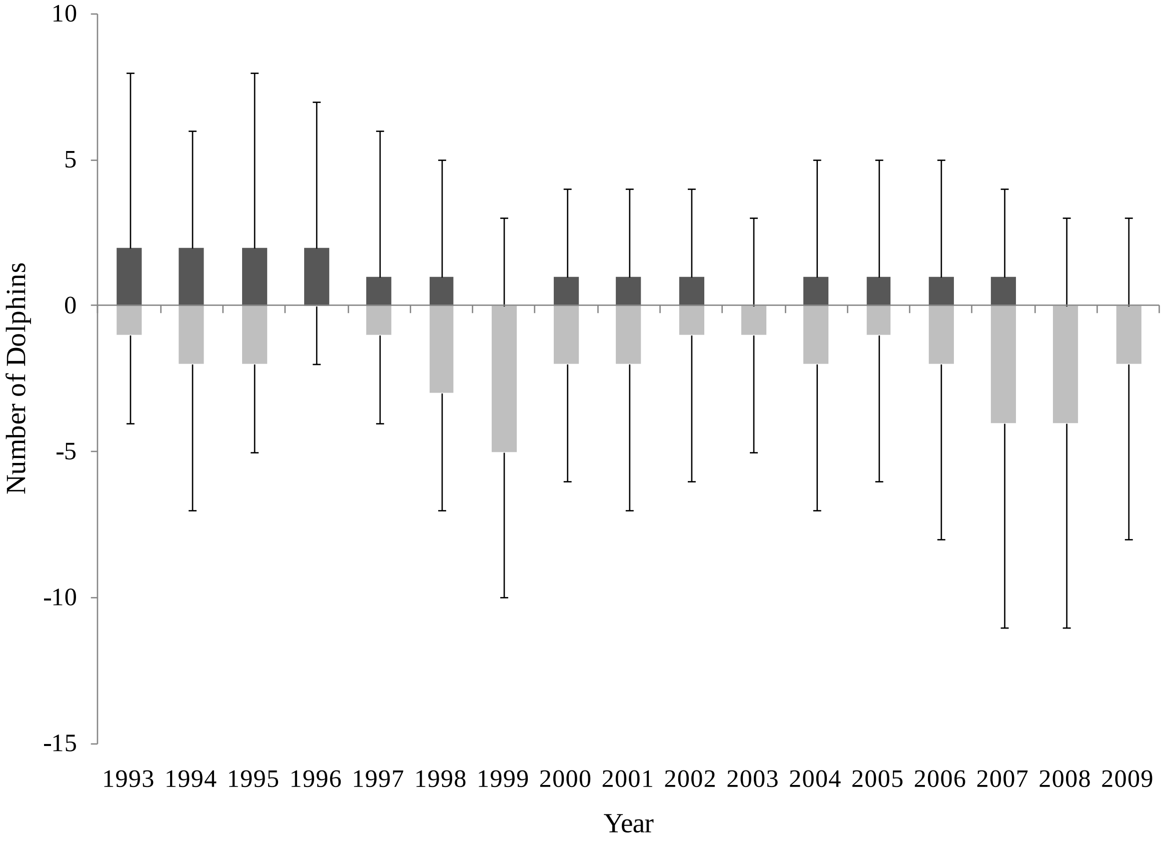

Figure 6. Annual estimates of apparent mortalities (lower light gray bar) and recruitments (upper dark gray bar) for the “resident” population of dolphins using the study area. Estimates are presented as posterior medians (bars), and upper 95% highest posterior density intervals are shown with vertical lines.

Notably, there was an anomalous drop in survival in 1999, with a survival rate estimate of 0.91 (95% HPDI = 0.78 – 0.97), representing 5 deaths (95% HPDI = 1 - 10). This was the largest annual departure from the average survival rate, with a probability of 0.83 that this annual estimate deviated from the average. This peak in apparent mortality corresponded to the largest between-year decline in abundance, with an estimated 11% drop (95 % HPDI = -88% – +58%) in the size of the “resident” population in 1999 (posterior median = 40, 95% HPDI = 25 – 55) compared to the previous year (posterior median = 45, 95% HPDI = 24 –

54). Despite uncertainty in these adjacent estimates, MCMC draws from the full posterior distributions and estimated a probability of 0.66 of a decline.

Although demographic estimates were less precise, these abundance trends were mirrored in the larger “superpopulation” that used the area, which declined from an estimated high of 187 dolphins in 1996 (95% HPDI = 154 – 221) to a low of 96 (95% HPDI = 72 – 117) in 2009, an overall reduction of 49% (95% HPDI = -32% – -62%). Again the largest drop (posterior median = -12 %; 95% HPDI = -44% – +31%) was estimated to occur in 1999 when the size of the “superpopulation” was estimated to decline from a posterior median of 175 to 154 (Figure 5), with a probability of 0.73 of a decline occurring between adjacent estimates.

Sighting frequencies during our October index months over six years showed a similar decrease in the frequency of dolphin sightings from 1999 onwards, despite comparable survey effort and extent (Figure 7). The total days of survey effort (median = 20, range = 14 - 25), and total kilometers surveyed (median = 1660, range = 1023 - 2029) were relatively high for the month of October for all six years. However, there was a marked decline in the number of dolphin sightings, and thus sighting frequency after 1999 (1999-2010: median encounters = 24, range = 19 – 35 and median encounters per km= 0.02 groups per km of survey effort, range = 0.01- 0.02) compared to 61 encounters and 0.04 groups per km of survey effort in 1998, with dolphins being sighted half as frequently in recent years (Table 4; Figure 7).

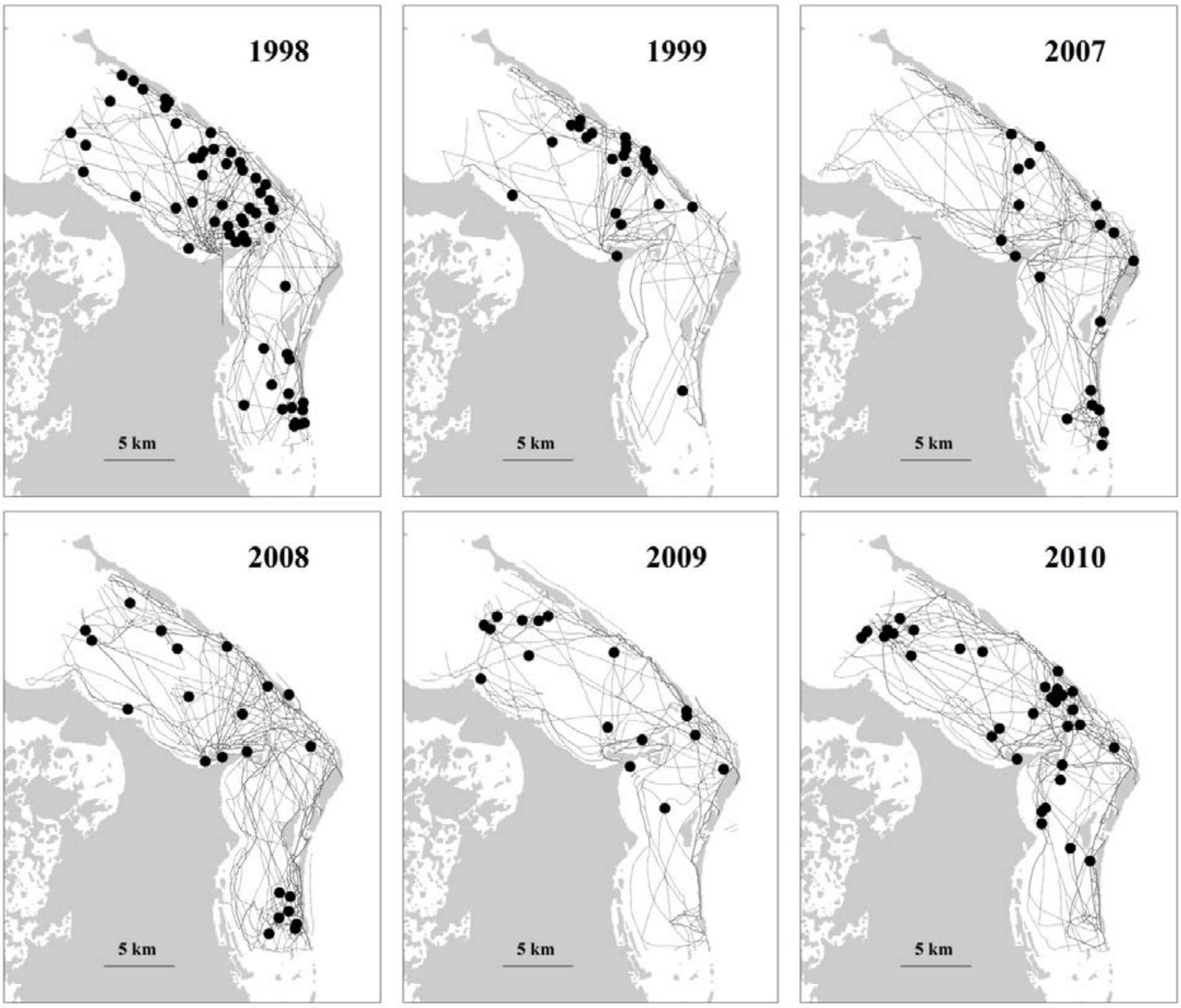

Figure 7. Map of the east Abaco study area showing all the tracks of the survey vessel during visual surveys (black lines) and bottlenose dolphin encounters (solid black circles) for the month of October for six years (1998-1999, 2007-2010).

Table 4. Survey effort for the month of October in six years (1998-1999, 2007-2010) with comparable survey effort (>1000 km) and spatial extent (Figure 9). Effort is shown as number of days with sightings surveys, total distance (km) surveyed, number of dolphin encounters and sighting frequency (ratio of number of encounters to total km surveyed).

Year	Effort (days)	Effort (km)	Number of Encounters	Sighting Frequency (Encounters/km)
1998	23	1458	61	0.04
1999	14	1023	25	0.02
2007	25	2029	21	0.01
2008	20	1724	24	0.01
2009	16	1616	19	0.01
2010	20	1704	35	0.02

Discussion

The bottlenose dolphins we surveyed displayed heterogeneous sighting frequencies in our study area, due to their mobility relative to the limited extent of the area which we could consistently survey using small boats. This presented problems for population definition and monitoring using conventional mark-recapture models. We overcame this by using a Bayesian mixture model to identify a defined cluster, or local population, from a larger superpopulation of dolphins that were more “transient” in their use of our study area (e.g. Conn *et al.* 2011). Although members of the local population likely did not spend their entire time within our study area, these comparatively “resident” dolphins had relatively high identification probabilities, which were essentially one (always identified) in years with high survey coverage. This not only indicated a high chance of encountering these in the study dolphins during the course of an annual survey period, but also provided increased power for monitoring their fates.

Less than half of the dolphins we documented could be classified as “resident”, and the size of this population declined to approximately half its earlier size over the course of the study. Although there are many factors that could have led to this decline, estimates of demographic parameters suggest that intense tropical cyclones may have an abrupt impact on mortality trends. Specifically, the greatest between-year decline in estimated abundance occurred in 1999, with a significant spike in apparent mortalities. This was the year when two intense hurricanes struck our study area just three weeks apart in August and September. One of these storms, Hurricane Floyd, was the largest and strongest during the study period (and strongest for more than 30 years), bringing sustained winds of 233km/hr when it passed directly over the study area (http://www.hurricanecity.com/city/abacoisland.htm; http://www.nhc.noaa.gov/sshws.shtml). This abrupt decline in abundance was mirrored in both the local population (~11% decline) and the larger superpopulation using the area (~12%). Furthermore, the population level-impact was supported by a decrease in the sighting frequency of dolphins in years following these storms.

This abrupt decline in abundance could be the result of movement (permanent emigration) away from the study area, perhaps due to habitat disturbance (e.g. Preen and Marsh 1995; Spiller *et al.* 1998; Gales *et al.* 2004; Gardner *et al.* 2005), but we suggest that real mortalities contributed significantly to the observed demographic changes. Mortality could occur through direct physical challenges posed by abrupt changes in environmental conditions, specifically wave heights and storm surge that likely make the shallow water sandbank system uninhabitable. However, it is likely that there are also indirect effects of abrupt environmental changes, specifically if dolphins are forced from their shallow-water habitat during intense storms to seek refuge, likely in deep, oceanic waters, where they are exposed to increased predation risk from oceanic sharks. We have documented an increase in the incidence of fresh shark-bite wounds on surviving dolphins following hurricanes (Chapter 2), providing support for an associated increase in predation risk. Although the plausible relationship between tropical cyclones and dolphin population dynamics is based on our observations of covariance in just a single year of anomalous hurricane activity, this is consistent with recent data suggesting that hurricanes may have impacts on the reproduction and social structure of coastal cetaceans (Miller *et al.* 2010; Elliser and Herzing 2011; Chapter 2) and abrupt mortality of even pelagic species (Mignucci-Gionanni *et al.* 1999).

In addition to the abrupt impact in 1999, our analyses suggest long-term declines in abundance from 1996 until the end of the time series in 2009, with relatively high mortality exceeding estimates of per capita recruitment. This is supported by continued low sighting frequencies in index survey months over the past decade. This long-term decline could represent mortality or permanent emigration resulting from the prolonged and combined effects from earlier storms (e.g. Preen and Marsh 1995): it is notable that mortality exceeded recruitment in all years following 1996, when the area experienced the first intense hurricane (winds >150km/hr) since 1965. Similarly, this apparently gradual decline could be a response to unobserved effects following later hurricanes: two further intense hurricanes passed through the study area in 2004, but an extremely low level of photo-identification effort in this year resulted in low capture probability and further non-linearities may have gone unobserved due to relatively high uncertainty in demographic estimates. The dolphins have likely also responded to variability in other natural and anthropogenic factors, perhaps compounding the effects of these storms. For example, both coastal development and recreational boat traffic escalated in the study area in recent years, likely creating a habitat that is increasingly undesirable for dolphins (e.g. Caron and Sergeant 1988; Lusseau 2005;

Bedjer *et al.* 2006), and perhaps leading to permanent emigration to other areas on Little Bahama Bank that remain largely undisturbed. It is also possible that predation risk by sharks may have increased in recent years due to a recovery of the sea turtle population following a ban on harvesting (Bahamas Marine Mammal Research Organisation, unpublished data). Dolphins have been shown to alter their use of certain habitats in response to fluctuations in predation risk resulting from shifts in the availability of key prey species for sharks (Heithaus *et al.* 2002; Heithaus and Dill 2002).

Despite uncertainty about the influence of environmental covariates, the ability to define a local population and estimate changes to its demographics has allowed us to frame discussions about the possible causes of population dynamics, which is rarely possible for cetaceans due to problems of population definition. In the presence of movement beyond a study area, inference from mark-recapture generally refers to the level of the “superpopulation”, which may be largely undefined unless unrealistic assumptions are made to separate temporary emigration from capture probability of locally available individuals (Whitehead 1990; Pollock 1990; Kendall and Nichols 2002). However, when the heterogeneity of ranging patterns induces a bimodal structure to capture probabilities, it is possible to distinguish “resident” and “transient” individuals based on capture histories alone (Pradel *et al.* 1997; Whitehead and Wimmer 2005; Conn *et al.* 2011). Our model generalizes this concept to two or more structural clusters, if they exist, and estimates individual effects to infer each individual’s cluster assignment (e.g. Durban *et al.* 2010). The Bayesian approach allows uncertainty to be effectively incorporated into inference about cluster membership, addressing problems caused by low capture probabilities. Although we estimated latent individual effects in our case, this formulation provides a promising direction for the future development of models that incorporate individual covariates for clustered capture probabilities, in order to learn about the mechanisms underlying heterogeneous space-use.

This structure of differential site fidelity by social clusters or “communities” is common in populations of bottlenose dolphins (Parsons *et al.* 2006; Lusseau *et al.* 2006; Urian *et al.* 2009; Conn *et al.* 2011), and we propose that this clustered mark-recapture approach will be useful for defining units to monitor in other similar open populations. However, we also suggest that its utility also extends more generally to mark-recapture studies where high-mobility and differential ranging patters of the target animals induces heterogeneous capture probabilities of individuals within local study areas (e.g. Hammond 1990b). The approach might be particularly suitable for opportunistic and non-standard mark-recapture samples (e.g. Petit and Valeriere 2006; Karanth *et al.* 2006), where it can be harder to design and control for appropriate spatial coverage.

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CHAPTER FOUR

SIZE AND LONG-TERM GROWTH TRENDS OF ENDANGERED FISH-EATING KILLER WHALES

Holly Fearnbach, John W. Durban, Dave K. Ellifrit, and Ken C. Balcomb

Endangered Species Research **13**, 173-180

CHAPTER FOUR

Size and long-term growth trends of endangered fish-eating killer whales

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Abstract

The endangered southern resident population of killer whales (*Orcinus orca*) has been shown to be food limited, and the availability of their primary prey, Chinook salmon (*Oncorynchus tshawytscha*), has been identified as a key covariate for individual survival and reproduction. Our study collected aerial photogrammetry data on individual size, to better inform energetic calculations of food requirements, and to compare size-at-age data to make inference about long-term growth trends. A helicopter was used to conduct 10 flights in September 2008, resulting in 2803 images from which useable measurements were possible for 66 individually-identifiable whales, representing more than three-quarters of the population. Estimated whale lengths ranged from 2.7m for a neonate whale in its first year of life, to a maximum of 7.2m for a 31 year-old adult male. Adult males reached an average (asymptotic) size estimate of 6.9m (SE = 0.2), with growth slowing notably after the age of 18; significantly larger than the asymptotic size of 6.0m (SE = 0.1) for females, which was reached after the earlier age of 15. Notably, there was no overlap between the ranges of estimated sizes of adult males (6.5-7.2m) and females (5.5-6.4m). On average, older adults (>30 years of age) were 0.3m (n = 14, p = 0.03) and 0.3m (n = 5, p = 0.23) longer than the younger whales of adult age, for females and males respectively; we hypothesize that that a long-term reduction in food availability may have reduced early growth rates and subsequent adult size in recent decades.

Introduction

Data on individual size can be used to address fundamental questions to inform conservation management of endangered populations. These include identification of taxonomic status (Perryman and Lynn 1993; Perryman and Westlake 1998; Pitman *et al.* 2007), assessment of health (Choquenot 1991; Perryman and Lynn 2002; Landete-Castillejos *et al.* 2002), estimation of energetic requirements (Williams *et al.* 2004; Noren 2011), and the identification of key life history and demographic patterns (Choquenot 1991; Koski *et al.* 1992; Read *et al.* 1993; Perryman and Lynn 1993; Lee and Moss 1995; Flamm *et al.* 2000; Shrader *et al.* 2006; Breuer *et al.* 2007). Notably, an individual's adult size is influenced by environmental factors during early growth (Metcalfe and Monaghan 2001; Catchpole *et al.* 2004), and as such information on size and size trends can be used to infer responses to environmental variability, such as the effects of nutritional stress due to limited food availability (Choquenot 1991; Catchpole *et al.* 2000; Trites and Donnelly 2003).

Free-ranging cetaceans at sea represent a challenge for collecting morphometric data, although live capture operations have been possible for some smaller species (e.g. Read *et al.* 1993). Photogrammetric approaches implemented from boat-based platforms have provided a simple alternative for measuring body features exposed above the surface (Durban and Parsons 2006; Jaquet 2006; Webster *et al.* 2010), but precise estimates of full body size typically require an aerial platform to obtain through-water images from directly above the whale (Koski *et al.* 1992; Perryman and Lynn 1993; Perryman and Westlake 1998; Perryman and Lynn 2002). Notably, helicopter platforms have proven to be extremely well-suited to providing precise photogrammetric measurements of cetaceans (e.g. Pitman *et al.* 2007), due largely to their ability to hover at a fixed (and known) altitude, and make relatively subtle adjustments in location to remain directly overhead of target animals. Although helicopters have been deployed for this purpose from pelagic research ships (Perryman and Lynn 1993), they offer particular utility for aerial photogrammetry of accessible coastal populations that can be surveyed during short (fuel-restricted) helicopter flights with minimal open water flying.

The endangered southern resident population of killer whales (*Orcinus orca*) is one of the most accessible populations of cetaceans. This distinct population comprises fewer than 100 whales that return to the coastal waters of Washington State (USA) and British Columbia (Canada) each summer to feed on returning runs of Pacific salmon (Ford *et al.* 2000; Krahn *et al.* 2004; Ford and Ellis 2006; Ford *et al.* 2010). As a result of their coastal habitat, this is one of the best studied mammalian populations: population size, individual life histories and demographics have been monitored through an annual photo-identification census of individuals dating back to the early 1970s (Bigg *et al.* 1990; Olesiuk *et al.* 1990; Ford *et al.* 2000). This monitoring has revealed changes in population size (Parsons *et al.* 2009) which have formed the basis for listing this population as “endangered” under the Species at Risk Act in Canada and the Endangered Species Act in the U.SA.

Long-term prey-habit studies of southern resident killer whales have shown distinct prey specialization on Chinook salmon (*Oncorynchus tshawytscha*) during the summer months (Ford and Ellis 2006), and recent analysis of long-term demographic data has shown this population to be food-limited, with declines in survival (Ford *et al.* 2010), fecundity (Ward *et al.* 2009) and social cohesion (Parsons *et al.* 2009) during years with low Chinook salmon availability. Our study aimed to collect aerial photogrammetry data on individual size, to better to inform energetic calculations of food requirements for this population (Noren 2011), and to compare size-at-age data to make inference about long-term growth trends.

Existing size data are available for >30 individuals from this population that were captured in a live-capture fishery for exhibition in aquaria, conducted in the 1960s and early

1970s (Bigg and Wolman 1975; Olesiuk *et al.* 1990). However, this fishery selected for physically immature animals (Olesiuk *et al.* 1990), and data on ages are not available, constraining a detailed assessment of the full size-at-age profile and preventing use of these data for examining size trends. A key feature of our approach was the use of an established long-term photo-identification catalog of individuals (Ford *et al.* 2000) to match aerial photographs and measurements to individual whales of known sex and age (Olesiuk *et al.* 1990; Ford *et al.* 2000). Aerial photographic surveys were directed in real-time by boat-based photo-identification surveys to maximize the coverage of different individuals and age/sex classes within the population.

Methods

We used a Robinson R44 Clipper helicopter to survey for whales from an airport at Friday Harbor, Washington State, during September 2008. To minimize search time, flights were only conducted on days when southern resident killer whales had been reported to be in the area, and a research boat had established contact with the whales. Guided by communications from the boat, the helicopter searched for whales at an altitude of around 1000ft (~305m), with descents to as low as 750ft (~229m) to photograph whales. All approaches below 1000ft were conducted under the authority of National Marine Fisheries Service permit (#532-1822) to conduct aerial surveys of southern resident killer whales under the Endangered Species Act and Marine Mammal Protection Act. One of the authors (JD) acted as an onboard guide to the helicopter pilot, using communication from the research boat to direct the helicopter over different target whales, to maximize the coverage of different individuals and age/sex classes within the population. Real-time whale identifications were made from the boat by one of the authors (DE) with more than 25 years of experience, and unique skill, in recognizing individual southern resident killer whales at sea. All boat approaches were conducted under the authority of permit No. 532-1822. The helicopter then hovered to hold position over each target whale until the photographer (HF) had captured suitable images of the whale.

The photographer was positioned in the passenger seat behind the pilot so that both could obtain a similar view from the same side of the helicopter, which facilitated positioning directly overhead of the whale. Wearing a seat harness, the photographer then leaned out of the open passenger door to shoot photographs vertically down on the target whale. A bubble-level was attached to the back of a hand-held digital SLR camera (Nikon D300), to ensure that the camera was orientated vertically, while the photographer used continuous shooting mode to capture as many images as possible of the surfacing whale. Photographs were taken when the whale was at the water surface and parallel to the water surface. High quality JPG images were shot at a resolution of 4288 x 2848 pixels (13.1 Megapixel resolution) in preference to RAW images in order to maximize the number of frames per second (to approximately 6fps). This ensured that the most elongated position of the whale was captured on each surfacing. A fixed focal length 180mm f2.8 AF Nikkor lens was used either with or without a 1.4x Kenko Pro extender, to achieve a realized focal length of either 378 or 270 mm (after accounting for the focal length factor of 1.5 inherent in the digital image sensor of the camera).

The altitude was recorded at one-second intervals throughout each flight using an onboard Garmin GPSMap 396 aerial Global Positioning System (GPS) unit. This WAAS-enabled differential GPS continuously received parallel signals from 12 satellites, and also calibration signals from shore-stations, to compute and update the position with advertised error of less than 3m (http://www8.garmin.com/aboutGPS/waas.html). The GPS and camera time were synchronized so that each image could be linked to a specific altitude using a relational database. To ensure that these two time stamps were precisely matched, a

Blue2Can Bluetooth receiver on the camera received wireless time signals from a second GPS unit (Holux M241), and this time was directly embedded into the metadata associated with each image. This ensured that both the altitude-linked aerial GPS time and the camera time were both derived from GPS signals, rather than relying on the pre-set camera clock that had to be manually updated.

Prior to measuring, every photograph was examined by one of the authors (DE) to match the image to an individual whale. The digital photographs were displayed on a 22-inch high-resolution flat panel monitor and were viewed through ACDSee photo manager (http://www.acdsee.com/). Photographs were linked to known individuals (of known age and sex class) by matching saddle patch pigmentation patterns (Figure 1) of individual whales to the long term (33-year) identification catalog (Ford *et al.* 2000; Ken Balcomb, Center for Whale Research, Unpublished Data). Photographic matches to the catalog were validated, where possible, by examining identification photographs obtained during the coordinated boat-based operations, and also using boat-based records of group composition and spacing at times coincidental to the aerial photographs.

Figure 1. Left and right side identification photographs obtained from boat platforms (left) of L78, a male first seen as a young of the year in 1989, displaying the distinctive saddle patch pigmentation used to confirm identification from aerial images (right).

Photographs of identified whales were then re-examined by one of the authors (HF) for measurement purposes, again using a 22-inch high-resolution monitor. ACDSee photo manager was first used to perform a second check of the individual identities by cross referencing the identification catalog, and then to select the best image(s) from each surfacing sequence of an identified whale. To ensure high quality, only images that were deemed to be vertical and with the whale in straight orientation (i.e. body axis of the whale was not tilted) were selected, and the most elongated image(s) of each whale was then chosen from the filtered set from each surfacing. The freely available software ImageJ (http://rsbweb.nih.gov/ij/) was used to measure the distance (in pixels) between the tip of upper jaw to the notch in the flukes (e.g. Pitman *et al.* 2007). All measurements in pixels were first converted to a true measurement based on the actual width of the digital sensor (0.036m) and the dimensions of this sensor width in pixels (4288). These measured distances were then converted to true lengths based on the scale of each image, which was calculated from the known altitude and realized lens focal length (scale = altitude / focal length). Images and associated data on individual identification, individual age, focal length, and size measurements were imported into a Microsoft Access relational database where they were linked to the GPS data on altitude based on the time matches.

To test the variability in our technique, we used aerial photographs to estimate the size of boats of known-length. To be consistent with the whale measurements, we used two research vessels, which were photographed in the same locations and at the same time as photographic encounters with whales. Conveniently, these boats were the same approximate size as whales from this population (see later results): one was a rigid hulled inflatable boat (RHIB) that measured 5.46m from the tip of the bow to the back of the outboard engine, and the other was a Boston Whaler measuring 6.50m for the same distance.

Average growth trends of whales were examined by fitting a generalized logistic (termed “Richard’s”) growth curve (Richards 1959) to the size-at-age data for each sex, separately. This curve is given by the equation:

$$L_t = A\,[1 - b{*}\exp(-ct)]^{M}$$

where A is asymptotic adult length, t is age in years, b and c are free parameters that adjust the slope and inflection point of the curve, and M describes the relative position of the inflection point relative to the asymptote. The Richards curve is a generalization of the classical growth curves that are commonly used, such as the Gompertz curve (e.g. Read *et al.*1993; Webster *et al.* 2010), with increased flexibility because the point of inflexion is not in a fixed proportion to the asymptote (instead, its position depends on the parameter M). We were particularly interested in estimating the timing and value for the asymptote (A) for each sex, as a measure of average adult size. Model fitting was accomplished using non-linear least square model fitting implemented using the R statistical package (http://www.r-project.org).

The ages of individually-identifiable whales born since the start of the photo-identification study in the 1970s were based on long-term longitudinal birth and sighting records (Ford *et al.* 2000; Ken Balcomb, Center for Whale Research, Unpublished Data), and the age estimates of whales born prior to the start of the study were based on the size development of dorsal fins for males and the age of oldest offspring for females, as described by Olesiuk *et al.* (1990, 2005) and presented in Ford *et al.* (2000). Following Olesiuk *et al.* (1990), ages were standardized by considering whales to be 0.5 years of age in their first summer (May-September) census period. Sex was determined by visual observation of genital anatomy and pigmentation (e.g. Ford *et al.* 2000), by the development of sexual secondary characteristics in males (particularly the dorsal fin), or by determining females by the birth of a calf (Ford *et al.* 2000; Unpublished data, Ken Balcomb, Center for Whale Research).

Results

Aerial photographs were collected during 10 flights in September 2008. Flights lasted an average of 77 minutes (min = 61, max = 118), and whales were typically encountered in Haro Strait, off the west side of San Juan Island (Figure 2). At least one of the research boats was photographed on each of 9 of the 10 total flights, with both boats being photographed on one flight, resulting in 147 measurable photographs of boats. There was some variability between length estimates of the same boat within days (Figure 3), but this improved across days as we quickly became better at positioning directly overhead of the research vessel, and selectively taking only vertical photographs. The maximum measurement for each boat was taken as the best estimate for that boat on each day, as smaller estimates were due to foreshortening as a result of photographs being taken when the boat was not directly under the helicopter. These estimates ranged from 5.41 to 5.57m across days for the RHIB and 6.22 to 6.59m for the Boston Whaler, representing an average bias of just 0.06m (range = 0.02 – 0.10m) for the RHIB and 0.08m (range 0.00 to 0.28m) for the Boston Whaler, which represented an average of just 1.1% of the true length (range = 0.3-1.9%) and 1.3% (range = 0.0 – 3.2%) for each of the boats respectively, and a combined average of just 1.2% (Figure 3).

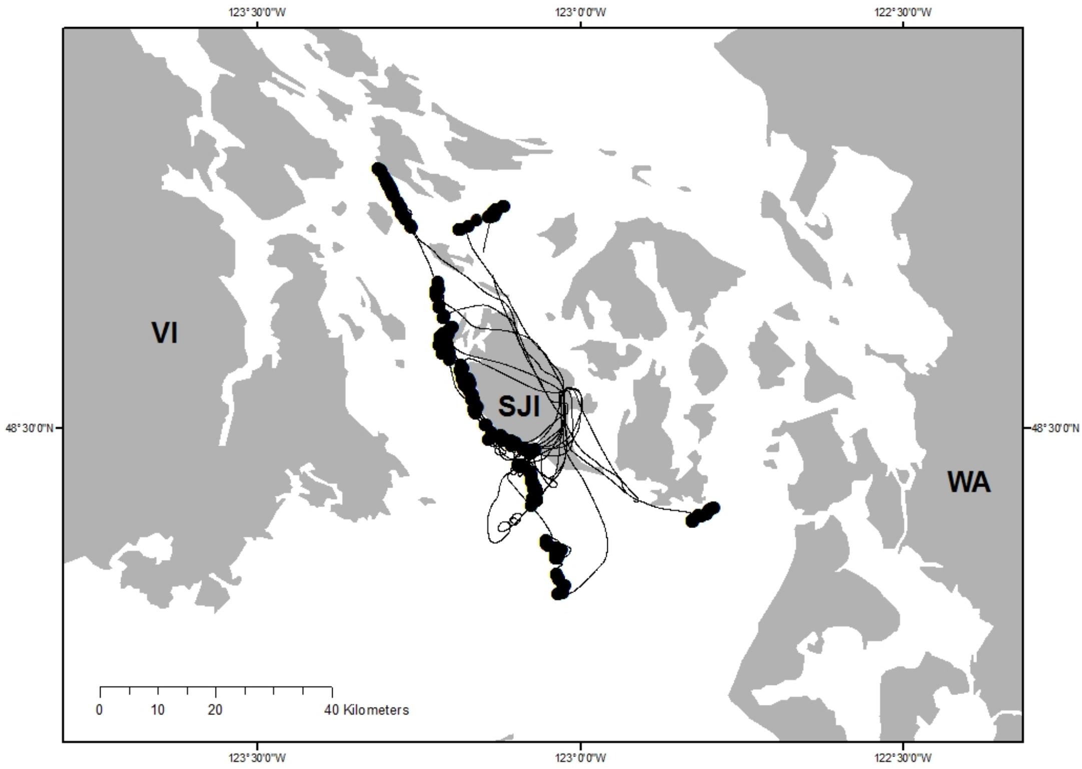

Figure 2. Map showing the tracks of the helicopter (solid lines) and the locations where measurement photographs were obtained (solid circles) during the 10 photogrammetry flights from San Juan Island (SJI), located between mainland Washington State (WA) in the USA and Vancouver Island (VI), in British Columbia, Canada.

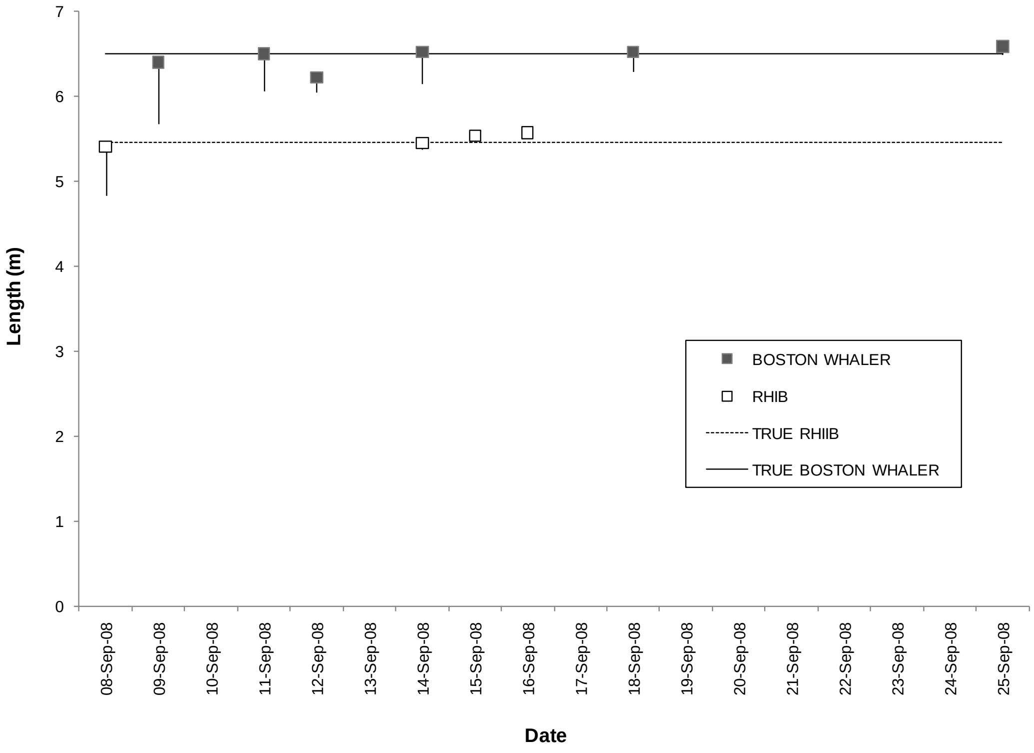

Figure 3. Length estimates for the two research vessels, a 5.46m RHIB and 6.50m Boston Whaler on 9 different survey days. Squares represent the best (maximum) estimate on each day, vertical lines represent the extent of the variability between estimates within days, and horizontal lines represent the true size.

Almost three thousand (2803) images were obtained from which useable measurements were possible for 66 whales of known identification, comprising 35 females, and 31 males. Whales were typically measured more than once (median = 7 surfacing sequences, range = 1-38). Variability within estimates of the same whale was likely due to a foreshortening effect of whales not being directly underneath the photographer and surfacing whales not being at their most elongated body position at the time of the photograph. The main bias was therefore likely to be negative, resulting in underestimates of length, and we thus chose to use the maximum estimate to be the best (least biased) for each whale. It should be noted, however, that even the maximum estimate may still have been negatively biased for full body length, and simply represented the longest body position measured for that whale. To reduce this effect, we only considered estimates to be reliable if measurements had been obtained from at least 5 different images. All further analysis was based solely on 46 whales for which this was the case (Table 1).

Table 1. Measurements of length (tip of snout to notch in tail) for whales with five or more measurements. Ages were estimated as per Olesiuk *et al.* (1990): "Birth Year" reflects the first May-September annual census period when present, at which time "Age" was standardized to be 0.5 years. Sex was determined by visual observation of genital anatomy and pigmentation (e.g. Ford *et al.* 2000), by the development of sexual secondary characteristics in males (particularly the dorsal fin), or by determining females by the birth of a calf (Ford *et al.* 2000; Unpublished data, Ken Balcomb, Center for Whale Research).

Whale ID	Birth Year	Age	Sex	# Measures	Min. Length (m)	Max. Length (m)
J41	2006	2.5	F	7	3.2	3.8
L103	2003	5.5	F	24	3.4	5.1
J37	2001	7.5	F	8	2.8	4.7
J36	2000	8.5	F	15	3.9	4.6
J35	1998	10.5	F	6	5.0	5.5
J31	1995	13.5	F	35	5.2	6.0
L91	1995	13.5	F	22	4.9	5.7
L94	1995	13.5	F	5	5.7	5.9
K27	1994	14.5	F	6	5.1	6.0
L82	1990	18.5	F	12	5.3	6.3
L83	1990	18.5	F	7	5.7	5.9
K20	1986	22.5	F	14	5.7	6.2
L72	1986	22.5	F	8	5.3	5.6
J22	1985	23.5	F	14	5.0	5.5
L67	1985	23.5	F	18	5.4	5.7
J19	1979	29.5	F	15	1.2	5.8
J17	1977	31.5	F	13	5.2	6.1
K14	1977	31.5	F	6	5.5	6.4
L55	1977	31.5	F	23	3.7	6.2
J14	1974	34.5	F	11	5.2	6.1
K13	1972	36.5	F	12	5.5	6.2
K40	1963	45.5	F	5	5.7	6.0
L7	1961	47.5	F	7	5.6	6.2
K42	2008	0.5	M	8	2.4	2.7
L109	2007	1.5	M	9	3.2	3.6
L110	2007	1.5	M	10	3.2	3.5
K38	2005	3.5	M	8	3.4	3.9
L105	2005	3.5	M	6	3.5	3.9
J38	2003	5.5	M	28	3.2	5.2
J39	2003	5.5	M	8	4.1	4.8
K35	2003	5.5	M	14	4.1	4.8
K34	2002	6.5	M	17	3.9	4.4
J34	1998	10.5	M	16	5.1	5.8
J33	1996	12.5	M	5	5.7	5.9
L95	1996	12.5	M	8	5.1	5.9
J30	1995	13.5	M	17	4.1	6.1
K26	1993	15.5	M	5	6.2	6.5
J27	1992	16.5	M	38	5.4	6.5
K25	1991	17.5	M	30	5.0	6.1
L84	1990	18.5	M	8	5.8	6.5
L78	1989	19.5	M	20	6.4	7.0
K21	1986	22.5	M	7	6.1	6.5
L74	1986	22.5	M	14	6.2	6.7
L41	1977	31.5	M	32	6.1	7.2
L57	1977	31.5	M	7	5.2	6.7
J1	1951	57.5	M	10	5.7	6.8

Estimated lengths ranged from a minimum length of 2.7m for a neonate whale in its first year of life (K42), to a maximum length of 7.2m for a 31.5 year-old adult male (L41). Estimates of length showed an asymptotic relationship with age, for both males and females, illustrating growth in body length through the mid teen years for females and the late teens for males (Figure 4). The fitted Richard's growth curve model estimated that adult males reached an average (asymptotic) size estimate of 6.9m (SE = 0.2), with growth slowing notably after an inflexion point at the age of 18 (SE = 4.7); significantly larger than the asymptotic size of 6.0m (SE = 0.1) for females, which was reached between the measured ages of 14.5 and 18.5, close to an inflection point at the age of 15 (SE = 1.8). These patterns are consistent with the ages of physical maturity based on repeated measures of dorsal fin growth in this population (Olesiuk *et al.* 1990), and we therefore followed these previous estimates to consider males of age 21 and older and females of age 15 and older to be adult in subsequent analyses. Notably, there was no overlap between the ranges of estimated sizes of adult males (6.5 - 7.2m) and females (5.5 - 6.4m). Comparison of the length older adults (>30 years of age) to the length of younger adults (<30 years of age) provided insight into long-term growth trends. On average, the older adults were 0.3m (t-test; n = 14, p = 0.03) and 0.3m (n = 5, p = 0.23) longer than the younger whales of adult age, for females and males respectively.

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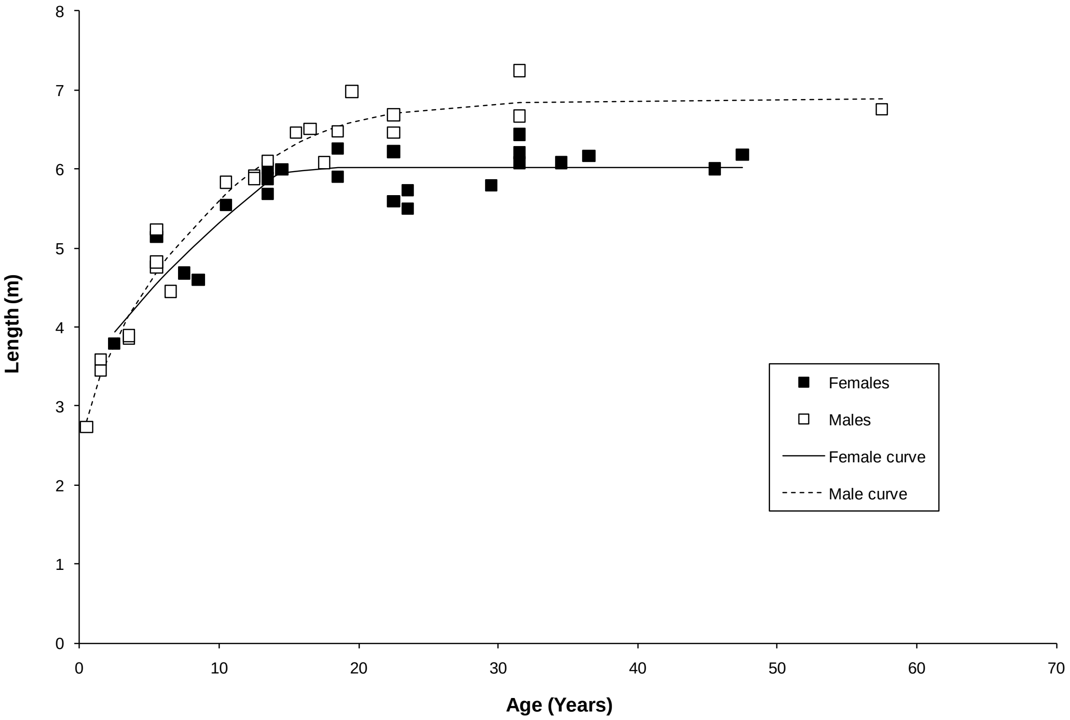

Figure 4. The maximum estimate of length for whales with five or more measurement photographs, plotted against their observed or estimated ages. Ages were estimated as per Olesiuk *et al.* (1990); Sex was determined by visual observation of genital anatomy and pigmentation (e.g. Ford *et al.* 2000), by the development of sexual secondary characteristics in males (particularly the dorsal fin), or by determining females by the birth of a calf (Ford *et al.* 2000; Unpublished data, Ken Balcomb, Center for Whale Research).

Discussion

Prior to our study, the available size data for southern resident killer whales came from a live-capture fishery (Bigg and Wolman 1975), in which size-selectivity constrained a full assessment of the size structure of the population (Olesiuk *et al.* 1990). In this study we used aerial photogrammetry to obtain length measurements from 66 whales, representing more than three-quarters of the population census of 83 whales in 2008 (Center for Whale Research, Unpublished data). Whales of both sexes were measured, ranging in age from a first-year neonate to old adults for both males and females (Olesiuk *et al.* 1990). Despite selecting for smaller whales, the size of the largest male (6.98m) and female (6.25m) in the live-capture data (Bigg and Wolman 1975) falls within the length ranges for adult males (6.5m - 7.2m) and adult females (5.5m - 6.4m) estimated in our study. This places southern resident killer whales at approximately the average size in the range of other killer whale populations throughout the world (Pitman *et al.* 2007).

Consistent and precise estimates of the length of research vessels of known size (and approximate whale size) served as an effective ground-truthing of our methods, with an average bias of just 7cm (1.2%). Additionally, the asymptotic length-at-age curves for both males and females were consistent with ages of physical maturity for this population estimated from repeated measures of dorsal fin growth (Olesiuk *et al.* 1990). For females, a defined asymptote in growth was reached for all measured whales in this study after the age of 14.5, in close agreement with the previous estimate of female maturity at 15 years of age. Although a small sample size of adult males constrained statistical power for curve fitting and prevented precise identification of the timing of the asymptote, there was notable slowing in growth after an estimated inflexion point at 18 years old, in agreement with the previous estimate of physical maturity by age 21 for male southern residents (Olesiuk *et al.* 1990) and after 18 for males from the neighboring northern resident population (Olesiuk *et al.* 2005). These growth curves can now be used to convert size-at-age data to a total population weight, using existing length-weight relationships (Bigg and Wolman 1975), and such mass calculations would provide key input into energetic calculations of food requirements (e.g. Noren 2011).

Energetic models for killer whales have previously relied on size assumptions for target populations based on published lengths from other killer whale populations (e.g. Williams *et al.* 2004; Williams *et al.* 2006), or mass from size-selective fisheries catches (e.g. Noren 2011), both of which may involve substantial bias that can be alleviated through the use of unbiased data from the target population. Furthermore, because the long-term photo-identification studies of southern resident killer whales have provided detailed demographic data on the age structure of this population in each of the past 37 years (Ford *et al.* 2010; Center for Whale Research, Unpublished data), it is now possible to reconstruct estimates of the size, weight and energetic requirements of the population at various times in the past and present. Understanding variability in the food requirements of this endangered population alongside patterns of variability in prey abundance would represent a significant contribution towards identifying risks and establishing conservation plans.

Our size-at-age estimates also provide an insight into long-term growth trends in this population. Notably, older adults were approximately 0.3m longer than the younger whales of adult age, for both males and females. This difference was only significant for adult females, as our statistical power was limited by a small sample size of adult males available to be measured, as a result of relatively high adult male mortality in the mid to late 1990’s (Krahn *et al.* 2004). This could represent continued somatic growth throughout life, as has been found in northern fur seals (*Callorhinus ursinus*; Trites and Bigg 1996), but we suggest this may be an indication of nutritional stress in recent decades. Specifically, a long-term reduction in returning stocks of Chinook salmon (Beamish *et al.* 1995; Ford *et al.* 2010) may have reduced early growth rates and subsequent adult size in recent decades, alongside the reported decreases in survival (Ford *et al.* 2010), fecundity (Ward *et al.* 2009) and social cohesion (Parsons *et al.* 2009). Similar patterns have been observed in other vertebrate populations subject to nutritional stress: feral donkey (*Equus asinus*) populations exhibited a decrease in juvenile body condition and growth rate, and an increase in mortality, as a result of food shortages (Choquenot 1991); increases in mortality and decreases in growth rates for both Soay sheep (*Ovis aries*) and red deer (*Cervus elaphus*) have been found to be correlated with decreased food availability (Catchpole *et al.* 2000, 2004); and an observed decrease in survivorship, fecundity and body length of Steller sea lions (*Eumetopias jubatus*) in Alaska has been linked to a decrease in the quality of available prey items (Trites and Donnelly 2003).

As the time series of demographic monitoring of this population continues to extend, repeated assessments of size and growth in relation to food availability allow an evaluation of this hypothesis, and may be an important tool for monitoring the success of management actions to protect prey resources.

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CHAPTER FIVE

SPATIAL AND SOCIAL CONNECTIVITY OF FISH-EATING KILLER WHALES IN THE FAR NORTH PACIFIC

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CHAPTER FIVE

Spatial and social connectivity of fish-eating killer whales in the far North

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Abstract

Describing the ranging and distribution patterns within wildlife populations is key to understanding population structure, identifying habitat relationships, and evaluating conflicts due to shared resources with humans. The productive far North Pacific waters of the Gulf of Alaska, Aleutian Islands and Bering Sea support a high density of “resident” type fish-eating killer whales (RKW, *Orcinus orca*), which overlap in distribution with lucrative commercial fisheries, producing both direct and indirect interactions. To provide a spatial context for these interactions, we analyzed a 10-year dataset of almost 80,000 photo-identifications from a large (linear distance ~ 4000 km) coastal study area to investigate the ranging and social patterns of 532 distinct RKWs between the Gulf of Alaska and western Aleutian Islands. Although capable of large-scale movements (up to 1443 km), we documented generally restricted ranges of less than 200 km on average, with high site fidelity across years. There was a social basis to these movements, and Bayesian analysis of pair-wise associations identified four defined clusters, likely representing groupings of stable matrilines with distinct ranging patterns, aligning with environmental shifts from continental shelf to shelf-edge waters to deep pelagic habitats. This provides evidence of structure within the Alaska stock of RKWs, important for evaluating ecosystem and fisheries impacts. Nonetheless, these clusters combined to form a large network of associated whales that ranged across most of the study area, and included whales photographed while depredating sablefish from longline

fisheries. This large-scale connectivity potentially facilitated the spread of depredation by killer whales on longline fisheries.

Introduction

Describing ranging and distribution patterns within wildlife populations is key to understanding population structure (Whitehead *et al.* 2008; Silva *et al.* 2008), identifying important habitat relationships (Jaquet and Whitehead 1996; Tufto *et al.* 1996; Elwen and Best 2004; Redfern *et al.* 2006; Ferguson *et al.* 2006; Friedlaender *et al.* 2006), and evaluating and mitigating conflicts due to shared resources with humans (Hoare 1999; Osborn 2002; Sigler *et al.* 2008; Mazur and Seher 2008; Whitehead *et al.* 2004; Whitehead 2010). In mammals, social organization may underlie ranging patterns, both by restricting movements and reflecting a response to a heterogeneous environment (Emling and Orling 1977; Clutton-Brock and Harvey 1977; Rubenstein 1986; Packer *et al.* 1990; Wittemyer *et al.* 2005; Whitehead *et al.* 2008). Understanding social structure and individual movement in the context of these social affiliations can therefore further our understanding of the spatial ecology and resource requirements of a population.

The influence of social structure on the spatial partitioning of populations is likely to be particularly important in the marine environment (e.g. Lusseau *et al.* 2005), where there is an absence of major physical barriers to movement. It is therefore not unexpected that some of the most stable social structures among mammals are found in the marine environment, notably the matrilineally-structured killer whale society (Bigg *et al.* 1990; Baird and Whitehead 2000; Parsons *et al.* 2009). Long-term studies in the eastern North Pacific have documented three sympatric lineages with differences in genetic composition (Stevens *et al.* 1989; Hoelzel and Dover 1991; Hoelzel *et al.* 1998; Hoelzel *et al.* 2002; Barrett-Lennard 2000), morphology (Baird and Stacey 1988; Ford *et al.* 2000), vocalizations (Ford 1989;

Barrett-Lennard *et al.* 1996; Deecke *et al.* 2005) and social structure (Bigg *et al.* 1990; Baird and Whitehead 2000). It has been suggested that the evolution of these lineages has been supported by cultural traditions, passed down generations within stable family groupings (Baird 2000; Rendell and Whitehead 2001; Yurk *et al.* 2002), and has recently been proposed that they may represent different species (Morin *et al.* 2010). These lineages have distinct prey specializations (Ford *et al.* 1998; Saulitis *et al.* 2000), with “transients” feeding on marine mammals, “residents” feeding on fish, notably salmon in some areas (Ford and Ellis 2006), and “offshores” thought to specialize on high trophic level fish (Herman *et al.* 2005; Krahn *et al.* 2007a), notably sharks in recent observations (Ford *et al.* 2011). Consequently, these lineages are often referred to as “ecotypes” (Ford *et al.* 2000).

Killer whale social and population ecology is well documented for the coastal waters of the NE Pacific. However, relatively few data exist for the more remote waters of the far North Pacific, despite the densities of killer whales in the Gulf of Alaska, Aleutian Islands and Bering Sea being among the highest in the world (Forney and Wade 2006). Recent work has shown that the dietary differences and ecotypic classification of killer whales from the eastern North Pacific also extends to these more remote waters (Herman *et al.* 2005; Krahn *et al.* 2007a), and the “resident” type of fish-eating killer whales is by far the most abundant (Zerbini *et al.* 2007; Matkin *et al.* 2007; Durban *et al.* 2010). This high density of “resident” type fish-eating killer whales overlaps in distribution with the most lucrative commercial fisheries in U.S. waters, producing both direct and indirect interactions between whales and fisheries (Yano and Dalheim 1995). There is still considerable uncertainty about the diet of “resident” type fish-eating killer whales that occur in this region (Herman *et al.* 2005; Krahn *et al.* 2007a), but observations have been made of whales feeding on commercially important species such as Atka mackerel (*Pleurogrammus monopterygius*), Pacific salmon (*Oncorhynchus spp.)* and Pacific halibut (*Hippoglossus stenolepis)* (Matkin *et al.* 2007;

NMML, unpublished data). Additionally, “resident” type fish-eating killer whales commonly depredate sablefish (*Anoplopoma fimbria*) and halibut from longline fisheries (Yano and Dahlheim 1995; Lunsford and Rutecki 2010), and whales are frequently observed feeding on the discards of trawlers (Yano and Dahlheim 1995; Matkin *et al.* 2007). Killer whales are known to have high calorific requirements (Williams *et al.* 2004; Noren 2011), and the impact of this competition for resources may be considerable (Lundsford and Rutecki 2010).

Assessment of the spatial extent, intensity and value of these interactions is required to develop mitigation strategies and account for this substantial natural mortality in ecosystem and fisheries assessments. This in turn requires data on the distribution and structuring of killer whales in this region. Currently all “resident” type fish-eating killer whales in the Gulf of Alaska, Aleutian Islands and Bering Sea are managed as the "Eastern North Pacific Alaska Resident” stock" (Allen and Angliss 2012), but there is substantial uncertainty about structure at finer spatial scales. In this study we use 10 years of sighting surveys and photo-identification of individual whales to explore the spatial connectivity of “resident” type fish-eating killer whales in coastal waters from the western GOA to the western Aleutian Islands, including the Bering Sea shelf edge. We include a quantitative description of the social structure underlying individual movements. Notably, we examine the social interactions and movements of whales that have been observed to depredate longlines to understand their social and spatial relationship within the population.

Methods

Study area and data collection

Photo-identification data were collected from 2001-2010, during sightings surveys conducted in coastal waters ranging from the northern Gulf of Alaska (~ 60^{o}N, 150^{o}W) to the western extent of US waters in the western Aleutian Islands (~ 55 ^{o} N, 175 ^{o}E), including the waters of the continental shelf edge in the Bering Sea. The area surveyed covered a linear distance of c. 4000 km, generally including waters less than 30 km from shore or the shelf edge (Figure 1). This large area is composed of a varied physical environment, ranging from continental shelf waters in the east to deep pelagic waters around the western Aleutian Islands, with highly productive passes between the Aleutian Islands (Hunt and Stabeno 2005; Ladd *et al.* 2005).

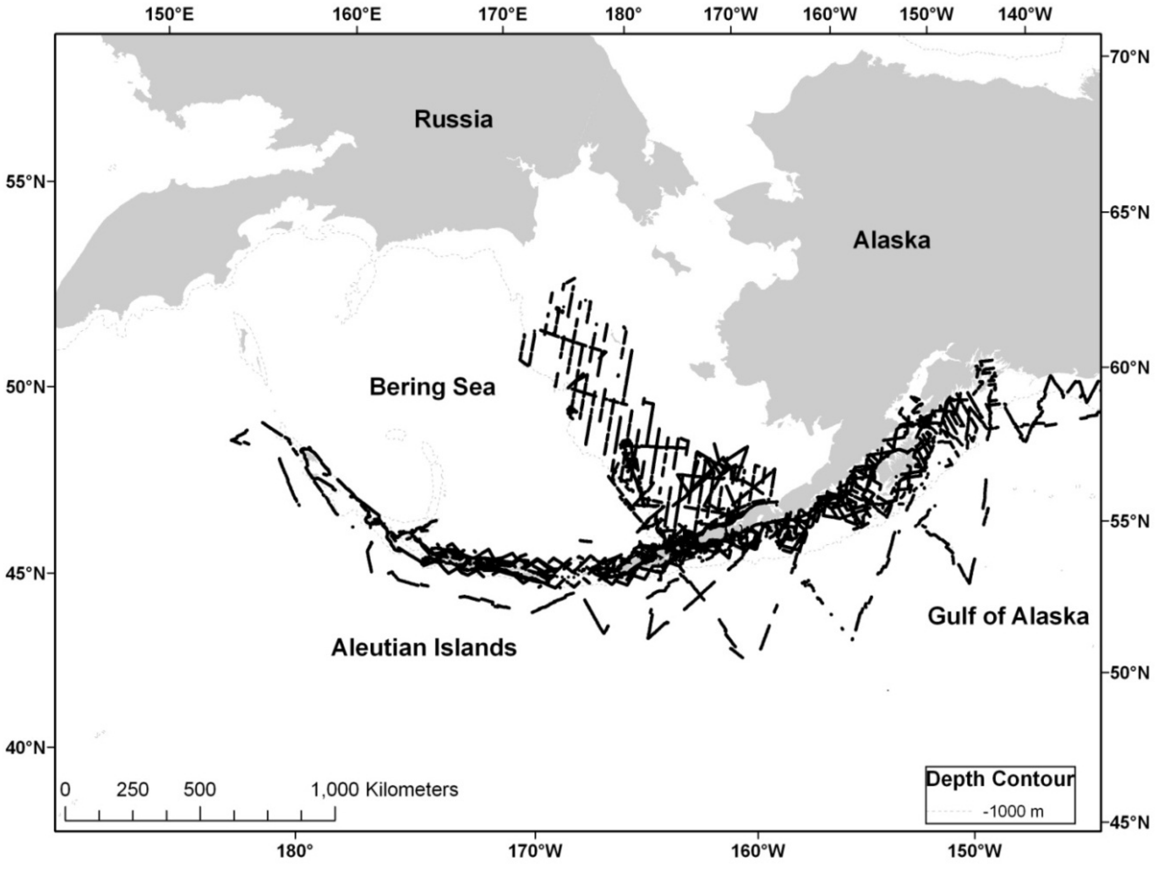

Figure1. Map showing vessel track lines (solid lines) during sightings surveys with photo-identification of killer whales, 2001-2010.

Sighting surveys were comprised of a combination of directed surveys to search for killer whales, and surveys when killer whale sightings and photo-identification data were collected opportunistically from other platforms (Table 1). These surveys were primarily conducted in the summer months between May and September, but there was additional survey effort in February and March 2008. The directed surveys were designed to investigate the distribution and abundance of killer whales throughout the study area; line-transect methods were employed for random-area coverage from 2001 to 2003 (Zerbini *et al.* 2007) and surveys from 2004 to 2010 adopted a more focused approach to survey in areas known to be regularly used by killer whales. Large charter vessels (40-60 m) were used for these surveys, and observers searched for killer whales using hand-held 7x50 binoculars or fixed-mount 25x magnification binoculars from heights of 5.5 to 10 m (e.g. Zerbini *et al.* 2007). Directed killer whale surveys were also conducted in a focused area of the eastern Aleutian Islands from 2001-2005 using smaller (10-14 m) charter fishing vessels (NGOS, Table 1; Matkin *et al.* 2007).

Table 1. List of dedicated (D) killer whale sighting surveys and opportunistic (O) platforms from which killer whale photo-identification data were collected. “Areas” lists the 5° latitude by 10° longitude areas that were covered by each survey area (see Figure 2) and IDs is the total number of distinct “resident” type killer whales identified from high quality photographs on each survey.

SURVEY	SHIP	DATES	TYPE	AREAS	IDs
01AH	F/V Alpha Helix	04-Jun-01: 17-Jun-01	O: Oceanographic	1,2 4,5,8	98
01AM	F/V Aleutian Mariner	20-Jul-01: 25-Aug-01	D: Killer whale	1,2,3,4,5,8	123
02AH	F/V Alpha Helix	21-May-02: 18-Jun-02	O: Oceanographic	1,2 4,5,8	99
02CP	F/V Coastal Pilot	12-Jul-02: 20-Aug-02	D: Killer whale	1,2,3,4,5,8	112
02MA	R/V MacArthur I	13-Jul-02: 29-Aug-02	O: Right Whale	1,2,3,4,7,8	14
02MF	R/V Miller Freeman	16-Jun-02: 28-Jul-02	O: Pollock Trawl	2,4,7,8	20
03CP	F/V Coastal Pilot	03-Jul-03: 14_Aug-03	D: Killer whale	1,2,3,4,5,8	153
03MF	R/V Miller Freeman	27-Jun-03: 15-Jul-03	O: Pollock Trawl	1,2	4
04AE	F/V Alaskan Enterprise	21-Jul-04: 27-Aug-04	D: Killer whale	2,3,4,5,7,8	58
04MA	R/V MacArthur II	29-Jun-04: 31-Oct-04	O: Humpback whale	1-8	100
04MF	R/V Miller Freeman	04-Jun-04: 04_Jul-04	O: Pollock Trawl	2,4,7,8	6
05AE	F/V Alaskan Enterprise	31-May-05: 11-Jul-05	D: Killer whale	2,4,5,6,7,8	131
05OD	R/V Oscar Dyson	02-Aug-05: 28-Sep-05	O: Humpback whale	1,2	20
06OL	F/V Ocean Olympic	31-May-06: 25-Jun-06	D: Killer whale	4,5,6,7,8	253
07OD	R/V Oscar Dyson	01-Aug-07: 28-Aug-07	O: Right whale	4,8	16
07OL	F/V Ocean Olympic	30-May-07: 16-Jun-07	D: Killer whale	4,8	9
08DA	R/V Oscar Dyson	15-Feb-08: 03-Mar-08	O: Pollock trawl	4,5	15
08OL	F/V Ocean Olympic	02-Aug-08: 12-Sep-08	O: Right Whale	2,4,8	5
09AQ	F/V Aquila	21-Jun-09: 14-Jul-09	D: Killer whale	4,5,7,8	79
10AE	F/V Alaskan Enterprise	24-Jun-10: 12-Jul-10	D: Killer whale	4,5,6	197
LL	F/V Alaskan Leader	May-Sep 06-10	O: Longline	2,3,4,5,7,8	41
NGOS	Various	May-Sep 01-05	D: Killer whale	4,8	288

Data were also collected on an opportunistic basis from a number of platforms: during wide-scale sightings surveys for humpback whales (04MA, 05OD; Calambokidis *et al.* 2008) and right whales (02MA, 07OD, 08OL; LeDuc 2004; Clapham *et al.* 2009;Wade *et al.* 2011); cetacean surveys aboard walleye pollock (*Theragra chalcogramma*) trawl research surveys (02MF, 03MF, 04MF; Moore *et al.* 2002; Waite *et al.* 2002); and oceanographic surveys (01AH, 02AH; Sinclair *et al.* 2005) (Table 1). Photographs of depredating killer whales were also taken by observers during standardized longline fishing surveys in the summers of 2006 to 2010 (Lunsford and Rutecki 2010), providing a sample of whales that were observed to be depredating on sablefish during longline fishing operations.

When killer whales were encountered during these surveys, identification photographs were taken from the ship platform or during closer approaches using a 6 m rigid hulled inflatable boat (RHIB). An attempt was always made to photograph as many different individuals within the group as possible. Groups were defined as all individuals typically within 500 meters that were moving in a coordinated fashion. During dedicated surveys, skin and blubber samples were also collected using remote biopsy techniques (e.g. Barrett-Lennard *et al.* 1996). These samples were used in combination with photographs to confirm lineage. Lineage assignment was made using the criteria established in previous studies in this region (Matkin *et al.* 2007; Zerbini *et al.* 2007; Durban *et al.* 2010), based on a combination of molecular genetic analysis from skin samples to corroborate assignments based primarily on morphological characteristics of the photographed whales. Killer whales of the “resident” lineage are by far the most frequently encountered in this region (Zerbini *et al.* 2007) and can be readily distinguished from “transients” and “offshores” in photographs by experienced observers (Durban *et al.* 2010). Specifically, there are key morphological differences in dorsal fin shape and saddle patch pigmentation that have been long established as diagnostic features to distinguish these lineages (Baird and Stacey 1988; Ford *et al.* 2000).

In this study, all photographic assignments were conducted by at least two of the authors, who analyzed the photographs independently, extending previous assessments of lineage in earlier examinations of this growing dataset (Zerbini *et al.* 2007; Matkin *et al.* 2007; Durban *et al.* 2010).

Photo analysis

Photo-identification images were taken with either 35-mm SLR cameras, shooting Fuji Neopan 1600 ISO black and white film (2000-2003), or with digital SLR cameras with a minimum resolution of 6MP (2004-2010). All 35mm photo-identification images were digitized using a slide copy adaptor to capture 6MP tagged image format files with a Nikon Coolpix digital camera. Once all images were in digital format, the best photograph of each whale, in each encounter, was selected.

Each best-in-encounter photograph was then matched to a master photo-identification catalog of individuals. If a match was found, then the whale was linked with the corresponding identification number, and if no match was found, then a new number was assigned. Although unique identification numbers were assigned to every whale that could be differentiated during an encounter, permanent numbers were only assigned to whales that were deemed to be distinctly marked so that they could be matched between encounters and across years. Temporary numbers were assigned to whales that could only be distinguished within the group and were not sufficiently distinct to track over time (Figure 2). Distinctiveness was based on a combination of features of the dorsal fin (e.g. distinctive shape, the presence of notches) and the adjacent saddle patch (distinctive pigmentation, scarring patterns) following Durban *et al.* (2010), with the distinctiveness of features being determined by the expert opinion of two of the authors (HF, DE). Only distinctive whales were used in the subsequent analysis. In addition, all best-in-encounter photographs were assigned quality grades (*Q*=1-3) for each of exposure, amount of fin and saddle captured, clarity and angle, and only high-quality photographs (*Q*>1 for each category) were included in the subsequent analysis.

Figure 2. Examples of high quality photo-identification images of three “resident” type fish-eating killer whales: photos 1 and 2 display two photographic sightings of the same distinctively marked whale 9 years apart; photo 3 displays another distinctive whale; photo 4 displays an identification photograph of a whale judged to not be sufficiently distinct to match across encounters.

Data analysis

Ranging patterns were examined for all distinctly marked individuals that were identified two or more times. We used ARCGIS 9.2 (www.esri.com) with Hawth's Analysis Tools (http://www.spatialecology.com/htools/tooldesc.php) to map encounter locations for each individual, and summarized two ranging parameters: maximum extent of movement and maximum longitudinal range using the great circle distance calculation. Spatial ranging was further summarized by examining the overlap of individual encounter locations relative to eight areas of dimension 5° latitude by 10° longitude (Figure 3).

Associations between individuals were evaluated for all whales seen more than once using the half-weight index (HWI, Cairns and Schwager 1987), also known as Dice's index (Dice 1945). We assumed that any two whales identified in the same encounter were associated, and the half-weight index of association was calculated for each pair of whales as HWI = $2X/(A+B)$, where X = the total number of times that individuals A and B were observed together, and $A + B$ represents the total number of times individuals A and B were observed (Cairns and Schwager 1987). The HWI therefore ranged from 0, when two individuals were never seen in the same encounter, to 1, if two individuals were always seen together.

To investigate population structure from the repeated pair-wise association measures, we adopted a Bayesian approach to fitting a social network model to identify significant clusters of associates. Specifically, we used the Latentnet package from the statistical software program R (R Development Core Team 2011) to fit latent position and cluster models to these association data (Krivitsky and Handcock 2008). This approach assumes the existence of a latent (unknown) space of sociality of the individuals, where the probability of a relationship between two individuals is modeled as a function of an estimated distance between two individuals in a two-dimensional Euclidean "social space"(e.g. Hoff, Raftery and Handcock 2002). Latentnet provides a way of assessing the significance of social relationships (distances) between individuals by assigning cluster membership for each individual based on their position in Euclidean space (Krivitsky and Handcock 2008). This Bayesian inference is probabilistic, estimating the probability of each whale belonging to each cluster, which is desirable given sparse observational data with limited numbers of re-sightings across this large study area. The package performs estimation using a Markov Chain Monte Carlo (MCMC) algorithm, and provides a way of assessing how many clusters there are by identifying the model (number of clusters) with the lowest Bayesian Information Criterion (BIC). As with other model selection methods, this criterion achieves a compromise between the goodness-of-fit and a penalty for the number of free parameters in the model; the model with the smallest BIC value was estimated to be the model that best fit the data.

Results

Data samples

A total of 331 encounters with “resident” type fish-eating killer whales were included in analyses (Figure 3), based on morphological assignment to the “resident” type. There were no disagreements between our two photo analysts, who were also in accord with previous assessments of earlier subsets of these data (Zerbini *et al.* 2007; Matkin *et al.* 2007; Durban *et al.* 2010). These assignments were corroborated by genetics for all 82 of these groups where biopsy samples were also obtained. Most of these encounters occurred around the central and eastern Aleutian Islands, largely reflecting the increased survey effort in this central area, although “resident” type fish-eating killer whales were encountered throughout the study area, ranging from the northern GOA to the western Aleutians and into the Bering Sea. “Resident” type fish-eating killer whales were always encountered in groups, ranging in size from 3 to 120 whales (median = 15).

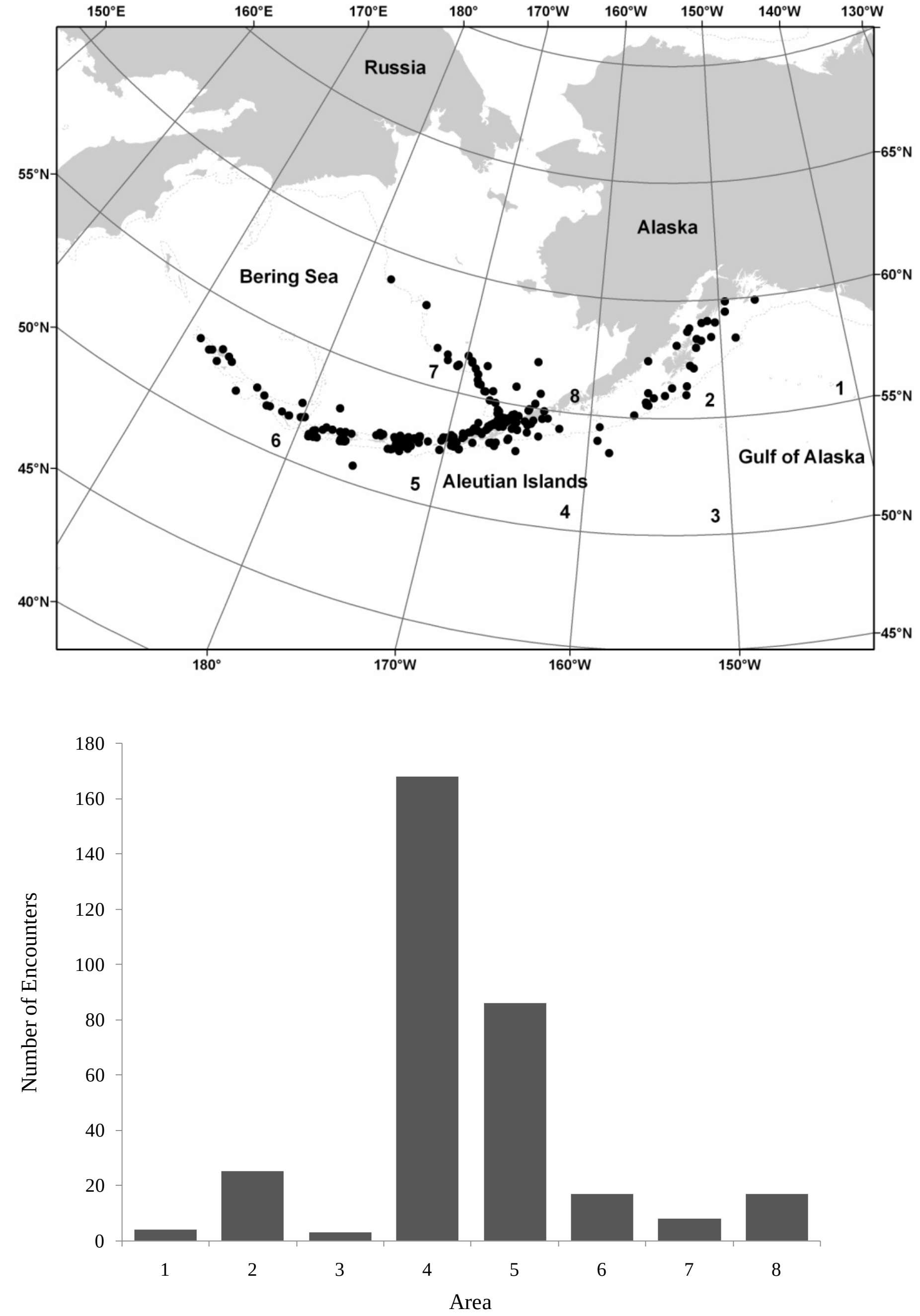

Figure 3. Top, map of the study area showing all encounters with "resident" type fish-eating killer whales from 2001-2010 (*n*=331); bottom, the number of encounters in each of eight spatial areas of dimension 5° latitude by 10° longitude (see top).

In total 77,815 photographs of “resident” type fish-eating killer whales were taken, resulting in 3058 unique identifications and 1220 distinct individuals. The majority (2705) of these unique identifications were judged to be of sufficiently reliable photographic quality, comprising 1186 distinct individuals. The re-sighting frequency varied for these individuals, with a median of 1 encounter per individual and a range of 1-7 encounters, and 417 whales were seen in more than one calendar year (median = 1 year, range = 1 to 6 different years). Most (1002) of these distinct whales were only seen in a single spatial area, with the highest number seen in the eastern and central Aleutians areas (areas 4 to 5), with re-sightings in the same area up to 10 years apart. However, 169 whales were photographed in 2 areas and 2 whales were documented in 3 areas. These spatial re-sightings were not solely in adjacent areas, indicating some relatively long distance movements (Table 2).

Table 2. Table of the total number of distinct individual “resident” type killer whales that were identified in each of eight spatial areas (diagonal cells) of dimension 5° latitude by 10° longitude (Figure 3), and overlap of individuals between areas (non-diagonal cells).

	AREA 1	**AREA 2**	**AREA 3**	**AREA 4**	**AREA 5**	**AREA 6**	**AREA 7**	**AREA 8**
AREA 1	**6**	10	0	0	0	0	0	0
AREA 2		**158**	1	21	0	0	0	0
AREA 3			**3**	0	0	0	0	0
AREA 4				**373**	35	1	7	64
AREA 5					**352**	31	0	0
AREA 6						**95**	0	1
AREA 7							**1**	4
AREA 8								**14**

Examination of re-sighting locations of whales identified during the winter survey (08DA) provided an initial indication of year-round site fidelity. Of the 15 distinct whales identified in area 5 during February 2008, 3 whales were re-sighted in the summer months, all in the same area 5. Two of these whales were seen during our surveys (02AH and 06OL) and the third whale (an adult male with distinctly white pigmentation) was photographed 8 years prior to the initial sighting (Renner and Bell 2008). The 41 whales observed depredating sablefish were seen at survey stations in 5 areas (2,3,4,5, and 7), but were not observed in areas 1, 6 and 8 (Figure 4), indicating that depredation is a widespread practice in the eastern and central Aleutian Islands, Bering Sea shelf edge and the western Gulf of Alaska, but is absent in the Gulf of Alaska waters east of Kodiak Island. Most (33/41) of these whales were also seen during other surveys, typically in the same or adjacent areas up to 9 years apart: 19 were observed depredating in two different areas, and also re-sighted in the same areas during other surveys; 14 whales were only seen in a single area both while depredating and during surveys. Whales observed depredating in the eastern Aleutians ranged across areas 4 and 5, with two whales moving between area 4 and area 7, along the Bering Sea shelf edge, and one whale restricting movements to area 5 (Figure 4). Whales observed depredating in the central Aleutians (area 5) and western GOA (areas 2 and 3) appeared to restrict movements within these regions (Figure 4).

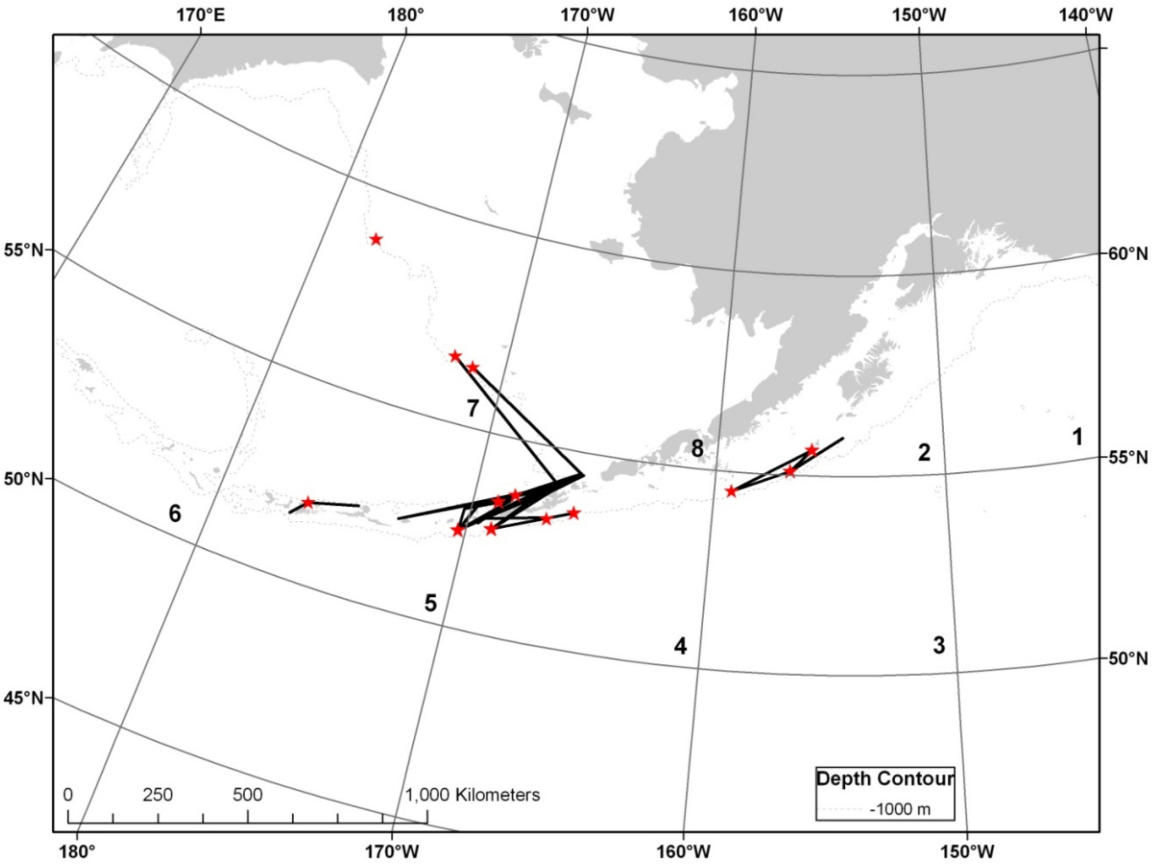

Figure 4. Map displaying sighting locations for *n* = 41 “resident” type fish-eating killer whales that have been observed depredating longline fisheries. Red stars depict locations where whales were observed depredating and black lines connect repeated sightings.

Movements

Movement analysis was conducted for all whales seen on more than one occasion (*n*=532). Examination of the longitudinal ranges of these whales (Figure 5) indicated limited east-west movements, and most (335 / 532) of these whales were observed in the same area in different years, indicating long-term site fidelity. Furthermore, the median “range” indicated by the maximum distance between repeated encounter locations was only 196.5 km (inter-quartile range = 88.5 – 304.5 km, maximum = 1443 km). The vast majority (469) of these whales had a maximum extent of their movement being less than 500 km, although long-distance movements (500 - 1450 km) were documented for 63 whales. Of these, 21 whales moved between 750 – 1000 km and four whales moved more than 1000 km (Figure 6).

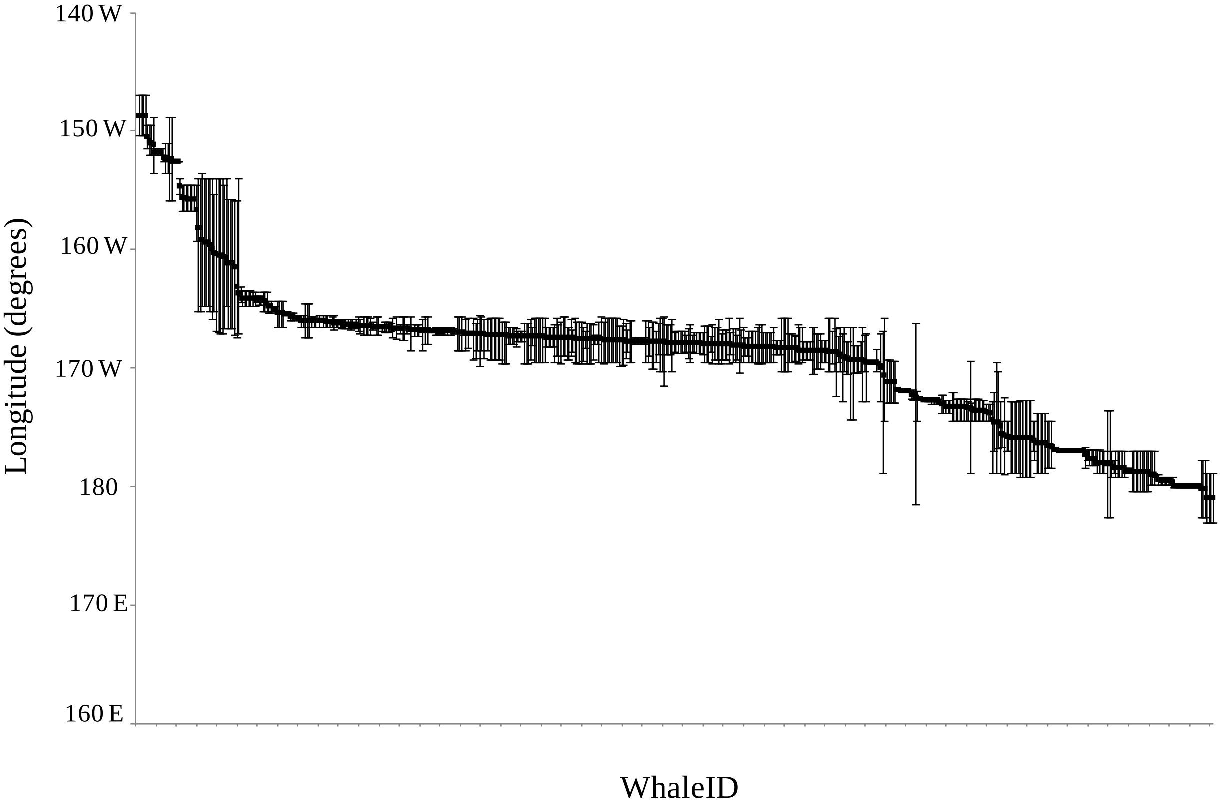

Figure 5. Maximum longitudinal extent (vertical lines) of movement for *n* = 532 “resident” type fish-eating killer whales identified in more than one encounter. Individuals are ordered based on mean longitude at which they were seen (solid line).

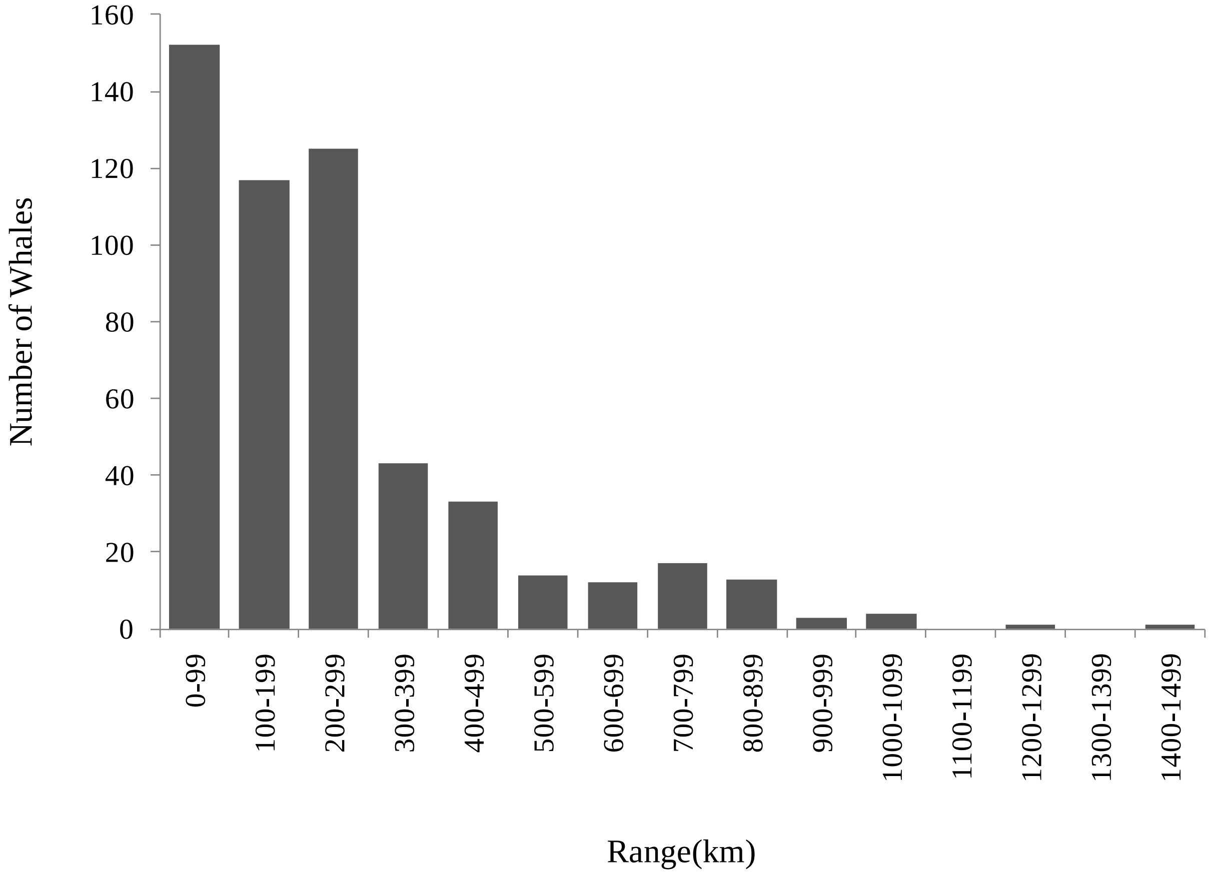

Figure 6. The range, indicated by the maximum distance between re-sighting locations for *n* = 532 “resident” type fish-eating killer whales identified in more than one encounter.

Maps of these typically short movements (Figure 7, top) illustrate significant spatial structuring, with movements primarily restricted within three regions: the northern Gulf of Alaska (areas 1 and 2), the eastern Aleutians Islands and Bering Sea shelf edge (areas 4, 7 and 8), and the central Aleutian Islands (areas 5 and 6). The relatively rare longer distance movements (Figure 7, bottom) do show some overlap between the central Aleutian Islands and the eastern Aleutians / Bering Sea shelf edge, and between the eastern Aleutian Islands and western Gulf of Alaska waters west of Kodiak Island (areas 1, 2 and 3).

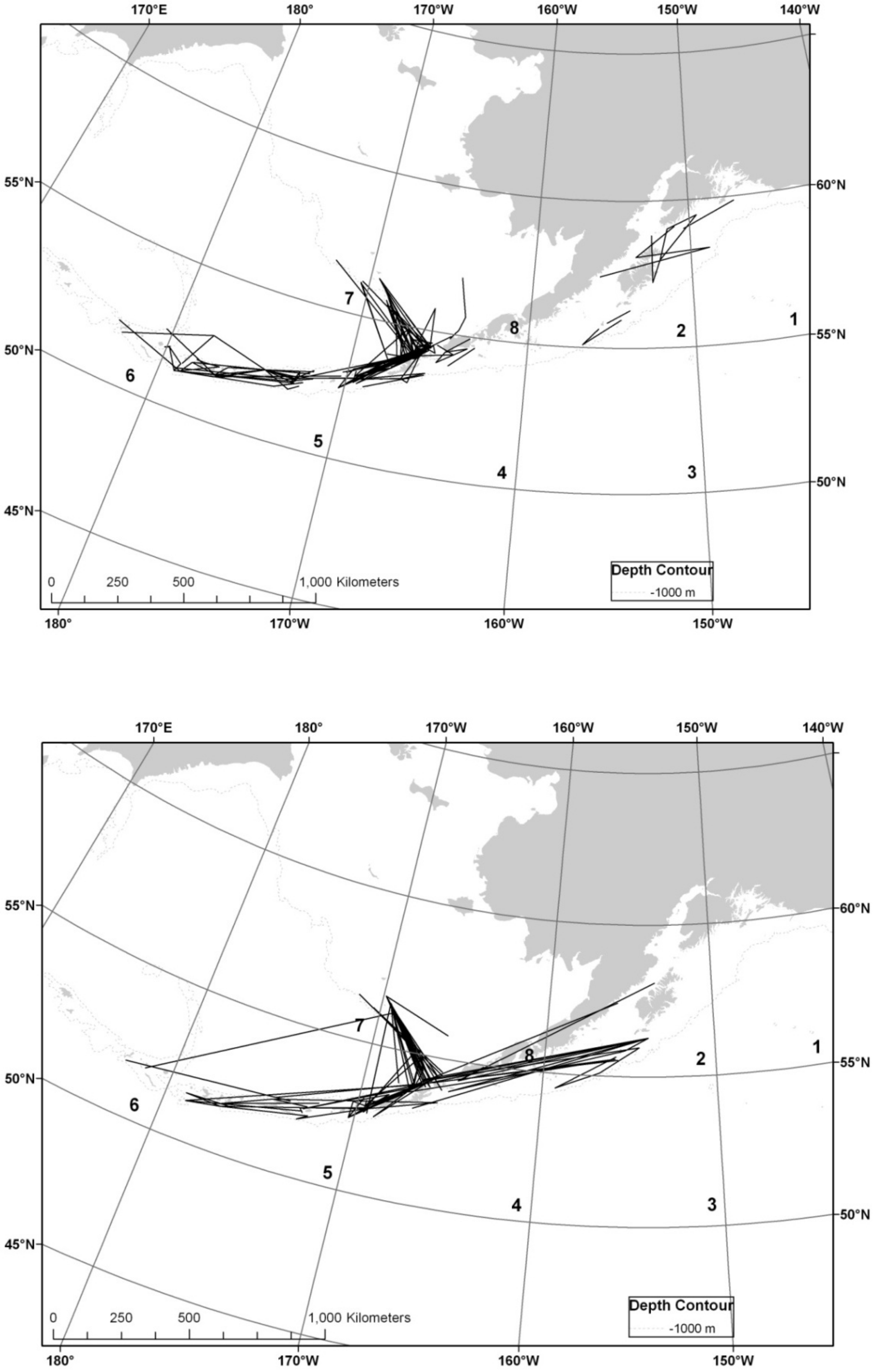

Figure 7. Map displaying connections of repeated sighting locations of "resident" type fish-eating killer whales with maximum ranges less than 500 km (top, *n*=469) and more than 500km (bottom, *n* =63).

Association network

Analysis of the associations between *n*=532 whales seen on more than one occasion revealed one large network of 441 connected individuals, and some peripheral groupings comprising 91 individuals that were unconnected to the large network. Of the 41 whales seen depredating the longline survey, 33 were seen more than once and were therefore included in the association analysis; 30 of these whales fell within the connected network and 3 were in the unconnected groupings.

The distribution of association values for all whales within the connected network was generally low (mean = 0.02, SD = 0.11), with a large number of unassociated whales (only 5% non-zero values). However, Bayesian cluster analysis revealed that the associations were not randomly distributed across the network. Bayesian measures of model fit indicated 4 distinct clusters of whales within this network (Figure 8), with the lowest BIC = 5639 for the 4-cluster model, compared to a next best fit of BIC = 5647 for the 5-cluster model. Although there was some uncertainty over the cluster assignment of some whales under the 4-cluster model, 327/441 whales could be assigned to a distinct cluster with high probability ($p \geq 0.75$; cluster 1 = 31 whales; cluster 2 = 169 whales; cluster 3 = 33 whales; cluster 4 = 94 whales). The 114 remaining whales could not be assigned with such high confidence to a specific cluster, although probability of cluster membership fell between 0.50 - 0.74 for 103 of these whales. Notably, of the 30 depredating whales included in the large social network, 17 whales were assigned to social cluster 2, 3 whales were assigned to social cluster 4, and 10 whales could not be assigned to a specific social cluster with high probability.

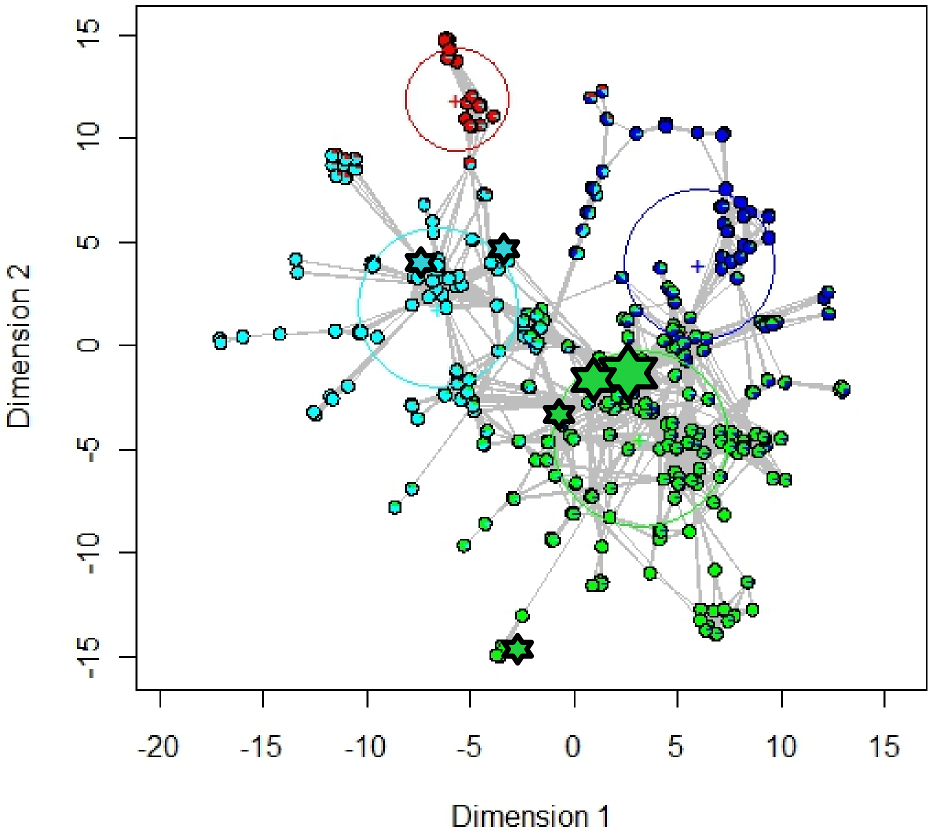

Figure 8. Cluster assignment in two-dimensional social space of *n*=441 "resident" type fish-eating killer whales seen more than once that were part of a connected network. Direct associations (seen together at least once) are indicated by solid lines, social positions for each whale (circular pie symbols) were estimated from association indices between each pair of whales: the color of the pie reflects the cluster assignment of each whale, with the proportion comprised of each color representing the probability of that whale being assigned to each cluster. Cluster 1 = red, *n* = 31 whales; cluster 2 = green, *n* = 169 whales; cluster 3 = blue, *n* = 33 whales; cluster 4 = turquoise, *n* = 94 whales. Cross symbols indicate the mean social space of each cluster' circles represent the estimated the standard deviation of the intra-cluster variances. Stars represent the estimated social position of whales that have been observed depredating: with star size proportional to number of whales (range: 1-10).

The levels of association between whales differed within these defined clusters, with mean association values of 0.36 (SD = 0.37, non-zero values = 56.1%), 0.07 (SD = 0.17, non-zero values = 18.9%), 0.23 (SD = 0.29, non-zero values = 42.2%) and 0.09 (SD = 0.22, non-zero values = 18.1%) for clusters 1, 2, 3 and 4 respectively. Notably, all four clusters contained some highly associated whales, with 53, 84, 20 and 100 pair-wise association indices equaling a value of 1, where two whales were always seen together. These consistent associations persisted for up to 10 years (maximum duration of the study).

This connected social network was comprised of whales with a combined range spanning more than half of the study area, covering a linear distance of almost 3000 km (Figure 9). The distinct social clusters of whales within this network also showed relatively distinct ranging patterns, with limited spatial overlap between clusters. Whales in cluster 3 ranged most widely (median range = 430km, range = 54 – 903 km), covering waters from the Gulf of Alaska to the eastern Aleutians (areas 1, 2, 4 and 8), followed by whales in cluster 2 (median range = 236 km, range = 6 – 1061 km), that predominantly used the waters of the eastern Aleutian Islands, with north/south movements along the Bering Sea shelf edge (areas 4, 7, and 8). However, whales in this cluster also undertook east/west movements to the central Aleutians (5). Whales in cluster 4 (median range = 162 km, range = 1 – 988 km) predominantly used the waters of the central Aleutian Islands (areas 5) but also ranged into the eastern Aleutians (4) and the western Aleutian Islands (6). Finally, whales in cluster 1 were encountered over more restricted ranges (median range = 91 km, range = 17 – 245 km) near Amchitka Pass, on the boundary of the central and eastern Aleutian Islands (area 5).

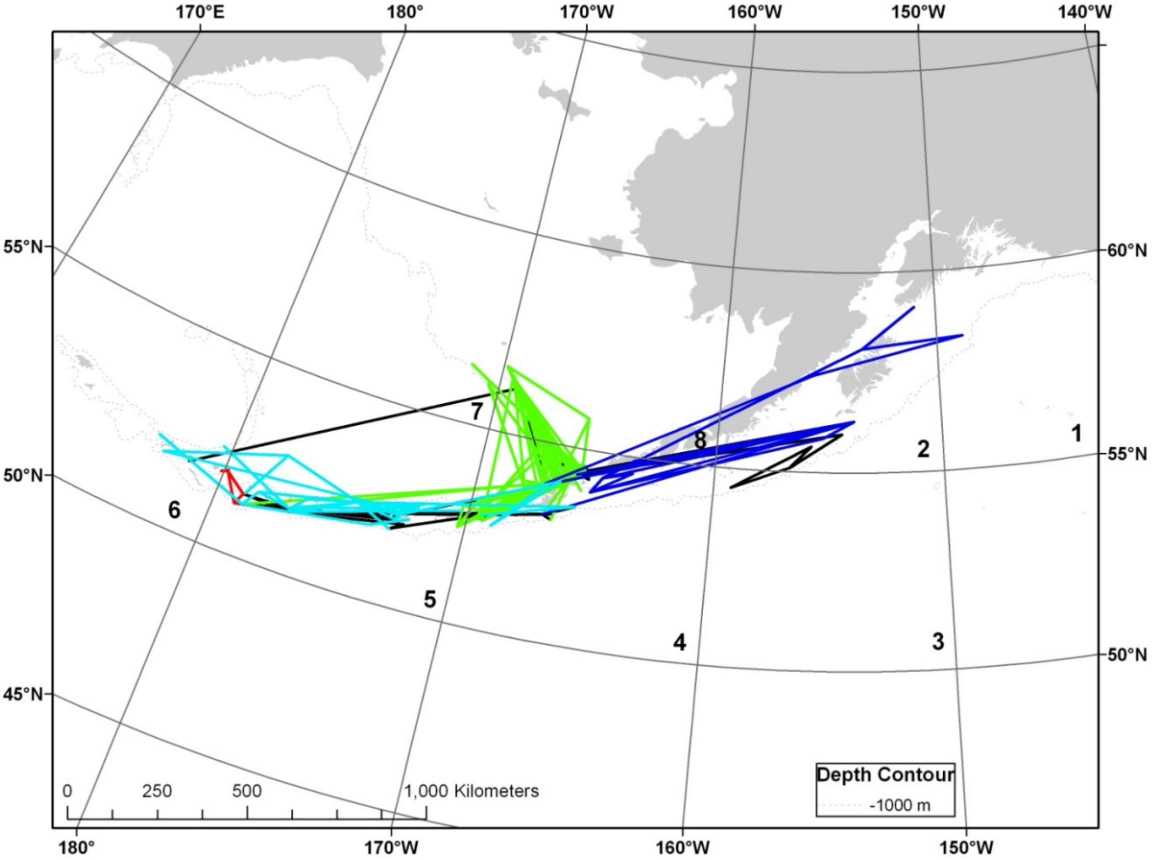

Figure 9. Map displaying straight-line distance between the repeated sighting locations for *n* = 441 “resident” type fish-eating killer whales within the large connected social network. Line color represents distinct cluster membership of whales assigned with high probability (p ≥ 0.75) as per Fig.7; cluster 1 = red, *n* = 31 whales; cluster 2 = green, *n* = 169 whales; cluster 3 = blue, *n* = 33 whales; cluster 4 = turquoise, *n* = 94 whales); black lines depict whales within the network that couldn’t be assigned to a specific cluster with high probability.

Discussion

We have documented significant spatial structuring within the Alaska Resident stock of “resident” type fish-eating killer whales between the northern Gulf of Alaska and the western Aleutian Islands. Although some long-distance movements (up to 1443 km) were documented, most whales had maximum observed ranges less than 200 km, with high site fidelity across years. The extent of this movement is much less than reported for other North Pacific ecotypes (e.g. maximum range of 2660 km for “transients”, Goley and Straley 1994; 4435 km for “offshores”, Dahlheim *et al.* 2008), but is comparable to the summer range of other populations of “resident” killer whales (e.g. Matkin *et al.* 1997; Ford *et al.* 2000). Because our photo-identification sample was largely collected during summer months, we cannot rule out longer, unobserved, seasonal movements: “southern resident” killer whales in the eastern North Pacific demonstrate a high degree of site fidelity to the inshore waters around southern Vancouver Island during summer months, but some groups range more 2000 km during winter (Krahn *et al.* 2007b). However, our small sample of winter “resident” type fish-eating killer whale identifications documented whales that were also seen in the same area in summer. Movements in mammalian populations are generally related to resource acquisition (Wrangham 1986; Wrangham and Rubenstein 1986), and the restricted range of these “resident” type fish-eating killer whales is likely a response to the highly productive environment, particularly around the Aleutian passes (Sinclair *et al.* 2005), reducing the need to move long distances.

The movements we documented were primarily restricted within three regions: the northern Gulf of Alaska, the eastern Aleutians Islands and Bering Sea shelf edge, and the central Aleutian Islands. This is consistent with dietary differences among whales in these three regions (Krahn *et al.* 2007a), which suggests spatial population structuring. However, the relatively rare longer distance movements did show spatial connectivity between regions, specifically between the central Aleutian Islands and the eastern Aleutians / Bering Sea shelf edge, and between the eastern Aleutian Islands and western Gulf of Alaska waters west of Kodiak Island. There were no direct movements of whales between the northern Gulf of Alaska waters east of Kodiak Island and the Aleutian Islands, or between the far western Aleutian Islands and areas to the east, possibly indicating population boundaries. Conversely, these could also be edge effects, resulting from sparser photo-identification data at the far eastern and western extents of our study area. The limited exchange of whales between these areas and the core of our study area nonetheless suggests a lack of social connectivity. Future molecular genetic investigations will help evaluate this hypothesis.

Our analysis of social connectivity suggested that this spatial structuring was mediated by social affiliations. Pair-wise associations were distributed into four distinct clusters, the largest three of which defined whales ranging in each of our three connected regions, respectively. The fourth, smaller, cluster consisted of whales sighted exclusively at the boundary of the central and western Aleutian Islands, and it is likely that we have not sampled sufficiently to resolve the social and spatial connectivity of whales further west, with only three surveys in the western Aleutians to date. Within these clusters, there were some very strong associations (20-100 pairs per cluster always together) that persisted across years (up to the 10 year study duration), indicating stable groupings. This is consistent with the stable matrilineal groupings described in “resident” type fish-eating killer whales over four decades of study in the eastern North Pacific (Bigg *et al.* 1990; Matkin *et al.* 1999; Ford *et al.* 2000; Parsons *et al.* 2009). Matrilines of females and their descendants in these well studied populations have remained stable for generations, with no dispersal from the natal groups (Parsons *et al.* 2009). However clusters of matrilines have associated to varying degrees, sometimes comprising “pods”, with dynamic associations coincident with changes in prey availability (Parsons *et al.* 2009; Ford *et al.* 2010). We suggest that the social clusters we defined represent preferred but temporary groupings of multiple stable matrilines, based on both strong and weak associations within each connected cluster. Future genetic work will help resolve the relatedness within and between clusters.

Many mammalian populations occur in social systems where changes in group membership are observed as individuals form temporary groups that fuse together and then break apart (Kummer 1971; Struhsaker and Leland 1979). The fission-fusion dynamics of populations that occur in a variable environment are likely to be less cohesive and are comprised of a few, large connected components, each consisting of highly associated "cliques" (Rubenstein *et al.* 2007; Aureli *et al.* 2008). In this case, our clusters of preferentially associating groups appear to align with key ecological variability: specifically an ecological gradient that shifts from continental shelf waters in the nearshore waters of Gulf of Alaska to shelf edge waters in the eastern Aleutian Islands /Bering Sea shelf, and finally to more pelagic waters off the shelf in the central Aleutian Islands (Figure1; Krahn *et al.* 2007a). Chemical analyses of skin biopsies from these "resident" type fish-eating killer whales revealed a similar gradient in skin stable isotope profiles (Krahn *et al.* 2007a) that supports an east-west shift away from prey found in shallower waters on the continental shelf. Gulf of Alaska whales (Saulitis *et al.* 2000) consume salmon as a substantial part of their diet, but it is likely that whales in the eastern Aleutian Island whales consume salmon to a lesser extent (Wade *et al*. 2006). Whales in the central Aleutian Islands likely consume alternative locally available prey in deeper waters (Krahn *et al.* 2007a). The socially-mediated spatial structure we have documented supports consistent use of different foraging areas by these clusters, helping to explain these spatial differences in dietary signals.

At a larger scale, the four defined clusters were linked by occasional associations to form a single large connected network, with an expansive longitudinal range (c. 3000km), including most (83%) of the photo-identified whales that were seen on more than one occasion. Due to limited sample sizes, we cannot assess the significance of the outliers: it is possible that they were simply not observed sufficiently often to be seen associating into the network. Such large, connected networks may facilitate the spread of information throughout the population through cultural transfer, likely enhancing success in resource acquisition (Lusseau and Newman 2004; Rubenstein *et al.* 2007) and fitness (Whitehead and Rendell

2004; Whitehead *et al.* 2004; Whitehead 2010). In this case, large-scale social connectivity may facilitate the widespread practice of depredation of longline fisheries, despite relatively restricted movements of individual whales.

Depredation of longlines by killer whales in Alaskan waters has been observed for several decades (Dahlheim 1988; Yano and Dahlheim 1995; Matkin *et al.* 1997), but there have been increased reports of incidence in recent years (Lunsford and Rutecki 2010). Whales that were photographed while depredating longlines in several areas throughout our study area were members of the two largest social clusters in the eastern Aleutian Islands / Bering Sea and central Aleutian Islands. This aligns with widespread depredation by killer whales along the Aleutian chain and into the Bering Sea (Yano and Dahlheim 1995; Lunsford and Rutecki 2010). Although our sample size is small, we did not confirm any depredation by whales assigned to the cluster that ranged into the western Gulf of Alaska or by the unconnected whales in the Northern Gulf of Alaska waters east of Kodiak Island, coinciding with a notable decrease in the incidence of killer whale depredation in the Gulf of Alaska (Yano and Dahlheim 1995; Lunsford and Rutecki 2010), despite frequent depredation by sperm whales (*Physeter macrocephalus*, Sigler *et al.* 2008). Therefore, we suggest a social mechanism for the spread of depredation, through cultural transmission of learned behaviors between highly associated individuals (Whitehead and Rendell 2004; Rubenstein *et al.* 2007; Aureli *et al.* 2008; Whitehead 2010). However, there was some depredation observed by apparently unconnected individuals in the Western Gulf of Alaska; it is possible that their connections to the network were undetected in our small sample, but it could also be that whales in some areas may have learned depredation behaviors by themselves. Further collection of association data will help to resolve finer details of the association network.

The spatial structuring we have documented within killer whales in the coastal waters between the northern Gulf of Alaska and the western Aleutian Islands needs to be considered when evaluating the ecosystem impact of these top predators (e.g. Guénette *et al.* 2006) and the extent of competition with fisheries (e.g. Lundsford and Rutecki 2010). Killer whales are known to have high caloric requirements (Williams *et al.* 2004; Noren 2011), and the density of fish-eating “resident” killer whales in these productive waters is known to be among the highest in the world (Forney and Wade 2006; Zerbini *et al.* 2007). Their impact in this region is therefore undoubtedly considerable, but likely underestimated (Lundsford and Rutecki 2010). Future assessments of the importance of killer whale predation are needed, and should incorporate area-specific abundance estimates, guided by the clustered space-use patterns we have reported.

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CHAPTER SIX

ABUNDANCE AND DEMOGRAPHIC STATUS OF RESIDENT-TYPE KILLER WHALES AROUND THE ALEUTIAN ISLANDS

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CHAPTER SIX

Abundance and demographic status of resident-type killer whales around the Aleutian Islands

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Abstract

Documenting abundance and population dynamics is integral to understanding the trophic impact of top predators, but can be difficult for wide-ranging marine mammals in remote environments. We used 10 years (2001-2010) of photo-identification data to estimate abundance and evaluate demographic parameters of “resident” type fish-eating killer whales that are particularly numerous in the highly productive North Pacific waters around the central and eastern Aleutian Islands. We adopted a spatially explicit Bayesian mark-recapture approach to reveal population structuring and account for this heterogeneity in abundance estimation. Abundance was very high during summer sampling intervals (maximum annual estimate of 2260, HPDI=1255-4112), more than twice as high as previous estimates from line-transect surveys. In the absence of a longer time series, we assessed demographic status by comparing the composition of adult males, a class known to suffer high mortality during periods of food shortages and population limitation, to well-studied ‘reference” populations of “resident” type fish-eating killer whales in the eastern North Pacific with contrasting population dynamics. The Aleutian population was comprised of a greater proportion (29%) of typically older (median age = 27; range = 16 – 62; 40 % of all adult males > 30 years;), and larger adult males with particularly large dorsal fins (maximum blowhole to dorsal fin length = 292 cm; maximum dorsal fin height = 225cm), and could be classified as adult (based on sexually dimorphic fin growth) at an early age (~13). These demographics show no

signs of population contraction in recent decades, and we suggest that they are indicative of a good feeding history leading to population expansion. The high abundance and high proportion of large males reflects high caloric requirements, which are likely to have a significant impact on the marine system around the Aleutian Islands, likely leading to competition with commercial fisheries and other protected marine mammal populations.

Introduction

Wildlife populations exist within and are ultimately regulated by the highly structured ecosystems in which they occur (Cochrane 2002). As a result, management and conservation measures require an understanding of abundance and population dynamics that can be related to ecosystem dynamics (Leibold *et al.* 2004). Specifically, there has been increasing recognition of top-down forcing on marine ecosystems (Pace *et al.*1999; Estes *et al.*2009), and an evaluation of these trophic impacts requires knowledge of the abundance of top predators at appropriate spatial scales for ecosystem considerations. Killer whales, in particular, are a top marine predator, whose high caloric requirements are capable of significant impacts on lower trophic levels (Springer *et al.*2003; Williams *et al.*2004), but assessments of realized impacts have been constrained by a lack of information on abundance and trends (e.g. Guénette *et al.*2006). Here we fill a key data gap by estimating the abundance and inferring demographic trends for “resident” type fish-eating killer whales in the far North Pacific, where they are particularly numerous (Forney and Wade 2006).

Three distinct lineages of killer whales (referred to as “residents”, “transients” and “offshores”) have been identified in the productive waters of the North Pacific Ocean based on differences in morphology, genetics, prey preferences and acoustics (Ford *et al.*1998; Matkin *et al.*1999; Ford *et al.*2000; Saulitis *et al.*2000; Yurk *et al.* 2002; Herman *et al.*2005; Morin *et al.*2010; Ford *et al.*2011), with the “resident” lineage occurring in highest abundance in coastal waters (Forney and Wade 2006; Zerbini *et al.*2007; Matkin *et al.*2007). Individual killer whales can be distinguished by distinctive and long-lasting natural markings, and photographs of individuals can be used to construct sighting histories over several decades (e.g. Balcomb *et al.*1982; Bigg 1982; Bigg *et al.*1990; Ford *et al.*2000; Parsons *et al.*2009; Ward *et al.*2010). Using this photo-identification approach, accessible populations of killer whales have been regularly monitored through direct photographic censuses to provide robust population estimates (Bigg *et al.*1990; Matkin *et al.*1999; Ford *et al.*2000; Matkin *et al.*2008).

However, in more remote environments, which are costly and challenging to survey, it is not possible to count all individuals within a population in annual censuses, requiring a sampling approach for abundance estimates. Although distance sampling from line transect surveys has been used in such circumstances (e.g. Branch and Butterworth 2001; Zerbini *et al.*2007), this approach is typically imprecise and can only result in estimates of abundance not demographics. In contrast, capture-recapture sampling is an alternative approach using photographic identifications and re-identifications as “captures” and “re-captures” to which analytical capture-recapture techniques can be applied to estimate both abundance and demographic parameters (Hammond 1990). Such photographic capture-recapture methods have recently been adopted to estimate abundance and structuring of mammal-eating “transient” type killer whales in the far North Pacific waters around the Aleutian Islands (Durban *et al.*2010), where the trophic impact of killer whales has been the subject of considerable debate (Estes *et al.*1998; Springer *et al.*2003; DeMaster *et al.*2006; Mizroch and Rice 2006; Wade *et al.*2007; Springer *et al.*2008; Wade *et al.*2009; Estes *et al.*2009). However, there is an absence of such assessments for the fish-eating “resident” type of killer whales that are thought to occur in much higher abundance in the same area (Zerbini *et al.*2007). As such, inference about current abundance and status of fish-eating killer whales around the Aleutian Islands is particularly important in an ecosystem context, with these killer whales likely having significant direct trophic impacts on commercially important fish species (e.g. Lunsford and Rutecki 2010) and indirect effects through prey competition with other protected marine mammal populations (e.g. Merrick *et al.*1997; Guénette *et al.*2006).

In this paper we analyzed 10 years (2001-2010) of photo-identification data to estimate abundance and assess demographic parameters of “resident” type fish-eating killer whales that occur in the highly productive waters of the central and eastern Aleutian Islands, including waters of the Bering Sea shelf edge. We applied a spatially explicit parameterization of the established Jolly-Seber mark-recapture model (Royle and Dorazio 2008; Gardner *et al.*2010; Chapter 3) to estimate abundance while incorporating heterogeneity resulting from spatial population structuring (Chapter 5). Although “resident” type killer whales in the Gulf of Alaska, Aleutian Islands and Bering Sea are currently managed as a single “Eastern North Pacific Alaska Resident” stock (Allen and Angliss 2012), there is evidence of significant structuring within this area (Chapter 5; Parsons *et al.* submitted). Our assessment focuses on an area used by a large connected social network of killer whales (Chapter 5), with repeat survey effort providing power to estimate abundance using photographic mark-recapture techniques.

Although photographic samples were only available for a 10 year-period, 2001-2010, we made inference about longer term demographic histories (and current status) by undertaking a comparative analysis of current population age/sex structure. Specifically, we examined the population composition of adult males, a class known to suffer high mortality during periods of food shortages and population decreases in other populations (Olesiuk *et al.*2005; Krahn *et al.*2007b; Ward *et al.*2010). We compared the relative abundance, age and size of adult males in the Aleutian Islands to two populations of “resident” type fish-eating killer whales with near complete longitudinal demographic records: the “Gulf of Alaska”

(GOA) population, that has been monitored annually since 1984 and primarily occurs in Prince William Sound and coastal waters of the northern Gulf of Alaska (Matkin *et al.*1997; Matkin *et al.*1999; Matkin *et al.*2008), and the endangered “southern resident”(SR) population, that has been monitored annually since the early 1970s (Balcomb *et al.*1982; Bigg *et al.*1990; Olesiuk *et al.*1990; Ford *et al.*2000; Ward *et al.*2009; Ford *et al.*2010; Ward *et al.*2010) in the coastal waters of British Columbia, Canada and Washington State, USA. These two “reference” populations have displayed contrasting population dynamics: The GOA population has been shown to be steadily increasing in recent decades (Matkin *et al.*2008), while the SR population has exhibited periods of prolonged population decline, with high mortality associated with food-limited years (see Olesiuk *et al.*2005; Krahn *et al.*2007b; Ford *et al.*2010; Ward *et al.*2009, 2010).

Methods

Survey area and data collection

Photo-identification data were collected from 2001-2010, during shipboard sightings surveys (Chapter 5) conducted in the coastal waters of Alaska, ranging from the northern Gulf of Alaska to the western extent of US waters in the western Aleutian Islands. However, we restricted our assessment to a central part of this study area (Figure 1) that was surveyed in multiple years of the study, including coastal waters around the eastern and central Aleutian Islands (~160°W to 180°), and also extending northwards up the Bering Sea shelf edge to the Pribilof Islands (~57°N). Previous analyses have revealed that this area is used by a large connected social network of killer whales (Chapter 5), which has limited connectivity to whales in the waters of the western Aleutians and the GOA to the east.

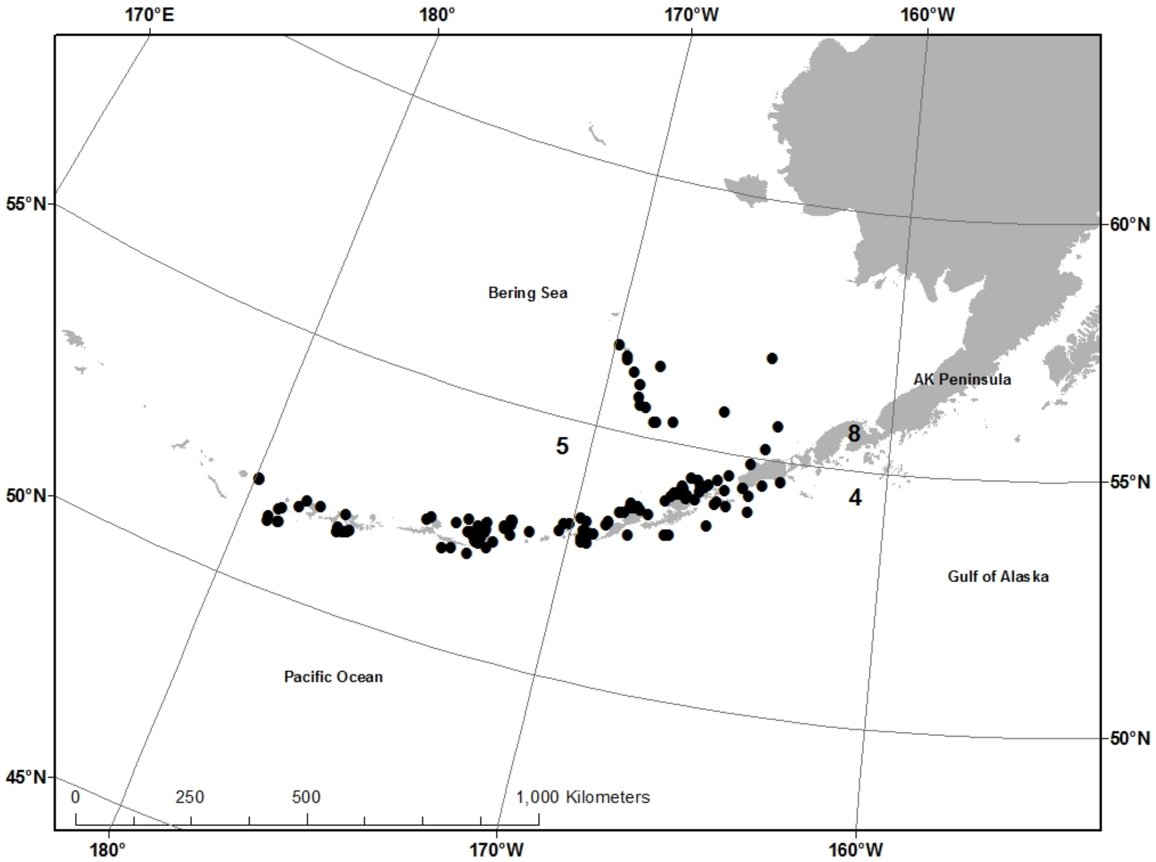

Figure 1. Map of the study area showing all encounters with "resident" type fish-eating killer whales during the summer sampling period (May-September) from 2001-2010 (*n*=138) in areas 4, 5 and 8.

This area is physically diverse, ranging from continental shelf waters in the east to deep pelagic waters in the west, with islands separated by extremely productive passes (Hunt and Stabeno 2005; Ladd *et al.* 2005). Surveys were primarily conducted during summer months (May-September), generally within 30 km from the shore or continental shelf edge. For this study, we limited analyses to include photo-identification data from dedicated killer whale sighting surveys and opportunistic surveys, where high priority was placed on collecting photo-identification data on killer whales (Table 1). Dedicated killer whale surveys from 2001-2003 employed line-transect methods for random-area coverage (Zerbini *et* *al.*2007) and surveys from 2004-2010 targeted areas of known killer whale occurrence. Large charter vessels (40-60 m) were used as survey platforms and observers searched for killer whales with either 7x50 handheld binoculars or fixed mount 25x magnification binoculars from heights of 5.5-10 m (e.g. Zerbini *et al.*2007). In addition, killer whale photo-identification images were opportunistically collected during oceanographic, fish trawl and dedicated right whale surveys from 2001-2008, although limited time was apportioned to photo encounters (Table 1).

Table 1. Table showing the survey history, number of encounters with “resident” type fish-eating killer whales, and number of distinct individuals identified from high quality, left side photographs collected during the summer (May-September) sampling intervals by year for each area and overall.

	Area 4				**Area 5**				**Area 8**				
Year	**Surveys**	**Dates**	**Encounters**	**IDs**	**Surveys**	**Dates**	**Encounters**	**IDs**	**Surveys**	**Dates**	**Encounters**	**IDs**	**Overall IDs**
2001	01AH, 01AM	June-August	10	100	01AH 01AM	June-August	2	36	------	------	------	------	**123**
2002	02AH, 02CP, 02MA	May-August	17	120	02AH, 02CP, 02MA	May-August	8	4	02MF, 02MA	June-August	5	14	**149**
2003	03CP	July-August	7	80	03CP	July-August	5	29	------	------	------	------	**104**
2004	04AE	July-August	6	48	04AE	July-August	2	5	04AE	July-August	1	6	**60**
2005	05AE, 05OD	June-September	4	30	05AE, 05OD	June-September	7	65	05AE, 05OD	June-September	7	41	**134**
2006	06OL	June	2	12	06OL	June	18	287	-------	------	-------	-------	**203**
2007	07OL, 07OD	June, August	3	15	-------	------	-------	-------	07OL, 07OD	June, August	1	8	**23**
2008	08OL	August-September	2	5	-------	------	-------	-------	-------	------	-------	-------	**5**
2009	09AQ	June-July	7	87	-------	------	-------	-------	-------	------	-------	-------	**78**
2010	10AE	June-July	4	50	10AE	June-July	6	87	-------	------	-------	-------	**132**
Overall	**15**	**May-September**	**62**	**400**	**11**	**May-September**	**48**	**383**	**7**	**June-September**	**14**	**66**	

Killer whales were approached following each visual sighting and photo-identification images were collected from as many individuals as possible from either the ship or a small launch (~6m). Photo-identification images were taken using either 35-mm SLR cameras, shooting Fuji Neopan 1600 ISO black and white film (2001-2003), or with digital SLR cameras with a minimum resolution of 6 MP (2004-2010). Groups were defined as all individuals typically within 500m that were moving in a coordinated fashion. When possible, skin and blubber samples were collected using remote biopsy techniques (e.g. Barrett-Lennard *et al.* 1996) and these samples were used in combination with photographs to confirm lineage. Lineage assignment was made using established criteria for this region (Matkin *et al.*2007; Zerbini *et al.*2007; Durban *et al.*2010; Chapter 5), based on a combination of molecular genetics and morphological characteristics (e.g. Chapter 5). Biopsy samples were preferentially taken from adult males, which were a slower and larger target (Herman *et al.*2008).

Digital photo-identification images taken in the field were converted to tagged format files (TIF) to allow examination of the maximum resolution possible. All 35-mm photo-identification images were digitized using a slide copy adapter to capture 6MP TIF files with a Nixon Coolpix digital camera, to allow standardized analysis alongside the native digital photo-identifications. The best photograph of each whale, in each encounter, was selected after all images were digitized. All best-in-encounter photographs were matched to a master photo-identification catalog of individuals and assigned an identification number (a new number was assigned if the whale could not be matched to a previously identified whale/existing identification number). Permanent identification numbers were assigned to whales of high quality that were distinct enough to be matched between encounters and years, and temporary numbers were assigned to whales that could be distinguished within a group, but were not distinct enough to track over time. Distinctiveness was based on a combination of features of the dorsal fin (e.g. distinctive shape, the presence of notches) and the adjacent saddle patch (distinctive pigmentation, scarring patterns) following Durban *et al.*(2010), with the distinctiveness of features being determined by the expert opinion of two of the authors (HF, DE). All best-in-encounter photographs were assigned quality grades *(Q*=1-3) for each of exposure, amount of fin and saddle captured, clarity and angle.

Photographic mark-recapture analysis

We treated the photo-identifications and re-identifications of individuals as “captures” and “recaptures” to which analytical mark-recapture methods could be applied. Only high-quality *(Q*>1 for each category), left side photographs of distinctive whales that were encountered in areas of relatively high survey effort (Figure 1, Areas 4, 5 and 8) were included in mark-recapture analysis to adhere as closely as possible to mark-recapture assumptions of correct mark-recognition, no loss of marks and population definition (Seber 1982). Additionally, we restricted data to only photographs taken during the summer months (May-September), to have as consistent a sampling interval as possible across years (Table 1). Owing to the spatially stratified patterns of movement and social connectivity presented in Chapter 5, we adopted a spatially explicit parameterization of the Jolly-Seber mark-recapture model (Gardner *et al.*2010; J. Durban, unpublished data). This method allowed us to incorporate spatial heterogeneity in identification probabilities when estimating parameters of abundance, survival and recruitment and concurrently learn about space-use. Identifications were stratified into each of the j=1,..,3 areas in each of the t=1,..,10 years. The areas were defined as areas of dimension of 5° latitude by 10° longitude (Figure 1; Chapter 5) that were consistently surveyed across the study period (Table 1). These represented a subset of the areas used in the analyses in Chapter 5, but represented the areas containing the majority of all killer whale encounters over the study period (2001-2010). Each individual could be identified in any number of the three areas during a particular year, but owing to the sparsity of repeat surveys in each year, we formatted the observed data as simple binary responses y_{ijt}, to indicate whether individual i was seen in area j in year t.

Because the total number of individuals available to be identified in the study area was not fixed, but unknown, and abundance estimation was a primary goal of inference, we adopted an augmented approach of Royle and Dorazio (2008) and Gardner *et al.* (2010). We augmented the list of n individuals observed with a large number (M=2000) of all zero identifications to represent a pool of identified individuals. We then linked these spatial identification histories to parameters of both a population model x_{it}, giving status (alive or not) of each individual in the population in each year (e.g. Chapter 3), and an observation model p_{ijt}, which described the spatial process of identification (capture) probability.

$$y_{ijt} \sim \mathrm{Bernoulli}(p_{ijt}\, x_{it})$$

The *observation model* used the mixture approach presented in Chapter 3 to identify clusters of whales with similar vectors of capture/identification probabilities, but here the similarity was expressed through identification probability effects stratified by areas, rather than time. Specifically, capture probability was modeled in terms of a mean capture probability for each area $\mu_j^{\,p}$ and effects that represented departures from these means due to annual variation in coverage of each area (ε^{p}) and clustered individual effects (θ) reflecting differential catchability of specific clusters in specific areas:

$$\mathrm{logit}(p_{ijt}) = \mathrm{logit}(\mu_j^{\,p}) + \theta_{z[i]=c,j} + \varepsilon_{jt}^{\,p}$$
$$\varepsilon_{jt}^{\,p} \sim \mathrm{N}(0, \sigma^{p})$$

where logit (a)= log(a/(1-a). Separate Uniform (0,1) prior distributions were placed on each of the three mean probabilities μ^{p}, and as such they were modeled as fixed effects, and a Uniform (0,10) prior was adopted for the random effects standard deviation σ^{p} to allow for temporal and spatial overdispersion. We adopted a mixture formulation where the area effect for each individual i was drawn from a specific cluster, c, with assignment of individuals to a cluster through estimation of the indicator variable $z_i = c$. For a ceiling of $C = 30$ potential clusters, we used a Dirichlet process to draw a set of C values of $\theta_{c,j}$ for each area from a baseline distribution and estimated which value $z_i = c = 1,\dots, C$ was appropriate for each individual (following Durban *et al.* 2010). The baseline distribution was hierarchically specified to be a multivariate Normal distribution, stratified into q=3 dimensions corresponding to the three areas:

$$\theta_{c,j} \sim N_3(0, \Sigma)$$

where Σ was a covariance matrix of the order 3x3. The principal (left to right) diagonal element of this matrix was the estimate of the variance of the cluster effects for each of the 3 areas, and the off-diagonal values represented covariances between pairs of areas in terms of how they captured the effects of each cluster. For example, a cluster with high catchability in area 1 would have high catchability in area 3 if a positive covariance existed. We adopted the Wishart distribution as the prior for the inverse covariance matrix Σ^{-1} (Fienberg *et al.*1999; Durban *et al.*2010), which is specified in terms of a scale matrix B and a degrees of freedom parameter w. We set diagonal values of $B = 1$ for the prior variance of the cluster catchability for each area, and the off-diagonals were assigned $B = 0$ for a prior assumption of no covariance between pairs of areas. Larger values of w represent stronger belief, and we therefore adopted a value of $w = q = 3$ to represent a vague prior to allow non-zero effects to emerge.

The population model used the same parameterization presented in Chapter 3, where the status was expressed in terms of annual probabilities of survival (φ) and recruitment (γ):

$$x_{i,t+1} \sim \text{Bern}\left\{\phi_{it}x_{it} + \gamma_{it+1}\left\{\prod_{k=1}^{t}(1-x_{ik})\right\}\right\}$$

with the initial state given by $x_{i1} \sim (y_{i1})$. Values of 1 were inputted for x in years when any whale was not identified ($h = 0$) between years of repeated identifications ($h = 1$), and similar imputation was based on identifications in the out-of sample months and areas subsequent to annual sampling periods when a whale was not seen, but was known to be alive. Where the status was unknown following the interval of last identification or before the first identification, and for all unobserved augmented individuals, we treated x_{ij} as a missing value about which inference may be made.

Temporal and individual variation in survival and recruitment probabilities were specified by modeling φ and γ as a function of mean (μ) and time-varying random effects terms (ε) which were drawn from a distribution stratified by the cluster indicators that were estimated from the spatial identification probabilities:

$$\text{logit}(\varphi_{it}, \gamma_{it}) = \text{logit}(\mu^{\varphi,\, \gamma}) + \varepsilon_{c,t}^{\varphi\, \gamma}$$

$$\varepsilon_{ct}^{\varphi,\, \lambda} \sim \text{N}(0, \sigma^{\varphi,\, \lambda})$$

Therefore the model did not estimate clusters of whales with similar survival or recruitment histories, but rather estimated survival and recruitment for the clusters with similar spatial identification probabilities. Uniform (0,1) prior distributions were placed on each of the mean probabilities $\mu^{\varphi\, \gamma}$ and a Uniform (0,10) was adopted for the standard deviations $\sigma^{\varphi\, \gamma}$ to allow annual percentages of the means to emerge, but also enabling “borrowing strength” across each set of parameters to allow for more precise estimates in sparse data years (Chapter 3).

Derived quantities

Annual estimates of abundance for each cluster and overall were therefore simply derived as a function of the latent state variables x_{it} and z_i indicating how many individuals from each cluster were alive in each year.

$$N_{ct} = \sum_{i=1}^{n+M} x_{it} (z_i = c)$$

$$N_t^{Tot} = \sum_{c=1}^{C} N_{ct}$$

Rescaling for non-distinctive individuals

Even with the use of high-quality photographs, there remained some individuals that were not judged to be distinctive (Figure 2). Reliable identification histories over time could not be constructed for such individuals, so they were not included in mark-recapture analysis. However, it was necessary to have some estimate of the proportion of these individuals in the population to re-scale the mark-recapture estimates upward to account for these non-distinctive animals. From the high-quality photographs, all individuals could be distinguished from other group members in a given encounter, based on subtle differences in acquired markings or inherent differences in pigmentation or fin shape (e.g. Wilson *et al.*1999; Durban *et al.* 2010). Therefore, even though some individuals could not be matched over time, we could produce an estimate of this non-distinctive proportion of the population in each year from the number of individuals with and without distinctive markings documented from high quality photographs in each encounter, averaged over each year (e.g. Durban *et al.*2010). Specifically, the number of distinctly marked individuals was treated as a binomial sample from the total individuals documented from photographs in each encounter, where the binomial probability represented the proportion of distinctive individuals (τ_t). Annual variation in this distinctive proportion was specified by modeling τ as a function of a mean and time-varying random effects term:

$$\text{logit}(\tau_t) = \text{logit}(\mu^{\tau}) + \varepsilon_t^{\tau}$$
$$\varepsilon_t^{\tau} \sim \text{N}(0, \sigma^{\tau})$$

A Uniform (0,1) prior distribution was placed on each of the overall mean distinctive proportion μ^{τ} and a Uniform (0,10) prior distribution was adopted for standard deviations σ^{τ} to allow annual differences if supported by the data and the borrowing strength to provide estimates in years with only sparse data. The mark-recapture and mark-rescaling components were linked to form a single probability model, by defining the overall abundance to equal $P_t^{Tot} = N_t^{Tot} / \tau_t$.

We used the WINBUGS software (Lunn *et al.*2000) to implement Markov Chain Monte Carlo (MCMC) sampling to estimate the posterior distribution for unknown parameters, missing data and derived quantities in the model. We based inference on 30,000 MCMC iterations after discarding a “burn-in” of 10,000 iterations prior to convergence of three different chains (Brooks and Gelman 1998; see Chapter 3). We also used MCMC sampling to assess the adequacy of model fit, adopting a posterior predictive approach (Gelman *et al*. 1996; Chapter 3). We obtained MCMC samples of predicted data from the posterior distributions of model parameters and calculated a discrepancy measure, *D*, for both the predicted Y^{new} and observed data *Y*. The discrepancy measures were stratified across years in order to provide annual measures of model fit:

$$D(Y)_t = \sum_{i=1}^{n} \sum_{j=1}^{3} \left| y_{ijt} - (p_{ijt} x_{ijt}) \right|$$

$$D(Y^{new})_t = \sum_{i=1}^{n} \sum_{j=1}^{3} \left| y^{new}{}_{ijt} - (p_{ijt} x_{ijt}) \right|$$

A posterior predictive p-value was calculated as the percentage of MCMC draws for which $D(Y^{new})_t$ exceeded $D(Y)_t$. Values close to 0.5 indicated that the realized discrepancy of the data was very similar to the model's predictions and values close to zero or one implied a poor fit (Gelman *et al*. 1996).

Figure 2. Photographs showing examples of one high quality, non-distinctive whale (a) and three high quality, distinctive whales (b-d) from "resident" type fish-eating killer whales around the Aleutians Islands.

Photogrammetric analysis: Distinguishing adult males

Killer whales are sexually dimorphic (Dahlheim and Heyning 1999), with males growing dorsal fins that can be at least two to three times the height of females' fins by adult age (Olesiuk *et al.*1990; Durban and Parson 2006). We therefore used this feature to distinguish photographed whales as adult males, following Olesiuk *et al.* (1990). Photo-identification images of all identified individuals (distinctive and non-distinctive from each encounter) were displayed on a 22-inch (56 cm) high resolution (4288 by 2848 pixels) flat panel monitor and were viewed through ACDSee photo manager (www.acdsee.com). Photographs were re-examined and only images where the whale was surfacing parallel to the camera were included in photogrammetric analysis. Corel Paint Shop Pro X2 (http://www.corel.com) was used to append a series of reference points on each image to define the height and width of the fin (Figure 3, bottom, following Olesiuk *et al.*1990; Durban and Parsons 2006) and the freely available software Image J (http://rsbweb.nih.gov/ij) was used to measure (in pixels) both the height and width of the dorsal fin. A height to width ratio (HWR= H/W) was then calculated for each whale, and all associated measurement data were entered into a Microsoft Access relational database and linked to previously imported image and encounter data. For consistency, an individual was defined as an adult male if the dorsal fin height to width ratio was equal to or greater than 1.4 (following Olesiuk *et al.*1990).

Figure 3 (top). A photograph showing the dorsal fin of an adult male killer whale with two projected green laser dots of known (10cm) separation laser dots (Durban and Parsons 2006). **(bottom)** A photograph showing the inserted lines used to measure dorsal fin width (W), defined as the distance between the anterior and posterior insertion of the dorsal fin (solid red dots), defined by Olesiuk *et al.*(1990) to be the mid-point of the curve between two intersecting reference lines (drawn to follow the main axes of the dorsal fin and adjacent back), dorsal fin height (H) defined as the distance from the dorsal fin base to the maximum height of the dorsal fin, and blowhole to dorsal fin (BHDF), defined as the distance between the center blowhole and the anterior insertion of the dorsal fins (following Olesiuk *et al.*1990; Durban and Parsons 2006). Measurements were scaled to actual size based on the known separation between the two projected lasers dots (L) (Durban and Parsons 2006).

For comparison, height to width ratios were also calculated in a similar way to assess the proportion of adult males in both the SR killer whale population, using images in a photo-identification catalog current through 2008 (Ford *et al.*2000; K. C. Balcomb, unpublished data) and the GOA population, using a catalog current through 2006 (Matkin *et al.*1999; C. O. Matkin, unpublished data). These catalog versions were used because they matched the years when absolute estimates of whale size were also made for these two populations, respectively (see below: "*Photogrammetric analysis: Absolute Size*"). Because the AI population was not completely photographed, unlike the reference populations, we constructed a simple Bayesian probability model (see Chapter 2) to estimate the proportion of males in this population and assess the difference between the proportion of adult males in the AI population and both the GOA and SR populations. Specifically, we treated the number of adult males in each AI encounter as a binomial sample of all whales (distinct and non-distinct) identified from high-quality photographs from each encounter, and assigned a uniform prior (0,1) distribution on the common binomial proportion, which represented a probability distribution for the proportion of males in the population. We used MCMC to update this prior distribution based on the identification data, and evaluated the probability that the proportion of adult males in the AI population was greater than the proportions of adult males from each of the reference populations by simply evaluating the proportion of the MCMC iterations (and therefore the proportion of the probability mass in the distribution) for which this was the case.

Photogrammetric analysis: Absolute size

We used an established method of laser photogrammetry (Durban and Parsons 2006) to estimate body size for adult males (as defined above), and compare between populations. Two green laser pointers (model# BTG10; www.z-bolt.com) were mounted onto the lens tripod mount of a digital SLR camera to project laser beams of a fixed and known (10cm) separation onto whales during photo-identification surveys of the AI population from 2006-2010, the GOA population from 2006-2007 (Figure 3, top; survey methods in Matkin *et al.*2008) and the SR population from 2004-2008 (survey methods of Durban and Parsons 2006). Again, laser-photogrammetry images were displayed on a 22-inch (56 cm) high resolution flat panel monitor and were viewed through ACDSee photo manager (www.acdsee.com).

Photographs were re-examined for measurement purposes and only images with both laser dots visible on whales that were surfacing parallel to the camera were included in the size analysis. Corel Paint Shop Pro X2 (http://www.corel.com) was used to draw a series of reference lines to define the dorsal fin (Olesiuk *et al.*1990) and the software Image J http://rsbweb.nih.gov/ij) was used to measure (in pixels) the distance between the two projected laser dots, the distance between the center of the blowhole and anterior insertion of the dorsal fin, and both the height and width of the dorsal fin (Figure 3). Following Durban and Parsons (2006), measured pixels were converted to actual size measurements using a scale factor derived from the pixel measurement of the known 10cm separation distance between the two projected laser dots. The fin metrics and the blowhole to dorsal fin measurements were not necessarily derived from the same photograph. Once the dorsal fin had been measured from projected laser dots, other photographs of the same whale, in the same encounter, that displayed both the dorsal fin and the back of the whale, could be used to derive the distance between the blowhole and dorsal fin, using the dorsal fin as a scale of known size. Where multiple measurements existed for the same whale, the largest measurement was taken as the least biased due to angle sensitivities (following Durban and Parsons 2006).

Age determination

When possible, skin and blubber samples were collected during encounters with whales around the Aleutian Islands using remote biopsy techniques (Barrett-Lennard *et al.*1996). Most of these samples were obtained from ostensibly larger adult males that were slower and larger targets, and the outer blubber layer of these samples was then used to estimate age of these whales through the ratios of fatty acids (Herman *et al.*2008). This approach has been shown to predict the ages of North Pacific "resident" type fish-eating killer whales, including those in Alaskan coastal waters, with good precision (standard deviation of residuals < 4 years). For comparison, ages for individual males from both the GOA and SR populations were derived as known from long-term longitudinal birth and sighting histories (Olesiuk *et al.*1990; Matkin *et al.*1999; Ford *et al.*2000; Chapter 4; C. O. Matkin, unpublished data). The age estimates prior to the start of the longitudinal photo-identification studies were based on the size development of the dorsal fins for males and the age of the oldest offspring for females as described by Olesiuk *et al.* (1990, 2005). Sex was determined by visual observation of genital anatomy and pigmentation (e.g. Ford *et al.*2000), by the development of sexual secondary characteristics in males (particularly the dorsal fin), or by the birth of a calf in females (Matkin *et al.*1999; Ford *et al.*2000; Chapter 4; K. C. Balcomb, unpublished data).

Age was examined relative to dorsal fin growth by integrating the HW ratio analysis (above: "*Photogrammetric analysis: Distinguishing Adult* males") with age estimates for whales that were both photographically identified and biopsy sampled for age estimation (or known for SR or GOA). To quantify this relationship, we fit a generalized logistic growth curve (Richards 1959) to the ratio-at-age data for all males with age estimates. This curve, describing the HW ratio at Age t (HWt), is given by the equation:

$$HWt = A\,[1 - b \times \exp(-ct)]M \quad (1)$$

where A is asymptotic HW ratio, t is age in years, b and c are free parameters that adjust the slope and inflection point of the curve, and M describes the relative position of the inflection point relative to the asymptote. This curve is a generalization of the classical growth curves that are commonly used, such as the Gompertz curve (e.g. Read *et al.*1993; Webster *et al.*2010), but with increased flexibility because the point of inflection is not in a fixed proportion to the asymptote (instead, its position depends on the parameter M) (e.g. Chapter 4). We were particularly interested in deriving from the model the average age at which individuals obtained adult status (HW ratio = 1.4). Model fitting was accomplished using the method of non-linear least squares implemented using the R statistical package (www.r-project.org)(R Development Core Team 2011).

Results

Mark-recapture sample

Photographs were taken during 138 encounters with “resident” type fish-eating killer whales in areas 4, 5 and 8 of our study area during the summer sampling period (May-September), resulting in 1329 unique identifications of 872 distinct individuals. These groups were designated as the “resident” type based on morphological features, and assignments were corroborated by genetics in 78 cases, representing total agreement where genetic samples existed (Zerbini *et al.*2007; Matkin *et al.*2007; Durban *et al.*2010; Chapter 5). After constraints for photographic quality and individual distinctiveness were applied, photographs were useable from 124 encounters, with 1169 unique identifications of 807 individuals

(Figure 1), and these were included in the mark-recapture analysis. Coverage was distributed across years and areas, but there was notably higher coverage in some areas and years (Table 1). For example, data were available from 3 different surveys in 2002, covering four different months. Area 4 had the most encounters (62), with encounters occurring in all survey years; Area 5 was surveyed in 7 years, resulting in 48 encounters, and area 8 was surveyed in 4 years, resulting in 14 encounters (Table 1). The restricted data represented 1011 non-zero entries in the whale-by-year status (x). Out-of sample re-sightings added 98 additional identifications of these same individuals, and 518 additional annual records that were imputed as "alive" (x_{it}=1) for years when whales were not identified between years of repeated identifications. The number of distinctive individuals that were identified in each annual sampling period varied across years (range = 5 - 203) (Table 1). Most individuals (n=609) were only identified in a single year, but sighting histories for whales identified in more than one year demonstrated site fidelity for the central and eastern Aleutians (median= 5 year sighting history, range = 2 - 10 year sighting history) (Figure 4). Evidence of an open population with regular recruitment is shown through a cumulative increase in the number of distinct individuals identified throughout the study period (Figure 5). The number of distinct individuals was highest in area 4 (400), then area 5 (383), with far fewer (66) individuals being seen in area 8. Most individuals were seen in a single area (n= 765), but there were 21 individuals seen in both areas 4 and 5, and 21 seen in areas 4 and 8: it is noteworthy that approximately one third of all individuals seen in area 8 were also seen in area 4; and no individuals were seen in both area 5 and 8.

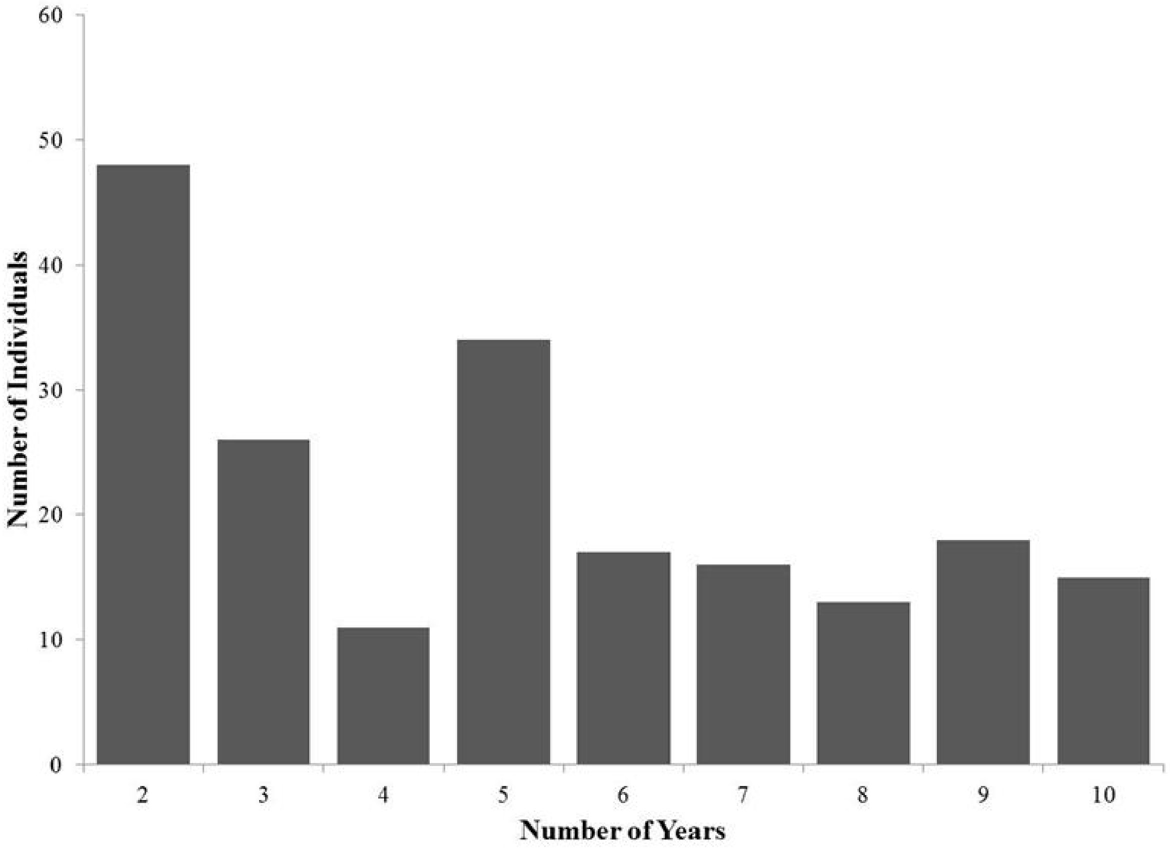

Figure 4. Frequency plot showing sighting histories (the number of years between first and last sightings) for all distinctively marked resident type fish-eating killer whales identified from high quality photographs in more than one annual sampling interval from 2001-2010.

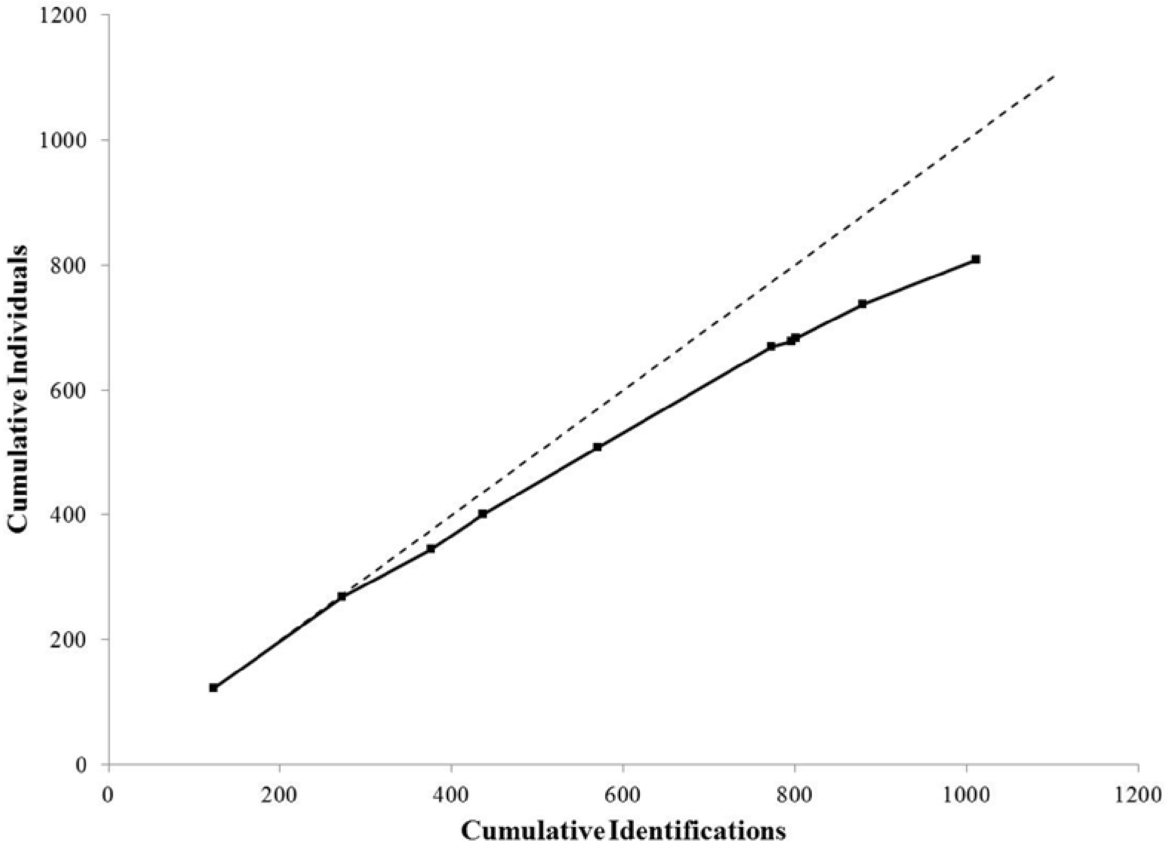

Figure 5. Discovery curve of the total number of distinctly marked individual resident type fish-eating killer whales identified in the central Aleutians from the growing number of cumulative high quality identifications made in summer sampling intervals each year between 2001 and 2010. The broken diagonal line represents the reference trend if no photographic recaptures had occurred.

Up to 10 different clusters were sampled during the MCMC iterations fitting the mark-recapture models, reflecting uncertainty about the number of clusters and cluster allocation of individuals. However, whales were only assigned to two clusters with maximum probability, with 442 of the observed individuals assigned to cluster 1 and 365 assigned to cluster 2. Cluster 1 had an above average probability of capture (positive θ values) in area 4 and area 8, and lower than average (negative θ values) capture effects in area 5. In contrast, cluster 2 had close to average probability of capture in area 5 (θ posterior median = 0.09), but notably lower than average (negative) capture effects in areas 4 and 8 (Table 2). In general, capture probabilities in each area were very low (Table 2), implying a large estimated abundance.

There was generally good agreement between the data and the model's predictions, with the posterior predictive p-value ranging between 0.34 and 0.73 for all years except the first year in 2001, indicating that the model was a plausible fit for the data (Gelman *et al.* 1996). The posterior predictive p-value for 2001 was only 0.09, implying relative poor fit to this initial year of data. Annual abundance of distinctive individuals, N_t^{Tot}, from the remaining years ranged from a high of 1326 (95% HPDI = 743-2415) to low of 530 (95% HPDI = 363-1144). Estimates of the proportion of the population that were distinctive were consistent across years, averaging around 0.67, and ranging from a low of 0.59 (95% HPDI = 0.53- 0.64) to a high of 0.73 (95% HPDI = 0.66-0.80). As a result, the rescaled estimates of total abundance, P_t^{Tot} , ranged from a maximum of 2260 (95% HPDI = 1255-4112) in year 2002 to a minimum of 732 (95% HPDI = 493-1561) in year 2010, displaying a marked drop in annual abundance over the time period (Figure 6). However, much of these abundance changes may have been due to permanent emigration, as estimates of apparent survival for the population were relatively low (μ^{φ} posterior median = 0.87, HPDI = 0.73-0.96), and new animals were not recruited as quickly as they were lost to the monitored population (median per capita recruitment, $\sum_{i=1}^{n+M}(1-x_{it})x_{it+1}/N_t^{Tot}$ =0.08, 95% HDPI = 0.06-0.18). It is notable that the highest abundance estimate came in 2002 when we had the most effective survey coverage of all areas, with 3 different surveys spanning 4 different months.

Table 2. Table showing the estimated departure effects θ_{cj} (positive or negative) from the overall average capture probability ($\mu_j^{\,p}$) in each area j for each cluster c = 1, 2. Estimates are presented as posterior medians (95% HPDI).

	Area 4	Area 5	Area 8
$\theta_{1,j}$	0.77 (-3.14-1.88)	-2.49 (-4.65-0.78)	1 (-3.20-2.29)
$\theta_{2,j}$	-2.03 (-5.79-1.66)	0.09 (-2.13-2.17)	-1.61 (-9.343-1.66)
μ^p	0.06 (0-0.41)	0.02 (0-0.26)	0.001 (0-0.01)

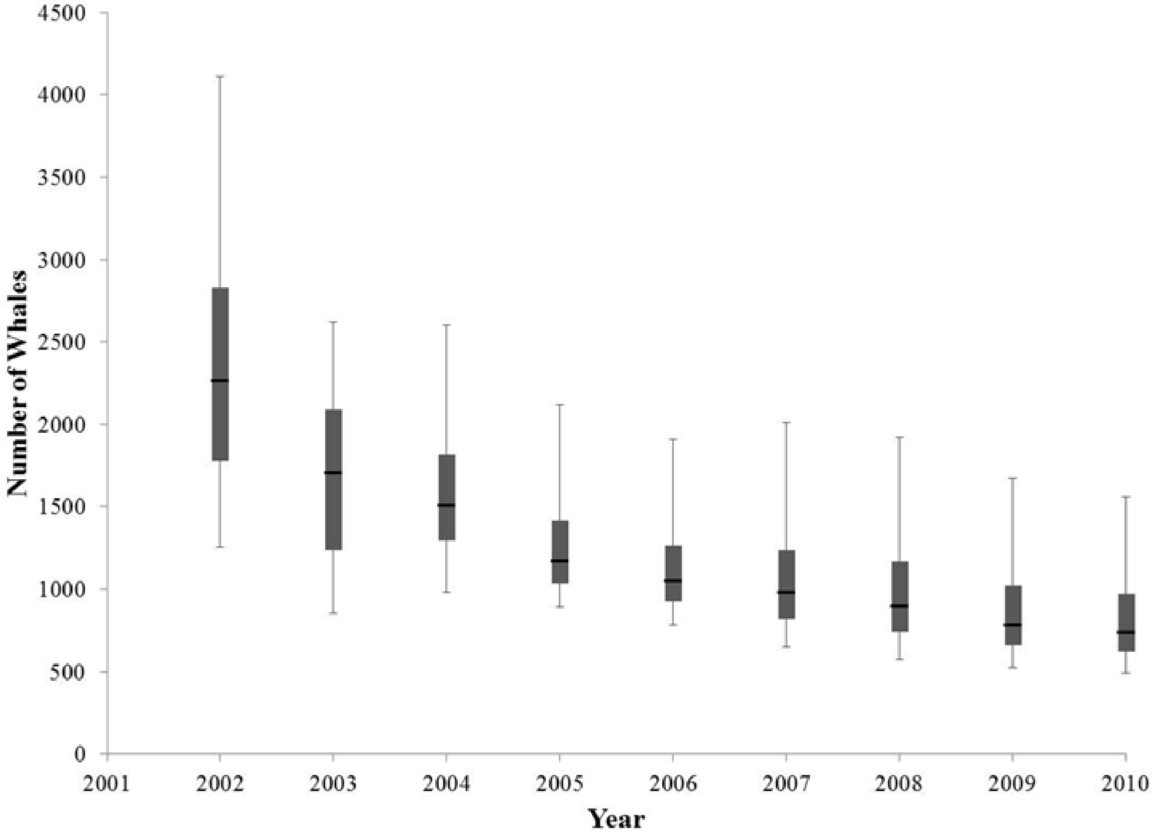

Figure 6. Annual estimate of total abundance, P_t^{Tot}, of killer whales using the study area (Figure 1) in each annual May-September sampling interval, *t.* Estimates are presented as posterior medians (horizontal line), with 75% (gray bars) and 95% (vertical lines) highest posterior density intervals.

Composition of adult males

A total of 368 individual whales from the Aleutian population were classified as adult males based on their height to width ratio equaling or exceeding 1.4. Of these whales, 324 were distinctive, representing 37% of all distinctive whales. However, to control for adult males possibly being more distinctively marked than other population classes, we estimated their proportion from all distinctive and non-distinctive whales. Because non-distinctive whales could only be distinguished within each encounter, we calculated the proportion of all whales identified from high quality photographs that were adult males in each encounter (median = 0.29, range =0.25-0.34). For the GOA population, a total of 48 individuals could be classified as males, comprising 24% of the population comprising regularly monitored pods (AB, AD, AE, AF, AG, AI, AJ, AK AN; Matkin *et al.*1999; Matkin *et al*. 2008). For the SR population, a total of 14 individuals could be classified as adult males, comprising 18% of the population. Using a Bayesian probability test, we estimated that these differences were highly significant, with the probability of l that the proportion of adult males in the AI population was greater than that in both the GOA and SR populations.

Size of adult males

Size data were available from 26 adult males with laser-metric images from the AI population, 10 from the GOA population and 11 from the SR population. This reflects the greater available pool of adult males in the AI population (above). There was no significant difference between the median blowhole to dorsal fin lengths (Kruskall-Wallis = 4.1, df = 2, $p = 0.1287$), with medians of 187 cm, 172 cm and 199 cm for males from the AI, GOA and SR populations respectively (Figure 7). However, despite the larger available pool of males, it is notable that the largest (longest) adult males were found in the AI population, with estimated blowhole to dorsal fin lengths up to 292cm. Similarly, the median dorsal fin height was highest from the AI males (151cm) compared to both the GOA (131cm) and SR (138cm) (Figure 8), and this difference has some level of statistical support at the $p<0.1$ level (Kruskall-Wallis = 5.1838, df = 2, p = 0.0749). Once again, it was notable that the tallest fins were found in AI males, with fin heights up to 225 cm.

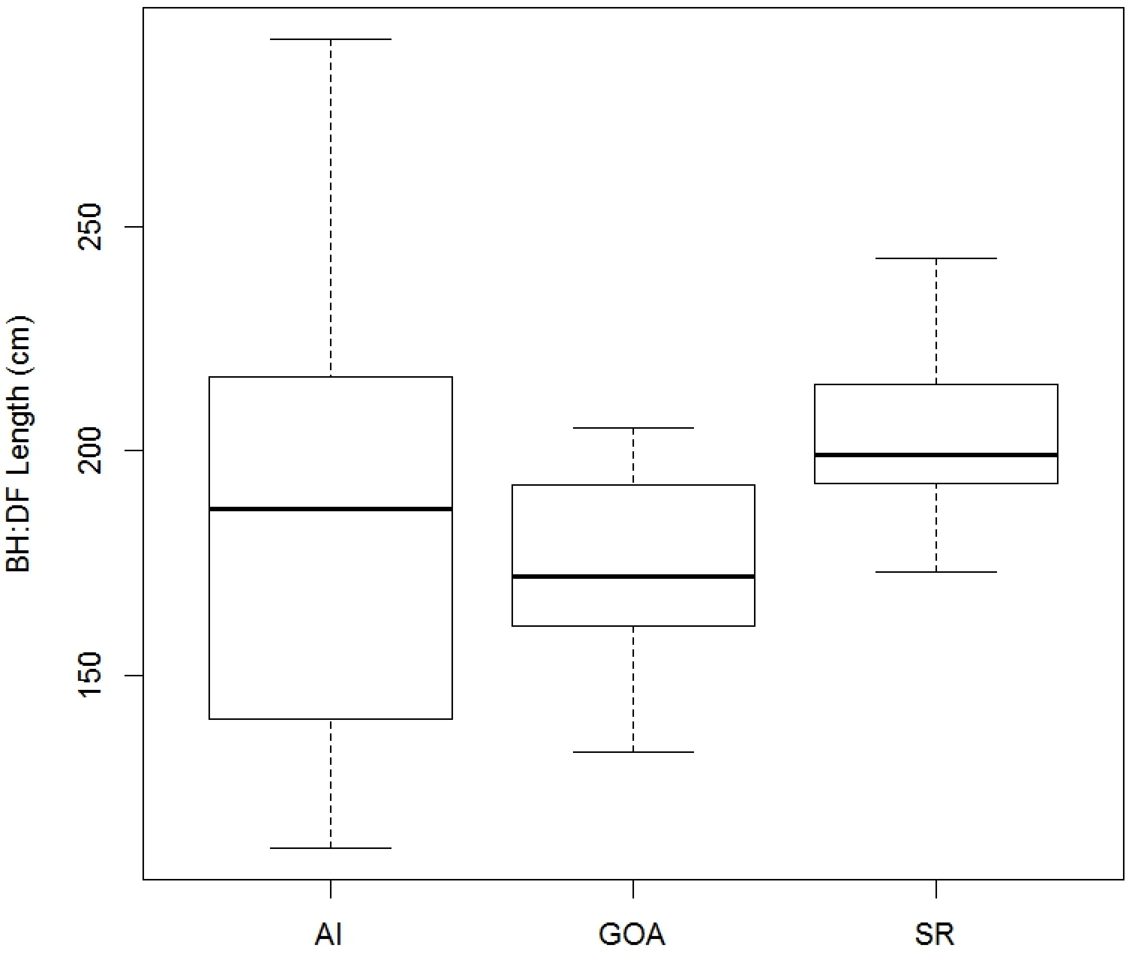

Figure 7. A boxplot showing the estimated blowhole to dorsal fin length (cm) for "resident" type fish-eating adult male killer whales (dorsal fin height to width ratio (HWR) >/=1.4) from the Aleutian (AI), Gulf of Alaska (GOA) and Southern Resident (SR) populations. Vertical dashed lines represent the extent of the distribution, the boxes represent the central 75% interquartile range and the horizontal lines represent the posterior medians.

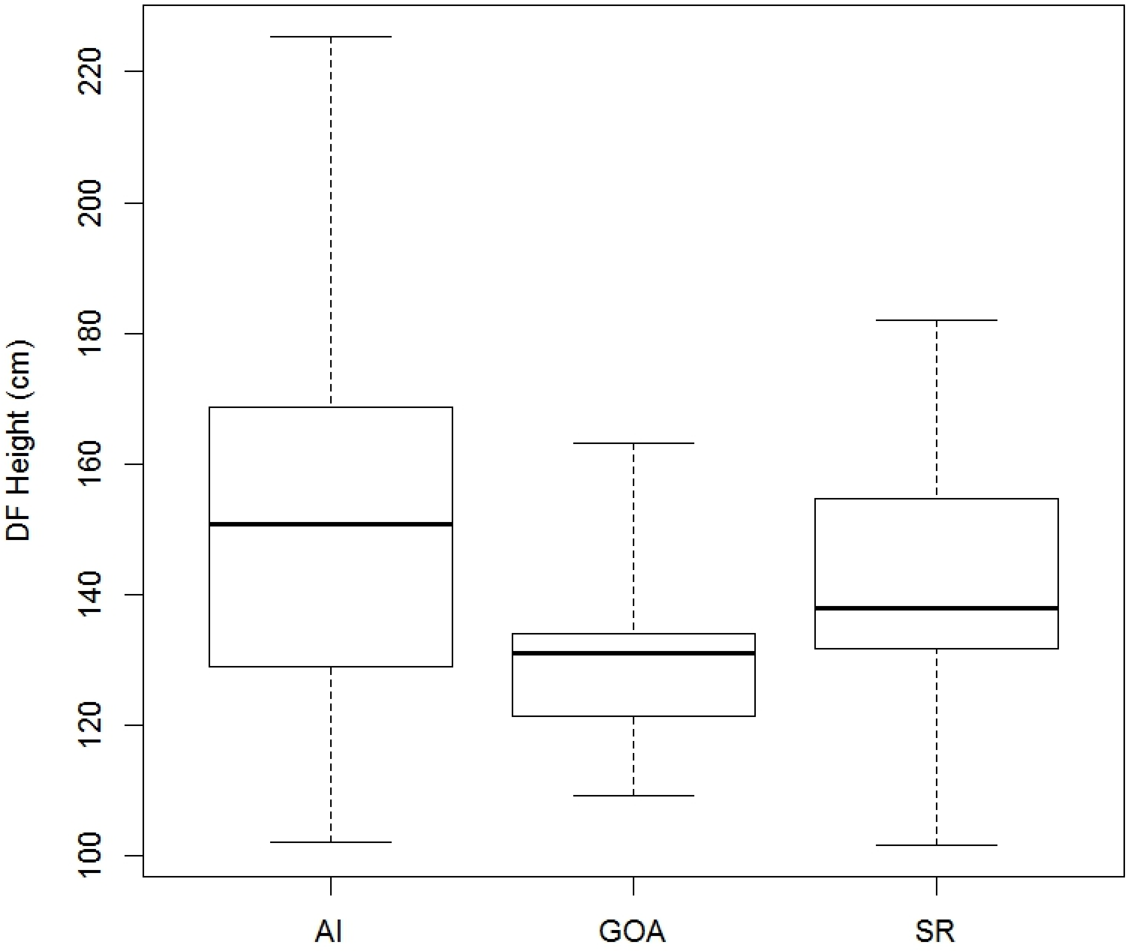

Figure 8. A boxplot showing the estimated dorsal fin height (cm) for "resident" type fish-eating adult male killer whales (dorsal fin height to width ratio (HWR) >/=1.4) from the Aleutian (AI), Gulf of Alaska (GOA) and Southern Resident (SR) populations. Vertical dashed lines represent the extent of the distribution, the boxes represent the central 75% interquartile range and the horizontal lines represent the posterior medians.

Age of adult males

Both HW ratios from photographs and age estimates from blubber biopsies were available from 20 males in the AI, and these could be compared to known ages from longitudinal sighting records for 48 GOA males and 14 SR males that also had HW ratios indicative of adult males. The median age for adult males (HW ratio of 1.4 or greater) was 27 (range = 16-62) for the AI population, compared to 23 (range = 12-42) for the GOA population and 19.5 (range = 16.5 to 57.5) for the SR population (Figures 9-11). The SR males were comprised mostly of young (</=20 years) adult males (64%), with 86% of all adult males aged less than 31 and only one male older than 51 (Figure 10). The GOA population comprised an equal proportion of young (</=20 years) and intermediate (21-30 years) adult males (40%), with 80% of all adult males aged less than 31 and no males greater than 51 (Figure 11). In contrast, the AI population had the highest proportion of intermediate (21-30 years) adult males (45%), with only 60% of males aged less than 31 and 85% of adult males aged greater than 20 (Figure 9). Additionally, there were 3 whales (15%) with ages greater than 51, including 1 whale estimated to be greater than 60 years old.

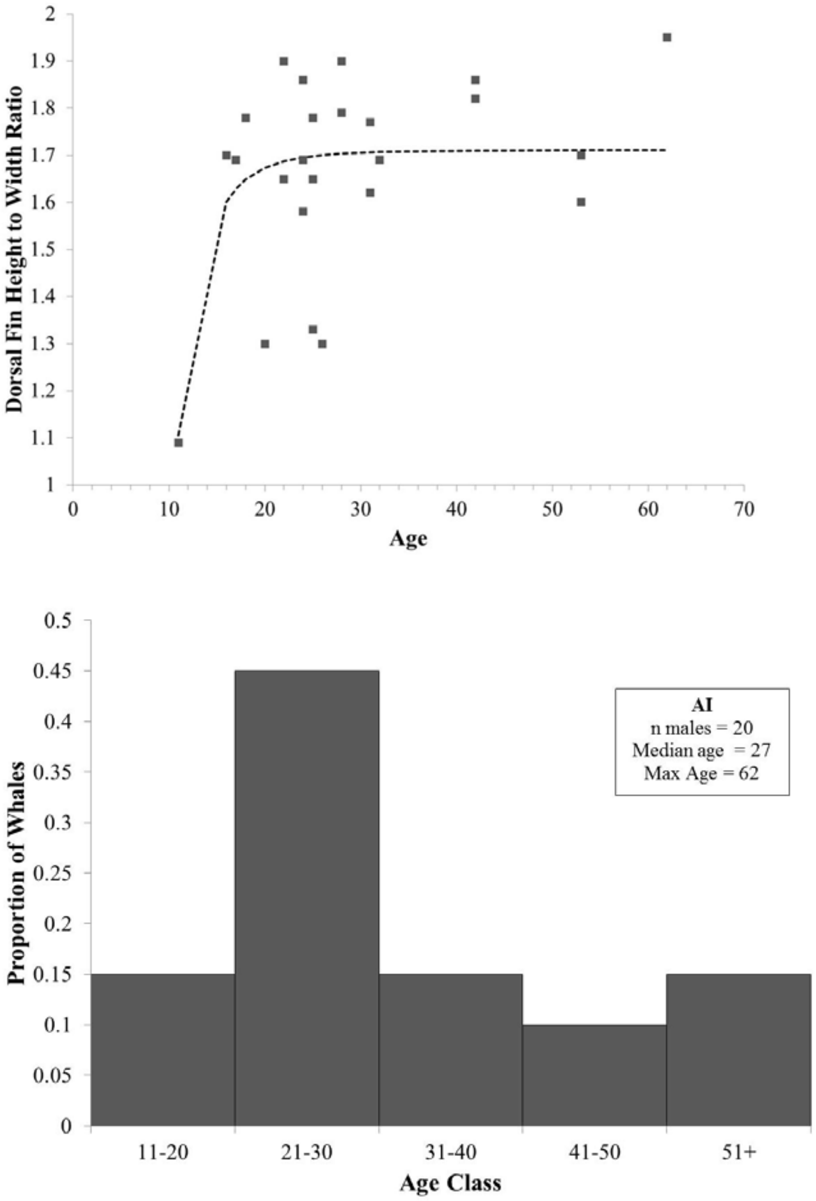

Figure 9 (top): Estimate of maximum dorsal fin height for known males from the Aleutian “resident” type fish-eating killer whales plotted against estimated ages. Age and sex were estimated as per Herman *et al.* (2008). Dashed line represents a generalized logistic growth curve fit and dotted line represents the reference point of dorsal fin height to width ratio >/= 1.4, used to define adult males (as per Olesiuk *et al.*1990). **(bottom):** Proportion of males (dorsal fin height to width ratio >/= 1.4) in each of five decadal age classes, for “resident” type fishing-eating killer whales from the Aleutian population.

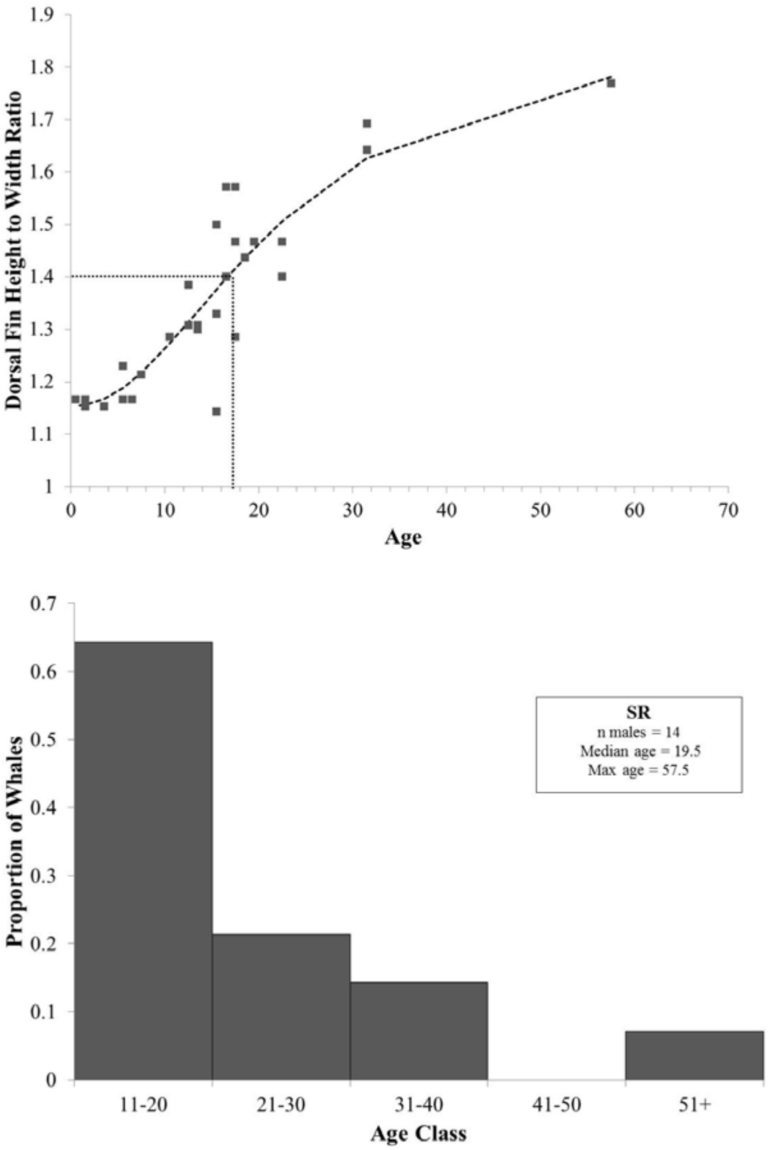

Figure 10 (top). Estimate of maximum dorsal fin height for known males from the Southern Resident (SR) population of "resident" type fish-eating killer whales plotted against observed or estimated ages. Age and sex were estimated as per Ford *et al.* (2000); Chapter 4; K.C. Balcomb, (unpublished data), from long-term longitudinal sighting histories and observations. Dashed line represents a generalized logistic growth curve fit and dotted line represents the reference point of dorsal fin height to width ratio >/= 1.4, used to define adult males (as per Olesiuk *et al.*1990). **(bottom):** Proportion of males (dorsal fin height to width ratio >/= 1.4) in each of five decadal age classes, for "resident" type fishing-eating killer whales from the Southern Resident population.

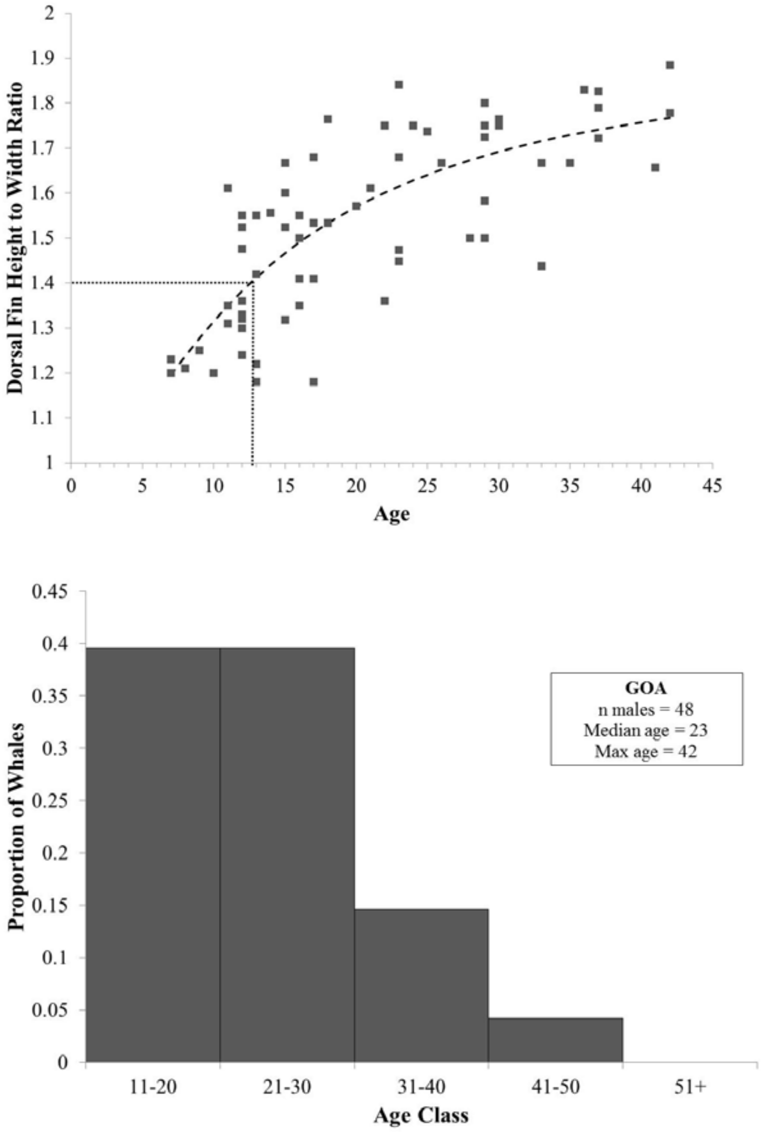

Figure 11 (top): Estimate of maximum dorsal fin height for known males from the Gulf of Alaska population of “resident” type fish-eating killer whales plotted against observed or estimated ages. Age and sex were estimated as per Matkin *et al* .(1999), Matkin (unpublished data), from long-term longitudinal sighting histories and observations. Dashed line represents a generalized logistic growth curve fit and dotted line represents the reference point of dorsal fin height to width ratio >/= 1.4, used to define adult males (as per Olesiuk *et al.*1990). **(bottom):** Proportion of males (dorsal fin height to width ratio >/= 1.4) in each of five decadal age classes, for “resident” type fishing-eating killer whales from the Gulf of Alaska population.

For the Aleutian (AI) population, estimates of dorsal fin height to width ratio (HWR) showed an asymptotic relationship with age, illustrating maturity of this sexual secondary characteristic (tall fins) through the late teens (Figure 9). The fitted growth curve model estimated that males in the AI population reached an HWR of at least 1.4 (adult status) at an average age estimate of approximately 13 years (Figure 9). Similarly, males in the GOA population reached HWR of at least 1.4 at the same estimated age of 13, but notably estimates of HWR did not show an asymptotic relationship with age, but appeared to show continual growth in fin height in dorsal fin throughout life (Figure 11). Males in the SR population showed a notable difference, reaching a HWR of at least 1.4 at the later estimated age of around 17 (Figure 10), and also did not display an asymptotic relationship of fin growth with age. However, the sample was limited with only one male aged greater than 31.5 years.

Discussion

Killer whales are known to be most abundant in higher latitudes (Forney and Wade 2006) with perhaps the highest density represented by “resident” type fish-eating killer whales inhabiting the productive waters around the Aleutian Islands and Bering Sea (Waite *et al.*2002; Sinclair *et al.*2005; Forney and Wade 2006; Zerbini *et al.*2007). However, previous abundance estimates for this region have been based on distance sampling methods from line-transect surveys, which are relatively imprecise and limited in their inference. In contrast, we took advantage of established methods of sampling individuals using natural markings (e.g. Bigg 1982) to estimate abundance, spatial structure and evaluate demographic parameters of these Aleutian “resident” type fish-eating killer whales using photographic mark-recapture approaches (e.g. Durban *et al.*2010). Our abundances estimates – up to 2260 (95%

HPDI=1255-4112) individuals using the area in a given summer (May-September) interval - were more than twice as high as previous estimates for the same area from line-transect surveys (991, 95% CI = 279-2585; Zerbini *et al.* 2007). This likely reflects movement of whales beyond the study area (Chapter 5), with mark-recapture surveys at multiple times within and between years affording greater opportunity to sample more individuals, therefore providing more complete population coverage compared to the instantaneous estimate of abundance possible from line-transect surveys (e.g. Zerbini *et al.*2007; Durban *et al.*2010). Furthermore, estimates of two distinct clusters of whales with differing area-specific capture probabilities indicated significant spatial structuring within this population: one cluster was documented in the coastal waters around the central Aleutian Islands, ranging westwards from 170^{o}W to at least Amchitka Pass at 180^{o}, distinct from a second cluster identified largely around the eastern Aleutian Islands (160^{o}W-170^{o}W) and adjacent shelf edge of the SE Bering Sea, ranging at least up to the Pribilof Islands (57^{o}N). This supports previous analyses (Chapter 5) and ongoing genetic investigations (Parsons *et al.* submitted) that there is significant structuring within this “Eastern North Pacific Alaska Resident” stock (Allen and Angliss 2012), with delineations perhaps at the population level.

Although we made inference from an open population model that was appropriate for our 10-year dataset, there was limited power to assess demographic trends due to the relatively sparse recapture data (most individuals only seen in a single year). Estimates of survival and per capita recruitment were lower and higher, respectively, than would be expected through deaths and births, and are likely the result of apparent immigration and permanent emigration events due again to animals ranging beyond the effective study area (Chapter 3). Furthermore, relatively sparse and geographically limited survey effort in some years likely combined with individual movements and had the effect of decreasing the extent of the monitored population. It is therefore not surprising that the annual intervals with the highest abundance were at the start of the time series in years with more survey coverage, in terms of the number of surveys, months and areas covered. However, we cannot discount that the apparent decline in abundance in recent years, although consistent with decreasing survey coverage, may reflect a decreasing abundance of “resident” type fish-eating type killer whales within the study area. There are anecdotal reports from fishermen of a dramatic decrease in killer whale sightings in recent years in the coastal waters near Dutch Harbor in the eastern Aleutian Islands, a hot spot at the start of or decadal study. This matches with reports of whales leaving the eastern Aleutians and being photographically documented to follow long-line fishing vessels northwards along the Bering Sea shelf edge beyond the Pribilof Islands (Megan Peterson, personal communication).

Due to our lack of power and limited time series, we adopted another approach to make inference about demographic status; namely by comparing the composition of adult males to observations from well-studied “reference” populations of “resident” type fish-eating killer whales in the eastern North Pacific with contrasting population dynamics. Because killer whales are sexually dimorphic (Dahlheim and Heyning 1999), larger adult males with their conspicuously tall dorsal fins are a component of the population that can be relatively easily sampled and monitored (Olesiuk *et al.*1990). Furthermore, adult and maturing sub-adult male killer whales suffer relatively high mortality during periods of food shortages and population decreases in well-studied populations (Olesiuk *et al.*2005; Ward *et al.*2010), presumably because of the higher caloric requirements associated with attaining and maintaining a larger body size and exaggerated features (Noren 2011). Increased caloric costs for the larger sex in dimorphic species can lead to decreased survival in food-limited environments (Clutton-Brock *et al.*1985, 1987; Promislow 1992; Toigo and Gaillard 2003; Issac 2005), contrasted by a high proportion of adult males following a series of years in which the population has experienced favorable feeding conditions (Kucera 1991; Catchpole *et al.*2004). Therefore, both the number and proportion of adult male killer whales can give a window into past feeding conditions and resultant population dynamics (Olesiuk *et al.*2005; Ford *et al.*2010). This is particularly true given that long-term studies have shown extreme philopatry to natal matrilines in populations of “resident” type fish-eating killer whales, including the GOA (Matkin *et al*. 1999) and SR (Olesiuk *et al*. 1990) reference populations. Therefore, we assumed the relative proportions of different age classes also represented the result of mortality in the AI populations.

In this context, Aleutian “resident” type fish-eating killer whales display signs of good demographic status relative to our two reference populations, most notably in comprising a higher estimated proportion (29%) of adult males than either the SR or GOA population (18% and 24 % respectively). The GOA population has increased at an average rate of 3.2% in recent decades (1984-2008; Matkin *et al.*2008), compared to the SR population with an average population increase of 1.1% over four decades, with periods of prolonged decline coinciding with reduced food availability (Ford *et al.* 2010). Olesiuk *et al.* (2005) provided a useful within-population comparison from the “northern resident” killer whale population that frequents the coastal waters of British Columbia: this population comprised 22% adult males during a period of population increase (2.5% growth, 1973-1996), but a lower proportion (18%) represented by adult males during a subsequent period of zero net population growth from (1997 to 2004). As further evidence of relatively high and long-term survival of adult males in the Aleutians, the males in this population were typically older than those in either of the two reference populations, with 40% of adult males greater than 30 years old, compared to just 14% and 20% in the SR and GOA populations respectively. Based on this evidence, we suggest the Aleutian population has likely experienced a prolonged period of stable or increasing abundance over recent decades, and has likely not experienced periods of food shortage.

Individual size has been suggested to be a proxy of fitness (Clutton-Brock *et al.*1985, 1987), and therefore we also examined size and size-at-age of adult males as a demographic index. Although there was no significant difference between the median sizes (proxied by blowhole to dorsal fin lengths) of adult males between the AI, GOA and SR populations, the largest males were documented around the Aleutian Islands (maximum blowhole to dorsal fin length = 292cm). Furthermore, AI males did have notably taller dorsal fins than either the GOA or SR whales, up to a maximum dorsal fin height of 225cm. Similarly, males in the AI population could also be classified as adult, based on sexually dimorphic fin growth (Olesiuk *et al.*1990; Durban and Parsons 2006) at an earlier age (~13) than those in the SR population (~17 years), and at a comparable age to those in the GOA population. Interestingly, growth of the dorsal fin only showed an asymptotic relationship with age in the AI males, illustrating maturity of this sexual secondary characteristic (tall fins) through the late teens; but appeared to show continual growth throughout life for GOA and SR males. This is notable because a separate analysis has demonstrated asymptotic growth of body length with age in SR males (Chapter 4), implying that additional resources may only be apportioned to the development of secondary sexual characteristics once body size development has been achieved. Because the development of secondary sexual characteristics incurs caloric costs (Noren 2011), this may be evidence that food availability in SRs and GOAs may be constraining the full development of secondary sexual characteristics.

Alternatively the differential development of secondary sexual characteristics may reflect variance in the strength of sexual selection as a result of differential competition for mates within the populations. Killer whales are an example of a male-biased, sexually dimorphic species (Dahlheim and Heyning 1999) with a highly polygynous mating system (Barrett-Lennard 2000; Ford *et al.*2011). As such, sexual selection is likely to favor large males (Trivers 1972), as larger body size and appendages would increase mating opportunities and reproductive success (Promislow 1992; Loison *et al.*1999; Toigo and Gaillard 2003; Issac 2005). For killer whales, the large body size and large appendages (notably dorsal fins, pectoral flippers and flukes) likely represents the quality of the male, as aggressive male-male competition for females has not been observed (e.g. Ford *et al.*2011). With a notably higher proportion of adult males in the AI population compared to SR or GOA populations, there is clearly more scope for mate competition and therefore a higher premium on advertising quality through secondary sexual characteristics.

The high, and likely increasing, population abundance of “resident” type fish-eating killer whales around the Aleutian Islands, and the notably high proportion of large adult males, reflects high caloric requirements (Noren 2011). These translate into significant, and probably increasing, trophic impacts on both their prey (e.g. Williams *et al.*2004) and competitors (e.g. Guénette *et al.*2006). Despite chemical signatures in skin and blubber samples supporting a diet of fish, there is still considerable uncertainty about the exact diet of “resident” type fish-eating killer whales in this region (Herman *et al.*2005; Krahn *et al.*2007a). In contrast to “resident” type fish-eating killer whales in the eastern North Pacific (including SRs and GOAs), that have been inferred to feed predominantly on Pacific salmon due to the collection of fish remains at the surface (Ford *et al.*1998; Saulitis *et al.*2000; Ford and Ellis 2006), relatively few prey remains have been collected from feeding killer whales around the Aleutian islands, likely reflecting a difference in diet and possibly a difference in foraging depth and behavior (Matkin *et al.*2007).

We do know that Aleutian whales are frequently observed feeding on the discards of trawlers (Yano and Dahlheim 1995; Matkin *et al.*2007) and particularly depredating sablefish (*Anoplopoma fimbria*) and Pacific halibut (*Hippoglossus stenolepis),* from longline fisheries (Dahlheim 1988; Yano and Dahlheim 1995; Lunsford and Rutecki 2010). The incidence of depredation on longline fisheries has been increasing in recent years, at a substantial financial cost to commercial fisheries (Lunsford and Rutecki 2010). It is possible that this depredation has provided killer whales with year-round access to high quality prey items, and may have contributed to their high abundance around the Aleutian Islands. Depredation behavior has been suggested to be culturally transmitted (see Chapter 5) and with the already high, and likely increasing abundance of killer whales, it will continue to be a major source of direct conflict with commercial fisheries.

Away from fishing vessels, killer whales around the Aleutians have been observed feeding on commercially important species such as Atka mackerel (*Pleurogrammus monopterygius*), and Pacific halibut, in addition to Pacific salmon spp. (*Oncorhynchus spp*) (Matkin *et al.*2007; NMML, unpublished data). Of these, observations of predation on Atka mackerel predominate, particularly in the central Aleutian Islands (NMML, unpublished data), correlating with east to west increases in Atka mackerel abundance (Logerwell *et al.*2005; McDermott *et al.*2005) and corresponding declines in salmon (Heymans 2005; Guénette *et al.*2006). There are correlations at a finer scale also, with the highest abundance of Atka mackerel found in passes and waters north of the Aleutian Islands (Lowe *et al.*2002; Zenger 2004; Logerwell *et al.*2005; McDermott *et al.*2005), displaying a similar pattern to the occurrence of “resident” type fish-eating killer whales (Sinclair *et al.*2005). This is similar to reports from Russian coastal waters to the west, where Atka mackerel is an important prey species for “resident” type fish-eating killer whales (Burdin *et al.*2007), and observed shifts in primary killer whale feeding areas are consistent with shifts in primary fishing areas of Atka mackerel commercial fleets (Burdin *et al.*2007).

Regular predation by “resident” type fish-eating killer whales on commercially important fish species has likely established significant competition with fisheries around the Aleutian Islands, and possible ecosystem impacts. Fishing pressure has been suggested to be a cause of declines in the biomass of multiple fish populations in this region, including salmon (e.g. Finney *et al.*2000), and Atka mackerel (Lowe and Fritz 1997; McDermott *et al.*2005), as well as a possible factor in the decline (and lack of recovery) of the western stock of Steller sea lions in recent decades (Sinclair and Zeppelin 2002; Guénette *et al.*2006). Although predation by mammal-eating killer whales has been hypothesized to also have had a role in the decline of sea-lions and other pinnipeds (Springer *et al.*2003; Williams *et al.*2004; Guénette *et al.*2006), prey competition with fish-eating killer whales has not, to date, been considered to be a major factor. However, the abundance estimates we present here far exceed previous estimates that were incorporated into previous ecosystem models (Heymans 2005), possibly warranting a re-examination of the potential trophic impact of “resident” type fish-eating killer whales on marine ecosystem around the Aleutian Islands.

In the case of Steller sea lions, both species are known to consume Atka mackerel in the same nearshore waters of the Aleutian Islands (Sinclair and Zeppelin 2002; Sinclair *et al.*2005; NMML unpublished data) and it is likely that a certain degree of prey competition has always existed between the two species. However, the effects may have become more pronounced with the depletion of the western stock of Steller sea lions, and possible concurrent increase in abundance of “resident” type fish-eating killer whales. The documented decline of more than 80% (Merrick *et al.*1987; Loughlin *et al.*1992; Trites and Larkin 1996; Calkins *et al.*1999) in the abundance of Steller sea lions in recent decades would have reduced interspecific competition on locally available prey (e.g. Atka mackerel), resulting in increased prey availability for the Aleutian “resident” type fish-eating killer whale population. Estes *et al.*(2009) noted that Atka mackerel were rarely seen in the shallow, nearshore waters in the central and western Aleutians, prior to the Steller sea lion declines, but are now very common, sometimes observed in large aggregations that extend the full depth of the waters. Similarly, it may be that competition with the high (and possibly) elevated abundance of the “resident” type fish-eating killer whale population may have partly driven the decline of sea lions, or may at least be hindering the recovery of this endangered population through increased prey competition. Further, fishery closures designed to protect prey resources and facilitate sea lion recovery (Steller sea lion protection measures, SSLPM, http://alaskafisheries.noaa.gov/sustainablefisheries/sslpm/) may have even created an even more reliable food source for fish-eating killer whales, further contributing to their competitive impact. Future efforts should be made to evaluate these hypotheses, most notably by incorporating updated input parameters for “resident” type fish-eating killer whales into energetic and ecosystem models.

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CHAPTER SEVEN

GENERAL DISCUSSION

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General Discussion

We are in a period of unprecedented climate change and discernible impacts on both terrestrial and marine ecosystems have already been documented (Parmesan 2006; Walther *et al*. 2002; Block *et al*. 2011). Apex predators are bio-indicators of the health of both terrestrial and marine environments (Estes *et al*. 2011) and long-term individual-based monitoring can enable researchers to monitor temporal changes in populations, such as shifts in size, structure, demography and distribution, that may occur in response to changes in environment (Clutton-Brock and Sheldon 2010). The removal of apex predators has been shown to have cascading effects on ecosystems (Pace *et al*. 1999; Berger *et al*. 2001; Terborgh *et al*. 2001; Estes *et al*. 2011) and monitoring data series are thus essential to adequately manage populations of top predators and the ecosystems within which they occur (Norris *et al*. 2004). However, there are great challenges and uncertainties when studying cetacean top predators in their entirely marine environment (Springer *et al*. 2003; DeMaster *et al*. 2006; Wade *et al*. 2007).

In this thesis, I have demonstrated the utility of using photographic data, combined with robust and appropriate statistical analyses, to evaluate the status of three populations of cetaceans. These populations inhabit a diverse range of environments and habitats, ranging from the tropics to the sub-arctic, and from relatively urban to very remote, and I have assessed population trends in the context of key ecosystem covariates, where possible, to quantify the impact of environmental variation in these status assessments. In addition to informing key management issues relative to these specific populations, the methods presented in this thesis should be transferable to other populations of cetaceans and other similarly mobile and cryptic species.

An Integrated approach

Despite a 30+ year history of photo-identification studies of cetaceans, relatively few studies have actually used these photo-identifications in a robust mark-recapture framework to estimate abundance (e.g. Hammond *et al*. 1990; Williams *et al*. 1993; Wilson *et al*. 1999; Stevick *et al*. 2001; Read *et al*. 2003; Calambokidis and Barlow 2004; Durban *et al*. 2005; Silva *et al*. 2009; Durban *et al*. 2010), and even fewer to estimate population dynamics (Whitehead *et al*. 1997; Cameron *et al*. 1999; Caswell *et al*. 1999; Fujiwara and Caswell 2001; Mizroch *et al*. 2004; Leaper *et al*. 2006; Corkery *et al*. 2008). Similarly, although photogrammetric studies of cetacean size and condition are growing (Koski *et al*. 1992; Perryman and Lynn 1993; Read *et al*. 1993; Perryman and Lynn 2002; Durban and Parsons 2006; Webster *et al*. 2010; Miller *et al*. 2012), there have been few attempts to incorporate photogrammetric data into assessments, which can greatly enhance the understanding of the status of populations (Croze 1972). This thesis used aspects of three case studies to form chapters that addressed key problems in photographic population assessment and offered solutions for making robust inference on populations using photographic data.

Photographs as observations

Observational data are required for studies on free-ranging marine mammals, but almost no marine mammal population (perhaps with notable exceptions; Ford *et al*. 2010) can be followed with sufficient resolution to allow direct inference from observational data. Therefore, population processes must be indirectly inferred from observations, which can be biased and may be sparse, requiring careful and robust treatment of the data. Chapter 2 demonstrated how careful treatment of photographs could be used simply to make inference on the timing of key events, namely predation attempts and birthing events, and relate these events to environmental covariates. Chapters 3, 5 and 6 used photographs in a mark-recapture context (as captures and recaptures of individuals) and photographs were processed for photogrammetric analyses in chapters 4 and 6. Together, these chapters demonstrated the utility of using individual-based photographs as sample observations to help understand the demographics and dynamics of cetacean populations.

Mobility of cetaceans presents problems for population definition

A key assumption of mark-recapture analysis is that all individuals have an equal probability of being captured (Seber 1982; Hammond 1990b). However, this assumption is essentially impossible to meet when dealing with highly mobile cetaceans, with wide-ranging individuals that can display heterogeneous site fidelity to a large area (Lusseau *et al*. 2006; Durban *et al*. 2010). Chapter 3 offered a novel mark-recapture solution to distinguish “transient” dolphins with low capture probabilities (and thus more difficult to monitor), from “resident” dolphins with high capture probabilities, allowing useful inference to be made about the dynamics of the “resident” dolphins. Chapter 5 used social and spatial analysis to identify distinct clusters within a large network of “resident” type fish-eating killer whales, and chapter 6 explicitly incorporated spatially-structured photo-identification samples into mark-recapture assessments of abundance for this same population of killer whales. The methodologies presented in these chapters highlighted the utility of applying robust statistical analyses to photo-identification data to make inference about the demography and dynamics of mobile populations and should be extremely useful for other studies, especially those monitoring cryptic or highly mobile species with heterogeneous movements and/or with limited monitoring opportunities.

Incorporating individual quality into assessments

With the continued development of analytical techniques for estimating abundance (e.g. Schwarz and Seber 1999; Buckland *et al*. 2000), there is an understandable focus on basing assessments on the quantity of individuals (Wade 1998; Read and Wade 2001; Morris *et al*. 2002). However, individual quality can tell us a great deal about responses to a changing environment (Post *et al*. 1999a; Gaillard *et al*. 2000) and in this thesis I used photogrammetry techniques to estimate individual attributes. Chapter 4 demonstrated the utility of using size-at-age data to inform about long-term growth trends in an endangered population of “resident” type fish-eating killer whales and chapter 6 adopted a comparative approach of using morphometric data from three different populations of killer whales to infer relative population status. These chapters showed how useful inference on population demography and long-term dynamics could be gleaned from data on individual quality. They also demonstrated how demographic assessments of populations can be greatly enhanced by employing a comparative approach when “reference” populations with known demographic histories (Olesiuk *et al*. 1990, 2005; Ford *et al*. 2000) are available.

Future Extensions: Quality not just quantity

In this thesis I demonstrated the utility of incorporating a variety of data sources to make inference about population status for cetaceans. I showed how individual quality can be combined with quantitative assessments for a more complete understanding of population status and dynamics. This approach could be extended further, taking into account key features of the life history and social structure of the target species.

Sexual dimorphism

Sexual dimorphism can be defined as the difference in the size, shape or traits between males and females of the same species (Lammers *et al.* 2001; Isaac 2005) and male-biased sexual size dimorphism, where males are bigger than females in body size and/or body weight, is common among mammals (Isaac 2005). Sexual selection is typically thought to favor large males (Trivers 1972), where larger body size would increase mating opportunities for males resulting in an increase in overall reproductive success, although it is unlikely that a single selective factor is driving sexual size dimorphism (Loison *et al.* 1999; Toigo and Gaillard 2003; Issac 2005). Increased size may be an advantage in physical competition over females (Darwin 1871), or may represent an advertisement of quality (Issac 2005). It has been shown that the degree of sexual dimorphism is less pronounced in female-biased populations and more pronounced in male-biased populations, indicative of the level of competition between males to gain access to females (Issac 2005). Therefore, for sexually dimorphic species, the extent of dimorphism itself might be informative, as it may reflect the current balance of sexual selection and environmental constraints on growth (Promislow 1992; Post *et al.* 1999a,b; Issac 2005).

Both killer whales and bottlenose dolphins are examples of a male-biased, sexually dimorphic species (although less pronounced for bottlenose dolphins; Read *et al*. 1993, Dahlheim and Heyning 1999), with a highly polygynous mating system (Connor *et al*. 1996; Barrett-Lennard 2000; Ford *et al*. 2011). For killer whales, the large body size and appendages (notably pectoral flippers and dorsal fin) likely represents the quality of the male, whereas large body size for bottlenose dolphins is likely advantageous in physical male-male competition for a access to mates (Parsons *et al*. 2003). Long-term studies on “resident” type fish-eating killer whales in the NE Pacific have documented relatively high mortality rates for adult and sub-adult males during years of food shortages (Olesiuk *et al*. 2005; Ford *et al*.

2010; Ward *et al*. 2010), suggesting that the large males incur a greater energetic cost as a result of these sexually dimorphic features (Demment and van Soest 1985; Promislow 1992; Toigo and Gaillard 2003; Issac 2005; Noren 2011), and as a result, both the size and endurance of males may well be an indication of their quality. The comparatively high proportion of adult males in the Aleutian population of “resident” type fish-eating killer whales (Chapter 6) likely reflects a low rate of mortality for adult males (increased endurance), but it also may represent increased male-male competition for access to females (increased attractiveness through increased size and physical attributes). Ford *et al*. (2011) showed that the reproductive success for the southern resident killer whales appeared to increase with both size (see Chapter 4) and age, but such analyses have not been conducted for the Aleutian or GOA populations. Future comparisons of the degree of sexual dimorphism within these populations could provide further information on nutritional and demographic status, in addition to making inference on the reproductive structure of these populations.

In addition to differential patterns of mortality and size, sex ratios at birth may provide a further link between environmental variability and demography. Sons are more costly to produce than daughters in many sexually dimorphic, polygynous species (Clutton-Brock *et al*. 1981; Post *et al.* 1999a), and Trivers and Willard (1973) predicted that in such species, mothers in good body condition (resulting from good feeding conditions) would invest in male offspring that could provide a better return in terms of future reproductive success. This theory has been supported by empirical data from a variety of terrestrial species, namely ungulates such as red deer (Catchpole *et al*. 2004) and mule deer (Kucera 1991), with high proportion of adult males following a series of years in which the population experienced favorable environmental conditions. However, gender at birth is generally difficult to ascertain for free ranging cetaceans with sparse observational data (Weller *et al*.

2009). Nonetheless, time series are now maturing that could be used for such analyses in future years (e.g. southern residents, Ward *et al*. 2010).

Social structure

Key information about the status of populations can also be drawn from social structure. The social structure of a population plays an important role in its ecology and can be a key determinant of population processes (Lusseau *et al.* 2006). At a fundamental level, social structure forms in response to the distribution of individuals within their habitat, which in turn is the result of environmental forcing that affects the distribution of prey resources and predators (Emlen and Oring 1977). As a result, variability in social systems may show a response to environmental changes (Lusseau *et al.* 2004), and we may expect the effect of environmental variability on demography to be mediated by social structure. Thus, quantifying the social and spatial connectivity of individuals within a population, and monitoring shifts in structure, can provide valuable insight into the stability of population, as well as the surrounding environment.

Long-term studies have documented sociality to be a key structural component of killer whale populations, as group membership remains stable over multiple years (Baird and Whitehead 2000) and even multiple generations (Bigg *et al.* 1990; Ford *et al.* 2000; Parsons *et al*. 2009). These social groups are comprised of maternally related whales, or “matrilines”, that are highly cohesive and rarely separate for significant time periods (Bigg *et al.* 1990; Oleisuk *et al.* 1990). Recent analyses of “resident” type fish-eating killer whale association histories have shown these matrilines to form a flexible social network, with consistent groupings of matrilines (termed “pods”) that are stable during years of relatively high availability of their prey (primarily Chinook salmon, *Oncorhynchus tshawytscha* ; Ford and Ellis 2006), and more ephemeral during poor food years (Parsons *et al.* 2009). Notably, a similar relationship has been discovered between survival (Ford *et al.* 2010), and fecundity (Ward *et al*. 2009), with relatively high mortality and low fecundity associated with poor salmon years, indicating that social structure may be a useful indicator of population status, perhaps even observable at an earlier stage. Sample sizes prevented me from a full description of the social structure of "resident" type fish-eating killer whales around the Aleutian Islands (Chapter 5). However, the Aleutian population appears to be structured similarly, with some very consistent associations persisting over multiple years. Large aggregations of whales were observed feeding in areas of high productivity (e.g. Seguam Pass, Hunt and Stabeno 2005; Ladd *et al*. 2005), and these aggregations are probably comprised of multiple matrilines, akin to the southern resident pods. Additional field efforts may allow for a more detailed social analysis in future years, including assessments of spatial and temporal variability in social cohesiveness that may reflect key environmental variation.

Case studies: Future considerations and implications

In this thesis I successfully used photographic data to fill key data gaps in each of the case studies. However, future field efforts can extend these datasets to enable a greater understanding of spatial and temporal variation in key population processes. These populations will continue to be impacted by both environmental and anthropogenic factors in future years, and it is important to continue monitoring and analysis so that trends in the dynamics of populations and their ecosystems can be detected in a timely manner.

Southern resident killer whales

This thesis used photogrammetric data to assess the size and growth trends of the southern resident killer whale population, a population that is listed as endangered under both the Endangered Species Act (USA) and the Species at Risk Act (Canada), and is an iconic symbol of the Pacific Northwest. Fewer than 100 individuals remain, and this population has experienced fluctuations in survival and fecundity in recent decades due to periods of decreased prey availability (Ward *et al*. 2009; Ford *et al.* 2010). For long-lived marine mammals, data on body condition and individual growth can provide important indications of individual health and population status (Perryman and Lynn 2002; Trites and Donnelly 2003; Miller *et al*. 2012), and I have shown the potential of using photogrammetry data to increase our understanding of size trends and nutritional status of this population. Future monitoring efforts for this population should focus on detecting changes in body condition (e.g. Miller *et al*. 2012), as well as monitoring fluctuations in growth rates across years, to identify periods of nutritional stress before it is manifested at the population level. Seasonal photogrammetric measures of condition can be used to identify critical feeding seasons, providing management agencies with critical times, as well as critical habitat (NMFS, 2008; Fisheries and Oceans Canada, 2011), that must be protected to ensure the viability of this population.

Aleutian Islands killer whales

This thesis described a high abundance of “resident” type fish-eating killer whales in the coastal waters of the western Gulf of Alaska, Bering Sea and particularly around the Aleutian Islands. I used individual-based photo data to describe the social connectivity, individual movements and abundance, and make inference on the demography and status of the population, despite the challenges of working in this remote region and limitations of a large-scale, but somewhat sparse dataset. Notably, the Aleutian population appears to be large and comprised of a high proportion of large, adult males; indicative of a high level of favorable past feeding conditions and likely population expansion. A high degree of site fidelity was apparent for individuals over years and seasons, and localized feeding by such a large number of whales likely has a significant trophic impact on the local ecosystem

(Williams *et al*. 2004), possibly including competitive impacts on endangered Steller sea lions (Loughlin *et al*. 1992). Future studies will need to incorporate the estimates of abundance and individual size presented in this thesis into energetic (Winship *et al*. 2002; Williams *et al*. 2004) and ecosystem models (Guénette *et al*. 2006) to fully evaluate the impacts of this large killer whale population.

Here I provide a "back of the envelope" estimate of energetic requirements for the ~ 2260 killer whales in the central and eastern Aleutian Island population of fish-eating residents. Given an average energy density of 5.9 kJ/g for Atka mackerel (Logerwell and Schaufler 2005), an average mass of 500g for an Atka- mackerel aged 3-4 years (Rand 2007), a 180,000 kcal daily energetic requirement for an average killer whale (Williams *et al*. 2004), this Aleutian population could ingest 116,245 tons of Atka mackerel annually, *if* their diet was composed completely of Atka mackerel. Furthermore, this is likely a considerable under-estimate, given my data on the relatively large proportion of adult males in the population that translates into an anomalously large average killer whale size. Winship and Trites (2003) estimated that Steller sea lions in all areas of Alaska consumed 104,000 tons of Atka mackerel annually, equaling 75% of the estimated exploitable Atka mackerel biomass dying naturally in the Aleutian Islands, and 181% of fisheries catches in the Aleutian Islands and GOA in 1998. The crude estimates presented here clearly indicate that the Aleutian population of "resident" type fish-eating killer whales could have an enormous direct impact on prey biomass, and indirect impact on competitors within this system, and as such should be considered in ecosystem models, fisheries assessments and recovery plans.

Bottlenose dolphins on Little Bahama Bank

This thesis provided evidence of a distinct calving period for bottlenose dolphins on Little Bahama Bank, perhaps a response to the threat imposed by the harsh environment during tropical cyclones in summer months. Similarly, survival trends appear to be punctuated by intense hurricanes, with potentially long-term effects due to habitat alteration. The predicted impact of climate change on terrestrial and marine systems is currently the focus of much research and much debate (see Parmesan 2006). However, it is not immediately intuitive that climate change may abruptly affect mobile and long-lived marine top predators. The frequency and severity of tropical cyclones are predicted to increase with future decades of warming (Landsea *et al.* 1996), which is likely to have acute and abrupt impacts on the marine environment of Little Bahama Bank and this island population of bottlenose dolphins. It is also likely that anthropogenic disturbance, such as recreational boat traffic and coastal development, will continue to increase, resulting in additional loss of suitable habitat for these dolphins.

In future years, survey efforts could be expanded to monitor adjacent habitats, as well as additional seasons, to allow for a more complete monitoring of this population. Specifically, an expansion of photo-identification monitoring would allow presumed mortalities to be better resolved from the process of permanent emigration, and allow for the detection of possible shifts in home ranges and habitat use (e.g. Wells *et al.* 1990; Wilson *et al.* 2004). In addition, satellite telemetry has been shown to be an extremely useful tool for monitoring the fine scale movements of cetaceans, specifically with the recent use of small, remotely attached tags to monitor the movements of larger delphinids (e.g. Durban and Pitman 2011; Baird *et al*. 2012). With further tag miniaturization, this approach could be used to assess the fine scale movements of these small dolphins in the future, specifically to monitor their response to tropical cyclones (e.g. Langtimm *et al*. 2006). To help relate movements and habitat shifts in the context of anthropogenic perturbations, fine scale GPS tracks from the growing rental boat fleet could be collated to quantify a “boat traffic intensity surface” that could be related to dolphin movements. As such, a multi-disciplinary approach to the monitoring of this population will help fill key data gaps on both the response to environmental and anthropogenic changes, and also facilitate more robust assessments.

Conclusions

We have come a long way since the onset of individual-based monitoring of cetacean populations. In early 1970s, Dr. Mike Bigg cut notches into the dorsal fin of an individual killer whale to prove the validity of the photo-identification technique (Ford *et al*. 1994; Ford *et al*. 2000). Now, photographs are a routine and accepted source of data for cetaceans (Hammond *et al*.1990), but most photographic population assessments still fall short of successfully identifying the drivers of population dynamics. This thesis highlighted the importance of using a variety of individual-based photographic data to assess abundance, demographics and trends for cetacean populations, and provided robust solutions to overcome a variety of key constraints.

However, cetaceans have long generation times (e.g. decades, Olesiuk *et al*. 1990; 2005), and appropriate time series are often difficult and expensive to compile. In the final data chapter of this thesis, I demonstrated how comparative analyses across populations can be an effective approach for inferring relative population status. I suggest this approach may offer a valid alternative when long-term series are not available from a target population, but ecosystem assessments and management requires scientific recommendations. Specifically, assessments can be made in a multi-population framework (e.g. Read and Wade 2000), akin to meta-analysis of key parameters in fisheries stock assessment (Myers and Mertz 1998). However, this should not be seen as a replacement of long-term photo-identification and photogrammetric monitoring, but may be a useful alternative approach in the shorter term. The development of tools used for photographic image capture, processing and statistical analysis is continuing to advance, and this will ensure that photographic population assessments will continue to be of great utility for monitoring cetacean populations.

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