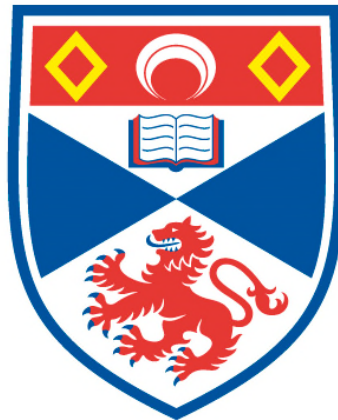


**ECOLOGY OF PACIFIC WHITE-SIDED DOLPHINS
(*LAGENORHYNCHUS OBLIQUIDENS*) IN THE
COASTAL WATERS OF BRITISH COLUMBIA, CANADA**

Erin Ashe

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**



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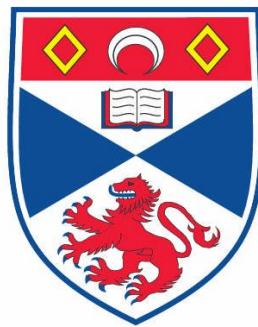
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Ecology of Pacific white-sided dolphins
(*Lagenorhynchus obliquidens*) in the coastal waters of
British Columbia, Canada

Erin Ashe



This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

August 2015

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Abstract

The ecology of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the Broughton Archipelago, British Columbia (BC), Canada was explored through photo-identification, mark-recapture, acoustics, and sociality studies. New population parameters were estimated from photo-ID data for the first time in this species. Abundance was highly variable, ranging from 546 (95% CI: 293-1,018) to 2,889 (95% CI: 1,424-5,863), after accounting for the proportion (0.57; 95% CI: 0.55 - 0.60) of marked dolphins. A “match uncertainty” analysis showed that less strict matching criteria caused negative bias in abundance estimates and an apparent improvement in precision. Estimates of survival rate ranged from 0.907 (SE=0.03) to 0.989 (SE= 0.066). Robust design analyses revealed random temporary emigration movement at 0.14 (SE=0.318) annually and no movement seasonally. The study revealed new evidence for philopatry and sociality: some individuals were resighted over 19-year periods, and associated pairs more than a decade apart. Evidence was found for a high degree of sociality. The mean proportion of calves was estimated as 0.0597 (SE=0.0083, 95% CI: 0.045-0.079) *per capita*, translating to an average probability of pregnancy in adult females of 0.238 (95% CI: 0.180-0.316) and an average interbirth interval of 4.2 years. Approximately 3.9% of dolphins bore injuries from killer whales, but only 0.5% showed evidence of interactions with fishing gear or propellers. Acoustic evidence for population structure was equivocal, but warrants additional, targeted research. Population viability analysis predicted an average rate of annual decline of -0.122 (95% CI: -0.143 to -0.101), given a range of input values in a sensitivity test, over the next 50 years.

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Chapter 1

GENERAL INTRODUCTION

1.1 The role of demography in ecology, conservation biology and resource management

Understanding the dynamics of animal populations is key to answering both fundamental research questions in animal ecology and applied questions that can inform reliable conservation and management measures to prevent species decline and extinction (Crouse et al. 1987; Lebreton et al. 1993). Such research is interdisciplinary in nature, and draws on expertise in both statistics and biology (Buckland et al. 2007). Analytical work is needed to provide dependable, quantitative measures of wildlife population health, but we also need an understanding of a species' basic biology to inform statistical models and provide context.

One of the most important tasks in conservation biology involves assessing a population's conservation *status*, which is usually interpreted to mean current state relative to some historic baseline level (Rodrigues et al. 2006). Regulatory bodies often set management or conservation objectives in terms of some "optimal" population size, such as some fraction of the maximum abundance ever recorded (Taylor et al. 2000). Intuitively, it makes sense that management should be more precautionary when making decisions about human activities that may impact vulnerable species than healthy ones. Problems in conservation biology have traditionally been thought of as falling into either a *small population paradigm* or a *declining population paradigm* (Caughley 1994). The small population paradigm is concerned with small populations on the brink of extinction, whereas the declining population paradigm focuses on the process of decline and how to detect, stop and reverse population declines (Caughley 1994; Soulé 1987).

In practice, it is rarely possible to count all individuals in a population; instead, a number of sampling methods are used to estimate abundance (Seber 2002). If these abundance estimates indicate a declining trend, understanding the processes that account for the decline is the key to designing management practices capable of halting or reversing the decline (Caughley 1994). Although populations fluctuate naturally, much of conservation biology addresses

declines caused when wildlife populations come into contact with harmful human activities. Many studies of wildlife populations suffer from such low statistical power that we are unable to detect all but the most catastrophic declines (Taylor and Gerrodette 1993).

Marine mammals are an interesting and challenging taxonomic group to explore fundamental questions in conservation biology, both because of their life-history traits (long life span and slow reproductive rates) and because of their exposure to anthropogenic impacts. Historically, many species of whales were heavily exploited and much of our knowledge of large whale biology comes from data collected during whaling operations (Clapham et al. 1999). The logistical constraints of marine research, coupled with the diving behaviour of the animals, mean that there are some major gaps in our understanding of the basic biology of some cetaceans (Reeves 2003). In fact, new species of beaked whales (Family Ziphiidae) are still being discovered (Dalebout et al. 2002).

In addition to being interesting study animals, cetaceans are also charismatic, and factors that affect their conservation status often become high-profile issues. Cetaceans receive special protection under the legislation of some countries and hunts that target cetacean populations are highly contentious (Hammond 2006). Even incidental harm to cetaceans can be controversial. For example, since the 1960s, purse seine fisheries for tuna in the eastern tropical Pacific Ocean have used the association of tuna with pantropical spotted (*Stenella attenuata*), spinner (*S. longirostris*) and common (*Delphinus delphis*) dolphins to facilitate catches of large yellowfin tuna by setting nets around schools of dolphins (Wade et al. 2007b). A consequence of this fishing method was the incidental killing of hundreds of thousands of dolphins annually before management measures were put in place when the US Marine Mammal Protection Act (MMPA) was enacted in 1972 and allowable mortality limits were subsequently set (Hall 1998). Public demand for action led to market-based pressure for dolphin-safe fishing practices.

The MMPA specifies minimum standards for collecting rigorous scientific information to manage species and populations, but collecting this information is logistically challenging and expensive. Information on trends is not available for 71% of marine mammal stocks found in waters under US jurisdiction (Roman et al. 2013). In parts of the world where there is no legal

obligation to monitor the status of marine mammal stocks, data gaps are even more extreme (Kaschner et al. 2012). Highly mobile or migratory marine mammals may pass through waters under the jurisdiction of several countries or regulatory authorities.

1.2 Pelagic dolphins: large schools, large challenges

Compared to coastal populations of bottlenose dolphins (*Tursiops truncatus*) off northern Scotland (Wilson et al. 1999) or Doubtful Sound, New Zealand (Currey et al. 2009b), some offshore species of dolphins travel in very large (>1000 animals) schools, and their pelagic habitat can be an inhospitable place for researchers to work (Lewison et al. 2004). In terms of context, the best estimate of average group size (411 individuals) of long-beaked common dolphin (*Delphinus capensis*) observed on line transect surveys in the eastern tropical Pacific (Ferguson et al. 2006) is much larger than the best estimate of the world's total population of the Critically Endangered vaquita (*Phocoena sinus*; ~ 97 individuals; Navy, 2014). Stocks of pelagic dolphins can be very abundant, numbering in the hundreds of thousands.

Although abundance is not the only criterion used to assess status, the International Union for the Conservation of Nature (IUCN) Global Mammal Assessment includes abundance estimates as an important criterion with which to assess conservation status (Schipper et al. 2008). Although it is difficult to generalize, marine mammals overall tend to be faced with higher threat levels than terrestrial mammals (Schipper et al. 2008). It has been my experience during the course of this study that the perception among some stakeholders, managers, funders and other scientists, is that “abundant” is synonymous with “not at risk”. The tuna-dolphin issue counters this argument well: both spinner and spotted dolphins are considered depleted stocks and have not recovered as expected, although they currently number in the hundreds of thousands (Gerrodette and Forcada 2005).

There appears to be a disconnect between conservation theory and practice, such that conservation biology places overwhelming priority on species at risk of imminent extinction (e.g., small, localised populations) over abundant species that may fall into the declining-population paradigm (Gaston and Fuller 2008). Gaston and Fuller (2008) note that common species are ecologically important, and relatively small changes in their abundance could have major consequences for ecosystem function. As they point out, the passenger pigeon

(*Ectopistes migratorius*) was once the most numerous bird on earth before its extinction in the early 1900s. In marine ecosystems, the decline and extinction of once-abundant marine species could result in ecosystem collapse (Jackson et al. 2001). We have relatively poor information on the status of pelagic dolphins. For ~70% of stocks of dolphins or porpoises in waters under US jurisdiction (i.e., up to 200 nautical miles offshore), surveys would fail to detect a precipitous decline (50% over 15 yr). Statistical power is even lower for cetaceans with highly pelagic distributions; statistical power to detect catastrophic declines is 0 for many pelagic species in waters under US jurisdiction (Taylor et al. 2007).

Pelagic dolphins warrant greater consideration in management of human activities in offshore waters. One consequence of the high abundance of pelagic dolphins is that many individuals may be affected by human activities, such as exposure to noise from offshore oil and gas exploration or military sonar events (e.g., Navy 2013). In contrast to the high profile of sound exposure in beaked whales, there has been little research on the effects of noise on pelagic dolphins. There seems to be little incentive to study impacts of that exposure, in part because few pelagic dolphin species are listed as at risk (i.e., considered to be at some risk of extinction by a conservation authority or listed under a country's endangered species legislation). This could lead to a vicious cycle, in which species can be exposed to threats because they are thought to have good conservation status; with no information on population consequence of that exposure/threat, they are never listed; and without a listing, they never rise to the level of a priority for funding to re-assess risks and conservation status (Gaston and Fuller 2008). One way to avoid this "data gap trap" is to monitor marine mammal species periodically, irrespective of conservation status, and to keep human-caused mortality sufficiently low that populations are never depleted below some agreed-upon level (Hammond et al. 2013).

Pelagic dolphins, with the notable exception of those subject to bycatch in Eastern Tropical Pacific tuna fisheries, are often overlooked in monitoring programmes (Taylor et al. 2007b). The US Marine Mammal Protection Act and Canada's Species at Risk Act are meant to promote even-handed monitoring of stocks to prevent declines as early as possible (Mooers et al. 2007) but, in practice, research funding is often prioritised toward the most critically endangered taxa. Some of the most difficult decisions to make in conservation biology relate

to prioritising the species on which to focus conservation efforts (Joseph et al. 2009; Kareiva and Marvier 2003; Restani and Marzluff 2002).

There is a requirement for use of “best available information” in natural resource management in Canada. If science becomes available outside government agencies responsible for marine mammal management (*e.g.*, Fisheries and Oceans Canada), it must be used in decision-making. It is understood that scientific knowledge accumulates over time, and the information is incorporated in an iterative fashion. This creates an opportunity for independent science to feed into conservation and management, and Canada’s Species At Risk Act makes explicit mention of the need for traditional ecological knowledge and research conducted by scientists who are independent of government agencies (Taylor and Pinkus 2013).

1.3 Pacific white-sided dolphins: the case study

The genus *Lagenorhynchus* currently includes six species – *Lagenorhynchus albirostris* (white-beaked dolphin; the type species for the genus), *L. cruciger* (hour-glass dolphin), *L. obscurus* (dusky dolphin), *L. australis* (Peale’s dolphin), *L. acutus* (Atlantic white-sided dolphin) and *L. obliquidens* (Pacific white-sided dolphin) – that are distributed anti-tropically (Hare et al. 2002). A wide degree of morphological variation exists within the genus. Independent lines of evidence are emerging to suggest that a reclassification of the some of these species within the genus may be warranted (Perrin et al. 2013). Both acoustic and genetic lines of evidence point to reclassification, and that some *Lagenorhynchus*, including Pacific white-sided dolphins, belong in the genus *Sagmatias*.

Pacific white-sided dolphins (*L. obliquidens*) are pelagic (Ferrero and Walker 1996; Leatherwood and Reeves 1983), abundant (Central North Pacific: 931,000, CV=0.90, , and widely distributed throughout the temperate North Pacific Ocean (Figure 1.1)(Leatherwood and Reeves 1983; Stacey and Baird 1991). They are also distributed along the continental shelf of the United States (59,274; CV=0.50; NMFS 2013) and occur in continental shelf waters of British Columbia (“BC”; 25,900; CV=0.35; Williams and Thomas 2007)(Heise 1996a; Morton 2000).

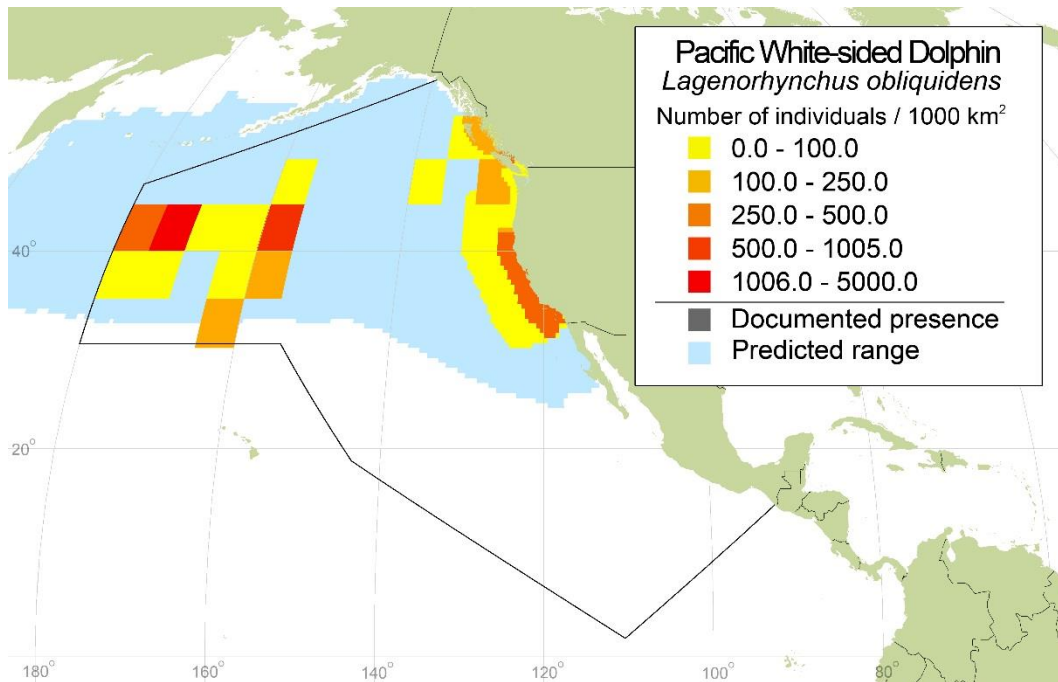


Figure 1.1: Density estimates and reported range of Pacific white-sided dolphins in the North Pacific Ocean from (Williams et al. 2011a). The light blue polygon indicates the presumed range of the species from niche envelope models. The coloured boxes illustrate reported density estimates from areas that have been covered by line transect surveys within the outlined area.

There are no time series of abundance estimates for the species. Even if there were, uncertainty in these abundance estimates would make it difficult to detect trends. The only density estimate across the vast majority of the species' range came from a spatially biased (non-randomised) survey, and with strong potential for positive bias due to bow-riding (attractive movement in response to the ship; Buckland et al. 1993).

Pacific white-sided dolphins are listed as 'Least Concern' by IUCN, 'not at risk' in Canada (Stacey and Baird 1991), and not considered 'endangered', 'threatened' or 'depleted' under the US MMPA (NMFS 2012). The combined mortality from commercial fisheries and research trawls in California, Oregon, and Washington stock of dolphins is high enough (exceeds 10% of Potential Biological Removal (PBR) to be classified as a strategic stock; however, under the MMPA only commercial takes are included (NMFS 2013). Although bycatch is currently not considered a major threat to Pacific white-sided dolphins (NMFS 2012), historically, it was a major problem. It is estimated that the high-seas driftnet fishery for squid and salmon killed

hundreds of thousands of dolphins during the 1970s and 1980s (Hobbs and Jones 1993). A moratorium on the fishery was called for by the United Nations in 1991 and implemented in 1992. However, some illegal driftnet fishing on the high seas continues today in the North Pacific (NMFS 2012). Pacific white-sided dolphins have been the target of live captures for display in aquaria, but the number of removals was low (Brownell Jr et al. 1999). The last dolphin capture in the US was in 1993 and there are no active permits for live capture (NMFS 2013). Each year hundreds of dolphins are targeted for live capture in the Japanese drive hunt (Hammond 2012). The impact of these threats is difficult to interpret in light of uncertainty in abundance estimates and lack of information on stock structure.

Assessing the conservation status of the species is hindered by lack of information on population structure, adult survival, trends in abundance, reproductive rate and anthropogenic threats (Hammond 2012). The primary objective of my study was to provide new information on demography, namely abundance and survival. A secondary objective was to assess the evidence for population structure in one part of the species' range.

Lack of geographic barriers is not a good predictor of population genetic structure in cetaceans (Hoelzel 1998). For example, Atlantic spotted dolphins (*Stenella frontalis*) assumed to be a large, panmictic population were found to have significant genetic variation (Adams and Rosel 2006). In fact, there is some acoustic, genetic and morphological evidence emerging to suggest that population structure can be found within Pacific white-sided dolphins. Two forms with overlapping ranges have been identified in waters between Mexico and the Southern California Bight based on genetic and morphological differences (Lux et al. 1996; Walker et al. 1986) and two populations have been identified between the coastal waters and offshore waters off Japan (Hayano et al. 2004). Lux et al. (1996) tested for and found evidence of genetic subdivision among dolphins from four geographic areas that correspond roughly to areas under different jurisdictions: Baja California, Mexico; California, Oregon and Washington; an 'offshore' stratum on the international high seas; and BC/southeast Alaska. Soldevilla *et al.* (2008) note significant acoustic differences between two echolocation click-types that may be attributed to the two putative populations in California waters. In previous assessments of genetics and acoustics, Canadian waters were poorly sampled (Lux *et al.* 1996; Soldevilla *et al.* 2008). My study provides new information on Pacific white-sided dolphins in a part of their range that is

unusually accessible but poorly represented in previous analyses.

1.4 Opportunity to investigate Pacific white-sided dolphins in inshore waters

Pacific white-sided dolphins recolonised the inshore waters of British Columbia (BC) in 1984 after decades of very few or no sightings (Morton 2000), although the dolphins had previously been observed in BC's offshore and continental shelf waters (Leatherwood et al. 1984; Morton 2000). Morton (2000) initiated a photo-identification study beginning in 1987 that documented the relative increase in dolphin abundance in BC's Broughton Archipelago region. The accessibility of inshore waters and long-term photo-identification and observational data created a rare opportunity to advance our knowledge on a species typically thought of as a pelagic dolphin. In doing so, it created a tractable study site for estimating demographic parameters and vital rates, investigating sociality, exploring evidence for population structure, and examining these in an ecological context. I took advantage of this opportunity and built upon the existing study through my own field and analytical investigation in 2008-2013.

Thesis outline

Chapter 2: accounting for uncertainty in mark-recapture data

Coping with uncertainty is a key aspect of ecological studies. This chapter illustrates a problem that is commonly encountered but rarely addressed in mark-recapture studies. Parameter estimation from mark-recapture analyses of photo-identification data hinges on correctly matching individuals from photographs and assumes that identifications are detected with certainty, marks are not lost over time, and that individuals are recognised when they are resighted (Hammond 1986). Matching photographs is an inherently subjective process that traditionally only considers two photographs a "match" when the analyst is 100% certain. This decision can carry serious implications with respect to sample size and the bias and precision of the resultant parameter estimates (Friday 2000; Friday et al. 2008; Stevick et al. 2001; Urian et al. 2015). I conducted a novel experiment to assign one of three levels of certainty that a pair of photographs represented a match. I then estimated abundance and survival using these three datasets to quantify the effect of match uncertainty on the bias and precision of the resulting estimates.

Chapter 3: survival and abundance

Chapter 3 builds on Alexandra Morton's long-term historical photo-identification dataset and incorporates the current study's new data to estimate survival rate and abundance using mark-recapture methods. A simple two-sample estimator is used to estimate abundance over pairs of years. Annual survival rates, recapture rates, rates of temporary emigration, and abundance are estimated using open population mark-recapture models. This first estimate of survival rate derived for this species using mark-recapture methods is discussed in the context of data sparseness, temporary emigration, and conservation status.

Chapter 4: impact of killer whale predation on Pacific white-sided dolphins

During the course of the study, killer whales were observed attacking and killing Pacific white-sided dolphins in the study area. A number of injuries that appeared to be consistent with killer whale rake marks were observed during the photo-ID matching and scoring process. In this chapter, four lines of evidence are explored to assess the degree to which mammal-eating killer whales could be impacting the survival of Pacific white-sided dolphins in the Broughton Archipelago study area: (1) direct observations of predation collected from personal observations, published reports, and interviews with researchers and mariners in the region; (2) examining photographs to estimate "injury rate" to estimate the prevalence of unsuccessful killer whale predation attempts; (3) modelling interannual variability in survival rate with an index of mammal-eating killer whale abundance as a covariate; and (4) a preliminary energetic analysis to examine the degree to which killer whale predation could impact Pacific white-sided dolphin abundance.

Chapter 5: hypotheses about stock structure from sociality and acoustics

It is important to know the population to which the estimates of survival and abundance apply. Acoustic attributes and sociality were explored for evidence of population structure within the study area. In many species, including killer whales (Barrett-Lennard 2000; Ford et al. 2000; Morton 1990) and harbour porpoise (Kyhn et al. 2013), acoustic variability between populations is consistent with genetic population differentiation. Acoustic recordings collected from photo-identified groups of dolphins are examined for evidence of differentiation. Social structure influences population structure (Hoelzel et al. 2007; Lusseau 2006; Sugg et al. 1996).

Observations of dolphin groups from 1987-2013 were analysed for evidence of sociality. Although assumed to be a social species (Connor 2000), the social structure of Pacific white-sided dolphins has never been examined due to lack of long-term photo-ID data from known individuals. This chapter presents the first evidence for social differentiation in this species.

Chapter 6: population viability analysis

Parameter estimates from Chapters 3 and 4 are incorporated into a population viability analysis (Lacy 2000), including an analysis of the sensitivity of population trend predictions to uncertainty in various demographic parameters. Given the best demographic estimates from the study, along with plausible bounds, the population is likely to decline over the next 50 years by -0.122 (95% CI: -0.143 to -0.101) per year. Predicting population growth rate over the next 50 years is hindered most by uncertainty in two parameters: survival of adult females; and the true number of dolphins killed by killer whales each year. Future research must involve developing methods to reliably determine sex of Pacific white-sided dolphins, either using photogrammetry or genetic testing. The accuracy and precision of the mortality estimates may emerge organically as the recovery plan for mammal-eating killer whales mandates studies to improve our understanding of diet and prey requirements.

Chapter 7: general discussion and directions for future research

This chapter recaps the key findings of the studies described in Chapters 2-5, including limitations, in the context of directions for future research and discusses the integration of ecology and behavioural ecology to guide decision-making. Pacific white-sided dolphins are illustrative of many of the problems faced when assessing the status of populations from sparse data, and many of the recommendations that will improve our understanding of this species would also apply to efforts to assess the regional dynamics and status of other widespread, common species. The effect of species falling below the research and conservation radar is discussed and recommendations made on ways forward with respect to species conservation status assessment for both common and data-limited species.

Chapter 2

EFFECT OF MATCH UNCERTAINTY ON PARAMETER ESTIMATION IN MARK-RECAPTURE ANALYSIS USING PHOTO-IDENTIFICATION DATA

2.1 INTRODUCTION

Identifying and following individual animals through time offers a powerful way to estimate survivorship and fecundity, which are essential parameters when modelling the dynamics and assessing the conservation status of animal populations (Lebreton et al. 1992; Pradel 1996; Seber 2002). A variety of methods are available for estimating demographic parameters in marine mammals (and other species) including enumeration methods (i.e., complete or incomplete counts; Eberhardt et al. 1979; Thompson et al. 1997), distance (e.g., line transect) sampling (Buckland et al. 2001; Forcada and Hammond 1998), spatial modelling (Buckland et al. 2004; Hedley and Buckland 2004), and mark-recapture approaches (Hammond 2010). Advantages of mark-recapture methods include use of the data to estimate annual survival rates (Lebreton et al. 1992) and, in some cases, obtaining better precision in abundance estimates compared to distance sampling (Hiby and Hammond 1989).

Photo-identification has become widely used to follow marine mammals since researchers first noticed that some individuals possessed naturally occurring, identifiable, and persistent features. The unique markings of bottlenose dolphins (*Tursiops truncatus*) were recorded and tracked as early as the 1950s (Caldwell 1955). Photo-identification of killer whales in the northeastern Pacific Ocean began in the 1970s (Bigg 1982), and the resulting demographic records now span decades. Other examples of photo-identification studies that have generated long-term datasets include bottlenose dolphins in Sarasota, Florida (Wells and Scott 1990), North Atlantic humpback whales (*Megaptera novaeangliae*; Smith et al. 1999), and southern right whales (*Eubalaena australis*; Best et al. 2001, 2005).

For some populations of killer whales in the northeastern Pacific, every individual is uniquely marked, and populations tend to be small (numbering in the hundreds) and seasonally resident

to a discrete area, making the probability of re-capture high and parameter estimation, in most cases, straightforward (Bigg et al. 1990; Olesiuk et al. 1990). For species found in larger populations that are highly mobile or migratory (e.g., humpback whales), or those in which not every individual possesses unique markings (e.g. bottlenose or dusky dolphins), obtaining appropriate data to estimate abundance becomes more complex. Hammond (1986) reviewed methods to estimate survival and abundance from cetacean photo-identification catalogues and highlighted the implications of violating model assumptions. These analysis methods along with data collection and photographic analysis standards were compiled into a Special Issue arising from a 1988 International Whaling Commission workshop (Hammond et al. 1990). This volume gave practical advice to field biologists interested in conducting photo-ID studies, and outlined the major limitations as they existed at that time.

Mark-recapture data must meet a specific set of assumptions if reliable parameter estimates are to be made. For a simple two-sample abundance estimate, the following assumptions hold (Seber 2002):

1. The population is closed,
2. Every marked animal in the populations has the same probability of recapture,
3. Capturing (or marking) does not affect the probability of recapturing the same animal,
4. The second sample is a random sample,
5. Marks are not lost or missed between samples, and
6. All marks are identified on recovery, and they are always detected without error.

Logistical constraints of working with free-ranging cetaceans can result in violation of these assumptions, which can in turn bias estimates unless statistical methods are used to allow these assumptions to be relaxed. The purpose of this chapter is to explore the variability inherent in correctly matching individuals among sampling occasions (i.e., assumption 6, above).

Errors in individual identification are known to occur (Langtimm et al. 2004; Payne et al. 1983), but few studies have addressed this issue explicitly. The few studies that have explored effects of misidentification have found that, even at small rates, errors in identification can bias parameter estimates (Lukacs and Burnham 2005; Stevick et al. 2001; Yoshizaki et al. 2009). Misidentification involves many factors, but a recurring theme involves the importance of

choosing the right features to use as a natural mark in order to satisfy assumption 5 (above). Anatomical features should be chosen so that the natural markings used in a mark-recapture experiment will last longer than the experiment, and should not change in such a way that might affect the ability to recognize it in future (Wilson et al. 1999). For killer whales, the shape of the dorsal fin and patterns in the saddle patch are most often used as natural marks. For humpback whales, pigmentation patterns on the underside of the flukes, as well as the edge of the flukes themselves, are used to identify individuals. In this study, naturally occurring nicks and notches in a Pacific white-sided dolphin's dorsal fin were used as a natural mark, such that it could be recognized from both left and right side photographs.

Observers tend to conflate photo quality with animal distinctiveness, because a well-marked individual is more easily recognized in a poor-quality photograph than a subtly marked individual. As a result, previous cetacean studies have relied on strict protocols when gauging whether two photographs are a match (Read et al. 2003; Wilson et al. 1999). The final dataset with which to estimate parameters is still subject to human error, because it is dependent on a somewhat subjective decision about whether a human observer is convinced that pair of photographs represent two encounters of the same individual or two different individuals. Little attention has been paid to the process by which analysts reach a final decision about whether two photographs constitute a match, but a recent survey has shown that researchers vary widely in their approach to defining a match (Urian et al. 2015). Historically, cetacean studies use conservative protocols, and after seeking advice from experienced colleagues in the case of any ambiguity, only score two photos as a match if there is consensus among observers (Friday 2000; Stevick et al. 2001; Urian et al. 2015). Most protocols reviewed by Urian et al. (2015) are inherently averse to false positives; the corollary to this is that false negatives will arise as a result (Stevick et al. 2001).

Erring on the side of false negatives is not always a precautionary approach. Deciding always to call ambiguous matches a non-match will cause recapture rates to be biased low, which will cause abundance estimates to be biased high and survivorship estimates to be biased low (Friday et al. 2008; Hammond 1986; Hammond et al. 1990). For management procedures that set allowable harm limits based on abundance (e.g., Wade 1998; Winship et al. 2006) a positively biased abundance estimate will allow overexploitation. The extent to which this is

a problem for real-world conservation and management decisions is case-specific, but few studies have estimated the magnitude of bias in abundance and survivorship estimates depending on match uncertainty.

There are two primary reasons for misidentification errors: (1) errors in identification due to changes in the natural markings; and (2) misidentification as a result of variation at the level of the matching process. The first can occur if individuals acquire new marks such as scars or damage due to predation (Gordon 1987; Steiger et al. 2008), or if marks such as scratches or pigmentation patterns heal and subsequently disappear (Dufault and Whitehead 1995). In one study (Dufault and Whitehead 1995), mark acquisition occurred at a higher rate than mark loss. Mark acquisition is less likely to cause misidentification, especially in small populations. For larger, wide-ranging populations, it is recommended that one estimate mark acquisition rates and use strict animal distinctiveness criteria that rely on markings that are unlikely to change over time (Urian et al. 2015). The second misidentification process, namely errors that occur at the level of the matching process, has received comparatively little attention. Previous analyses have shown that conflating photo-quality with individual distinctiveness biases the matching process and, subsequently, the parameter estimates from mark-recapture analyses (Arnbom 1987; Friday 2000; Friday et al. 2008). False rejections of true matches, and field protocols that photograph individuals using non-symmetrical markings on left and right sides, can result in a dataset containing multiple encounter histories for an individual (Hiby et al. 2012). The extent to which match uncertainty biases resulting estimates of demographic parameters requires investigation for each study. A recent exercise suggests that the differences in protocols among individuals and labs will result in different biases in parameter estimates, as long as protocols require investigators to force an inherently subjective matching process into a binary (match/not-a-match) outcome (Urian et al. 2015). This issue has become increasingly important as long-term cetacean studies have switched from film to digital photography (e.g., Chapter 3), which may introduce heterogeneity in matches (Urian et al. 2015). Ideally, one would quantify the level of uncertainty associated with any given match, and incorporate that uncertainty into resulting demographic parameter estimates (Urian et al. 2015).

The aim of this chapter was to acknowledge explicitly the uncertainty in the photo matching process using six years of photographic data from Pacific white-sided dolphins (Chapter 3), and quantify the extent to which match uncertainty affects the bias and precision of abundance and survival estimates. This chapter also describes the photo-identification methods used in this chapter and Chapter 3.

2.2 METHODS

2.2.1 Study area

The Broughton Archipelago is located between Vancouver Island and mainland British Columbia (BC), Canada. This remote region is characterized by a complex geography of hundreds of islands, and narrow inlets, and fjords (Figure 2.1).

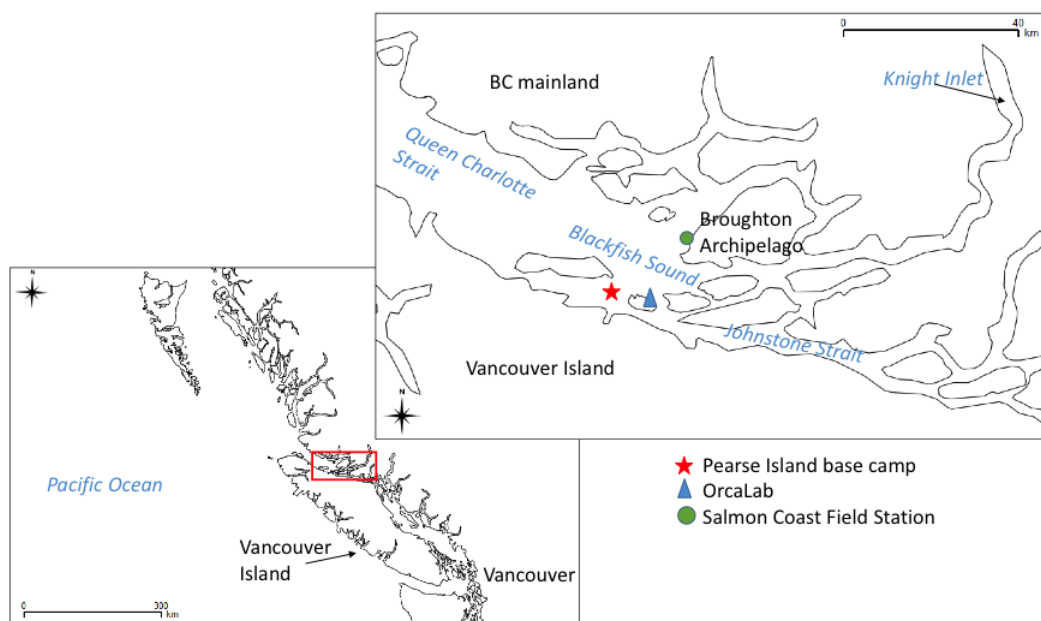


Figure 2.1: Map of the Broughton Archipelago study area in British Columbia, Canada.

2.2.2 Data Collection

To ensure the greatest possible consistency in data collection with an existing, long-term catalogue and to maximise the number of long-term resightings (Chapter 3), field protocols in the current study followed those of the previous study (Morton 2002) as closely as possible.

Photo-identification surveys for Pacific white-sided dolphins in the Broughton Archipelago were conducted by Alexandra Morton (“AM”, Raincoast Research Society) using small (3-6m) research vessels from October 1984 to 2005 (the “historical” study or catalogue) and by Erin Ashe (“EA”) from 2008-2013 (the “current” study). Photo-ID effort was distributed throughout the year, but was restricted by weather conditions. In both the historical and the current studies, groups of dolphins were found using a combination of boat-based searches and from radio reports and communication from local mariners. The historical study was conducted from a research station in the Broughton Archipelago study area. Land-based dolphin detections were made from the research station through regular visual scans and from constant monitoring of stationary hydrophones for dolphin vocalisations (Morton 2002). Reports from a second, stationary hydrophone network (Orcalab) monitored 24 hr/day (Deecke et al. 2010; Morton 2002), were used in the current study to direct dolphin searches. Searches and photographic encounters were limited to a maximum Beaufort sea state of two due to safety and sightability constraints (Evans 2004).

For each encounter during the historical study, general location and an estimate of group size was made in the field and recorded. Total group size was estimated by tallying the number of individuals in smaller subgroups (typically 2-8 individuals) at intervals throughout the encounter (Morton, 2000). In the current study, a group was defined as all of the dolphins encountered in a discrete location in a day. Finer scale information (e.g., groups defined using a 15m ‘chain rule’; Smolker 1992) on group composition was collected from 2011 onwards to inform studies of sociality. Encounters with dolphins lasted a minimum of 20 minutes during which I recorded: an estimate of group size (minimum, maximum, and best estimate); location; predominant group activity state (although scan-sample data were collected at 5-minute intervals during longer encounters), and number of calves in the group (minimum, maximum, and best estimate). Photographs were collected with SLR (1987-2005) and digital SLR (2008-2013) cameras.

The historical study aimed to collect photographs of as many members of the group as possible, using a SLR with high-speed (1600 ASA) black and white film. When complete coverage was impractical, due to large group size, erratic behaviour, or logistical constraints (e.g. weather, daylight), an effort was made to prioritise photographing every well-marked individual.

Groups of dolphins were approached slowly in an effort to reduce the probability of bow-riding behaviour, which brings some individuals, especially juveniles, very close to the boat and makes other individuals less available for photographic capture. Large groups were generally traversed in two passes to try to obtain photos of both left- and right-hand sides. In the first pass, individuals were photographed in sub-groups as each sub-group came into photographing range until the far edge of the group was reached. In the second pass, the group was traversed in the opposite direction and at the same angle as the first pass and individuals were photographed in sub-groups in the same manner as the first pass. The encounter ended when all animals had been approached at least once or when conditions changed.

Both left and right sides of the dorsal fins were photographed. As each dolphin came into range, a decision was made as to whether the animal had already been photographed during the session or if the animal was not well-marked enough to warrant subsequent identification. In each of these cases, AM refrained from taking photographs. Dolphins were photographed almost exclusively while engaged in slow, milling (non-directional) behaviour in tight groups (behaviour typically observed following medium to high speed travel). The non-directional/milling behaviour facilitated photographing both right and left sides of the dorsal fin.

Photo-ID data collection in the current study adopted many of the field methods of the historical study, with the advantage that digital photography allowed far more photographs to be taken than during the historical study. In the current study, no attempt was made to target well-marked individuals. Instead, the photographs were collected with the aim of giving marked and unmarked dolphins an equal probability of being photographed. When all group members could not be photographed due to weather, unworkable behavioural state (e.g. high-speed travel and active foraging), or large group size (>100), an effort was made to collect a representative sample of the group as a whole.

In both studies, photo-ID efforts ended when dolphins were engaged in activity states (e.g., high-speed travel) that resulted in water splashing around the dorsal fin, which results in poor quality photographs. An encounter ended when all of the members of the group had been approached, if a representative sample had been collected, if weather conditions changed or, in

the current study, when the time limit of the research permit (30 minutes per sub-group) was reached.

2.2.3 Photo-processing methods

2.2.3.1 Photo-scoring: black and white film photographs from historical study

Film canisters were mailed to a photographic laboratory where a contact sheet could be developed and mailed back to AM. To save costs, AM then examined the contact sheets and selected for printing those images of marked individuals that appeared to be of sufficient quality to make an identification. The images were developed into 9 x 13 cm prints. A Peak loupe eyepiece (8X) was used by AM to identify individual dolphins from the prints developed from each encounter. All blurry images, images with fins blocked by water splash and photos of animals with insufficient marks to be identifiable animals were rejected. As a coarse filter, AM's cost-saving measure to print only high-quality photographs of distinctive animals was considered roughly equivalent to the scoring criteria (outlined below) used in the current study. I subsequently scored these photos according to standardised criteria for scoring photo quality and animal distinctiveness, but it should be noted that the historical catalogue represents a subset of the photographs that AM took. With few exceptions, I found that AM's subjective decision of which negatives to print corresponded roughly to the current study's criteria with respect to photo quality (3.0 or higher) and distinctiveness (D1 or D2). Photographs of sufficient quality and distinctiveness were included in the mark-recapture analysis.

To facilitate ease of matching (see below), dorsal fin photographs were catalogued according to categories based on their most obvious feature. Presumed males were catalogued as "males" based on the hypothesis that old males in this species possess an extremely falcate or drooping, "banana-shaped" fin (Morton 2000). The identification categories included: male; square notch; V-notch; little nicks; leading edge nick; and triangular.

2.2.3.1 Photo-scoring and matching: digital photographs from current study

All photographs of a dorsal fin were graded for quality and distinctiveness in two independent stages (Urian et al. 2015). Information on quality, distinctiveness and other attributes were

entered into Photo Mechanic 5 (Camera Bits¹) photo-processing software. First, photographs were graded for photographic quality using a standardized set of photographic quality criteria (Appendix 1) ranging from 1 (poor quality) to 3.3 (high quality) adapted for this study from image quality scoring criteria used in studies of Moray Firth bottlenose dolphins (Wilson et al. 1999). The dorsal fin was chosen as the feature for evaluating natural markings (rather than markings on the flanks, for example), to maintain consistency with the historical study (Morton 2000) and to allow left and right side markings to be pooled, because data were expected to be too sparse for separate left and right side analyses (Wilson et al. 1999). Dorsal fins of Pacific white-sided dolphins varied among individuals from extremely well marked with nicks and scars, to completely clean, unmarked fins. Thus, not all dolphins were distinctive enough to be included in mark-recapture analyses. A separate analyst scored each photograph of quality 3.0 or higher to grade the distinctiveness of each individual. The distinctiveness score ranged from D1 (Highly distinctive) to D4 (Unmarked) (see Appendix 1). A separate set of analysts conducted the matching step (below).

2.2.3.2 Photo matching: both studies

In the historical study, each dolphin in the photo-identification catalogue was assigned a unique alpha-numeric identification code once an identification was made. In the current study, a team of six analysts (including EA) conducted the photographic matching of the current study's catalogue in Photo Mechanic 5. A team of two analysts (trained by EA) conducted the photographic matching between the historical and current catalogues.

The pattern of nicks on the trailing edge of the dorsal fin was the primary mode of identification. Fin shape provided a secondary indicator. Dorsal notches had to match in size, angle of tear and other details. The definition of a match allowed for acquisition of marks over time, but no loss of nicks, that is, if there was an additional notch on the more recent photo, but the original nick or notch was present in both photographs, then this was scored as a potential match. Restriction of matches to nicks, notches and tears meant that both left- and/or right-side photographs could be used to identify individuals.

¹ <https://store.camerabits.com/products/photo-mechanic-version-5>

Only photographs of quality 3.0 or higher and with a distinctiveness score of D1 or D2 (i.e., symmetrical markings that would be recognized from both sides) were included in the analysis (Appendix 1). This protocol was chosen to reduce misidentification errors, while allowing both left and right side photographs to be included in the analysis. Photographs of individuals believed to be calves (i.e., small, ruffled dorsal fin, orange colouration, foetal fold marks on the body, photographed alongside mother) were excluded from the analysis. The photo-matching protocols from the historical study were not well documented (i.e., only photographs of high quality were ever printed, but the negatives could not be scanned to estimate the proportion discarded). The photographs from the historical study were all of relatively high quality, but to ensure between-study consistency, I subjected the photographs from the historical study to the same quality scoring protocols as the current study. In that process, 71% of the photographs were of sufficient quality to enter into the analysis (i.e., quality score 3.0 or higher, and distinctiveness of D1 or D2). In contrast, only 10% of digital photographs in the current study were of sufficiently high quality to enter into the analysis. This suggests that AM's decision to print only the highest quality photographs served as a good coarse filter to eliminate poor quality images, and that the subsequent quality scoring made the photographs from the two studies as comparable as possible. The high-quality subset of photos from both studies was then matched within each photographic encounter, and each individual was assigned a preliminary identification code. Individuals within an encounter were matched and a certainty score of "Certain", "Likely", or "Possible" was assigned to putative matches between pairs of photos based on the degree of confidence in each match. "Certain" was assigned if the analyst was 100% confident, "Likely" if $\geq 90\%$ confident, and "Possible" if $\geq 50\%$ confident in the match.

An encounter history of 1s and 0s, corresponding to whether a putative individual was or was not detected during each sampling encounter, respectively, was created for each individual and certainty level for this analysis.

2.2.4 Available data

The number of sampling occasions and the months in which sampling took place each year varied widely throughout this study. Between 2008 and 2013, a total of 34 photographic

encounters with dolphins occurred. Of these, 32 encounters contained photographs of sufficient quality and distinctiveness to enter the analysis for the “Certain” and “Likely” certainty levels, whereas all 34 encounters contained photographs that were of sufficient quality to create encounter histories at the “Possible” certainty level. The single encounter from 2008 was not included in the analysis due to low sample size (only 2 individuals were identified; Figure 2.2).

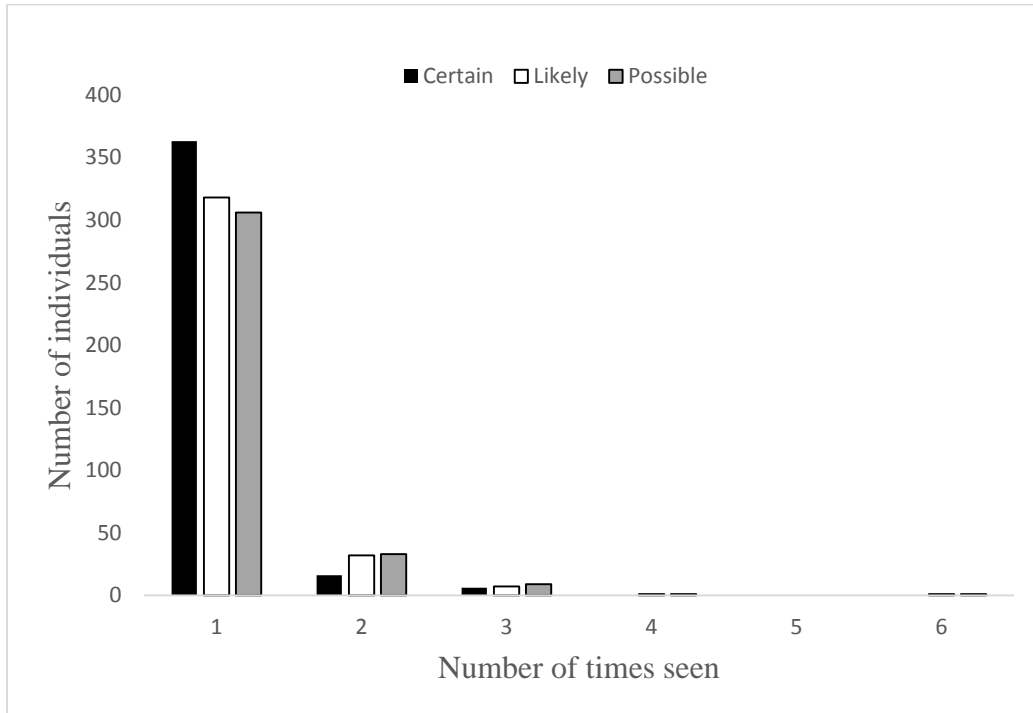


Figure 2.2: Number of times an individual was seen, tallied for each certainty level.

2.2.5 Estimation of abundance

The three sets of encounter histories for each certainty level were analysed to produce three estimates of abundance. Chapman’s modification to the Lincoln-Petersen two-sample estimator to account for small sample bias was used to estimate abundance at each certainty level (Hammond 1986; Seber 2002).

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

where

\hat{N} =abundance estimate; estimate of population size

n_1 = the number of individuals detected during the first sampling occasion

n_2 = the number of individuals detected during the second sampling occasion

m_2 = the number of individuals re-sighted. That is, the number of animals captured during the first sampling occasion that were also captured during the second sampling occasion.

For this analysis, each year was treated as a sampling occasion, such that recaptures were restricted to individuals seen in adjacent pairs of years. Given the low number of resightings in adjacent pairs of years and the comparatively large number of photos taken in 2010, a separate within-year analysis was conducted for 2010 (details below).

Variance was estimated as:

$$Var(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

Log-normal 95% confidence intervals were calculated (Borchers and Buckland 2002) as \hat{N}/d to $\hat{N} * d$, where

$$d = \exp\left\{z_{\alpha} \sqrt{Var[\ln(\hat{N})]}\right\}$$

$z_{0.025} = 1.96$ for a 95% CI

and

$$Var[\ln(\hat{N})] = \ln\left\{1 + \frac{Var(\hat{N})}{\hat{N}^2}\right\}$$

2.2.6 Meeting model assumptions

Population closure was assumed over the time intervals used in the abundance estimation analysis. Assuming demographic closure (no recruitment or mortality) over a year is

reasonable, considering the exclusion of calves and juveniles from the analysis, the comparatively long inter-birth interval predicted for this species (as long as 4.7 yrs), and the maximum longevity (e.g., reports of 46-year-old reproductive-age females) of Pacific white-sided dolphins (Taylor et al. 2007a). Geographic closure (no immigration or emigration) was also assumed for the sake of convenience in this analysis of the effect of match uncertainty, but it was no doubt violated. There are records of resightings of individuals over long time periods, however the data to assess within- and between-year movement rates are sparse and the closure assumption was likely to have been violated to some unknown degree. The primary objective of this exercise was to assess the relative importance of match uncertainty on the resulting abundance estimates, rather than generating a robust abundance estimate for use in decision-making (Chapter 3).

The random sampling approach used during photographic encounter occasions reduced the chance of violating the assumption of equal probability of capture within a sampling occasion. However, this assumption is difficult to meet fully for any cetacean population (Hammond 1986). Heterogeneity in capture probabilities can stem from differences in age, sex, social factors and variation in site fidelity among individuals (Pollock et al. 1990) and individual variation in behavioural responses to boats (Lusseau 2003; Williams et al. 2002b; Williams et al. 2002c). A higher probability to capture and recapture well-marked individuals can also introduce heterogeneity. Protocols to subset based on minimum photographic quality and distinctiveness criteria, along with the separation of these two factors at the matching stage, reduced the chance of introducing heterogeneity due to variation in distinctiveness.

Photo-identification sampling methods are unlikely to affect the probability of recapture in most cetacean studies (Hammond 1986). Dolphins are not expected to become trap-happy or trap-shy as a consequence of being photographed. There was no obvious behavioural reaction to photo-identification in this study, with the exception of dolphins being attracted to the boat. To minimise this effect, once dolphins close to the boat were photographed once, the research boat speed was reduced or the engine shut down until the “bow-riders” travelled away from the research boat, or a different part of the group was available for sampling.

Random sampling was prioritised both within and between encounters. The vast majority of encounters occurred on different days, often separated by weeks or even months. Given the low rate of recapture, it is unlikely that the study resulted in a major violation of the assumption that the second sample was a random sample with respect to the first, but it is difficult to assess whether this assumption was violated.

Dolphins acquire distinctive, long-lasting marks over time (Hammond 1986; Wilson et al. 1999; Würsig 1990) and there is qualitative evidence for mark-acquisition in this study. Nick acquisition may have occurred over the course of years, but this was not explicitly quantified. Nicks acquired after first identification were unlikely to obscure the marks used for subsequent identification, because other indicators (e.g., fin shape) were also used. In some cases, two photographs taken years apart could be scored as a “likely” or “possible” match if they differed in a way that is consistent with nick acquisition over time. The probability of mark loss was reduced by restricting the data to photographs of individuals with seemingly permanent, distinctive features and excluding those with less-permanent marks such as conspecific tooth-rakes. However, several individuals with dorsal fins missing may have lost their fins during the course of the study, and a few individuals with fresh wounds were observed. Misidentification was reduced by the photo-processing criteria and investigated here using the certainty scoring criteria.

2.2.7 Estimating adult annual survival rate

Sets of annual encounter histories at each certainty level from 2009-2013 were created to estimate annual survival rate using a Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965)(Chapter 3). The analysis was carried out in Program MARK (White and Burnham 1999) version 6.1. The primary objective of this exercise was to assess the relative importance of match uncertainty on the resulting survivorship estimates, rather than generating the best estimate for use in decision-making (Chapter 3). No goodness of fit tests were conducted to test whether the resulting estimates were accurate; instead, the aim was simply to explore how the estimates changed as less-certain matches were added to encounter histories.

2.3 RESULTS

The number of individual dolphins photographed and recaptured in each sampling period and at each certainty level is shown in Table 2.1. Including less certain matches resulted in fewer individual dolphins overall because previously unmatched dolphins initially categorised as two individuals, were then matched, resulting in a single animal. One of the aims of this analysis was to examine the effect that match certainty had on abundance estimates. For the current study, sampling effort was greatest during 2010 and high in 2011, resulting in the most number of recaptures between these years. Given the low number of recaptures in 2009 and 2011-2013 and the low resulting precision, data from 2011-2013 were combined in an attempt to boost the number of recaptures. However, 2010 had a substantially higher number of recaptures within the year, so data were also analysed within 2010 (Table 2.1).

A two-sample abundance estimator at each certainty level produced abundance estimates of individually identifiable dolphins in the population from 2008-2012. Abundance of marked dolphins at the “Certain” certainty level, ranged from a low of 985 (CV=0.55) in the “2011-2012+2013” sample, to a high of 2,005 (CV=0.31) in 2010 (Table 2.2). As expected, the “Certain” matching level produced abundance estimates that were greater than the estimates at the “Likely” or “Possible” levels in the same pairs of years (Table 2.2).

In 2010-2011, for example, abundance was estimated as 1,404 (CV=0.34) at the highest level of certainty (“Certain”) and at 1,159 (CV=0.31) at the “Possible” match level. Using only the “Certain” match level also lowered precision of the abundance estimates across certainty levels (Table 2.2).

Table 2.1: Number of individual dolphins photographed in the two sampling periods to be compared (n1, n2), and the number of matches between these (m2), for each of three certainty levels. Data were compared for one year to the next from 2008-2013, and additionally for 2011 compared to 2012-13, and for two time periods within 2010.

	2008:2009	2009:2010	2010:2011	2011:2012	2012:2013	2011:2012+2013	2010a:2010b
Certain							
n1	1	37	247	33	2	33	106
n2	37	247	33	2	55	57	149
m2	0	4	5	0	0	1	7
Certain+Likely							
n1	1	37	245	33	2	33	140
n2	37	245	33	2	55	51	244
m2	0	4	5	0	0	2	18
Certain+Likely+Possible							
n1	1	37	239	33	2	33	137
n2	37	239	33	2	55	57	241
m2	0	5	6	0	0	2	24

Table 2.2: Two-sample estimates of abundance for pairs of years from 2009-2011, within 2010, and for 2011 with pooled data for 2012 and 2013.

Certainty	Nhat	log-normal	
		95% CI	CV
2009-2010			
Certain	1,884	(922, 3,848)	0.38
Certain+Likely	1,869	(915, 3,816)	0.38
Certain+Likely+Possible	1,513	(787, 2,907)	0.34
2010-2011			
Certain	1,404	(736, 2,680)	0.34
Certain+Likely	1,393	(730, 2,659)	0.34
Certain+Likely+Possible	1,159	(640, 2,103)	0.31
Within 2010 only (April-June and July-November)			
Certain	2,005	(1,103, 3,645)	0.31
Certain+Likely	1,817	(1,233, 2,678)	0.20
Certain+Likely+Possible	1,335	(962, 1,852)	0.17
2011-2012+2013			
Certain	985	(359, 2,701)	0.55
Certain+Likely	656	(276, 1,564)	0.47
Certain+Likely+Possible	656	(275, 1,564)	0.47

2.3.1 Estimates of annual survival rate

Apparent annual survival rate for well-marked adult dolphins was estimated using a CJS model at each certainty level from 2008-2012. The model for constant survival and time-varying capture probability had the best support from the data. The estimates of adult annual survival for the “Certain” matches was estimated as 0.458 (SE=0.288) (Table 2.3). The implausibly low estimates (i.e., much lower than the estimates from models using more data in Chapter 3) presented in Table 2.3 are likely due to the low capture probability over the sampling period. However, as less certain matches were included in the analyses, the apparent survival estimates increased slightly and the precision of the estimates also increased slightly (Table 2.3).

Table 2.3. Survival rate estimates derived from three different levels of certainty in photographic matching from 2008-2012.

Certainty level	Survival	SE	95 % CI
Certain	0.458	0.288	(0.183, 1)
Likely	0.460	0.287	(0.184, 1)
Possible	0.468	0.276	(0.191, 1)

2.4 DISCUSSION

The study demonstrated that as less certain matches were included, abundance estimates decreased (assumed to become negatively biased) with an increase in precision. Although the sample size is low, this effect was most obvious in the within-2010 analysis, when effort was highest and where there were a substantial number of matches. Estimates of survival rate also increased and showed an apparent increase in precision.

The trade-off illustrated in this study exemplifies the need for researchers and end-users of science to make an explicit decision about whether it is better to include uncertain matches to increase sample size to get a more precise (albeit biased) estimate, or to prioritise accuracy over precision. This decision is inherently case-specific. If monitoring for overall trends in abundance (Gerrodette and Forcada 2005; Wilson et al. 1999), precision may be paramount and bias less of a concern, as long as the bias remains constant over the period of interest

(Taylor and Gerrodette 1993; Taylor et al. 2007b). For assessing sustainable limits to human-caused mortality under frameworks such as Potential Biological Removal or modelling extinction probability, accuracy may be prioritised over precision, because, while PBR is robust to uncertainty, it is not robust to bias (Wade 1998). When the trade-off makes the difference between having a biased estimate versus no estimate at all, then it is better to report an estimate, as long as the sources of bias are acknowledged transparently. Ideally, one could quantify that bias using an approach such as the one presented here. Where sample sizes are modest, one should try to strike a balance between bias and precision.

In this study, abundance estimates were found to vary among years and certainty levels. Because of inter-annual variation in effort and the relatively low rate of recapture in 2009 and 2011-13, it is most informative to compare within-year estimates from 2010. Within 2010, the abundance estimates ranged from 2,005 (95% CI: 1,103-3,645) for “Certain” matches to 1,335 (95% CI: 962-1,852) for “Certain+Likely+Possible” matches. The “Possible” and “Likely” categories may contain false positive matches, which will cause negative bias in abundance estimates (Yoshizaki et al. 2009). However, false positive errors typically arise from inclusion of poor-quality photographs (Barlow et al. 2011; Friday et al. 2008; Stevick et al. 2001) and only the highest quality photographs were included in this analysis.

It is difficult to be prescriptive about when to err on the side of including or excluding uncertain matches. Some rules of thumb may be inferred from the assumptions of the statistical models used. For example, the Chapman modification to the Lincoln-Peterson estimator is robust to small-sample bias as long as the sum of captures and recaptures (n_1+n_2) exceeds abundance (Robson and Regier 1964). This condition was not met in this study owing to variability in effort over the course of the study and the low probability of recapture due to the large population size. For highly mobile species, movement may already affect precision and that may lend support for prioritising accuracy – random movement in and out of the study area does not introduce bias but does lower precision (Kendall et al. 1995). If movement is non-random or when there is heterogeneity in capture probability among individuals, simple two-sample estimators produce biased estimates of abundance (Kendall 1999).

In the current study, my decision about the certainty threshold to use for demographic parameter estimation in Chapter 3 was dictated by my aim to provide encounter histories that could be used to accomplish multiple objectives simultaneously. I intended to use the data to make some preliminary inferences about social structure and acoustic behaviour in this species (Chapter 5), which had not been explored previously. As a result, I decided to be consistent with the historical study and with traditional mark-recapture studies and used only certain matches. Using the two other levels of certainty could have consequences for association patterns and assigning recordings of vocalisations to a group containing a certain individual. With respect to demographic analyses, the appropriate quality threshold was constrained by having inherited a long-term photo-ID catalogue that used pre-existing thresholds with respect to photo quality. In retrospect, the protocols used in the historical catalogue (Morton 2000) turned out to be quite comparable to the standards I used for the “certain” matching criteria. Consequently, I used the “certain” threshold to determine a match to allow me to use both the earlier and newer data in the same analyses. If I were initiating a new study with the exclusive aim of estimating demographic parameters, I would probably have included an analysis with a lower matching threshold (e.g., “Likely”) in order to increase the number of recaptures.

The Chapman estimator can be robust to violation of the closure assumption. If variation in capture probability is only associated with time, the estimator produces an unbiased estimate for the first sampling occasion if only additions from birth or immigration into the study area occur or an unbiased estimate for the second sampling occasion if only removals from death or emigration occur, as in breeding colonies or in migratory species (Kendall 1999). Pacific white-sided dolphins are not known to be migratory (Forney and Barlow 1998; Leatherwood and Reeves 1983) and evidence from this study (Chapter 3) for short and long-term residency to the study area supports this.

2.4.1 Future directions

It is a well-known problem that traditional mark-recapture methods do not allow for misidentification of animals that are recognised from natural markings (Link et al. 2010). Previous studies have considered effects of photo quality and animal distinctiveness on bias and precision in abundance and survivorship estimates (Friday 2000; Stevick et al. 2001). Although match certainty is clearly confounded with photo quality and animal distinctiveness,

the current study is novel in terms of examining match uncertainty explicitly. The aim was to evaluate how big a problem uncertainty in individual identification could be in mark-recapture models for Pacific white-sided dolphins, and it demonstrated that abundance estimates could potentially be biased by ~33% if this source of uncertainty were ignored (Table 2.2).

It is difficult to evaluate the effect of match uncertainty on precision of estimates, due to low number of recaptures. The next problem, of course, is how to resolve this.

This study has looked at misidentification in a novel way by examining the impact on abundance and survival estimates that arises at the processing level. Conventionally, technicians processing ID photographs are instructed to assert that two photographs are or are not a match. The current study shows that there is value to having matchers record data on their level of certainty that two photos represent a match, because there is useful information contained in that certainty level. It may be unusual that point estimates of abundance could vary by as much as a third due to match uncertainty, as was found in this case, but the approach could easily be incorporated in other photo-ID studies (Urian et al. 2015). In many cases, the (effect size of match uncertainty may be negligible, but it will be impossible to know this unless matching protocols instruct matchers to record their level of confidence in a match so that this information can be used at the analysis stage.

The study also shares a common theme with previous studies of misidentification in mark-recapture studies arising from issues of data quality. As a result, much of the advice for coping with this source of misidentification repeats what has been said in other studies. Mark misidentification can arise when the sampling (e.g., photo-ID) introduces heterogeneity in the observer's ability to recognise marks. One study that identified a minimum quality level when including photographic data in a mark-recapture analysis used two kinds of tags (i.e., photo-ID and genetics), placed bounds on the uncertainty, and incorporated that uncertainty in a bootstrap estimate of the variance around the abundance estimate (Stevick et al. 2001). Conceptually, the recommendation of Stevick et al. (2001) could apply here as well: encounter histories corresponding to the three certainty levels could be resampled via a bootstrap, to incorporate this source of uncertainty in estimates of abundance, survival and their variances. This will be more pragmatic in the short term than the suggestion to use double-tagging to

minimise or avoid misidentification in the first place (Link et al. 2010; Lukacs and Burnham 2005).

Misidentification can also arise when the marks change through time. With a large enough number of individuals followed through time, one may be able to build mechanistic models to understand how marks evolve. Quantifying this effect can then allow analysts to account for misidentification in the resulting demographic parameters. Unfortunately, simulation studies suggest that these mechanistic models will only work when capture probability is higher than was observed during this study (i.e., >0.2) and the absolute number of resightings is sufficiently large to have enough data to estimate demographic parameters and changes in marks simultaneously (Yoshizaki et al. 2009).

Statistically, the process of misidentification that this study discusses is quite challenging to address using traditional likelihood methods, but could be handled in a straightforward way using Bayesian methods (Link et al. 2010). Bayesian mark-recapture methods are an active research area (Schofield et al. 2009). As Bayesian survival estimators become more commonly used and associated code made accessible to population ecologists (Gimenez et al. 2009), addressing misidentification in a Bayesian framework may be the next logical step. By integrating all known sources of uncertainty into a single analytical framework, Bayesian methods offer the potential to assess whether misidentification (or any other source of uncertainty) has the potential to affect what is perhaps the most important decision – does any of this uncertainty affect the ultimate category of risk to which we assign a species (Brooks et al. 2008)?

Chapter 3

ESTIMATING SURVIVAL AND ABUNDANCE OF PACIFIC WHITE-SIDED DOLPHINS FROM PHOTO-IDENTIFICATION DATA USING MARK-RECAPTURE METHODS

3.1 INTRODUCTION

3.1.1 The importance of monitoring wildlife population health

The study of vital rates (life history parameters) is fundamental to understanding wildlife biology and ecology, conserving, and managing species and populations (Lebreton 1992, Matthiopoulos et al. 2008) and to inform conservation status assessments (Crouse et al. 1987, Doak et al. 1994, Thomas 1996, Wisdom *et al.* 2000, Eberhart 2002). Monitoring vital rates through time allows assessments of population dynamics, is important to help understanding of how species interact with each other and their environment, and enables prediction of how wildlife populations may respond to a changing environment that is increasingly affected by human activities (Ceballos and Ehrlich 2002; Vitousek et al. 1997). Population dynamics result from a trade-off between mortality and recruitment.

3.1.2 Monitoring vertebrate populations

With few exceptions (e.g., southern resident killer whales (*Orcinus orca*; Bigg 1987; Ford et al. 2000); North Atlantic right whales (*Eubalaena glacialis*; 1994), it is rare to have a complete census of a marine mammal population. Imperfect detection is the rule, rather than the exception. Methods to sample portions of populations are routine in studies of terrestrial species that burrow or are camouflaged (Bailey et al. 2004; Karanth and Nichols 1998; Seber 2002). Cetaceans can be distributed across difficult-to-access oceans and spend the majority of their time underwater. A number of methods are available for sampling marine mammal populations (Forney 2002, Evans and Hammond 2004) including photo-identification of natural markings of individuals (Hammond 1990, 2009, 2010). A number of statistical methods are available to use those samples to make robust inference about abundance or

density of individuals, including: inference from cue counts; mark-recapture from individual identification photos (Hammond 1986); distance sampling methods, which include point and line transects (Buckland et al. 2001); emerging methods to estimate density from acoustics (Küsel et al. 2011; Marques et al. 2009); and model-based approaches such as density surface modelling (Hedley et al. 1999; Hedley and Buckland 2004). Although most of these methods estimate population size, mark-recapture methods can be used also to estimate survival (and its complement, mortality) and reproductive parameters (e.g., calving probability, age at first reproduction, and inter-birth interval) (Hammond 1990).

In a sense, mark-recapture studies in cetaceans began with the use of *Discovery* tags, which were marks shot into the blubber of commercially targeted species and recovered during whaling operations as a way to understand movements, including migration (Brown 1975). For a variety of practical and statistical reasons, estimating abundance and survival from *Discovery* tags was not very reliable, but the *Discovery* tagging efforts did accomplish their primary objective to provide useful information on migratory destination and movement rates (Buckland 1990; Buckland and Duff 1989). By the 1960s and 1970s, a number of non-lethal studies were reporting that many whale species, including humpback whales, were naturally marked (Schevill and Backus 1960) and, as a result, individual whales could be sighted repeatedly (Katona et al. 1979). Sighting records can be used in statistical models to allow estimation of demographic parameters such as survival and abundance, but secondarily, good photographs can also facilitate assessment of individual body condition (e.g. scars, skin condition), improve understanding of social structure (Connor et al. 1998; Gowans et al. 2001), infer migratory destination (Baker et al. 1986; Calambokidis et al. 2001; Darling 1983), and estimate frequency and severity of human interactions (Knowlton and Kraus 2001; Kraus 1990).

Photographs of individually identified animals provide “encounter histories” that can be used to track individuals through time, and this means that photo-ID datasets lend themselves to the kind of mark-recapture statistical analyses that have been in use for decades with terrestrial species (Hammond 1986, 1990a, b). Mark-recapture methods are widely used to estimate abundance and survival. When estimating abundance, mark-recapture methods use information from the sampled (captured) animals to make inference about those that have

not been captured, and therefore the population as a whole. When estimating survival, the statistical inference is only for the sampled animals, which are assumed to be representative of the population (Seber 1982).

In the simplest case of a two-sample study to estimate the size of a “closed” population (i.e., a population that is assumed to be closed geographically and demographically to births, deaths, permanent immigration and emigration), the approach is to photograph a sample of marked individuals over an explicit sampling period, recapture a second sample at a later date, and use the resulting information on the proportion recaptured to estimate the total number of animals in the population (Le Cren 1965; Lincoln 1930; Seber 1982). Mark-recapture statistical models make several assumptions (see Chapter 2) to make abundance estimation tractable, such as geographic and demographic closure for certain periods, assuming that all individuals are equally likely to be sampled, that sampling is random, and that all individuals can be identified with certainty (either on the initial capture or on the recapture; Hammond 1986; Seber 2002). Many real-world studies fail to meet all of these assumptions (Pollock et al. 1990; Seber 2002; Williams et al. 2002a) and, as the field of mark-recapture statistics has matured, a variety of models have been developed to allow certain assumptions to be relaxed (Amstrup et al. 2010; Williams et al. 2002a).

Key tasks in mark-recapture studies include the need to understand the assumptions in any given method, to assess how likely it is that a given study has violated those assumptions, and the direction and magnitude of bias likely to be introduced as a consequence of violating assumptions. Many methods are robust to some violation, whereas other violations could introduce sufficient bias to yield abundance estimates that are of questionable use in conservation and management. Most studies involve a balancing act between bias and precision. One example of one such trade-off between bias and precision was shown in Chapter 2.

Quantifying and understanding patterns of individual survival probability is key to understanding population biology (Lebreton et al. 1993), but it can be challenging to estimate average survival probability, because time of death is usually unknown and undetected (Lebreton et al. 1992). Identification of factors that explain variability in the probability that

individuals will or will not survive is essential to making defensible management decisions about genetic bottlenecks, whether culling predators will help prey species recover (Matthiopoulos et al. 2008; Morissette et al. 2012), how to target certain age or sex classes to improve recovery of endangered species (Beissinger and Westphal 1998) and, ultimately, to understanding what is driving declines so we can prevent or reverse them (Currey et al. 2009b; Slooten et al. 2000).

Variation in adult survival rate has the greatest potential to influence population growth rate of long-lived animals (Sandercock 2006). Survival rates for cetacean species have been estimated using a variety of mark-recapture methods for several species, including humpback whales (*Megaptera novaeangliae*, Barlow and Clapham, 1997; Larsen and Hammond 2004; Ashe et al. 2013; Currey et al. 2009; Mizroch et al. 2004), grey whales (*Eschrichtius robustus*, Bradford et al. 2006; Bradford et al. 2008), and bottlenose dolphins (Currey et al. 2009b; Silva et al. 2009a). This approach can be especially useful in cases where the statistical power to detect trends in abundance is low, as is often the case in studies of long-lived, slowly reproducing taxa, including cetaceans (Gerrodette 1987, Wilson et al. 1999, Taylor et al. 2007a). In the North Pacific, empirical estimates of survival rate for small cetaceans are rare (Taylor et al. 2007b). As a result, our ability to understand which species are most in need of protection relies heavily on estimates of abundance, but imprecision in some cetacean abundance estimates can result in an inability to detect all but the most catastrophic declines (Taylor et al. 2007a). Even in well-surveyed waters under the jurisdiction of the U.S., statistical power to detect even catastrophic declines in offshore (pelagic) dolphin species is 0 for many stocks (Taylor et al. 2007a).

Survival rate has not been estimated using photo-ID data from Pacific white-sided dolphins anywhere in the species' range, in part due to difficulty of conducting research in their pelagic habitat, although a prediction has been made from life-history tables based on oldest age of bycaught animals (Taylor et al. 2007a). Generally, in the absence of any obvious anthropogenic threat, Pacific white-sided dolphins are considered a low priority for allocation of scarce funding for conservation and monitoring efforts and a low research priority (Stacey & Baird 1991). Because long-term data are required to calculate good estimates of survival (Hammond 1990), it is not surprising that an estimate of survival rate has not been reported for

Pacific white-sided dolphins anywhere in their range. It is somewhat surprising that Canada has not assessed the status of the species since April 1990, given Canada's obligation to consider status of wildlife populations every 5 years; however, that 1990 assessment did call for a re-evaluation if new, quantitative data on demography or threats became available (Stacey & Baird 1991).

In the mainland waters of British Columbia (BC), Canada, a substantial number of Pacific white-sided dolphins can be found year-round in fjords and passageways that can be accessed in good weather using small boats (Morton 2000). Previous research has documented the recolonisation of this species in inshore waters of BC in the late 1980s (Morton 2000) and that study noted that some individuals appeared to be sufficiently well-marked to initiate a small-scale photo-ID study. This study uses the photo-ID data from that study (Morton 2000), adds additional years of data, and uses mark-recapture methods to make inference about the demography of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in an accessible part of their range in inshore, coastal waters of BC.

3.2 METHODS

3.2.1 Study Area

The Broughton Archipelago (Figure 3.1) is a region in BC representing a ~400 km² network of islands and fjords, including 90 km of narrow passages and 200 km of inlets with depths that reach over 500m (Morton 2000). The area is fed by several productive rivers that serve as spawning grounds for five species of Pacific salmon (Morton 2000, Morton *et al.* 2005).

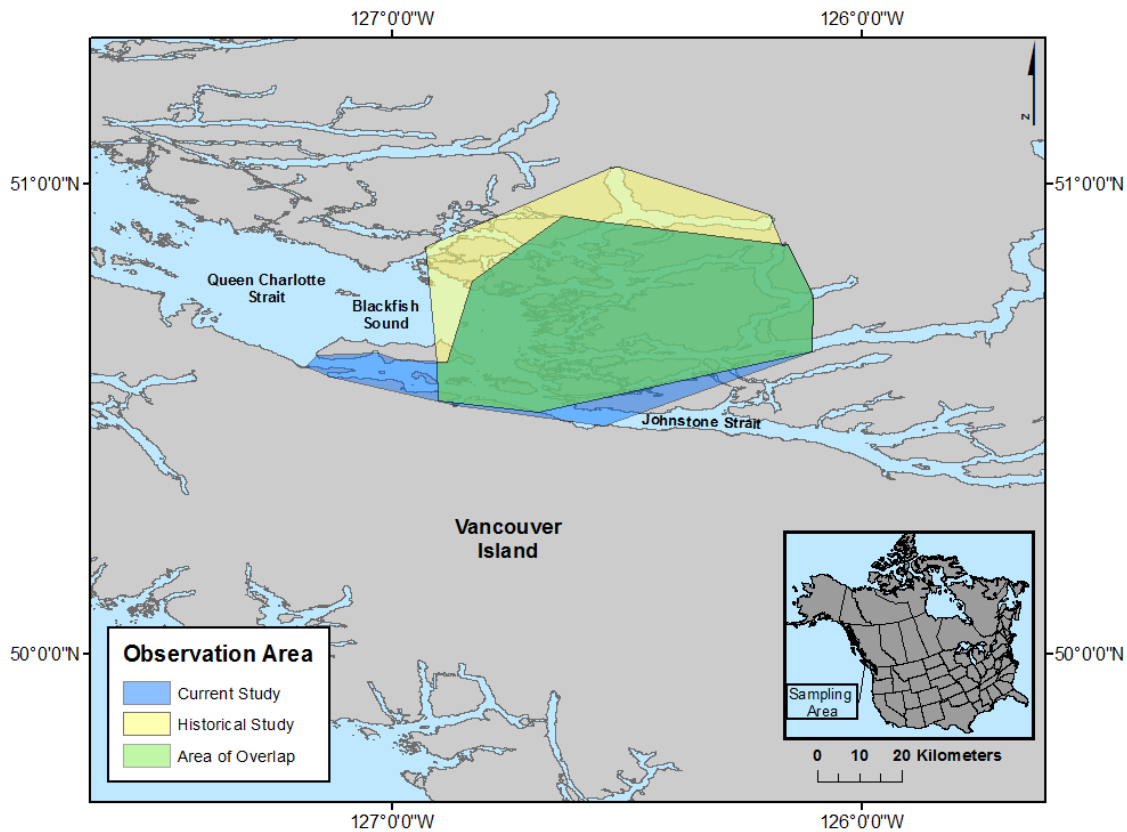


Figure 3.1: Map of the Broughton Archipelago study areas in British Columbia, Canada. The current study area is shown in blue, and the historical study area is shown in yellow. The area of overlap (approximately 70%) is shown in green.

3.2.2 Field methods

Details of the Pacific white-sided dolphin photo-identification survey field methods in the Broughton Archipelago are outlined in Chapter 2.

Although the two studies were based from different field stations (Figure 3.1), they covered largely the same areas (Figure 3.1). The current study tried to search the same areas previously found to be important to Pacific white-sided dolphins (Morton 2000), in an attempt to save costs and reduce search time, increase time spent with the animals, and to maximize the probability that the same animals were being sampled in both studies. The core study areas of the historical and current studies are shown in Figure 3.1, and the polygons representing the core search areas overlap by ~70% (using a spatial join in ArcGIS). At the site of greatest spatial disparity between the two studies, the current study went ~20km farther west than the

historical study; the historical study sampled mainland inlets ~10km farther north than the current study (Figure 3.1). To put this in ecological perspective, the two study areas differed at their widest point of disparity by a distance that an oceanic dolphin school could transit in approximately one hour while swimming at an optimal cruising speed of 5 m/s (Fish and Rohr 1999).

3.2.3 Photo-identification process

All photographs of a dorsal fin were graded for quality and distinctiveness in two independent stages (Urian et al. 2015). First, photographs were graded by an analyst for photographic quality using a set of photographic quality criteria (Appendix 1) ranging from 1 (poor quality) to 3.3 (high quality) adapted for this study from image quality scoring criteria used in studies of Moray Firth bottlenose dolphins (Wilson et al. 1999). Photo-identification photographs were processed and converted into encounter histories using only “Certain” matches (Chapter 2).

3.2.4 Population size estimation

3.2.4.1 Abundance between pairs of years

Abundance was estimated between pairs of years using Chapman’s modification to the Lincoln-Peterson estimator for small sample size (Seber, 2000; Hammond, 1986):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

\hat{N} =abundance estimate; estimate of population size

n_1 = the number of individuals sighted and marked during the first sampling occasion

n_2 = the number of individuals sighted during the second sampling occasion

m_2 = the number of individuals re-sighted. That is, the number of marked animals captured during the second sampling occasion that were also captured during the first sampling occasion.

Variance was estimated as:

$$Var(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

Log-normal 95% confidence intervals were calculated for the abundance estimates (Borchers *et al.* 2002), where \hat{N}/d forms the lower confidence limit and $\hat{N} * d$ forms the upper limit and

$$d = \exp\left\{z_{\alpha} \sqrt{Var[\ln(\hat{N})]}\right\}$$

where $z_{0.05} = 1.96$ for a 95% CI, and

$$Var[\ln(\hat{N})] = \ln\left\{1 + \frac{Var(\hat{N})}{\hat{N}^2}\right\}$$

3.2.4.2 Estimates of abundance from multi-sample closed population capture-recapture models

Heterogeneity in capture probability can introduce bias to abundance estimates derived from mark-recapture analyses (Pollock *et al.* 1990). If the level of bias does not vary among estimates, it may be possible to interpret trends in abundance. However, if bias varies among estimates in the study, interpretation of trends can be compromised. Although population structure and seasonal movements in Pacific white-sided dolphins is poorly understood, differences in movement patterns or residency could influence the rate at which individual dolphins are resighted and therefore introduce variable bias.

To minimise the introduction of heterogeneity from seasonal differences in distribution (and potentially populations), multi-sample closed population capture-recapture models were fitted in Program MARK using data from the winter months (October-March) only. Data from the winter months were only available in years during the historical study, 1991-2002. Days were pooled to form a number of sampling occasions within the six-month winter season in each year. The sampling occasions were formed to maximise captures within the sample and

maximise recaptures between samples. The population was assumed to be demographically closed throughout the sampling interval and geographically closed within the study area.

Abundance estimation was estimated independently for each year by fitting the multi-sample closed population capture-recapture models available in Program MARK (Cooch and White 2012; Otis et al. 1978). Models in which capture probability did not vary (model Mo in CAPTURE terminology, see below) and models in which capture probability varied over time (sampling occasion – model Mt) were fitted. Models that account for a behavioural response to capture (model Mb) were excluded from the model set because there is no evidence that dolphins respond behaviourally (e.g., “trap-happy”, “trap-shy”) to photo-identification collection methods (Hammond 1986) and because small sample size required me to limit the number of candidate models. Abundance of well-marked individuals was estimated independently for each year containing winter (October-March) sampling periods (1991-2002). For each year, model fit was assessed using AIC (Burnham and Anderson 2002).

Using the same datasets for each year, models Mo and Mt were also fitted in program CAPTURE implemented from within program MARK (Otis et al. 1978; Pollock et al. 1990; Rexstad and Burnham 1991). The Selection Criteria based on goodness of fit hypothesis tests of the recapture probability-related model assumptions implemented in program CAPTURE were used to indicate the most likely models for the data (Rexstad and Burnham 1991).

3.2.4.3 Adjusting for proportion of unmarked individuals

Total population size (N_{total}) was estimated by dividing the number of marked dolphins (N_m) by an estimate of the proportion of marked individuals in the population:

$$N_{total} = N_m / \theta$$

The parameter θ was estimated from the proportion of marked individuals using photographs as a sampling unit (i.e., using the data on the proportion of marked animals in each photograph). Note that $\theta = 1 - U$, where U = proportion of photographs containing unmarked individuals (Williams et al. 1993). The proportion of marked individuals was estimated using photographs

from the current study (2008-2013) as the sampling unit and the estimated proportion was assumed to be the same in the historical study as in the current study (Chapter 2).

Variance for the estimated total population size was estimated using the Delta method (Seber 2002):

$$var(N_{total}) = N_{total}^2 \left(\frac{var(N_m)}{N_m^2} + \frac{var(\theta)}{\theta^2} \right)$$

3.2.5 Survival rate estimation: Cormack-Jolly-Seber model

The Cormack-Jolly-Seber (CJS) model is an open population method (Cormack 1964; Jolly 1965; Seber 1965) to estimate apparent survival probabilities (ϕ) and recapture probabilities (p) (Lebreton et al. 1992) from mark-recapture data. Recapture probability is defined as the probability that an animal available for recapture (i.e., alive) is captured. Apparent adult survival is defined as the probability that an animal survives from one sampling occasion to the next, but permanent emigration cannot be distinguished from mortality. The CJS model estimates survival probability between each pair of sampling occasions with the exception of the final interval (Lebreton et al. 1992).

The CJS model assumes that: (1) all marks are permanent and correctly identified, (2) sampling is an instantaneous event, (3) all marked individuals have an equal probability of recapture in a given sampling occasion, (4) all marked individuals have an equal probability of survival between a pair of consecutive sampling occasions, (5) emigration is permanent, and (6) individuals behave independently of each other (Williams et al. 2002a).

Violation of the first assumption can result from including poor-quality photographs, including non-distinctive individuals, and from individual marks changing over time (Hammond 1986; Stevick et al. 2001; Urian et al. 2015). Only high-quality photographs of distinctive individuals were included in this study to maximise the chance of meeting this assumption. Instantaneous sampling was effectively met, because the duration (one day) of each sampling occasion was very short relative to the time between sampling occasions (weeks or months).

Field methods were designed to minimise the chance of violating the assumption of equal catchability. Photo-identification is relatively non-invasive and should not influence behaviour of animals in subsequent sampling occasions (Hammond 1986). The random sampling approach used during photographic encounter occasions reduced the chance of violating the assumption of equal probability of recapture within a sampling occasion. However, this assumption is difficult to meet fully for any cetacean population (Hammond 1986). Heterogeneity in recapture probabilities can stem from differences in age, sex, social factors and variation in site fidelity among individuals (Pollock et al. 1990) and individual variation in behavioural responses to boats (Lusseau 2003; Williams et al. 2002b; Williams et al. 2002c). The attempt to sample the group randomly, photographing as many individuals regardless of distinctiveness, and minimising bow-riding reduced the chance of violating this assumption.

Although an attempt was made to photograph the entire group, in the historical study, certain groups were also targeted: namely, additional effort was expended to photograph sub-groups presumed to contain distinctive males (i.e., animals with large, drooping dorsal fins). Targeting well-marked, putative males likely introduced heterogeneity in the early years of the study. Protocols to select data based on photographic quality and distinctiveness criteria, along with the separation of these two factors at the matching stage, likely reduced the chance of introducing heterogeneity due to variation in distinctiveness.

The CJS model was implemented in Program MARK (White and Burnham 1999) for well-marked, adult Pacific white-sided dolphins in the Broughton Archipelago from 1987-2013. Encounter histories were created where each individual dolphin was scored as “1” (resighted) or “0” (not sighted) for each year. No attempt was made to model survival by age-sex class, because ages were not available for all individuals, all age estimates are minima, and there is no reliable way to sex individuals from photographs.

A set of four candidate models was constructed to estimate apparent survival rate and recapture probabilities for adult dolphins over the course of the study. The models included combinations of both time-varying and constant survival and recapture probabilities. Missing years (1990, 2003, 2006, and 2007) were entered as 0s in the encounter histories and recapture probability was fixed to 0 for those years.

Program MARK offers two primary approaches for assessing model fit and estimating overdispersion; both methods were used. The first approach uses Program RELEASE (in this case run from within Program MARK) to generate goodness of fit statistics for the global (fully time-dependent) model (*i.e.*, TEST2 and TEST3).

The second approach is to estimate an overdispersion parameter. Evidence for overdispersion in the data was assessed by calculating a variance inflation factor, \hat{c} (Lebreton et al. 1992). If \hat{c} is estimated to be greater than 1 but less than about 3, it is difficult to assess whether this is because of excess variation in the data or poor model fit (Lebreton et al. 1992). Estimation of \hat{c} is typically carried out on the time-specific (global) model. In this case, the time-specific model was unable to estimate non-boundary values for all parameters (e.g. recapture probability = 0 and survival probability = 1), so the overdispersion parameter was estimated for the reduced parameter model.

3.2.5.1 Model selection

Candidate models in all analyses conducted in Program MARK were assessed and selected using an information theoretic approach. Akaike's Information Criterion (AIC) was used to select among candidate models (Burnham and Anderson 2002).

To account for differences in sample size, model selection was based on AICc, the default calculated in MARK (Anderson et al. 1994; Burnham and Anderson 2002). Support for a given model was assessed using the $\Delta\text{AICc} < 2$ 'rule of thumb' when comparing two models. When the difference in AICc between two models was less than two, the two models were considered to have equal support. If the difference in AICc scores was between two and seven, this was evidence for support for a true difference between the two models. A difference in AICc scores greater than seven was considered strong support for a difference between the two models (Burnham and Anderson 2002). Normalised AICc weights were also considered to assess relative support for a given model.

To quantify the uncertainty associated with each parameter estimate, profile likelihood confidence intervals were used. Profile likelihood confidence intervals perform better than standard (Wald's) confidence interval when sample size is small, when recapture probability is low (i.e., <0.2), and when parameter estimates are near the boundary of 0 or 1 (Lebreton et al. 1992; Williams et al. 2002a). Parameter estimation in MARK is achieved using the maximum likelihood method (Pradel 1996; Williams et al. 2002a).

3.2.5.2 Simulated annealing – an alternative maximum likelihood algorithm

Simulated annealing was used in all modelling procedures (CJS, Robust Design, and Pradel model for transient) carried out in Program MARK with the exception of the closed capture modelling. Simulated annealing is an alternate optimization algorithm to the default algorithm for finding the maximum of the likelihood function in Program MARK. Simulated annealing is a method that makes a determination between local optima when maximizing the likelihood. This is achieved by starting from an initial point from which the algorithm moves a step and “decides” whether to take another random step and in which direction (up or down) or to stay at the same point to minimize a function. This step is repeated until a point is reached where no other point is a better solution. The advantage to simulated annealing is that it is a “global optimization” procedure and avoids “getting stuck” at local minima. This can be a problem when the likelihood profile has more than one local minimum. Simulated annealing avoids getting stuck by randomly jumping to new parameter values along the profile likelihood, thereby maximizing the chances of finding the global maximum. In MARK, this option can be chosen over the default by selecting the “alt. opt.” option. The simulated annealing option is useful for models with convergence issues, which is often the case with sparse data and parameter estimates approaching the boundaries of 0 or 1.

3.2.6 Pradel model for transients

Transients are individuals that are photographed once but permanently emigrate from the study area so that they are no longer available for capture in during future encounters (Pradel et al. 1997). Including these animals can negatively bias survival estimates. To discriminate between the two types of individuals in the data, a two age-class model for survivorship was

used. Animals captured only once are considered the first age-class, and animals captured more than once, the second.

3.2.7 Robust design for estimating survival, temporary emigration, and abundance

Program MARK was used to implement Kendall's (Kendall et al. 1997; Kendall et al. 1995; Pollock 1982) extension, the closed robust design, of Pollock's robust design model (Pollock 1982). Robust design models were used to estimate survival rate, temporary emigration, and abundance (Williams et al. 2002a). The robust design uses two sampling levels (primary sampling sessions and secondary sampling occasions) and combines open and closed mark-recapture modelling approaches. Each primary session consists of at least two (ideally more) secondary sampling occasions. Between primary sessions, the population is assumed to be open. Population closure is assumed within primary sessions (*i.e.*, across secondary sampling occasions). Encounter histories from the historical dolphin study and the current study were combined to form primary sampling sessions and secondary sampling occasions. Years formed primary sampling sessions, within which there were a variable number of secondary sampling occasions (groups of days) from year to year (Table 3.1). Sampling days were pooled to: 1) maximise the number of recaptures between samples, 2) meet model assumptions, and 3) use data from all years in both the historical and current study.

Table 3.1: Number and extent of secondary sampling sessions in each primary session (year) used to form the encounter history for the robust design.

Year	Dates of secondary sampling occasions	No. secondary sampling occasions
1991	6.11-31.12	2
1992	2.9-31.12	4
1993	22.4-15.7	2
1994	3.2-18.3	2
1995	6.2-3.5	2
1996	7.7-22.10	2
1997	23.9-25.12	3
1998	28.8-27.10	3
1999	6.11-31.12	2
2000	20.10-31.12	3
2001	14.11-10.12	2
2002	1.11-21.12	2
2005	26.5-28.6	2
2009	9.9-22.11	2
2010	22.6-21.9	4
2011	12.5-15.4	2
2012	1.8-7.8	2
2013	9.7-13.8	2

3.2.7.1 Robust design model assumptions

In addition to the CJS assumptions, the following assumptions applied to the robust design analysis: (1) population closure is assumed across all secondary sampling occasions within a primary sampling session, (2) all individuals in the population have the same survival rate, and (3) probability of temporary emigration between primary sessions is assumed to be Markovian or random (Kendall 1999).

Years formed primary sampling periods (1987-2013) and groups of days formed secondary sampling periods. A secondary sampling period consisted of a minimum of 5 days and a maximum of 90 days, depending on data available in a given year, which were pooled to maximise captures within a sampling period and maximise recaptures between sampling periods. Secondary sampling occasions were kept to a sufficiently short interval to maximise the chance to satisfy the closure assumption. Photographic encounters occurred at relatively sparse intervals throughout the course of the historical and current studies (Table 3.1).

3.2.7.2 Robust design: winter only

A second robust design analysis was carried out on data from winter months only (October-March) to assess any influence of seasonality on parameter estimates. Years (1991-2001) formed the primary sampling period and days were pooled across the six months in each year to form secondary sampling occasions and to maximise the number of recaptures. The secondary sampling periods were the same as the sampling occasions used in the multi-sample closed capture analysis (section 3.2.4.2).

3.2.7.3 Estimating survival, temporary emigration, and abundance

In robust design models, apparent survival rate (ϕ), is defined as the probability of surviving between two primary sampling sessions and remaining in the study area. Capture probability (p) can vary among primary sessions and within primary sessions (i.e. among secondary occasions). The probability of recapture, (c), is estimated within secondary occasions. In this study, c was set equal to p and only varied in time among primary sessions. Temporary emigration is modelled with two parameters. The first, “emigration” parameter (γ), is defined as the probability that an individual is outside the study area in a primary sampling session given that it was inside the study area in the previous sampling session. The second, “immigration” parameter (γ'), is the probability that an individual is outside the study area in a primary sampling session given that it was also outside the study area during the previous sampling session. Thus, $1 - \gamma'$ represents immigration. Population size (N) is derived across secondary sampling occasions within each primary session. Table 3.2 summarises these parameters.

A set of 14 candidate models composed of parameters for apparent survival rate (ϕ), temporary emigration rates (γ , γ'), recapture probability ($c=p$), and abundance (N) was considered and parameters estimated in Program MARK (Table 3.2). Recapture probability was set to either time-specific or constant over each primary session. Models with time-specific capture and recapture probabilities over secondary sampling occasions were not considered. Only models with time-varying N were considered in this analysis. Both γ and ϕ were allowed to vary with time or remain constant (Table 3.2).

Table 3.2: Parameters estimated in robust design mark-recapture model used in this study. The notation t indicates that a parameter was allowed to vary with time and ‘.’ indicates that a parameter was kept constant.

Parameter	Time variation	Movement restrictions
Survival (ϕ)	$\phi(t), \phi(\cdot)$	
Recapture probability (p)	$p(t), p(\cdot)$	
Emigration (γ'', γ')	$\gamma''(t), \gamma''(\cdot), \gamma'(t), \gamma'(\cdot)$	$\gamma'' \neq \gamma'$ (Markovian), $\gamma'' = \gamma'$ (Random), $\gamma'' = \gamma' = 0$ (No movement)
Abundance (N)	$N(t)$	

Three temporary emigration scenarios were explored in the model set (Table 3.3): (1) Markovian movement ($\gamma'' \neq \gamma'$), the probability of being present and available for capture in the study area depends on whether the animal was present and available for capture during the previous sampling period; (2) Random movement ($\gamma'' = \gamma'$), the probability of an individual being present and available for capture in the study area is independent of whether the individual was present and available for capture during the previous sampling period; and (3) No movement ($\gamma'' = \gamma' = 0$), no temporary emigration (Kendall and Nichols, 1995; Kendall et al. 1997(Williams et al. 2002a).

There are no goodness of fit testing options available for robust designs in Program MARK. One approach is to collapse the closed portion of the encounter histories to a single sample (essentially a CJS model) and carry out GOF testing on this model. This approach was taken here.

Table 3.3: Set of 14 candidate robust design models considered. Recapture and capture probability were set equal in all cases. The notation (t) indicates that a parameter was allowed to vary with time and $(.)$ indicates that a parameter was kept constant.

Model	Restriction
$\varphi(.)\gamma''(t)\gamma'(t)p(t)$	$\gamma''=\gamma'$
$\varphi(.)\gamma''(t)\gamma'(.)p(t)$	
$\varphi(.)\gamma''(t)\gamma'(t)p(t)$	
$\varphi(t)\gamma''(t)\gamma'(t)p(t)$	$\gamma''=\gamma'$
$\varphi(t)\gamma''(t)\gamma'(.)p(t)$	
$\varphi(t)\gamma''(t)\gamma'(t)p(t)$	
$\varphi(t)\gamma''(.)\gamma'(t)p(t)$	
$\varphi(.)\gamma''(.)\gamma'(.)p(t)$	$\gamma''=\gamma'$
$\varphi(.)\gamma''(.)\gamma'(.)p(t)$	
$\varphi(.)\gamma''(.)\gamma'(t)p(t)$	
$\varphi(t)\gamma''(.)\gamma'(.)p(t)$	$\gamma''=\gamma'$
$\varphi(t)\gamma''(.)\gamma'(.)p(t)$	
$\varphi(t)\gamma''(.)\gamma'(.)p(t)$	$\gamma''=\gamma'=0$
$\varphi(.)\gamma''(.)\gamma'(.)p(t)$	$\gamma''=\gamma'=0$

3.3 RESULTS

3.3.1 Photo-identification

Photographs of well-marked individuals were taken on 189 days from November 1987 to June 2005 (historical study) and 44 days from September 2008-August 2013 (current study) (Figure 3.2). Visual estimates of group size were not recorded in every encounter in either study. In the 51 cases when group size was recorded in the historical study (average group size = 155; SE = 22), there was no significant difference from the 31 visual estimates of group size in the current study (average group size = 125; SE = 27; unpaired, two-sided t test with unequal

variance, $p=0.39$). With the switch from film to digital photography between the historical and current studies, the proportion of individuals identified within each group did increase (average proportion identified in historical study=0.056 (SE=0.009); current study=0.33 (SE=0.009); unpaired, two-sided t test with unequal variance, $p=0.0001$). The absolute number of identifications made on each sampling date throughout the study is shown in Figure 3.3.

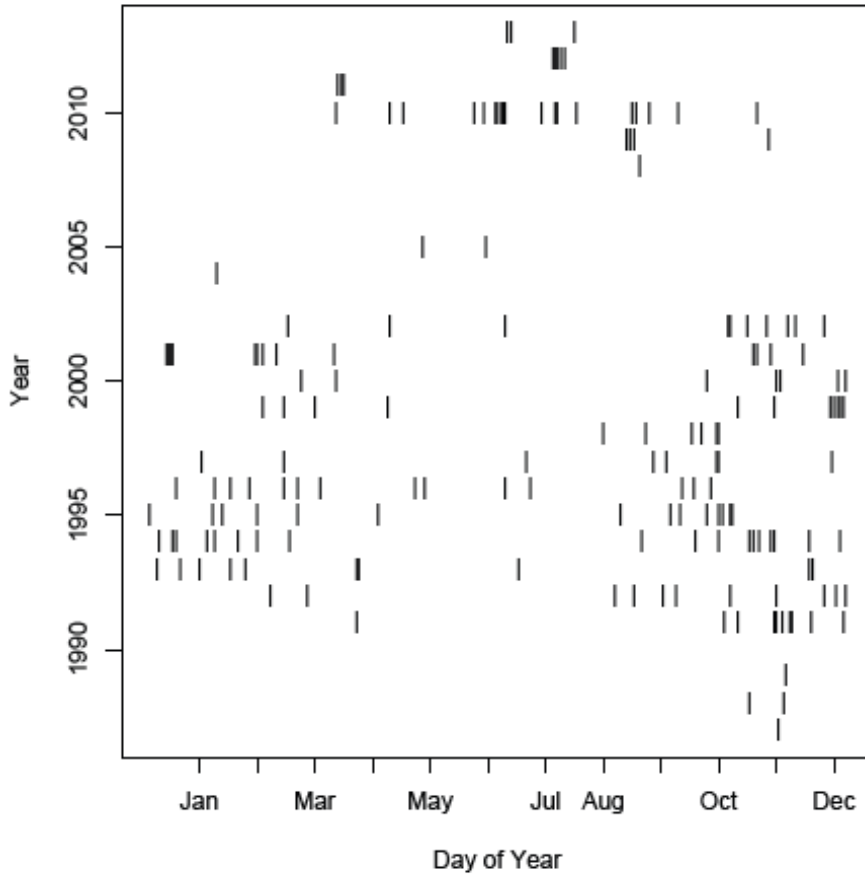


Figure 3.2: Plot of photo-identification effort each month in each year from 1987-2013. Lines indicate sampling days.

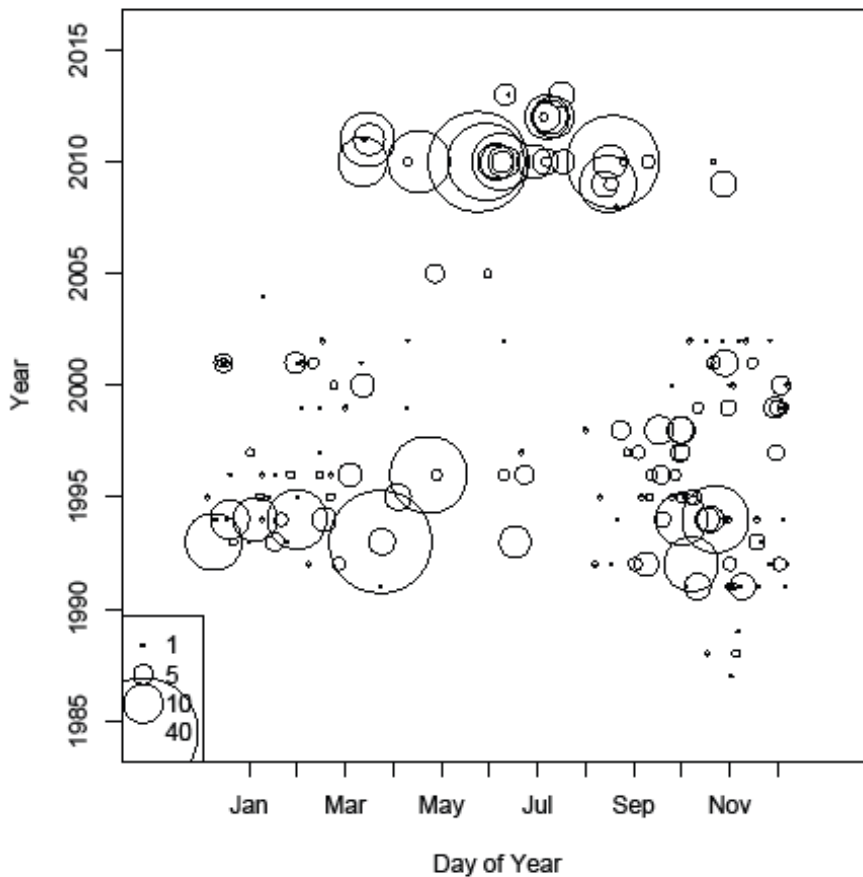


Figure 3.3: Plot showing the number of identifications collected on each sampling date throughout the study from 1987-2013. The size of the circles are proportional to the number of identifications collected on the sampling date.

Search routes (yellow lines) and sighting locations (red dots) from the current study are shown in Figure 3.4. No sightings were available from 1990, 2003, 2006, or 2007. Many young animals were excluded from the analysis based on both the historical and current studies' quality and distinctiveness criteria. The final dataset, pooling both the historical and current studies, included 909 distinctly marked individual dolphins, the majority of which were seen only once (Figure 3.6). A discovery curve shows an increase in the number of identifications throughout the historical study and then a levelling off. The number of identifications grew sharply when the current study began and does not appear to be levelling off (Figure 3.6).

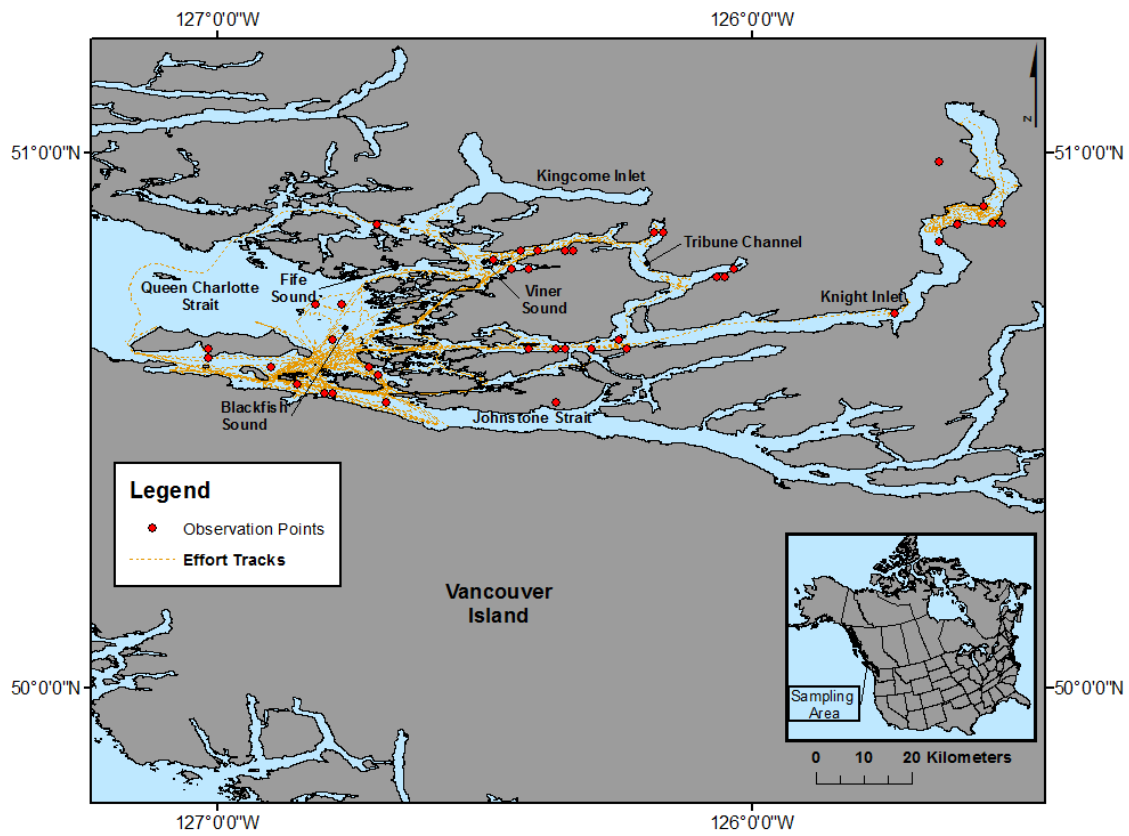


Figure 3.4: Vessel effort tracks (yellow lines) in the Broughton Archipelago study area and sightings (red dots) of Pacific white-sided dolphins used for photo-identification.

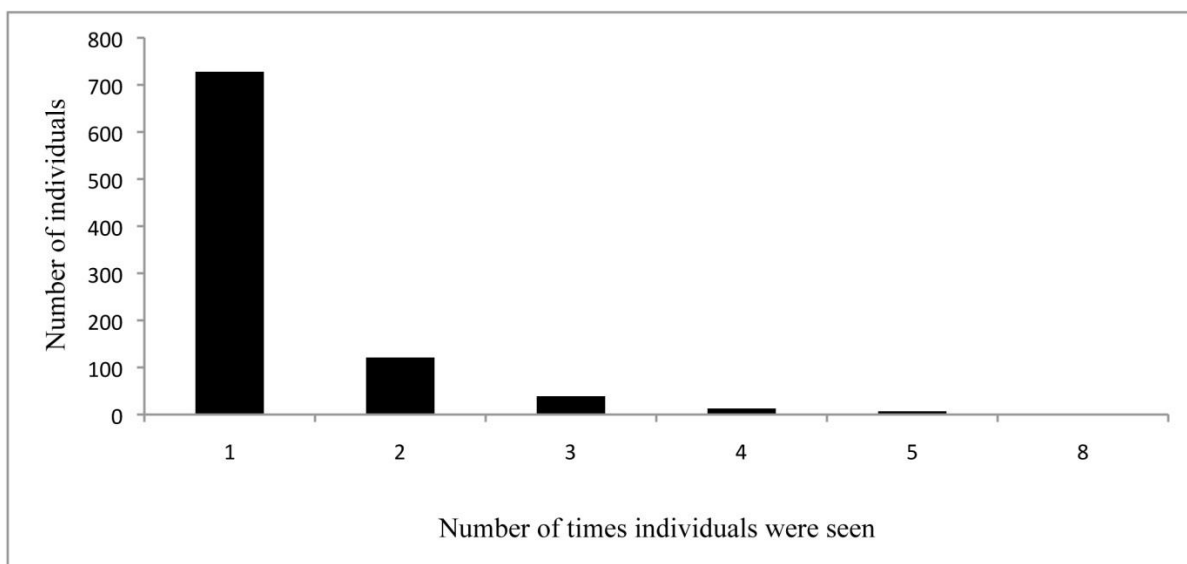


Figure 3.5: Number of times each of the 909 uniquely marked dolphins were seen.

Table 3.4: Number of days of photo-identification effort, number of individuals marked and recaptured each year, and total number of individuals recaptured each year.

Sampling occasion	Number of sampling days	Individuals Marked	Individuals recaptured													Total recaptured										
			1988	1989	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001		2002	2004	2005	2008	2009	2010	2011	2012	2013	
1988	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1989	5	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
1991	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	30	26			4	2	8			0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	10	
1993	57	46				2	2	8		0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	18
1994	103	82				2	6	13		0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	23
1995	152	126				2	0	1		0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	14
1996	45	43				5	0	1		0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	5
1997	81	72				0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	9
1998	33	29							1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	3
1999	41	38								0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4
2000	35	29								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2001	25	24								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2002	53	46													0	0	0	0	0	3	0	0	0	0	0	4
2004	13	12													0	0	0	0	0	0	0	0	0	0	0	0
2005	10	1													0	0	0	0	0	0	0	0	0	0	0	0
2008	1	7													0	0	0	0	0	0	0	0	0	0	0	1
2009	47	1													0	0	0	0	0	0	0	0	0	0	0	0
2010	279	37													0	0	0	0	0	4	0	0	0	0	0	5
2011	35	245													0	0	0	0	0	0	5	0	0	0	0	8
2012	60	33													0	0	0	0	0	0	0	0	0	0	0	0
2013	19	55													0	0	0	0	0	0	0	0	0	0	0	1

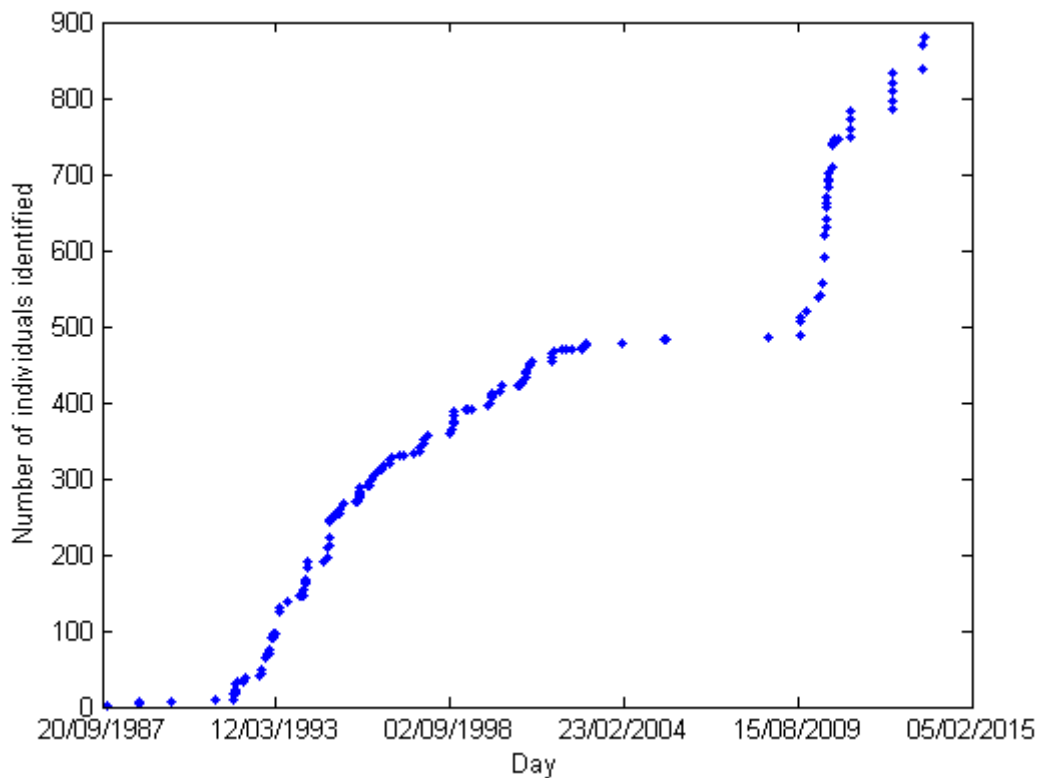


Figure 3.6: Discovery curve showing individual identifications of Pacific white-sided dolphins in the Broughton Archipelago 1987-2013.

3.3.2 Abundance estimates

3.3.2.1 Estimates from Chapman two-sample estimator

The estimates of total population size from the two-sample abundance estimator were highly variable. Abundance ranged from a low of 546 (95% CI: 293, 1018) in 2011-12 to high of 2,889 (95% CI: 1,424, 5,863) in 2010-2011 (Figure 3.7). It was not possible to calculate an abundance estimate for several pairs of years (before 1992, between 2000 and 2010, and after 2012) because of the low rate of recapture in adjacent years.

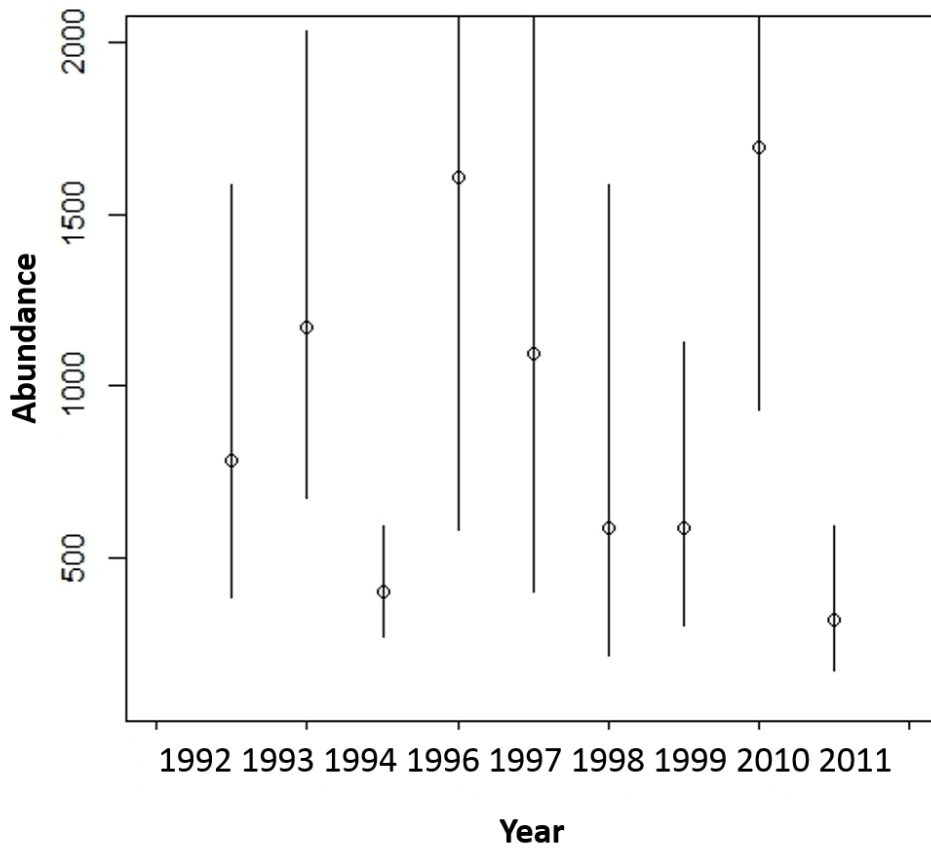


Figure 3.7: Abundance estimates and associated log-normal 95% confidence intervals for pairs of years from 1992-1999, 2010-2012 estimated from Chapman’s two-sample estimator.

3.3.2.2 Estimate of the proportion of marked dolphins

In total, 1,664 photographs from the current study were used to estimate the marked proportion of individuals in the population as 0.578 (CV=0.02, 95% CI: 0.55, 0.60).

3.3.2.3 Population size from multi-sample closed capture-recapture models

For all years, the Mt model for abundance was best supported by the data (Table 3.5) for closed capture modelling conducted within MARK. This suggests recapture probability varied throughout the sampling interval.

Table 3.5: Closed capture model diagnostics for winter data (October-March) 1991-2001 from analyses conducted in program MARK.

Year	No. trapping occasions	No. animals captured	Total no. captures	No. recaptures	Model	AIC	Residual deviance
1991-1992	11	32	34	2	Mo	-97.317	5.811
					Mt	-96.332	6.259
1992-1993	11	60	65	5	Mt	-216.261	9.119
					Mo	-200.964	28.570
1993-1994	10	68	69	1	Mo	-337.550	6.016
					Mt	-335.465	6.016
1994-1995	14	74	79	5	Mt	-272.901	9.221
					Mo	-245.372	42.916
1997-1998	3	16	17	1	Mt	-24.300	4.958
					Mo	-22.471	4.344
1998-1999	7	32	33	1	Mt	-103.669	5.162
					Mo	-101.864	9.169
1999-2000	9	28	29	1	Mt	-87.121	4.965
					Mo	-80.467	13.854
2000-2001	13	41	43	2	Mt	-123.970	6.950
					Mo	-112.426	22.733

Estimates of capture probability for each secondary sampling occasion during winter months in the historical study were relatively low overall with the lowest at 0.015 (SE=0.098) in 1991, but reached 0.157 (SE=0.144) for one secondary sampling occasion in 1999-2000 (Table 3.6).

The abundance estimates from the best performing models from closed capture modelling of the winter data carried out in Program MARK are shown in Table 3.7. The total abundance estimates were calculated using the proportion of marked dolphins (0.578). Total population size estimating from fitting closed capture models of winter data (October-March 1991-2002) in MARK were highly variable. Total abundance ranged from a high of 2,058 (95% CI: 416-10,162) in 1993-1994 to a low of 111 (95% CI: 25-485) in 1997-1998 (Table 3.7). There were either few or no recaptures in 1995-1996, 1996-1997, and 2001-2002. These years were not analysed. A regression of the abundance estimates (Figure 3.8) predicted a decline of ~2%/year, but the model was not significant ($p=0.8$).

Table 3.6: Estimated capture probability for each secondary sampling occasion during winter months (October-March) from the Mt model for each year from 1991 to 2001.

Year	p(t)	SE
1991-1992	0.106	0.071
	0.015	0.098
1992-1993	0.029	0.016
	0.118	0.050
	0.126	0.054
1993-1994	0.030	0.030
	0.030	0.030
1994-1995	0.013	0.008
	0.070	0.034
	0.063	0.031
1997-1998	0.049	0.047
	0.097	0.092
1998-1999	0.045	0.047
	0.097	0.092
1999-2000	0.157	0.144
	0.050	0.048
2000-2001	0.064	0.045
	0.092	0.063
	0.016	0.013

Table 3.7: Abundance estimates from 1991-2001 of marked dolphins seen in winter months. Estimates were calculated from the best fitting closed capture models in MARK (Mt for all years). Total abundance was estimated after accounting for the proportion of marked dolphins in the study (0.578).

Year	N	SE	CV	95% CI	Ntotal	SE	CV	95% CI
1991-1992	137	85	0.62	58-452	247	85	0.62	77-724
1992-1993	238	91	0.38	128-527	418	91	0.38	199-848
1993-1994	1,190	1,156	0.97	280-6,009	2,058	1,156	0.97	416-10,162
1994-1995	478	222	0.46	222-1,181	827	222	0.46	347-1,964
1997-1998	64	56	0.88	24-309	111	56	0.88	25-485
1998-1999	226	209	0.92	67-1,118	391	209	0.93	84-1,823
1999-2000	140	125	0.89	47-682	242	125	0.89	54-1,085
2000-2001	248	162	0.65	95-841	429	162	0.65	133-1,379

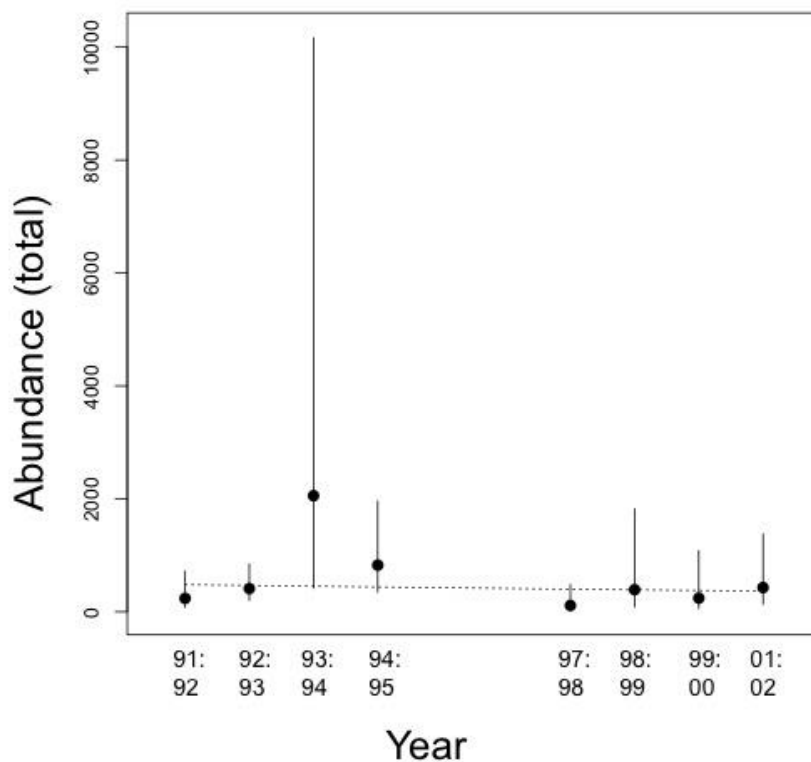


Figure 3.8: Estimates of total abundance of dolphins in study area in winter months from Table 3.7. The dotted line shows a fitted linear regression (weighted by inverse of CV^2). Although the regression predicted a decline of $\sim 2\%$ /year, the model was not significant ($p=0.8$) and had negligible explanatory power ($R^2=0.008$).

3.3.3 Estimates of apparent survival rate, 1987-2013

The CJS model (all data, both studies) with constant survival and time-varying recapture probability had much more support from the data than any other model (Table 3.8). This model estimated adult annual apparent survival rate as 0.924 (SE= 0.02, 95% CI: 0.881, 0.969) for well-marked individuals from 1987-2013. Recapture probabilities varied from 0 in several years to 0.172 (SE=0.034) in 1994. For the poorer fitting models, survival and capture probability estimates were estimated very close to the bounds of 0 or 1 in many years.

Table 3.8: Model selection diagnostics for CJS models with recapture probability varying by time for the years 1987-2013. Models with constant recapture probability had much higher AIC values.

Model	AICc	Δ AICc	AICc Weight	Model Likelihood	Number of parameters	Residual Deviance
$\Phi(.) p(t)$	1000.4	0	1	1	23	245.45
$\Phi(t) p(t)$	1048.7	48.39	0	0	48	239.85

3.3.3.1 Goodness of fit testing

The goodness of fit testing procedure was run in Program RELEASE on the fully time-dependent (global) model ($\phi(t) p(t)$) and the reduced parameter, top ranked model, $\phi(.) p(.)$. The results from TEST2 and TEST3 for the global model suggest that the model meets the assumptions ($p > 0.4388$). However, the test output also showed that most encounters lacked sufficient data for the test. The results of TEST2 and TEST3 for the reduced parameter model returned the same p-value and similar number of encounters that lacked sufficient data.

The variance inflation factor, \hat{c} was estimated from the best fitting model ($\phi(.) p(t)$). The bootstrap method estimated a \hat{c} of 1.46 and the logistic regression approach (median \hat{c}), estimated a \hat{c} of 1.14 using the simulated annealing algorithm, which were not significantly different from 1, indicating good model fit (no overdispersion). The default procedure in MARK failed to estimate median \hat{c} . However, probability of recapture was inestimable in many years either due to sparse data or parameter values approaching 0. The bootstrap

procedure suggested that the deviance of the observed model had a 1/1000 chance of being observed, ($P < 0.001$), suggesting a lack of fit to the data. Adjusting for \hat{c} did not change the model selection result or the estimate of survival rate.

3.3.4 Pradel model for transients (historical and current study)

The two age-cohort model with constant survival for both cohorts was the best performing model (Table 3.9), suggesting the presence of transient dolphins in the data. Survival rate was estimated as 0.497 (SE=0.09, 95% CI: 0.353-0.732) for transients and 0.942 (SE= 0.245, 95% CI: 0.871-0.975) for non-transients.

Table 3.9: Model diagnostics for Pradel model for transients.

Model	AICc			Likelihood	Num. Par	Residual Deviance
	AICc	Δ AICc	Weight			
$\varphi(a2-./.)p(t)$	952.3	0.00	0.971	1.000	23	219.74
$\varphi(.)p(t)$	959.4	7.03	0.029	0.030	22	228.88
$\varphi(a2-t.t)p(t)$	978.1	25.77	0.000	0.000	42	204.57
$\varphi(a2-t/t)p(t)$	1006.6	54.22	0.000	0.000	58	197.12
$\varphi(.)p(.)$	1098.4	146.03	0.000	0.000	2	409.01

3.3.5 Robust design model estimates of survival, temporary emigration, and abundance (historical and current study)

The Markovian movement model with constant survival, constant emigration, time-varying immigration (model 1) was the highest ranking model (Table 3.10). However, model convergence was suspect for this model and it was therefore discounted. The random movement model with constant survival, constant temporary emigration (model 2) and the model with Markovian movement, constant survival, and constant temporary emigration (model 3) were within 2 Δ AICc units of one another (Table 3.10).

Table 3.10: Model selection diagnostics for robust design mark-recapture models fitted to the capture histories of Pacific white-sided dolphins to estimate parameters for survival (ϕ), capture probability (p), emigration (γ), and abundance (N).

Model	Emigration restriction	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par
1. $\emptyset(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$ *		-2028.35	0.00	0.616	1.000	35
2. $\emptyset(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma'$	-2026.25	2.10	0.215	0.350	36
3. $\emptyset(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$		-2025.75	2.60	0.168	0.273	37
4. $\emptyset(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma' = 0$	-2006.20	22.16	0.000	0.000	48
5. $\emptyset(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$		-2006.17	22.18	0.000	0.000	48
6. $\emptyset(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma'$	-2006.15	22.20	0.000	0.000	48
7. $\emptyset(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma'$	-2005.80	22.55	0.000	0.000	46
8. $\emptyset(t)\gamma''(\cdot)\gamma'(\square)p(t)$		-1995.99	32.36	0.000	0.000	53
9. $(\emptyset(\cdot)\gamma''(t)\gamma'(\cdot)p(t)$		-1992.86	35.49	0.000	0.000	53
10. $\emptyset(t)\gamma''(t)\gamma'(\square)p(t)$	$\gamma'' = \gamma'$	-1975.94	52.41	0.000	0.000	61
11. $\emptyset(\cdot)\gamma''(t)\gamma'(\square)p(t)$		-1969.4	58.95	0.000	0.000	67
12. $\emptyset(t)\gamma''(t)\gamma'(\cdot)p(t)$		-1964.85	63.50	0.000	0.000	66
13. $\emptyset(t)\gamma''(t)\gamma'(\square)p(t)$		-1933.87	94.48	0.000	0.000	82
14. $\emptyset(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma' = 0$	22672.94	24701.29	0.000	0.000	17
*convergence suspect						

A number of parameter estimates in all three top models were approaching the boundary of either 0 or 1. Data cloning was used to assess whether the parameters were truly estimable close to 0 or 1, or whether they are being estimated near the boundary because of insufficient data (Lele et al. 2007; Lele et al. 2010).

Parameter non-identifiability was discovered in Model 3. To determine whether the non-identifiability was extrinsic or intrinsic, profile likelihood confidence intervals were selected for the original data, cloned, and the resultant confidence intervals examined. Because profile likelihood confidence intervals were used, model averaging across the two models was not possible.

Model 2 was considered the best fitting model. Model 3 was discounted based on a higher AIC score and parameter non-identifiability. For model 3, the estimate for survival was estimated as 1 (95% CI: 0-1). The data cloning procedure indicated non-identifiability for the survival rate and the immigration parameter estimates in addition to two recapture parameters.

The survival estimate from model 2 was estimated as 0.907 (SE=0.03, 95% CI: 0.843-0.972). The model suggested random temporary emigration in which the probability of an individual being in the study area in a particular year is independent of whether the animal was present in the study area in the previous year. Temporary emigration rate was estimated as 0.14 (SE=0.318). Data cloning carried out for model 2 did not reveal non-identifiability in any parameters. Abundance varied greatly among years (Figure 3.9) and precision was low. GOF testing was carried out to assess model fit for the CJS model (a collapsed version of the same data used in the robust design) and no evidence for overdispersion was found.

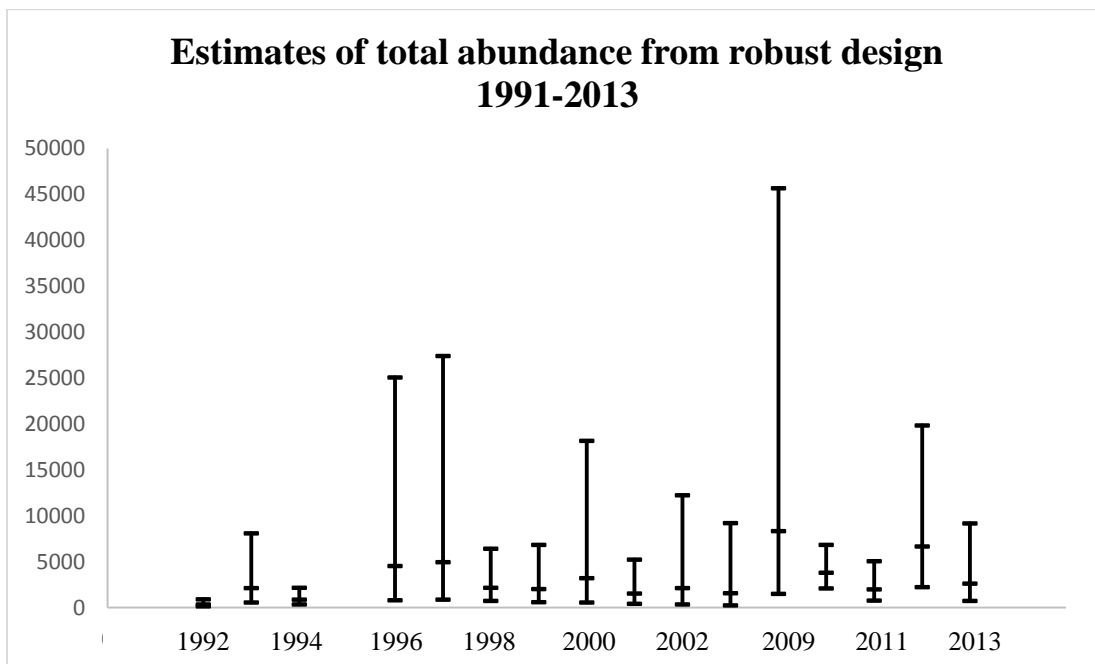


Figure 3.9: Population size estimated from robust design model and adjusted for the proportion of marked dolphins in the population. The first (1991) and fifth (1995) years were removed from the plot due to extreme upper confidence interval values.

3.3.6 Robust design restricted to winter months

When the data were restricted to winter months only, a ‘no movement’ model with constant survival was the best fitting model (Table 3.11). An adult survival rate of 0.989 (SE= 0.066, 95% CI: 0.866-1.000) was estimated. Recapture rates were variable, but low overall and approached zero in some sampling intervals. The highest rate of recapture was estimated as 0.032 (SE=: 0.019, 95% CI: 0.010-0.035). The three best fitting models were < 2 Δ AIC of one another, however, the confidence intervals for the second and third ranking models range from near zero to one, indicating poor fit and non-identifiability.

Table 3.11: Robust design mark-recapture model diagnostics for models fitted to winter (October-March) capture history data of Pacific white-sided dolphins to estimate parameters for survival (ϕ), capture probability (p), emigration (γ), and abundance (N).

Model	AICc		Model Weight	Model Likelihood	Num. Par
	AICc	Δ AICc			
$\phi(.)\gamma''(.)=\gamma'(.)=0$ p(t)	-737.147	0.000	0.440	1.000	58
$\phi(.)\gamma''(.)\gamma'(.)$ p(t)	-736.847	0.300	0.379	0.861	61
$\phi(.)\gamma''(.)=\gamma'(.)$ p(t)	-735.369	1.779	0.181	0.411	60
$\phi(.)\gamma''(t)=\gamma'(t)$ p(t)	-722.399	14.748	0.000	0.001	67
$\phi(.)\gamma''(.)\gamma'(t)$ p(t)	-721.495	15.652	0.000	0.000	69
$\phi(.)\gamma''(t)\gamma'(.)$ p(t)	-721.361	15.786	0.000	0.000	70
$\phi(t)\gamma''(.)=\gamma'(.)=0$ p(t)	-714.782	22.365	0.000	0.000	67
$\phi(t)\gamma''(.)=\gamma'(.)$ p(t)	-711.103	26.044	0.000	0.000	69
$\phi(t)\gamma''(.)\gamma'(.)$ p(t)	-709.823	27.325	0.000	0.000	69
$\phi(t)\gamma''(.)\gamma'(.)$ p(t)	-709.144	28.003	0.000	0.000	71
$\phi(.)\gamma''(t)\gamma'(t)$ p(t)	-704.691	32.456	0.000	0.000	78
$\phi(t)\gamma''(.)\gamma'(t)$ p(t)	-692.608	44.540	0.000	0.000	79
$\phi(t)\gamma''(t)\gamma'(.)$ p(t)	-692.024	45.123	0.000	0.000	80
$\phi(t)\gamma''(t)\gamma'(t)$ p(t)	-690.756	46.391	0.000	0.000	78
$\phi(t)\gamma''(t)\gamma'(t)$ p(t)	-674.255	62.893	0.000	0.000	88
$\phi(.)\gamma''(.)\gamma'(.)$ p(.)	-606.923	130.225	0.000	0.000	26

3.4 DISCUSSION

This study satisfied its primary objectives by generating the first time-series of abundance estimates for the species and the first estimate of adult survival from encounter histories of known individuals, rather than ages of bycaught or stranded animals (Heise 1996b; Taylor et al. 2007a; Walker et al. 1986). The confidence intervals of all survivorship estimates spanned 0.95, which is the value expected for this species (Heise 1996; Taylor et al. 2007a). With the exception of the winter-only estimate from the robust design model, the point estimates (0.907-0.942) dip below this value. Although precision is low due to sparse data, it is important to know that the estimates are in the range of what one would expect for this species given other known life history parameters (Taylor et al. 2007a).

In the process of collecting data to estimate these demographic trends, the study has also catalysed efforts to understand human and ecological stressors that may be impacting dolphin demographics (Chapter 4) and offers new insights into social patterns in this poorly studied species (Chapter 5). But the demographic parameters require some careful interpretation. All of the estimates presented and discussed here are preliminary, but new for this population and, indeed, for the species and the genus as a whole. Although this new information is tentative, it is hoped that this study can inform the design and execution of additional studies to improve inference before the parameter estimates are used to assess conservation status or make management decisions for Pacific white-sided dolphins.

These results show that Pacific white-sided dolphins are abundant in the study area, but that these numbers are highly variable and imprecise from year to year. Chapman estimates of population size were in the hundreds of animals in most years and in the thousands on four occasions (Figure 3.7). The estimates from the closed capture modelling of winter data from this historical study suggests a small, possibly resident (Chapter 5) dolphin population in winter (Figure 3.8). However, this relatively small population increased to 2,058 (95% CI: 416-10,162) between 1993-1994. This sharp increase in abundance may be due to an influx of dolphins from outside the study area following a shift in prey availability. But, this estimate is imprecise due to a low rates of recapture when restricting the data to the winter months only. Similarly, rates of recapture were very low between pairs of years, making it difficult to

produce estimates in many pairs of years. The low rate of recaptures is responsible for the poor precision of the abundance estimates. Until the precision improves, it is impossible to interpret the variability or detect a trend in abundance.

The number of individuals available for capture was relatively high, but the number of recaptures was low. This was likely due to relatively low effort, on average, over the 27-year duration of the study. Fitting models to sparse data is a perennial problem in ecological studies (Chao 1989; Doak et al. 2005). This is an inevitable situation for monitoring the status of species for which sample sizes will likely always be small, such as cryptic, rare, severely depleted or critically endangered species. For larger populations such as this one, meeting assumptions and increasing capture probability is key. This section will summarize the main findings of the data I have available, and ends on recommendations (*“Directions for future research”*) for field and analytical methods that may increase sample size or strengthen our ability to make inference about demography.

3.4.1 Discussion of model assumptions

Before reaching any firm conclusions about the degree of confidence to have in the parameters estimated in this study, it is important to assess whether they may be biased due to violation of model assumptions. I consider each of these below:

3.4.1.1 Bias due to mark change

Following recommended best practice (Friday 2000; Read et al. 2003; Stevick et al. 2001; Urian et al. 2015; Wilson et al. 1999), photo quality and individual animal distinctiveness were assigned during separate processes, and only the highest quality photographs of distinctive individuals entered the analyses. Although I scored every photo in the historical catalogue for quality and distinctiveness to ensure uniform standards between the historical and current studies, and oversaw every putative match made by the technicians who assisted me with matching, there is some subjectivity inherent in the quality and grading process (Chapter 2). The switch from film to digital photography could have introduced some bias due to unmodelled changes in the ability to detect subtle marks as technologies improved. There will

be a need to maintain consistent protocols as technicians leave and join the study over time, and as technology changes.

3.4.1.2 Independence of sampling occasions

There is very little information on the social structure of Pacific white-sided dolphins; however this study has revealed some evidence for long-term associations from the photo-identification catalogue (Chapter 5). The assumption of truly independent captures may not have been met, nor can it ever be accomplished for highly social species. This is unlikely to bias point estimates of abundance or survival, but may underestimate standard errors (Williams et al. 2002a).

3.4.1.3 Geographic closure

The geographic closure assumption was certainly violated in the Chapman two-sample estimators, introducing some bias. The assumption of geographic closure in the secondary sampling occasions in the robust design could have been violated for the longer sampling periods. Nevertheless, the top model estimated random rather than Markovian movement. Simulations have shown that if movement is random and the assumption of geographic closure is violated, heterogeneity in capture probability is unlikely to introduce major bias in estimates of capture probability and abundance (Kendall et al. 1997; Kendall et al. 1995).

3.4.2 Abundance

Total abundance estimated from pairs of years ranged from a low of 546 (95% CI: 293, 1018) in 2011-12 to a high of 2,889 (95% CI: 1424, 5,863) in 2010-2011 (but were not estimable in cases in which there were no recaptures in adjacent years). There was no obvious trend in the data, so the best estimate is the average abundance of marked dolphins from the two-sample estimator over the period 1992-2012 of 911 (95% CI: 526-1,297) and total abundance for the same period of 1,577 (95% CI: 910-2,243).

Abundance during the winter months was estimated using multi-sample closed capture models. Again, due to low rates of recapture, precision was low and point estimates of abundance were highly variable.

It proved challenging to collect data to correct these abundance estimates to include unmarked individuals. Standard methods rely on data from encounters in which one can be certain that all individuals were photographed, usually from small groups (Nicholson et al. 2012b; Wilson et al. 1999). However, in both of those cases, the dolphin populations were much smaller (115-208; Nicholson et al. 2012 and ~129 Wilson et al. 1999b) than in the current study. Mark rates have been estimated in a similar-sized population of dusky dolphins in New Zealand by estimating proportion of marked dolphins in a random sample of photographs (~1,090; Markowitz et al. 2004). Because the population in the current study is large, and often occurs in groups of hundreds, I relied on methods that use photographs, rather than individual dolphins, as the sampling unit (Lusseau et al. 2006; Urian et al. 2015; Williams et al. 1993).

The estimated proportion of high quality photographs that contained a marked dolphin was surprisingly high at 0.578, which increased the abundance estimates of the marked population by ~73%. Previous studies had postulated a low mark rate as a barrier to mark-recapture for this species (Black 1994; Tsutsui et al. 2001) and my impression in the field was that the proportion of marked individuals was substantially lower than this. This mark rate is on a par with well-studied populations of bottlenose dolphins such as the Moray Firth bottlenose dolphin population (0.56-0.68; 1999) and the bottlenose dolphins in Doubtful Sound (0.65; Williams et al. 1993), but lower than dusky dolphins in New Zealand (0.76; Markowitz et al. 2004). This has implications for practical methods (see *Directions for future work*, below) for improving this study in future. It would seem that the limiting factor is getting a large number of high-quality photographs, rather than a low mark rate *per se*.

3.4.3 Survival rate

Three methods were used to estimate adult survival rate. For each of the three methods, the best estimates were: (1) CJS, 0.924 (95% CI: 0.881-0.969), (2) robust design, 0.907 (95% CI: 0.843-0.972), robust design (winter data only), 0.989 (95% CI: 0.866-1.000), and (3) the Pradel

model, 0.914 (95% CI: 0.867-0.947) for non-transients and 0.497 (95% CI: 0.353-0.732) for transients. The confidence intervals for all three methods overlap with the adult survival rate of 0.95 predicted by (Taylor et al. 2007a) and also found in the Sarasota Bay bottlenose dolphin population (Wells and Scott 1990). This similarity in adult survival between the two species is to be expected, given that the oldest age of a reproductive female in Taylor's analyses was similar in Pacific white-sided dolphins (46 years) and bottlenose dolphins (48 years). All of the survival analyses in the current study had low recapture probabilities. Given the sparseness of the data, there is certainly a need for additional data to increase accuracy and precision.

There are insufficient data to determine whether permanent emigration could cause negative bias in the survival estimates. One dolphin (D297) was photographed twice in 2013, but the only other time it was seen was in 1994. When periods of temporary emigration can approach the predicted 21.8-year generation time of the species (Taylor et al. 2007), the line between permanent and temporary emigration becomes blurred. Many dolphins were only photographed once. These individuals may truly be transient and are just passing through the study area or it may be due to a very low rate of recapture from sampling heterogeneity. Although the data were too sparse to detect transience using TEST3 in the CJS model, the two age-class model performed best, implying that there are transient dolphins in the dataset. When transients were explicitly modelled in the Pradel model for transients, there was support from the data to suggest transients are present in the data and the study area.

3.4.4 Temporary Emigration

Some individual dolphins were recaptured within a year and within a few days, suggesting some level of residency but many individuals were resighted over periods exceeding a decade (discussed in light of sociality in Chapter 5). However, several individuals have been photographed >300 km from the study area and later resighted within the study area (discussed in light of movement rates in Chapter 5). These dolphins lie somewhere along a spectrum between remaining fully resident to this small study area, and displaying transient or obviously migratory pattern that brings the dolphins to the area in an unmistakable seasonal pattern like humpback whales. This study found evidence for both site fidelity and random temporary emigration. Markovian movement could explain a negatively biased survival estimate, but the robust design model of all of the data results favoured random movement, which suggests that

emigration and immigration are equal and survival estimates should be unbiased (Kendall et al. 1997). However, with random temporary emigration, capture probability is lower and precision of the parameter estimates is reduced (Kendall et al. 1997; Kendall et al. 1995). The favoured model in the robust design analysis of the winter data was a “no movement” model, which suggests seasonal residency.

3.4.5 Directions for future work

Although this study satisfied its primary objectives, these analyses have identified several weaknesses. These cluster in four main areas, relating to funding, survey design, field protocols, and data analysis.

3.4.5.1 Funding

This study was initiated and run voluntarily over more than 20 years (Morton 2000). There was no dedicated funding for this research until 2010 (despite fundraising campaigns and numerous submitted grant proposals). During the years when there was dedicated funding for this study, one can see an increase in captures (Table 3.1), because resources were available to spend more time on the water and to buy a camera with a longer telephoto lens. Although the 2013 field season was also funded, the aim of the 2013 funding was to satisfy multiple objectives simultaneously (i.e., small-boat, multi-species surveys), and capture probability in 2013 was not particularly high. The lessons learned in these analyses can be brought to bear on future, more strategic proposals that emphasise factors now known to lead to success. The two years of greatest success were in 2010 when funding was available for year-round research effort and in 2011 during a spring expedition when a sponsor donated use of a live-aboard vessel for a week in an area and at a time of year that otherwise would have been inaccessible to our small research vessel. This allowed me to access a site (Knight Inlet) in April when dolphins aggregate to exploit a brief surge of eulachon as the fish travel to spawn in a local river. A combination of the two approaches may be a way forward to increase recapture probability in future.

3.4.5.2 Study design

In the current study, the secondary sampling intervals were chosen retrospectively to capture as many encounters as possible for the longest period that was reasonable to assume closure in order to maximise recaptures. This *ad hoc*, pragmatic approach is less desirable than a designed experiment (Nicholson et al. 2012a). For the specific purpose of this study, my next task will be to use this study to inform simulations in MARK to guide optimal sampling intervals for robust design and other models that will maximise accuracy and precision of the estimates.

3.4.5.3 Data collection

The fact that some dolphins approach the boat and others avoid it may represent an opportunity. Currently, with one driver and one photographer, my field protocols involve slowing down when the dolphins start to bow-ride, so that they lose interest in the boat. Then, I attempt to photograph the entire group. This results in some loss of efficiency. If I maintain a boat speed that encourages dolphins to bow-ride, I find that those dolphins are too close and too unpredictable in their surfacing patterns to collect high quality, parallel photographs that can be used for individual identification, whereas dolphins that avoid the boat are too far away to be identified with the current equipment. It may be possible to address this in future by using a larger boat, with more than one photographer on board. With one person using a wide-angle lens and another using a telephoto lens, it may be possible to use the dolphins' behaviour to our advantage (i.e., with one photographer photographing bow-riding animals and another photographing animals that stayed far from the boat). Another option would be to have two or more boats working simultaneously when there are very large (500-1,000) groups of dolphins. It would be powerful to turn each encounter into its own mark-recapture experiment, with one boat serving as the capture and the other as the recapture (Read et al. 2003). This approach could increase capture probability of the database as a whole, but will also improve studies of sociality (Chapter 5) and improve accuracy and precision of estimates of school size, which will in turn improve estimates of mark rate. Having two boats may also reduce any heterogeneity introduced by dolphins responding to the boat. It has been shown that stereotyped zig-zag avoidance responses of killer whales to boats disappear when more than three boats approach simultaneously (Williams and Ashe 2007). Perhaps photo-ID of large schools of Pacific white-sided dolphins will become slightly more tractable with a team effort. On a final note, it became apparent in 2010 that much of the budget was being spent transiting

from our field station to the Broughton Archipelago sites where dolphins were found most reliably. It may be possible to base a portion of the research effort from AM's Broughton field station to improve efficiency. By reducing transit time, I would maximise time spent photographing dolphin groups.

3.4.5.4. Analysis

The best way forward to improve precision in the estimates of abundance and survival rate is simply to collect more data, and maximise capture probability. In my case, the above-mentioned approaches will do that (funding, design & field protocols). As number of recaptures increases, this will allow more sophisticated analytical techniques to be explored to improve accuracy and precision of the estimates.

As recapture probability increases, mark-resight models (McClintock and White 2009; McClintock et al. 2009a) may be a useful approach to take advantage of data from unmarked individuals. Newly developed methods (Bonner 2013; Hiby et al. 2012; McClintock et al. 2013) to include photographs of individuals with distinctive marks that are visible from only one side would increase sample size. Unfortunately, these cannot be used with AM's historical data, because the information on unmarked animals is unavailable, but as the database of digital photographs grows, I will pursue these models. Bayesian approaches have been shown to help detect trends from sparse data (Moore and Barlow 2013).

3.4.6 Conclusions

It is possible to estimate demographic parameters for Pacific white-sided dolphins using mark-recapture methods from photo-identification of individually identifiable dolphins. Although the estimates of abundance and survival are imprecise, the precision can be improved with an increase in capture probability. With adequate resources to support continued photo-identification effort, capture probability is likely to improve given the high mark rate. Although there may be low statistical power to detect trends at this stage given the low precision in abundance estimates (Taylor and Gerrodette 1993; Taylor et al. 2007b), the estimates are useful for calculating initial sustainable limits to human-caused mortality from bycatch (Wade 1998; Williams et al. 2008) in the region.

Estimating population growth rate using stochastic population models (Currey et al. 2009b) or from realized population growth models (Pradel 1996; Sandercock and Beissinger 2002) may reveal a temporal pattern and provide insight into the pattern of growth and the current population status.

The newly derived parameter estimates presented here in addition to the reproductive estimates in presented in Chapter 5 were used to assess threats and uncertainty in parameter estimates through stochastic population trajectory models (e.g. Population Viability Analysis (PVA) (Boyce 1992; Lacy 1993) in Chapter 6. Similar approaches have been used for bottlenose dolphins (Currey et al. 2009b; Thompson 2000) and Hector's dolphins (Slooten et al. 2000). An assessment of viability could inform an updated conservation status assessment of Pacific white-sided dolphins in Canada's Pacific Region (Stacey and Baird 1991), and also inform IUCN status assessments. In addition to the species-level conservation assessments, IUCN is now conducting regional assessments of populations. The new demographic information derived in this study coupled with an increase in information on population structure means that these dolphins could be assessed using the IUCN regional criteria for conservation in the near future (Currey et al. 2009a; Gardenfors et al. 2001).

Pelagic dolphins illustrate many of the problems that challenge the study and conservation of wide-ranging species, but low capture probability has also been found in extensive photo-ID surveys in fin and beaked whales off southern California (Falcone and Schorr 2014). When a species is cryptic or highly mobile, or when a study site is small relative to a population's range, capture probability may be low, despite a researcher's best efforts. Capture probability can also be low in cases when depleted populations are recovering, but funding and search effort remain constant. Such a situation appears to be happening in the U.S. West Coast population of humpback whales. Capture probability is decreasing rapidly, and variance increasing, as the population recovers toward pre-whaling abundance (John Calambokidis, pers. comm., 2 February 2015). This is reducing power to detect trends and identify the point at which a recovering stock has fully recovered. Statistical guidance is needed for data-sparse situations like these, because increased survey effort is not always possible in an era of declining funding and conservation triage.

Two philosophically different approaches have been used successfully to improve our understanding of highly mobile or migratory species, and these approaches are complementary rather than mutually exclusive. First, large-scale, international collaborations offer a powerful way to study species at the ocean basin-wide scale at which some species live. For humpback whales, the SPLASH (Calambokidis et al. 2008) and YONAH (Smith et al. 1999) projects brought together researchers from several countries around the North Pacific and North Atlantic, respectively, to estimate abundance, survivorship and movement patterns with unprecedented precision. International collaborations would no doubt improve our understanding of the biology of Pacific white-sided dolphins, just as they have for pelagic seabirds (Wolf et al. 2006), turtles (Hamann et al. 2010), and sharks (Camhi et al. 2009). An alternative approach is to shift away from the need for demographic data in management plans, and focus instead on anthropogenic threats (Bottrill et al. 2008; Master 1991; Wilson et al. 2007). But, it may not be necessary to choose between approaches. When relying on sparse data to inform decisions about the health of wildlife populations, methods are needed to integrate the best available information on both demography and threats (Moore and Read 2008).

INFLUENCE OF KILLER WHALE PREDATION ON PACIFIC WHITE-SIDED DOLPHIN ECOLOGY

Personal motivation

On my first day in the field for my PhD research, I spent a few hours photographing several subgroups of Pacific white-sided dolphins in a long, narrow fjord called Knight Inlet. There were a few hundred dolphins spread across a diffuse school spanning a few kilometers. As my study progressed, I would come to consider this a fairly typical encounter. The dolphins were no more or less approachable than they were on any other day. A small group of dolphins would approach and leave the boat, possibly to encourage me to speed up so they could ride the boat's wake. Another group, which seemed to include mothers and calves, would maintain a distance. All of the dolphins in the group would undergo rapid changes in activity state, from resting to socializing to feeding and back. Keeping track of the highly fluid and dynamic position, activity state and composition of each subgroup was just as challenging as ever.

Suddenly, everything changed. Every individual disappeared underwater in an instant, and then a wall of dolphins could be seen swimming away at the fastest speed I would ever witness in 6 years of studying this species. Local mariners call this behaviour "squalling", because the dolphins churn up the surface of the water in exactly the same way as a sudden wind and rainstorm. For a few minutes, I hesitated to follow, fearing that this was the dolphins' way of demonstrating that they were bothered by my boat. Then, out of the corner of my eye, I saw a large male killer whale breaching just behind

the group of dolphins. Although I had spent years studying killer whales, and my field protocols involve scanning the study area thoroughly every few minutes, there was absolutely no sign of the killer whales until they were a body's length from the dolphins. In some respects, the attack that followed (described below) was anti-climactic, but this awesome event shifted the focus of one part of my thesis. Until this event, I planned to study the effects of human activities (e.g., bycatch in fishing and aquaculture nets, or propeller wounds) on Pacific white-sided dolphins. Now, I knew that I wanted also to explore killer predation as a factor in the ecology of Pacific white-sided dolphins in the inshore waters of British Columbia (BC), Canada. I wanted to know if the event I had just witnessed was truly rare, or simply rarely observed or reported.

4.1 INTRODUCTION

4.1.1 Background

Pacific white-sided dolphins are generally considered a pelagic species (Leatherwood et al. 1984), but in 1984, they began to appear regularly in inshore waters of British Columbia (BC), Canada (Morton 2000). It seems that this inshore movement represented a re-colonization of this habitat rather than an entirely unprecedented distribution shift. Evidence from First Nations' archaeological middens in the area show that Pacific white-sided dolphins have been using the area for thousands of years (Morton 2000). The dolphins appear to use this particular habitat in part to take advantage of predictable prey sources like herring and eulachon. However, finding herring or other fish in this complex network of narrow fjords and bays carries a risk.

Pacific white-sided dolphins have few natural predators. Only one published record of a recovered carcass from the Oregon coast reports injuries consistent with an attack from an unknown shark species (Stroud and Roffe 1979). Apart from sharks, killer whales are the only known (non-human) predator of Pacific white-sided dolphins.

The killer whale is the largest member of the family Delphinidae. It is a generalist predator at the level of the species, with prey ranging from seabirds to great whales (Ford et al. 2005; Ford and Reeves 2008; Ford et al. 1998), but a specialist at the level of the population (Ford et al. 1998). Globally, killer whales have been reported to attack or consume 20 species of cetaceans (Jefferson et al. 1991). Killer whale populations specialise in both prey and prey acquisition strategies around the world. Killer whales specialise in carousel feeding on herring in Norway (Simila and Ugarte 1991), intentional stranding on beaches to capture seals in the Crozet Archipelago (Guinet 1991) and Argentina (Lopez and Lopez 1985), and 'wave-washing' seals off ice floes in Antarctica (Visser et al. 2008).

Two ecotypes are seen frequently in the coastal waters of BC: a fish-eating, *resident* ecotype that feeds primarily on Chinook salmon; and a mammal-eating, *transient* (or "Bigg's") ecotype that feeds on marine mammals (Baird and Dill 1995; Ford et al. 2000; Ford et al. 1998; Morton 1990; Saulitis et al. 2000). A third, offshore, ecotype thought to specialise on elasmobranch

species rarely visits the study area (Ford et al. 2000). The transient ecotype most often feeds on harbour seals in BC, but harbour and Dall's porpoise are also regular prey items (Jefferson et al. 1991). Pacific white-sided dolphins are rarely reported as prey of BC's transient killer whales (Dahlheim and Towell 1994; Ford et al. 1998; Saulitis et al. 2000; Wade et al. 2007a), but the transient killer whale diet studies have not been updated since the 1990s, when Pacific white-sided dolphins had only recently returned to BC's inshore waters (Morton 2000).

Since their 1984 reappearance in the study area, there has been an increase in relative abundance of Pacific white-sided dolphins in inshore waters of BC (Heise 1996a; Morton 2000) and Alaska (Dahlheim and Towell 1994). In 2004-2005, when the first systematic surveys were conducted in BC, an estimated 25,900 (95% CI: 12,900-52,100) Pacific white-sided dolphins were found in BC's continental shelf waters during summer months (Williams and Thomas 2007). The first record of killer whale predation on Pacific white-sided dolphins was made in 1992 (Dahlheim and Towell 1994). Alexandra Morton has studied Pacific white-sided dolphins in the region since 1984 and never observed predation (AM, pers. comm.). Ford et al. (1998) note four attacks on Pacific white-sided dolphins and only one successful predation event out of 166 observations of attacks on marine mammals from 1973 to 1996.

The abundance of seals and cetaceans in BC is thought to have changed markedly over the last 20 years, as whales have recovered from commercial whaling and seals and sea lions have recovered from culling programmes, although few abundance estimates are available (Williams and Thomas 2007). I initiated this study to investigate recent evidence for transient killer whale predation on Pacific white-sided dolphins, in part because information on prey abundance and quality is required under the recovery planning strategy for transient killer whales under Canada's Species At Risk Act (Canada 2007) and in part to better understand a factor that may be influencing the ecology of Pacific white-sided dolphins. The killer whale diet inferred in the 1990s may not represent current prey consumption, because prey acquisition in mammal-eating killer whales is plastic and is expected to respond to changing availability (Smout et al. 2010).

4.1.2 The landscape of fear

Information on predator-prey interactions can also improve our understanding of how the dolphins are using these inshore waters, which they have recolonised after a decades-long absence (Morton 2000). Direct predation can have a population-level effect on abundance, survival and population growth rate, but predators can also exert indirect pressure on prey populations (Seidensticker and McDougal 1993; Williams et al. 2004). If prey species are constantly distracted from feeding or mating in order to remain vigilant in the presence of predators, this can affect activity budgets, fitness and vital rates, without any direct predation ever taking place (Creel and Christianson 2008; Heithaus and Dill 2002). This has been called a “landscape of fear” and it has been shown that predation risk, not only predation, can affect the dynamics of prey species (Laundre et al. 2001). Perceived predation risk is a function of both distance to and number of predators (Beale and Monaghan 2004). From ecological theory, one predicts that the more predators present, the lower the probability of survival (Abrams 1993).

Two classes of predator impacts other than direct lethal effects have been identified (Peckarsky et al. 1993), namely: (1) indirect effects at the community level, such as keystone predator effects and top-down trophic cascades; and (2) non-lethal effects on prey populations. These indirect effects do not directly result in the mortality of individuals, but have negative consequences for the prey population as a whole due to predator avoidance, reduced food acquisition, and reduced growth rate and fecundity as a result of the cumulative effect of vigilance behaviour. Animals make decisions (i.e., choosing one particular behaviour from a set of alternatives) that involve balancing conflicting objectives, such as finding food while avoiding being eaten (Dill 1987). Prey species are expected to face increased risk of predation if the predator learns to spend a disproportionate time where the prey species’ food is abundant. Animals can change habitat to avoid predation, but altering behaviour to reduce risk can carry costs. This can lead to “behavioural resource depression,” whereby predators are less successful because of behavioural modifications on the part of the prey such as increased aggression, greater alertness, or a reduction in risky activities. Although the prey may escape predation, engaging in these avoidance activities may reduce foraging opportunities, thereby affecting fitness through reduction in energy intake. All of these decisions can end up having large effects on the ecosystem. Over time, these decisions are expected to conform to an optimal solution. Importantly, the magnitude of these sub-lethal and indirect predation effects

can cause greater impacts on prey population density and reproduction than direct predation itself (Dill 1987).

Quantifying the role of predators in marine ecosystems can be challenging, because predators may be cryptic, highly mobile, and occur in low densities. Owing to the difficulty of observing predator-prey interactions directly, top-down effects can be assessed by modelling studies that integrate information on abundance, diet, and *per capita* consumption rate (shaped by predator metabolic rate and prey quality) (Williams et al. 2004). A modelling study has found that another *Lagenorhynchus* species, the dusky dolphin (*L. obscurus*) may experience population-level consequences of predation and predation risk by virtue of feeding in fjords that increase vulnerability to attack (Srinivasan et al. 2010). The physical setting of the New Zealand study is reminiscent of the fjords in BC where the current study took place (Morton 2000).

4.1.3 The acoustic arms race

When hunting, transient killer whales adopt stealth behaviour (e.g. long, slow dives, infrequent vocalizations) to remain undetected by their marine mammal prey (Barrett-Lennard et al. 1996; Morton 1990). Once a group of killer whales captures a dolphin, porpoise or seal, the whales may become quite vocal (Deecke et al. 2005; Morton 1990). Some marine mammals can detect killer whale calls from distances of several kilometers (Deecke et al. 2002; Miller 2000). Source levels are not available for the calls of transient killer whales or Pacific white-sided dolphins, but an estimate of the acoustic footprint of predator and prey may be available from proxies. Miller (2000) measured the active space of stereotyped (pulsed) calls of resident killer whales in Johnstone Strait at a range up to 26.2 km (mean=13.1 km, s.d.=4.5 km). However, transient killer whales produce pulsed calls significantly less often than residents (Deecke et al. 2005) (0.05 calls per individual per minute versus 0.34 calls per individual per minute, respectively), presumably to avoid detection (Barrett-Lennard et al. 1996; Morton 1990). Therefore it appears that transient killer whales produce quieter vocalizations and clicks than residents, but it is unclear how much quieter these signals might be. Nevertheless, Pacific white-sided dolphins are capable of hearing killer whale acoustic cues at ranges of several kilometers. The range at which a killer whale can hear a dolphin is unknown because source levels of dolphin vocalisations are needed to quantify the range at which killer whales can detect dolphins (Kyhn et al. 2013).

4.1.4 Objectives of this study

Like all species, Pacific white-sided dolphins in inshore waters of BC are engaged in a balancing act for survival (Morton 2000; Stacey and Baird 1991). Over evolutionary time, these dolphins may have adapted to minimise the risk of predation from sharks or killer whales (e.g. colouration, vocalisations, social structure). However, predation risk varies on shorter, ecological time scales in which dolphins may respond behaviourally to varying risk of predation on a seasonal, daily, or hourly basis.

This chapter reports direct observations of killer whale attacks (successful and unsuccessful) on Pacific white-sided dolphins, in order to identify common themes with respect to predatory behaviour of killer whales and anti-predatory responses of dolphins. Following previous analyses of cryptic sources of anthropogenic and natural mortality in marine ecosystems, e.g., natural predation (George et al. 1994; Steiger et al. 2008; Williams et al. 2004), ship strike (George et al. 1994; Knowlton and Kraus 2001), bycatch in unmonitored fisheries (Knowlton and Kraus 2001; Moore et al. 2013; Williams et al. 2008), I considered four lines of evidence to assess whether killer whale predation on Pacific white-sided dolphins in BC is rare, or rarely witnessed and reported in the primary literature.

First, I report direct observations of predation attempts, based on my own experience and interviews with mariners. Secondly, I examined photographs of well-marked individuals (Chapters 2 and 3) for evidence of injuries and scars that are consistent with killer whale rake marks and human activities, to assess the rate at which Pacific white-sided dolphins are exposed to killer whale attacks and anthropogenic activities that they survive. Thirdly, I examined demographic evidence by including frequency of occurrence of mammal-eating killer whales in the study area as a covariate in a mark-recapture analysis of dolphin survival. Finally, I ran simple bioenergetics models to estimate how many killer whales it would take to consume the number of dolphins that go missing each year through natural mortality and emigration (Chapter 3).

4.2 METHODS

4.2.1 Direct observation

I interviewed local researchers, mariners, whalewatch operators, tour guides, and fisheries observers about their observations of killer whale predation and predation attempts on Pacific white-sided dolphins. I compiled a list of standard questions, and used an online survey tool (Survey Monkey), telephone interviews, and correspondence to compile responses. My goal was to compile as many opportunistic observations as possible of such predation events, and to evaluate these first-hand accounts for commonalities with respect to physical setting, group size, predatory behaviour and anti-predatory tactics (behavioural responses) of the prey species. Although these observations could, in theory, provide a bare minimum estimate of the frequency of occurrence of attacks, no information was available to quantify the degree of underreporting or underestimation, and therefore the number of observations was not intended to provide an annual mortality rate. The number of times predation attempts on other marine mammal species were observed was also recorded.

Using the subset of mariners whose record-keeping allowed them to estimate the number of dolphin attacks relative to those of all other marine mammal species, the average proportion of transient killer whale attacks that involved Pacific white-sided dolphins was estimated in the following way. The number of dolphin kills and total kills were modelled as an intercept-only GLM, using a logit link, and the binomial family, such that the response was a proportion (dolphins and total kills), with all records of a given observer treated as an independent sample.

4.2.2 Indirect evidence (proportion of dolphins with scars)

Photo-ID data from live animals have been used successfully to make inference about lifetime exposure of those individuals to cryptic events, such as historic entanglement in fishing gear (e.g., humpback whales; Robbins 2007). In the process of examining ID photographs (Chapters 2 and 3), I noticed several photographs that could have been indicative of fresh or healed wounds from killer whale teeth. Following recent recommendations on the need for objective criteria for attributing an anthropogenic cause to marine mammal mortality or morbidity cases (Moore et al. 2013), I solicited feedback from experienced marine mammal stranding coordinators and veterinary pathologists to assess whether a sample from these photographs

were indeed consistent with killer whale rake marks, and to distinguish between fresh wounds and healed scars. I selected 22 photos of dolphins with injuries that included missing and mangled dorsal fins, parallel scars on the dorsal fin and/or body, and non-parallel or random scars on the body. The selected photographs were of high enough quality to assess the source of injury, but the photos used to solicit expertise were not screened for photo quality or animal distinctiveness (Chapter 2) because they were not being used for identification purposes in this exercise. Of this sample of 22 photographs, 8 seemed consistent to me with serious injury from human activities (propeller wounds or damage from fishing gear), 6 were what I considered injuries with unknown origin, and the remaining 8 I considered likely injuries resulting from killer whales.

I used the following to inform my judgement about the likelihood that a case could be attributed to killer whales. I attributed scars to killer whale teeth when 3 or more parallel marks were found in close proximity (Steiger et al. 2008) and “highly structured”, i.e., “long, thin, and parallel”(George et al. 1994) . Teeth marks from other predators were ruled out, based on the assumption that shark wounds are characterised by numerous penetrations in an oval configuration and by jagged serrations (Brodie and Beck, 1983; Riedman, 1990). The 14 photographs of injuries that I believed to be either anthropogenic or of unknown origin served as a control group for the quality control step of expert solicitation. The control photos were also used to inform judgement about the likelihood that injuries recorded from high-quality photographs of distinctive dolphins were from anthropogenic activities.




	<p>Example of a dolphin with mark thought to come from a killer whale attack.</p>
	<p>Example of a dolphin with mark (on the leading edge of the dorsal fin) thought to come from a fishing line or net.</p>
	<p>Example of a dolphin with mark of unknown origin.</p>

Figure 4.1. Examples of the three types of photos included in the marine mammal injury expert survey. I included a sample of photos I thought were injuries caused by (1) killer whales, (2) human activities, and (3) unknown origin. Responses from experts were used to guide subsequent categorization of injuries for the well-marked dolphins in the digital photo-ID catalogue.

I circulated the set of photos to 18 scientists with expertise in marine mammal injury assessment. I used a survey template to guide responses via a web-based interview/questionnaire site, and asked each respondent to gauge whether they considered the wounds in a given picture had been caused by killer whales, other dolphins, boat propellers, fishing nets, or another source of injury. Multiple-choice questions were asked to assign the injuries shown in each photograph to one of the three causes in Table 4.1, with respondents encouraged to skip any photographs they felt they could not interpret reliably. The survey response section for each photograph included space for free-form comments as well.

The feedback from the survey on the 22 photographs was used to guide my decision-making when examining the photographs of 415 of marked individuals in the digital photo-identification catalogue (Chapter 2) to estimate the proportion of killer whale rake mark scars in the population.

4.2.3 Dolphin demographic evidence (killer whale presence as covariate in dolphin survival analysis)

Formal and informal sightings networks have been instrumental in monitoring cetacean habitat use of my study area since 1986 (Morton 2000; Morton 2002). Using long-term, year-round acoustic and visual monitoring data from a land-based research station called Orcalab (Figure 2.1) was recorded. Although vocally active species such as resident killer whales are thought to spend little time unobserved in the study area during the busy summer months, transient killer whales are acoustically cryptic, and the number of days when transient killer whales were reported certainly underestimates presence, especially in winter. The minimum number of days that transient killer whales were observed is thought to be a reliable index of interannual variability in area usage, however, because observer effort at Orcalab has been consistent since 1986 (Morton and Symonds 2002). This tally was used as a candidate covariate in a Cormack-Jolly-Seber analysis of Pacific white-sided dolphin survival (see Chapter 3). These models tested whether interannual variability in exposure to transient killer whales (i.e., a proxy for predation risk) explained sufficient variation in dolphin survival to warrant the addition of an extra parameter. Model selection was accomplished using AIC (Burnham and Anderson 2002).

4.2.4 Bioenergetic models

The Pacific white-sided dolphin abundance and survival rate estimates reported in Chapter 3 were used to estimate the number of dolphins that “disappear” each year from the local dolphin population via natural mortality and/or emigration. I used long-term sightings data from Orcalab to estimate the minimum number of daily visits by transient killer whales in the study area each year. I used previously published methods to conduct simple bioenergetic analyses (details below) to assess whether it is theoretically possible for the transient killer whales that use the study area to consume the dolphins that go missing from the dolphin population (Baird and Dill 1996; Trites and Pauly 1998; Williams et al. 2011b; Williams et al. 2004).

Orcalab’s minimum daily counts of killer whales were treated as a daily census of killer whales to serve as a minimum estimate of abundance (in units of whale-days) in each year from 1987-2012. Orcalab protocols (Morton 2002) use visual and acoustic cues, both from their own land-based vantage point and the on-the-water observations of local researchers and whalewatchers, to identify killer whales to matriline, or at least ecotype (*i.e.*, fish-eating residents or mammal-eating transients). Records are reconciled each day to give a best estimate of the number of resident and transient killer whales that visited the study area that day. The best, daily estimate of number of transient killer whales was considered an estimate of the number of “whale-days” that transient killer whales were in the Orcalab study area. For days when transient killer whales were present, but the estimate of number of whales was missing, the median group size was used. The number of whale-days was calculated for each year (1987-2012) from the Orcalab database.

I estimated the caloric value of an adult Pacific white-sided dolphin, because no direct measurements from bomb calorimetry are available (Williams et al. 2004). I assumed that dolphins were comparable to harbour seals in terms of proportional composition of protein, fat and non-digestible carbohydrate material (Baird and Dill 1992), with a mean body mass of 85 kg (Walker et al. 1986). Caloric values of blubber and muscle tissue were taken from the literature (Williams et al. 2004). No information is available from captive transient killer whales on digestive efficiency of marine mammal tissue, so I assumed that dolphin flesh is as digestible to killer whales as fish with a mean digestive efficiency of 84.7% (Williams et al. 2004).

There is considerable uncertainty in the estimates of killer whale body size (Trites and Pauly 1998; Williams et al. 2011b; Williams et al. 2004) and metabolic rate (Ford 2010; Kriete 1995; Noren 2011; Williams et al. 2004) as well as Pacific white-sided dolphin body size (Ferrero and Walker 1996; Heise 1996b) and energy density. Due to the inherently speculative nature of an exercise aimed at exploring how many dolphins a group of killer whales could eat, no attempt was made to incorporate all of this uncertainty into a single parameter estimate with reliable confidence intervals. Instead, a range of scenarios was considered to try to provide plausible ranges for illustrative purposes, given the uncertainty in killer whale (a) body mass, and (b) mass-specific metabolic rate estimates.

A range of body mass and mass-specific metabolic rate scenarios were considered for killer whales (Table 4.1): combinations of “conservative”, “medium”, “high”, and “best” estimates for body mass of males and females and mass-specific metabolic rates from different sources were used (Baird 1994; Trites and Pauly 1998; Williams et al. 2011b; Williams et al. 2004). For example, a global analysis of whaling records found that killer whales taken from the North Pacific were much larger than those taken from Iceland, with a best estimate of asymptotic body mass reported for North Pacific killer whales as 4,616 kg and 6,199 kg for adult females and adult males, respectively (Williams et al. 2011b). These estimates of mass combined with a mass-specific metabolic rate of 30 kcal/kg/day (Williams et al. 2004) are used in scenario ‘Best-Best’ (Table 4.1).

I estimated the number of dolphins that disappear annually from the local dolphin “population”, based on the total population size from the two-sample estimator (Chapter 3), and the geometric mean of the annual survival rates from the CJS model with killer whales as a covariate (0.902) (Table 4.5). Based on these three estimates of mass and mass-specific metabolic rate, I then calculated how many killer whale-days it would take to account for the number of dolphins that disappear from the local population each year if the dolphins met killer whales metabolic requirements at a range of levels. Scenarios at a range of consumption estimates were explored at four levels: (1) 9.5% level based on responses from interviews (see Results below); (2) 25%; (3) 50%; and (4) 100%. Finally, I compared this to the annual number of transient killer

“whale-days” observed from the Orcalab data during the same years as the current study (with the exception of 2013): 1987-2012.

Table 4.1: Scenarios of mean mass and average daily mass specific energy demand for male and female killer whales from “conservative”, “medium”, and “best” estimates from the literature. Each mass and metabolic rate scenario assumes a 285,090 kcal gross caloric value for dolphins at an 84.7% digestive efficiency (Williams et al. 2004).

Scenarios	kcal/kg per day	Mean mass adult male killer whale	Dolphins per day required by adult male killer whale	Mean mass adult female killer whale	Dolphins
					per day required by adult female killer whale
Conservative mass; Conservative energetic requirement	30	2587	0.32	1974	0.25
Conservative mass; High energetic requirement	62	2587	0.66	1974	0.51
Best mass; Best energetic requirement	30	6199	0.77	4616	0.57
Medium mass; Medium energetic requirement	55	4733	1.08	2800	0.64
Best mass; Medium energetic requirement	55	6199	1.41	4616	0.72
High mass; High energetic requirement	62	6199	1.59	4616	1.19
Best mass; High energetic requirement	62	6199	1.59	4616	1.05

4.3 RESULTS

4.3.1 Direct observation

A total of 13 mariners responded to my request for information. This effort to compile previously unreported observations has added 32 first-hand reports of killer whale attacks on Pacific white-sided dolphins (Table 4.2) to the seven previously reported in the literature (Ford et al. 1998; Wade et al. 2007a).

Some details of each predation event are given in Table 4.2. The vast majority (69%) of the predation events took place in confined waters, either a shallow bay or a narrow passageway, with eight respondents indicating that the killer whales used the local topography to actively herd the dolphins into a place where they could be killed easily. The anti-predatory tactics used by the dolphins generally started with high-speed chases (“squall”) and, when that failed, eight respondents noted that the dolphins entered shallow waters to avoid predation, sometimes beaching themselves on shore in the process. In three cases, there was evidence for surplus killing or injury (i.e., dolphins that died during escape, but not consumed by the whales).

Based on records kept by 9 local mariners, 24 attacks on dolphins were observed, collectively, out of a collective 252 observed attacks on all species (Table 4.3). An intercept-only GLM estimated that the average proportion of transient killer whale attacks that they observed to include dolphins was 0.095 (95% CI: 0.061, 0.142).

Table 4.2 Reports of killer whale predation on Pacific white-sided dolphins in the region collected from the published literature, web or news reports ('web'), reports submitted to me by mariners and researchers ('interview'), and personal observation. Site attributes indicates whether the location of the attack took place in relatively open water or in confined waters (e.g. enclosed bay). The anti-predatory response of dolphins is reported as 'beached' to indicate dolphins stranding, 'shore' for dolphins traveling toward and/or very close to shore, 'squall' for high-speed travel, 'cryptic' for behaviour that appeared to be an attempt to avoid detection.

Event	Year	Location	Site features	Dolphin group size	KW group size	anti-predatory	predatory behaviour	Outcome	Source
1	1992	Dixon Entrance, AK	confined waters	5 to 6	15	refuge	kill	at least 1 dolphin killed	Dahlheim and Towell 1994
2	1992	Clarence Strait, AK	NR	NR	NR	NR	kill	NR	Dahlheim and Towell 1994
3	1993	Petersburg, AK	NR	6 to 8	NR	NR	kill	NR	Dahlheim and Towell 1994
4	1995	Queen Charlotte Sound, BC	open water	"small group"	5	refuge, aerial	kill	NR	web
5	1995	Nigei Island, BC	open water	NR	NR	aerial	kill	1 dolphin on beach	interview
6	1996	Kent Inlet, BC	confined waters	NR	NR	NR	NR	NR	interview
7	1996	Kent Inlet, BC	confined waters	NR	NR	NR	NR	NR	interview
8	1999	Hardy Bay, BC	confined waters	NR	NR	NR	kill	NR	interview
9	2000	Viner, BC	confined waters	50	NR	squall	chase	NR	interview
10	2004	Columbia River, WA	open water	NR	NR	NR	NR	unknown	interview
11	2007	Johnstone Strait, BC	confined waters	1000	6	squall	attack from	5 dolphins killed	interview
12	2010	Viner, BC	confined waters	NR	NR	squall, shore	kill	NR	interview
13	2010	Goose Bank	open water	2 to 3	5	high speed	chase	abandoned chase	interview
14	2010	Goose Bank	open water	200	8	high speed	chase	abandoned chase	interview
15	2010	Broughton Strait	confined waters	300+	6	squall	breach,	at least one kill, likely more	interview
16	2011	Telegraph Cove, BC	confined waters	NR	NR	NR	NR	NR	interview
17	2011	Hyacinte Bay, BC	confined waters	100-300	NR	squall, shore	NR	NR	web
18	2011	Campbell River, BC	confined waters	NR	NR	NR	NR	4 on beach, 1 w/ fresh teeth marks	news report
19	2011	Turn Island	NR	NR	6+	squall	breach	beached dolphin likely died	interview
20	2011	Broughton Strait	confined waters	100	4	squall	breach	NR	interview
21	2011	Phillips Arm	confined waters	25+	4+	NR	breach	NR	interview
22	2011	Broughton Strait	confined waters	500-1000	6	squall	chase	abandoned chase	interview
23	2011	Broughton Strait	confined waters	100+	9	high speed	attack	at least one kill	interview
24	2011	Knight Inlet	confined waters	15-20	4 to 8	high speed	chase	kill	interview
25	2011	Donegal Head	open water	15-20	4 to 8	high speed	chase	kill	interview
26	2012	Bute Inlet, BC	confined waters	NR	10	squall, shore	kill	at least one kill	interview
27	2012	Bute Inlet, BC	confined waters	150	NR	high speed	NR	NR	interview
28	2012	Johnstone Strait	confined waters	1	16	NA	breach	kill	interview
29	2012	Cormorant Channel	confined waters	12	8	high speed	chase	abandoned chase	interview
30	2013	Denny Island, BC	confined waters	NR	NR	NR	NR	NR	interview
31	2013	Wells Passage	confined waters	15-20	4 to 8	high speed	chase	kill	interview
32	2014	Bute Inlet, BC	confined waters	10	4 to 6	high speed	attack from	let dolphin go	interview
33	UNK	Johnstone Strait, BC	confined waters	10 to 20	3 to 5	high speed	NR	NR	interview
34	UNK	Hecate Strait	open water	100	10	NR	NR	NR	interview
35	UNK	Georgia Strait	open water	NR	10	NR	NR	NR	interview

Table 4.3 Results from interviews from observers who kept records of the total number of killer whale attacks on dolphins compared to total number of killer whale attacks on all marine mammal species observed.

Observer	Total no. of dolphin attacks observed	Total no. of all killer whale attacks observed
1	1	6
2	3	7
3	7	99
4	1	4
5	4	100
6	1	5
7	3	15
8	3	4
9	1	12

Several common themes emerge in observers’ reports of killer whale and dolphin behaviour. In some respects, the attack I describe at the beginning of this chapter (November, 2009) appears to be fairly typical of the commonalities in witness reports of killer whale predation on Pacific white-sided dolphins in NE Pacific coastal waters. Some common killer whale hunting tactics include: dividing a large group of dolphins into subsequently smaller groups; focusing on a small group; using the shoreline and the seabed as tools to help corral/herd the dolphins; and ramming the dolphins either from below the surface, and/or to launch the dolphin in the air and plunge down on top of the dolphin. In nearly all interviews, observers noted that they did not notice the killer whales, or that the dolphins appeared not to have noticed the killer whales, prior to the attack. However, in one report, apparently naïve dolphins approached a group of killer whales before the killer whales attacked the dolphin group. In some cases, the killer whales abandoned chase altogether or appear to have had no intention of consumption. One mariner reported a killer whale ripping a small piece of flesh from a dolphin head and leaving the area without eating the dolphin.

There are also common themes to the anti-predatory response of the dolphins. The dolphins often “squall” or travel at extremely high speeds to escape. If trapped in enclosed waters, the dolphins may head to shallow waters intentionally to escape the whales or accidentally. In one

case, the observer watched the dolphins attempt escape up a small creek. In some cases, dolphins beached themselves in the ensuing panic. One unwitnessed, but potential predation event not included in Table 4.2, stemmed from finding 22 dolphins stranded on a beach where two killer whale attacks had occurred previously (Table 4.2). The observers were convinced that the stranding must have been the result of a killer whale attack (and some dolphins possessed what looked to be fresh killer whale rake marks), but they did not witness the attack.

4.3.2 Indirect evidence (injury proportion analysis)

Of the 18 experts solicited for their opinion on photographs of dolphin injuries, only 7 responded. For most photos, the respondents indicated that the injuries were of unknown origin (Table 4.4). Two of the photos were thought to be from killer whales, two from conspecific interactions, and the rest were divided among unknown, fishing, and conspecific interactions. Those who responded to the photographs that I originally thought were indicative of injuries from killer whales concurred with my opinion in all cases. Experts were uncertain of the cause of injury in 13 (59%) of 22 cases and also left no response when uncertain (Table 4.4).

After expert responses helped diagnose cause of injury from photos, I revisited photos of 415 individuals identified between 2008 and 2013. Of these, 16 individuals were found to have scars or injuries that were consistent with killer whale rake marks (like the first dolphin pictured in (Figure 4.1) and only two had marks consistent with fishing activities. This translates to 3.9% of the marked individuals in the study showing evidence of having survived a killer whale attack and 0.5% of the marked dolphins showing evidence of interaction with fishing gear at some point during their lifetime, or at least during the 6-year period during which I took the photographs.

Table 4.4: Summary of responses from seven experts asked to assess 22 sample photographs of scarred dolphins. In several cases, experts declined to leave a response when uncertain about origin of the scar or injury.

Source of Injury	Number of photos
Killer whale	2
Dolphin	2
Fishing	3
Equivocal among dolphin, fishing, and unknown	1
Equivocal between fishing and unknown	1
Unknown	13
Total	22

Fresh and healed killer whale wounds were observed in photographs of unidentified dolphins as well. Photographs from an encounter in April 2011 showed fresh killer whale rake marks (top photo, Figure 4.1). This photo was from an encounter during which vigilance behaviour was observed. Immediately after ending the encounter, I observed a small group of dolphins that appeared to be patrolling the opening of a narrow inlet. The rest of the ~1,000 dolphins I had encountered previously were engaged in high-speed travel. I had photographed a group of mammal-eating killer whales in the area 4 days prior to this event.

4.3.3 Demographic evidence (killer whale presence as covariate in dolphin survival analysis)

After killer whale and dolphin observations from visual and acoustic observation records from 1985-2012 were collected, I calculated that killer whales were present in the study on 728 days and dolphins were present on 774 days (Figure 4.2). On 94 occasions, mammal-eating killer whales and dolphins were observed on the same day. Both killer whales and dolphins were observed in every month and in each year of the 27-year observation period. Sightings of killer whales peaked in October (Figure 4.3).

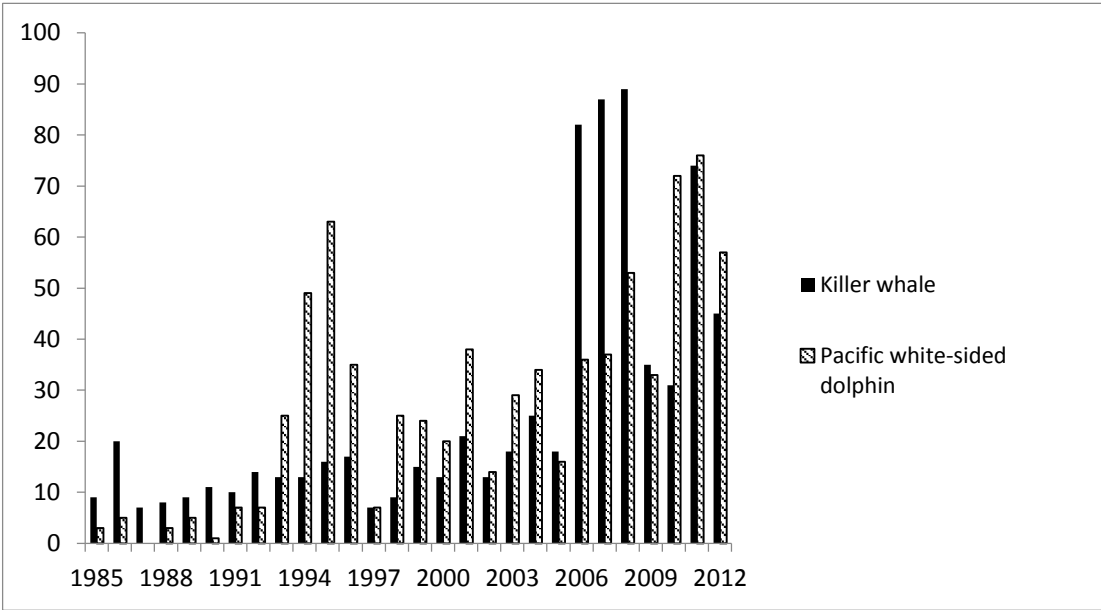


Figure 4.2: Number of mammal-eating killer whale sightings and acoustic detections from the Orcalab monitoring station 1985-2012.

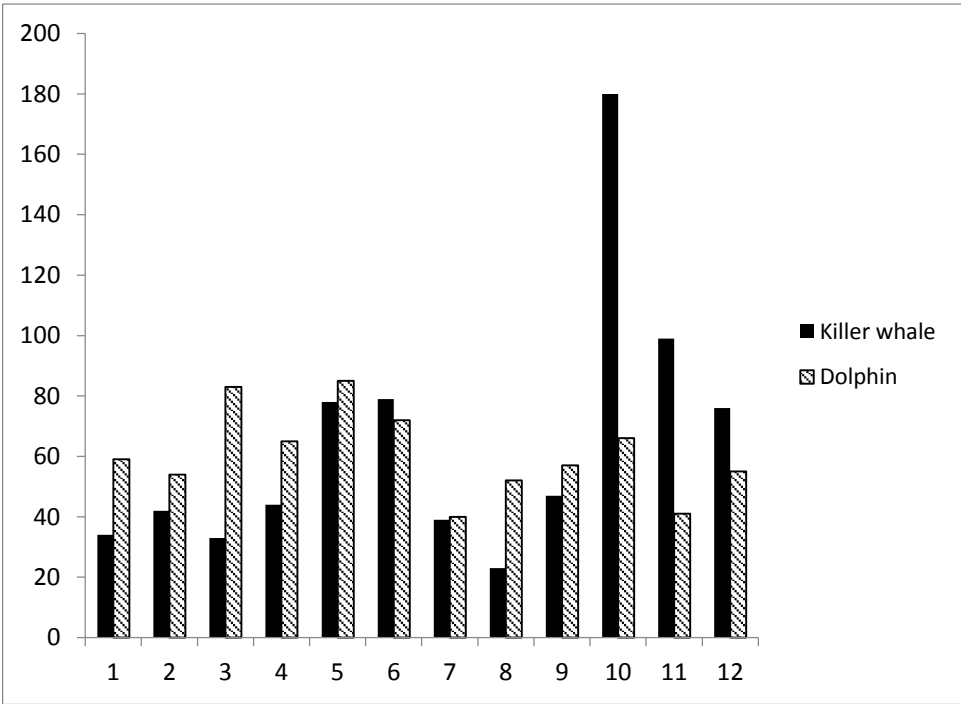


Figure 4.3: Seasonal sightings and acoustic detections of mammal-eating killer whales and Pacific white-sided dolphins from the Orcalab monitoring station 1985-2012.

The CJS model (Chapters 2 and 3) with killer whale presence as a candidate covariate was ranked as the second best fitting model. However, the top two models had a $\Delta AIC < 1$, giving

equal weight to both models (Table 4.5) (Burnham and Anderson 2002). Thus, there was equivocal support from the data for including a term describing the minimum number of days that transient killer whales were in the same study area as the dolphins. Both models are cases where capture probability was “restricted” to four different parameters due to the variability in capture probability. With the additional explanatory power offered by the killer whale term, the best estimate of adult survival of Pacific white-sided dolphins was 0.92 in most years, but declined when numbers of killer whales increased in the area (Figure 4.4).

Table 4.5: Candidate model outputs from CJS model to estimate survival rate and recapture rate with killer whale presence (kw = number of “whale-days” per year) as a covariate. In the “4 p” models, capture probability was modelled as four parameters that represented four groups of similar capture probabilities across years.

Model	AICc		Model	Num.	
	AICc	ΔAICc	Weights	Likelihood	
$\varphi(\cdot)p(t)$ "4 p" model	937.2	0.0	0.529	1.000	4
$\varphi(kw)p(t)$ "4 p" model	937.5	0.2	0.471	0.892	5
$\varphi(\cdot)p(t)$	959.4	22.1	0.000	0.000	22
$\varphi(kw)p(t)$	960.2	23.0	0.000	0.000	23
$\varphi(t)p(t)$ "4 p" model	975.5	38.3	0.000	0.000	28
$\varphi(t)p(t)$	1005.8	68.6	0.000	0.000	46
$\varphi(t)p(\cdot)$	1097.3	160.0	0.000	0.000	26
$\varphi(kw)p(\cdot)$	1098.3	161.1	0.000	0.000	3
$\varphi(\cdot)p(\cdot)$	1098.4	161.1	0.000	0.000	2

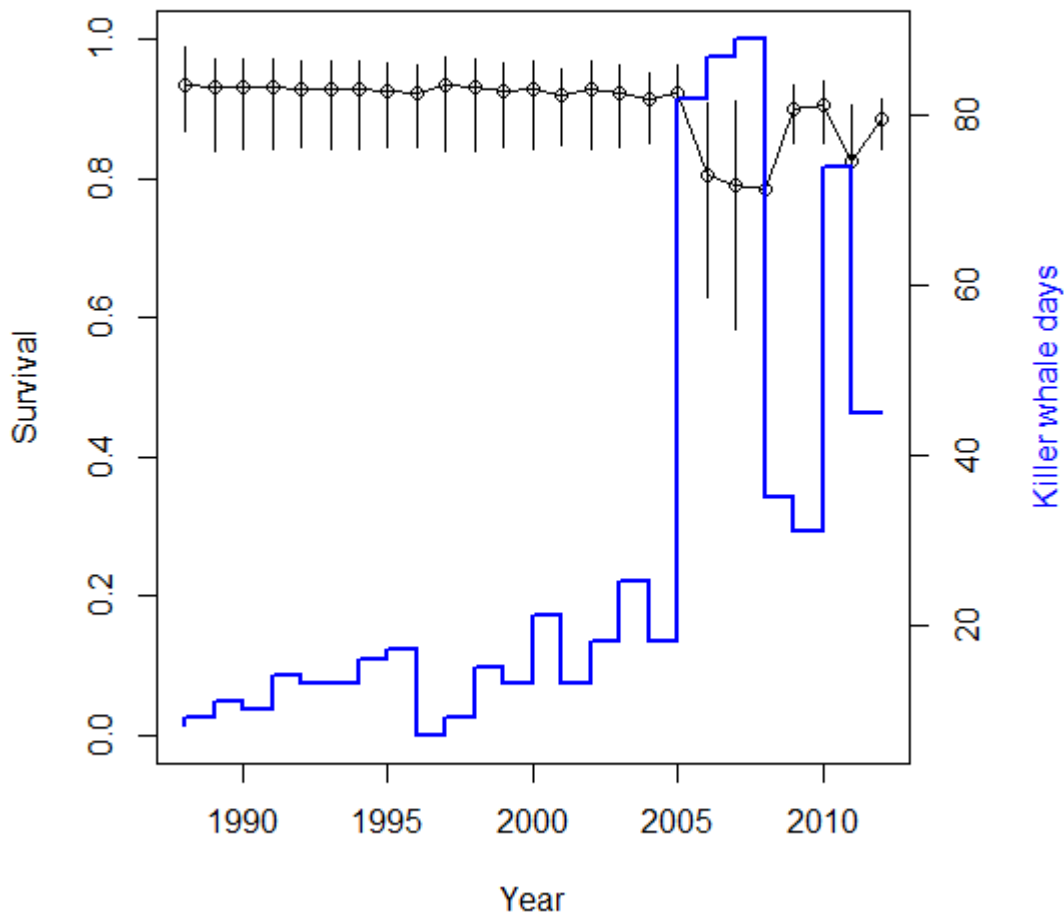


Figure 4.4: Plot of dolphin annual survival rate as a function of killer whale presence and the number of killer whale days in each year (1988-2012).

4.3.4 Bioenergetic models

An adult white-sided dolphin weighing 85 kg is estimated to provide 285,090 kcal (gross) of energy, given the tissue composition of a harbour seal (Baird and Dill 1992) and energy density values for marine mammal blubber and muscle (Williams et al. 2004). Assuming an 84.7% digestive efficiency (Williams et al. 2004), an average-sized dolphin represents a net caloric value to a killer whale of 256,581 kcal.

Observations from the Orcalab database were used to calculate the number of observed transient killer whale-days in the study area (Table 4.6). Note that Orcalab's estimate of

transient killer whale usage of the area is a minimum estimate of presence; unlike the highly vocal fish-eating resident killer whales, mammal-eating killer whales often hunt silently and could have gone undetected at night or in rough conditions. This minimum tally of whale-days is presented to show interannual variability in transient usage of the study area. The number of transient killer whales in the study area ranged from 1 to 30 individuals during the period 1985-2012, with a mean group size of 5.2 (SE=0.294) individuals. Median group size was 5. Transient killer whales were observed in the study area an average of 27 days per year. With a median group size of 5 killer whales, this translates to 135 transient killer whale-days in a typical year.

Estimates of dolphin abundance and mortality (1-survival) from Chapter 3 were used to estimate the number of dolphins that “disappeared” from the population each year. Using the “Best energetics; Best mass” scenario (Table 4.1) with respect to body mass and mass-specific metabolic rate, I estimated how many killer whale-days it would take to account for the number of dolphins that went missing from the area each year if killer whales met their energetic demand exclusively by feeding on dolphins (the “100% scenario”). To include uncertainty and incorporate new information on diet composition of transient killer whales (e.g., interview results from Table 4.3), I estimated this value (number of whale-days needed to consume the number of dolphins estimated to go missing from the area each year) with dolphins comprising a range of levels of the killer whales’ diet: 9.5% (the best estimate from Table 4.3); 25%, 50% and 100%). I found that killer whales could be responsible for about one-third of dolphin deaths from 2011-2012 (Table 4.6) at the 9.5% level calculated from interviews with observers of killer whale predations in the study area (Table 4.3). The only scenario in which killer whale predation is capable of accounting for all of the missing dolphins is an unlikely one, namely if the whales were meeting 100% of their energetic requirements from dolphin predation (Table 4.6).

Table 4.6: The total dolphin population size estimated from the two-sample estimator (Chapter 3), the number of dolphins that 'disappear' annually based on an annual survival rate of 0.924, the number of killer whale days required to account for annual dolphin mortality assuming scenario “Best-Best” (Table 4.1) killer whale body masses and mass-specific metabolic rate, and the number of killer whale days from Orcalab year-round sightings and acoustic detections.

Year	Dolphin abundance (N)	No. of dolphins that disappear annually	No. of kw days required to account for annual dolphin mortality assuming 9.5% of diet	No. of kw days required to account for annual dolphin mortality assuming 25% of diet	No. of kw days required to account for annual dolphin mortality assuming 50% of diet	No. of kw days required to account for annual dolphin mortality assuming 100% of diet	Minimum observed Number of KW Days
1992-1993	1346	102	1607	611	305	153	65
1993-1994	2022	154	2414	917	459	229	65
1994-1995	688	52	821	312	156	78	80
1995-1996	2773	211	3311	1258	629	315	85
1996-1997	1890	144	2257	858	429	214	35
1997-1998	1009	77	1205	458	229	114	45
1998-1999	1009	77	1205	458	229	114	75
2010-2011	2889	220	3450	1311	655	328	370
2011-2012	546	41	652	248	124	62	225

4.4 DISCUSSION

Mammal-eating killer whales are attacking Pacific white-sided dolphins far more often than one would expect from the literature (Deecke et al. 2005; Ford et al. 1998; Wade et al. 2007a). They are capable of eating substantial numbers of dolphins (Table 4.6), but if they were meeting the majority of their metabolic demands by consuming dolphins, we would expect see it more often – the attacks are highly conspicuous in contrast to the subtle cues that accompany predation on harbour seals (Deecke et al. 2005; Ford et al. 1998). Overall, it seems that transient killer whales are capable of exerting non-trivial predation pressure on dolphins in my study area from all four lines of evidence:

- many more observed predation events since the last review in 1996;
- 3.9% of dolphins show evidence (scar or injury) consistent with surviving a killer whale attack;
- survival model provides some evidence that killer whale presence explains some heterogeneity in survival probability; and
- the number of dolphins that killer whales could consume at is high relative to dolphin abundance in the study area even at the lowest percentage of diet explored here (9.5%).

4.4.1 Direct observation

The reports from mariners are extremely valuable not only because predation events are relatively rare to observe, but also because the observations can provide additional information on the behaviour of both killer whales and white-sided dolphins during an attack.

The dolphins' anti-predatory response to head towards shore, up a river, or toward a beach may work together to cause more dolphins to be killed than are actually consumed or needed to meet energetic demand. This so-called "surplus killing" can result in predators causing bigger population-level effects on prey species than one may infer from studies of predator diet.

It has been postulated that some cetaceans respond to mid-frequency sonar signals (even when this signal is outside the frequency range of a species' peak hearing sensitivity) because it may be perceived mistakenly as a killer whale call (Tyack et al. 2011; Zimmer and Tyack 2007). Killer whale vocalizations have elicited the strongest behavioural avoidance responses ever documented among cetaceans (Cummings and Thompson 1971; Tyack et al. 2011; Zimmer and Tyack 2007). Consequently, killer whale vocalizations are often used as the aversive treatment in sonar behavioural response studies. But, there is little direct evidence to demonstrate that animals display an aversive response to killer whale calls. In playback experiments, grey whales abruptly changed direction and swam away from the sound source when exposed to recorded killer whale calls (Cummings and Thompson 1971). Here I show that behavioural response of an oceanic dolphin to actual killer whale predation attempts can lead to stranding. This predator-prey system may be a useful one to study to better understand population consequences of disturbance of sonar and other anthropogenic activities; to understand how disturbance could lead to population consequences (New et al. 2013).

4.4.2 Sublethal evidence and impacts

A scar proportion of 3.9% is low compared to other studies. Bottlenose dolphins in Shark Bay have a 74.9% scar rate from shark attacks (Heithaus 2001). Killer whales may be extraordinarily efficient predators (i.e., few dolphins survive attacks), or killer whale attacks may be relatively rare. It may also be the case that killer whales may occasionally wound a

dolphin and abandon it without killing it. Surplus killing of harbour seals has previously been reported in killer whales (Gaydos et al. 2005).

The survivors of killer whale attacks may obtain information about the attacks and communicate this information to the rest of the group (Dill 1983). Similarly, dolphins may engage in predator inspection. In addition, dolphins regularly interact with non-predatory, fish-eating killer whales and have taken refuge by “hiding” among fish-eating killer whales following an attack from mammal-eating killer whales (Garry Henkel, personal communication, February, 2015). Predator inspection may serve to teach younger animals about the predator (FitzGibbon 1994). Vigilance behaviour requires exclusive attention, however, and may come at the expense of other activities such as time spent feeding (Cowlshaw et al. 2003).

Dolphins are constantly making decisions about where to travel, when to rest and where to forage: choosing one behaviour from a set of alternative behaviours involves weighing risks and trade-offs (Dill 1987). When mammal-eating killer whales are present, and dolphins are at risk of predation, these decisions are made in an “ecology of fear” (Brown et al. 1999; Schmitz et al. 2004). A dolphin’s ability to survive and reproduce hinges on its ability to successfully trade-off between competing needs to feed and avoid predation. Repeated episodes of disturbance due to predation risk may affect the dolphin’s energetic balance, which can affect its ability to survive, reproduce and feed its offspring (Bejder et al. 2006; Lusseau 2004; Williams et al. 2006). Ultimately, predation risk can negatively impact the population as a whole. In fact, these “risk-effects” can have a greater impact than the direct effect of mortality from predation itself (Creel and Christianson 2008; Terborgh and Estes 2010). Taken together, killer whales may be driving the dynamics of Pacific white-sided dolphin populations, both directly and indirectly.

4.4.3 Demographic and energetic evidence

The results of the CJS model with killer whale presence as a covariate provides equivocal evidence that the presence of mammal-eating killer whales in the study area may affect adult annual survival rates of Pacific white-sided dolphins. Dolphin survival rate declined markedly

in years where the number of killer whales was high (Figure 4.4). Similarly, in years where the number of killer whale days was high enough to account theoretically for the estimated dolphin mortality in that year, there is a decline in dolphin abundance (Figure 4.4). The decline in abundance could be due to mortality or displacement of a fraction of the dolphin population from the study area to reduce predation risk.

4.4.4 Future research

Collecting observations from mariners was a useful approach to increase the sample size of a rarely witnessed event and the observations were useful in setting the behavioural context of both predator and prey. I plan to continue to solicit observations from mariners in the region because their observations added information on the diet of mammal-eating killer whales (what proportion of the diet is dolphin), providing context to predatory behaviour of killer whales and the anti-predatory behaviour of dolphins. These observations would continue to add value to future directed research on killer whale predation on Pacific white-sided dolphins.

The proportion of the diet composed of white-sided dolphins has apparently either increased since the 1990s (Ford et al. 1998) or dolphins were underrepresented in previous diet studies. The information on transient killer whale diet (Baird and Dill 1995; Ford et al. 1998) should be updated to encompass the dolphin recolonisation as a new food resource. The energetics calculations would benefit from a more accurate estimate of the caloric value of a Pacific white-sided dolphin through bomb calorimetry (Williams et al. 2004). Conducting focal follows of mammal-eating killer whales when in the area will increase the sample size of mammal-eating killer whale feeding events, provide insight into the proportion of the diet comprised of dolphins, and identify whether a few individual killer whales or matriline may be specialising on Pacific white-sided dolphins. Given the evasive tactics used by the dolphins, it may take a great deal of time for killer whales to learn how to catch this species, and a dedicated study on dolphin-killer whale interactions may result in new insights about killer whale cultural transmission of hunting techniques (Deecke et al. 2000).

Dolphin anti-predatory behaviour is worth exploring further in an ecological context and from a conservation perspective. One priority for future research is to improve understanding of the

natural and anthropogenic sources of injury in these dolphins, which could not be determined in 59% of my photographs (Table 4.4). Veterinary pathologists who participated in the survey noted that full necropsies would be required to determine cause of death, and this would require making Pacific white-sided dolphins a higher priority for stranding response and pathological analyses (Moore et al. 2013). For sub-lethal effects, estimating an activity budget in the presence and absence of killer whales may reveal behavioural responses to predation risk that can improve our understanding of energetic and ultimately population-level consequences of disturbance (Christiansen et al. 2013; Stockin et al. 2008; Williams et al. 2006).

Conducting playback experiments of killer whale calls while collecting stress hormone samples from the dolphin blows (Hogg et al. 2009; Hunt et al. 2012) might provide another method to assess the non-lethal impact of killer whale presence. This would provide insight into both the physiological impact (Gobush et al. 2008) and behavioural responses (Deecke et al. 2002) to killer whales. If marine mammals do respond to tactical sonar in a predator avoidance framework, this sort of investigation may inform future mitigation (Tyack et al. 2011; Zimmer and Tyack 2007).

Chapter 5

PRELIMINARY EVIDENCE FOR POPULATION STRUCTURE IN PACIFIC WHITE-SIDED DOLPHINS FROM ACOUSTIC AND SOCIALITY DATA

5.1 INTRODUCTION

A central theme in conservation biology involves identifying evolutionarily significant units to conserve (Moritz 1994). For global conservation status assessments, the species may be the default scale to consider (Miller and Prideaux 2013), but it is important to note that even globally abundant species are composed of biological populations, some of which may be facing serious threats at a regional scale (Currey et al. 2009b; Krahn 2004). For example, although false killer whales (*Pseudorca crassidens*) are globally distributed in tropical and subtropical waters, a genetically distinct population in Hawaiian waters is threatened by direct mortality from commercial long-line fishing activities (Baird et al. 2008).

Understanding population structure is essential to interpret to which population of animals estimated demographic parameters apply and, ultimately, to identify units to conserve (Taylor 1999). For my research, I need to be able to evaluate whether my estimates of abundance or survival rate applied to Pacific white-sided dolphins across a wider region of the northeast Pacific or, conversely, if the dolphins in my study area form a unique, “resident” population.

There are a number of methods that can provide information to help define population units, including genetics (Baker et al. 1998; Hoelzel et al. 2007; Mendez et al. 2011), morphology, movements and association patterns from photo-identification (Aschettino et al. 2012; Calambokidis et al. 2001), chemical markers (Krahn et al. 2007), acoustics (Ford 1991; McDonald et al. 2006; Whitehead et al. 1998), or timing of reproduction (Bigg 1982; Krahn et al. 2007; Perryman and Lynn 1993; Wade and Angliss 1997). My long-term goal is to conduct genetic analyses to improve understanding of the relatedness of the dolphins in my study area

to those in adjacent Canadian, US and offshore waters. Conducting that genetic analysis was beyond the scope of this study and it would have been difficult to obtain a permit for biopsy sampling until a preliminary analysis could develop some hypotheses that could only be tested with genetic data from free-ranging animals.

Range-wide population structure of Pacific white-sided dolphins is not well understood. In the western north Pacific, there is genetic evidence for an inshore and an offshore population (Hayano *et al.* 2004). In the eastern North Pacific, genetic evidence supports division along the following US management units: (1) Baja California; (2) California, Oregon, Washington; (3) British Columbia and Alaska, and (4) “offshore” (*i.e.*, central North Pacific). Additionally, there is morphological evidence to support two forms of Pacific white-sided dolphins off the coast of California based on skull features (Walker *et al.* 1986). It is currently unclear whether these two forms off California are sympatric or whether the two forms occur in the same area at different times.

Acoustic evidence also supports two putative forms of Pacific white-sided dolphins off southern California. Echolocation click trains with two distinct centroid frequencies were detected in a site where the two forms overlap (Soldevilla *et al.* 2008).

In addition to the north-south division in the eastern North Pacific, genetic evidence supports differentiation between dolphins in inshore and offshore waters (Lux *et al.* 1997). An exception to this inshore-offshore split is found in the California-Oregon-Washington region, which was not found to differ significantly from the offshore “stock” (Lux *et al.* 1997). Results from analysis of samples collected in recent years in US waters lend additional support to four putative populations (Robert W. Brownell, personal communication, January 2010), but funding constraints in recent years have hindered genetic analyses of tissue samples held in both Canada and the US.

In addition to the evidence for population structure within a species (Taylor 2005), there is a need to explore whether individuals demonstrate social structure within populations. Highly structured social organisation can occur in cetaceans for defence against predators, cooperative

feeding, or complex mating systems (Connor 2000; Connor et al. 1998; Whitehead and Mann 2000). Highly social odontocetes seem to be less resilient to overexploitation than less socially differentiated species (Wade et al. 2012). In addition to life-history traits, anthropogenic threats can be clustered in space and time (Madsen et al. 2006; Nowacek et al. 2007), so knowing something about the tendency for individuals to be associated over long time periods can give insight into disease propagation initiated from human activities (Acevedo-Whitehouse et al. 2003; Gulland and Hall 2007) or vulnerability to stochastic events like oil spills (Williams et al. 2009).

There is an ecological basis for expecting Pacific white-sided dolphins to be a highly social species. Although there is no sexual dimorphism in this species, there is a smaller than expected testes size relative to body mass (Connor 2000), suggesting that there is likely to be a highly derived behavioural system (i.e., other than sperm competition or male mating rate) that governs male access to females. An approximately 4-year inter-birth interval has been inferred from bycaught and stranded animals (Heise 1996b; Taylor et al. 2007a), which is much longer than is typically observed in baleen whales or many small cetaceans (Whitehead and Mann 2000). These features, while inconclusive individually, collectively point toward a reasonable expectation of high sociality. Pacific white-sided dolphins are seen in very large groups, often numbering in the thousands (Williams and Thomas 2007). While these very large groups likely represent ephemeral situations of dolphins aggregating around a common food resource (Benoit-Bird and Au 2003), it seems plausible that the smaller group sizes encountered in the historical and current study (Chapter 3), represent long-term social units that have previously received little scientific attention.

Information on reproduction can also be useful in forming hypotheses about boundaries of the stock or biological unit to which demographic parameters may apply (Chapter 3). Differences in timing of reproduction have been noted in bottlenose dolphins (Urian et al. 1996) and two populations of harbour porpoise (Börjesson and Read 2003). As sea otters (*Enhydra lutris nereis*) expand to new areas, juvenile males may scout habitat, with females and pups being the last to arrive in a new site (Tinker et al. 2008). Conversely, when prey resources are limited, male-maintained breeding territories and exclusion of juvenile females by adult females moderate the effects of prey reductions on reproductively active females (Bodkin et al. 2000).

Monitoring the occurrence of calves in Pacific white-sided dolphin groups observed during the recolonisation event (Chapter 3; Morton 2000) may reveal patterns that could guide cetacean conservation and management of human activities in other regions as cetacean populations recover from overexploitation. From the predator-prey literature, one would also predict that females with calves should be the last to recolonise a new area in which predation risk is high (Chapter 4).

The first aim of this study was to examine evidence for population structure in Pacific white-sided dolphins by evaluating characteristics of dolphin vocalisations in a hypothesis-testing framework. The second aim was to investigate evidence of sociality from patterns of association in photo-identification data collected from dolphin groups. Because this is the first investigation into sociality in Pacific white-sided dolphins, there was no information to gauge whether or not the groups for which I have recordings maintain a stable group composition: in other words, the sociality and acoustics components of the study were intended to progress in tandem. The study was intended to allow the development of hypotheses to test in future with new data collection and analyses, eventually using genetic data. Given the low capture probability overall (Chapter 3), there was a large, known potential to fail to detect an individual that was present. Consequently, analyses were not intended to provide a quantitative comparison of vocalizations of two definitive social groups, but instead were meant to explore whether variability in the dolphins' vocalizations were more consistent with a single social unit or multiple units. In addition, reproductive patterns were investigated to examine the level of sociality further and to place the demographic findings (Chapter 3) in context of a known recolonisation event (Morton 2000).

5.2 METHODS

5.2.1 Acoustic field methods

Acoustic recordings were collected from dolphin groups during photo-identification encounters in the study area (Chapters 2 and 3) from 2010 to 2012. Information on group size, location, and activity were collected at the beginning of an encounter (Chapter 2). An effort was made to collect recordings when no other boats were present. The research boat engine was shut off during all recording sessions. Because the primary objective of the study was to collect identification photos (Chapters 2 and 3), not all encounters resulted in a recording. The

decision to record or not to record was determined by logistical constraints, and was not influenced by the composition of the dolphin group.

Dolphin vocalisations were recorded using a Sensor Technology Ltd. SS03 Seaphone hydrophone (Collingwood, ON) connected to a Fostex FR2 field memory recorder (Fostex America, Foster Electric, USA, Inc., Gardena, CA). The Fostex FR2 can sample at 128 kHz per channel, giving a Nyquist frequency of 96 kHz and a flat frequency response of ± 3 dB from 80 Hz to 20 kHz. Without access to a multi-element hydrophone array, I was unable to collect echolocation clicks in a way that would allow cross-study comparisons of source level or centroid frequency (e.g., Kyhn et al. 2013) but, because the same equipment and settings were used for all recordings, the recordings are comparable from one group to the next. Vocalisations were directly recorded onto a 4 GB Compact Flash memory card (CoreMicro Canada, Richmond Hill, ON) and downloaded onto a hard drive.

5.2.1.1 Acoustic data processing

Each recording was screened using Adobe Audition (Adobe System Corporation, San Jose, CA) for overall recording quality. Recordings were assessed on whether dolphin vocalisations were present and whether boat noise or other ambient (e.g., wave) noise interfered with or masked the dolphin vocalisations. Recordings without dolphin vocalisations and/or high levels of boat noise were removed from the dataset.

5.2.1.2 Assigning dolphins to putative groups

Recordings were divided into two groups, labelled A and B, to test whether there was significant variation in vocalisations (burst pulse call contours and rates of echolocation clicks) between the two groups, which would be consistent with population structure. A recording was assigned to Group A if at least one dolphin photographed in that group had been seen in the historical catalogue (i.e., had also been photographed in the study area >7 years earlier).

My working hypothesis is that Group A dolphins form a core group that can be considered ‘resident’ dolphins, because at least some have been seen in the study area over a period of

many years. Of the 879 individuals included in this study, 108 (11.9%) were photographed on more than one occasion. Given the generally low capture probability in this study and large size of this population, this suggests some degree of fidelity to this small study area (Chapter 2). Some resightings of dolphins in the study area spanned particularly long time periods. Sightings of animal D297 spanned the longest period (19 years). Other sightings that represent particularly long periods included animal D170 (17 years), animal D413 (15 years) and animal D986 (11 years). All of these dolphins are considered part of a putative resident population, and were therefore assigned to Group A.

Group B included recordings only from encounters where no putative ‘resident’ dolphins (as defined above) were identified. In other words, Group B dolphins were assumed to have been seen only in the recent study (i.e., between 2008 and 2013). The low capture probability (Chapter 3) means that an unknown number of Group B dolphins may have been present prior to 2008, but not detected. Evidence for random temporary emigration from the study area (Chapter 3) suggests that some fraction of the population may be ‘visitors’ rather than part of the ‘core’ group. The low capture probability raises the potential for failure to detect long-term usage of the area, and therefore to assign a previously undetected dolphin to Group B incorrectly. Under the working hypothesis, the opposite is not a concern, because once a dolphin has been seen in both the historical and the current study, it is assigned unambiguously to Group A. However, it is possible that a “resident” dolphin present and available for capture in the historical study was not photographed until the current study or that Group A includes “non-resident” dolphins.

I compared the differences in vocal behaviour between groups A and B to differences one would expect to see from chance alone, by creating two new groups from files sampled at random (i.e., Group A_random and Group B_random). Acoustic files were randomly chosen (half from Group A and half from Group B) using the random number generator in Microsoft Excel until two files of approximately equal file size (a proxy for number of whistle contours) were created.

5.2.1.3 Testing between-group differences in calls

The automatic whistle classifier in PAMGuard acoustic detection software (Gillespie et al., 2008, www.pamguard.org) developed by (Gillespie et al. 2013) was used to test for differences between Group A and Group B. PAMGuard contains a “Whistle and Moan detector” that was developed to detect the presence of cetacean calls in passive acoustic monitoring data. PAMGuard’s detector is called a “whistle” detector, but it detects tonal signals (Caillat 2013; Gillespie et al. 2013; Watkins 1968). Burst pulse calls have a rapid inter-click interval, which appears tonal with a long enough fast Fourier transform (FFT) sampling window (Watkins 1968). Although my analyses were conducted on burst pulse calls, I use the term “whistle” to be consistent with the terminology used in the PAMGuard software (Gillespie et al. 2013; Caillat 2013).

Within the presence/absence detector, PAMGuard contains a whistle classifier that can detect and distinguish whistles among odontocete species and attempts classification based on the groups of whistle contours rather than individual whistle contours. Relying on single calls and complete whistle contours has known technical limitations, and the whistle classifier was designed to be robust to these concerns about imperfect detection and fragmentation of whistle contours (Gillespie et al. 2013). Bayesian methods have been developed recently to automate the detection and classification steps in PAMGuard (Caillat 2013). I treated Group A and B dolphins as putative species in PAMGuard, to allow me to take advantage of these new automated methods.

Whistle classification in PAMGuard is a six-step process. Most of these are automated and a portion of these are user-controlled (Caillat 2013; Gillespie et al. 2013):

1. For each group, whistle contours were divided into small whistle fragments of equal length (to mitigate poor classification due to imperfect detection of the complete whistle contour in recordings), for which the mean frequency, slope of the frequency, and curvature of the fragment were calculated;
2. For each set of fragments within a group, a random starting point within the fragment was initiated and 2/3 of the fragments encountered from that point onwards were used to train the classifier. Caillat (2013) showed that this was the optimal allocation of data to balance false positives and false negatives. The remaining 1/3 of the fragments were used for testing the

classifier;

3. In both the training and testing datasets, once a sufficient collection of fragments had been accumulated, a distribution was produced from which the mean, standard deviation, and skew of the mean frequency, slope of the frequency and curvature of the fragment collection were estimated. Thus, a total of nine parameters were extracted from each collection of fragments;

4. A Linear Discriminant function Analysis (LDA) was performed on the training dataset using these nine parameters;

5. The output of the LDA was a relative probability of correct classification for each classification group; and

6. The classification was compared to the test data and a confusion matrix was created to quantify the performance of the classifier.

The six-step process was carried out in PAMGuard using acoustic data from Group A and Group B and from the randomly split data. I trained the non-random whistle classifier by randomly selecting two-thirds of the data from Group A and two-thirds of the data from Group B. The random whistle classifier was trained in the same way. The remaining third of the data from each group was retained for classification.

In two separate stages, the training data from each group were imported into PAMGuard. PAMGuard first processed the acoustic files (“collected training data”) using the Whistle and Moan Detector to identify whistle contours before breaking these into smaller, equal length fragments. Next, the LDA (step 4) was carried out on the contours generated from the Whistle and Moan detector. This step requires the user to select fragment length, section length (how many fragments accumulate before a distribution is produced), and the number of bootstraps to run while testing the performance of the classifier. The “Batch Testing of Multiple Values” option was selected and a range of parameter values was entered to evaluate the probability that the classifier was correctly identifying whistles given particular fragment and section lengths.

Steps 2-6 were repeated using the bootstrap function in PAMGuard using a range of parameter

values beginning with the range used by (Caillat 2013); i.e., fragment length 5-35 bins (26-187ms) and section length 10-60 fragments) and by (Gillespie et al. 2013); i.e., fragment length 10-84 bins (53-448ms) and section length 20-200 fragments). The bootstraps returned an output including a confusion matrix that assigned a probability as a measure of classifier performance. Bootstraps were run on each set of parameters (fragment length, section length) for 100 trials. This step was repeated until classification returned a high classification probability (i.e., additional trials no longer produced improved classifier performance) at a given fragment length section length (see Results). Once the bootstraps were complete, the LDA algorithm was calculated using these fragment and section lengths to create the classifier algorithm specific to my data (i.e., Group A and Group B, and Random data).

Classification performance with two species can be tested in PAMGuard using a Receiver Operator Characteristic curve which shows the rate of false positive classifications versus false negative (Caillat 2013). However, in this case the two groups are putative (i.e., a hypothesis to test using the data), and it is unknown whether true division exists. Once the classifier was trained, previously unprocessed data from Groups A and B were run through the classifier.

5.2.1.4 Testing between-group differences in click rate

As a complementary analysis, I also compared click rate between Group A and B recordings. Recordings from Group A and Group B were processed using the Click Detector in PAMGuard. PAMGuard appends an Access Database with summary statistics (number of clicks, sample duration, amplitude) of the echolocation clicks from each recording. The output from the Click Detector was used to summarize click features within and between groups. Click duration and number of clicks were calculated from the PAMGuard data summary database. Pacific white-sided dolphin echolocation clicks range from 20 kHz to more than 100 kHz (Evans 1973; Richardson et al. 1991; Soldevilla et al. 2008). This range exceeds that of the hydrophone used in the study, therefore click features such as start and end frequencies, bandwidth, minimum and maximum frequencies, fundamental frequency and source level could not be estimated.

5.2.2 Social analysis methods

Records of individual observations from photo-identification encounters from 1987-2013 (Chapter 3) were used to measure sociality in Pacific white-sided dolphins.

5.2.2.1 Defining associations

Observations of associations, or the spatial-temporal synchrony of individuals, can act as a proxy for measuring actual behavioural interactions when direct observation is logistically constrained. An association index is a measure of the strength of an association and is used to provide an estimate of the proportion of time that a pair of animals spend either with one another or apart (Whitehead 1997). Various association indices (e.g., ‘simple ratio’, ‘twice weight’, ‘half-weight’) are reviewed in (Cairns and Schwager 1987; Whitehead 2008a; Whitehead and Dufault 1999). Here, a ‘half-weight index’ (HWI) of association was used as a relationship measure among dyads in the social network. This index has been shown to be most robust to the failure to identify all individuals within a sampling period (Cairns and Schwager 1987), a bias common to photoidentification techniques. A HWI is given as:

$$\frac{x}{x + yab + 1/2(ya + yb)}$$

Where x equals the instances in which individuals a and b located together; Yab is the number of sampling periods in which both individuals a and b are identified separately (in this case, Yab is always 0); Ya is the number of sampling periods in which just individual a is identified; and Yb is the number of sampling periods in which only individual b is identified (Cairns and Schwager 1987; Whitehead 1997; Whitehead 2008a; Whitehead and Dufault 1999).

A group was defined as all dolphins seen during an encounter (i.e., on the same day). Finer scale information on group composition (e.g., groups defined using a 15m ‘chain rule’; Smolker 1992) was collected from 2011 onwards, but for this analysis it emerged that sample size limitations required relaxing that definition to a temporal scale of a day in order to (a) include data from the historical study and the first half the current study (both of which defined groups on the scale of a day) and (b) have sufficient sample size for models to converge. Group

membership was used to determine associations. This assumed that all interactions take place within the group, and interactions occur at the same rate among all pairs within a group, the so-called ‘gambit of the group’ (Whitehead and Dufault 1999).

I then estimated the correlation coefficient (r), between the “true”, or observed proportion of time two dolphins are seen associated and the estimated association indices (HWI) to measure the accuracy of the association index in measuring sociality. The correlation coefficient, r , provides a *post hoc* measure of accuracy, that is, how well my observed association data are represented by the expected association index. A daily sampling period was used as it was true to our sampling methods at sea (data were collected each day that dolphins were observed). It also helps account for demographic effects such as birth, death, immigration and emigration (Whitehead 2008a). To calculate r , the CV of the true association index (S , calculated below), or variability of association indices within a population was divided by the CV of the estimated association indexes (Whitehead 2008a, b). The accepted rule of thumb is that $r=1.0$ indicates that the association index (HWI in this case) is an “excellent” representation of social structure, $r=0.8$, a “good” representation, and $r=0.4$, a “somewhat representative” view (Whitehead 2008a, b).

Homogeneity in social relationships within the population was approximated by the variability of association indices within the population, or social differentiation (S), which was estimated from the CV of the “true”, or observed association indexes. While not a measure of effect size, social differentiation provides a useful measure of social homogeneity. Values of S ranging from 0-0.3 indicating a virtually homogeneous society, values greater than 0.5 suggestion some level of social differentiation, and values greater than 2.0 indicate a highly differentiated society (Whitehead 2008a, b).

Measuring sociality in wild animal populations is a trade-off between power and precision (Whitehead 2008b). In this study, social differentiation (S) was estimated for datasets restricted by the number of times individuals were seen: dolphins seen one or more times (1+); two or more times (2+); three or more times (3+); or four or more times (4+), the maximum possible in these data because only seven animals were seen more than four times. These thresholds are all lower than the five or more sightings that (Whitehead 2008b) recommends as a minimum

number of observations needed to provide an unbiased picture of association patterns in animal societies. A resolution of integration of 0.001, with 100 bootstraps, using a Poisson approximation, was implemented in SOCPROG 2.4 (Whitehead 2009) on the 2+ to 4+ datasets. When all sightings were included (*i.e.*, dataset 1+), social differentiation could not be estimated. The data were also divided seasonally into summer (April-September) and winter (October-March) to explore seasonal social patterns.

5.2.2.2 Hypothesis testing-random associations

Social differentiation estimates the variability of the dyadic associations and confidence in the metric, but not whether observed associations differ from random association patterns. If dolphins were in the same place at the same time for a common purpose, such as exploiting the same prey patch, for example, a certain number of putative associations would be expected by chance alone. To investigate whether the associations observed differed from those expected from chance alone, a permutation test analysis was implemented in SOCPROG 2.4. The permutation tests contrast a null hypothesis that animals were associating randomly (*i.e.*, no preference for social partners) with an alternative hypothesis that there were preferred social partnerships and avoidances among individuals (Bejder et al. 1998; Whitehead 2008b).

In SOCPROG, a random sample of alternative datasets was produced, which contained the same number of dolphins and groups as in the original data, matrices of association indices were permuted within the daily sampling period, and coefficient of association indices were generated as a test statistic. At each step, two individuals and two groups were chosen such that each individual was identified in only one group and each group contained only one of the individuals. Then, the positions of each of the four group assignments were exchanged, or 'flipped' (*i.e.*, the dolphin in group I was then in group II and the dolphin in group II was then in group I). After each random simulation of the data, the HWI indices for each dyad were recalculated. The average HWI of all permutations (the estimated HWI for each dyad) was compared to the observed HWI. A test statistic was calculated at each 'flip' producing a randomised frequency distribution from which a probability value was calculated.

In the current study, preferred/avoided associations with the null hypothesis of random association were tested in SOCPROG 2.4 (Whitehead 2009) using modifications (Whitehead et al. 2005) of the Bejder/Manly permutation test (Bejder et al. 1998; Miklos and Podani 2004). Permutation tests were carried out on the datasets for which dolphins were seen on 3+ and 4+ occasions, using day as a sampling period. The number of randomisations (e.g. 1000, 10,000, 20,000) was increased incrementally to identify the point at which the p-values stabilised (Bejder et al. 1998; Whitehead 2009).

5.2.2.3 Hierarchical cluster analysis

Hierarchical cluster analysis using association indices is a useful method to classify and visualise relationships between individuals. Results are typically shown as a dendrogram, or tree diagram. A dendrogram represents the society in a hierarchical structure where “branches” represent individuals with low association and higher levels of association are represented by groups of “twigs” from the branches. A hierarchical cluster analysis using average weight linkage was carried out in SOCPROG 2.4 (Whitehead 2009) on the 2+ and 3+ datasets. In SOCPROG, clusters for the hierarchical cluster analysis were created by an agglomerative process, which begins at the level of the individual in its own cluster and, based on the strength of the association, adds links with other individuals. In SOCPROG, the results of a hierarchical agglomerative cluster analysis can be illustrated as a dendrogram, in which individuals are plotted along one axis and their degree of association on another. A cophenetic correlation coefficient (CCC) was used to discriminate between a dendrogram of random and observed associations. A CCC of 1.0 is a perfect fit, and values >0.8 are generally considered a fair representation of the association matrix (Whitehead 2008a).

5.2.2.4 Network analysis

If the sociality analyses described above suggest that the observed associations differed significantly from random association, network analyses are often used to evaluate which individuals typically associate with each other. A network analysis graphically displays a society as a system where the “nodes” or points represent levels of social structure (e.g., individuals) and the nodes are connected by “edges” or lines that represent the association. The combination of graphical display and quantitative analysis provides an accessible

representation of social systems, even in large populations. Network analyses are used for drawing and viewing networks, analysing statistical properties of networks, modelling networks, and predicting the behaviour of a network (Whitehead 2008a).

Small sample size restricted the ability to conduct rigorous social network analyses. Using the 2+ dataset, the number of dyads was large, but most dyads were only seen twice (akin to trying to interpret a pattern from seeing only two coin tosses in a row). Using the 4+ dataset maximised the ability to infer relationship strength, although four times is still a low number of observations by the standards of studies of animal sociality (Whitehead 2008a), but the number of individuals ($n=7$) that met this sample size criterion was very small. Consequently, as a pragmatic compromise between sample size and representativeness, most of the interpretation was restricted to the cluster analysis conducted on the 3+ dataset ($n=40$).

The association data were exported as a list of edges and nodes in the form of a .VNA (virtual network architecture) file, which was mapped in Gephi, the open-source network analysis software (www.gephi.org). The network was drawn using the Force Atlas 2 attractive/repulsive algorithm in Gephi. The network analyses were conducted to illustrate, graphically, the outputs of the SOCPROG 2.4 cluster analyses.

5.2.3 Reproduction

Several methods exist to provide some rough measure of annual reproductive rate from field observations of adults and calves. To improve our understanding of the dynamics of this population, it would be ideal to estimate fecundity in terms of young-of-the-year (YOTY) per mature female, but it is difficult to distinguish adults from immature animals from field observations alone, and methods to sex adults from fin shape remain unreliable (Walker et al. 1986). As a pragmatic alternative, I estimated YOTY *per capita*.

During the latter part of the current study (2009-2012), I approached 40 subgroups with the specific aim of estimating YOTY *per capita*. During these 40 occasions, I recorded a best estimate of total group size, and total number of YOTY. Using school as a sampling unit, I subsequently estimated the mean proportion of YOTY *per capita*, along with a standard error.

This assumes that (i) these 40 schools were representative of the population, and (ii) schools were independent observations. The assumption of independence was likely violated, because some subgroups were observed on the same day and some individuals may have been observed more than once. This should not bias the resulting estimate, but may underestimate variance.

To test whether the proportion of YOTY *per capita* varied with school size, I used generalized linear models (Faraway 2005) with and without school size as a covariate. I used a quasibinomial family with a log link and error proportional to the mean, which accounted for overdispersion (with a dispersion parameter estimated to be 1.9).

5.3 RESULTS

5.3.1 Acoustic analysis

In total, 127 recordings were collected over 20 sampling periods (days). After selection based on quality (described in Methods), 83 files over 10 sampling periods remained. During the recording sessions, 10 individuals were matched to the historical catalogue (Chapter 2), which meant that 57 files could be assigned to Group A and the remaining 16 files were assigned to Group B for the purposes of training and classification (Table 5.1).

For the randomly assigned data, Group A_random contained five recordings and Group B_random contained six.

Table 5.1: Acoustic recording sampling dates and number of samples used for training and classification.

Recording Dates	Group	'Resident' dolphin IDs	No. Original samples	No. 'high-quality' samples	No. Samples for Training	No. Samples for Classification
6-Oct-10	A	D022, D302	44	13	9	4
14-Apr-11	A	D074, D413	27	18	12	6
7-Aug-12	A	D986	10	4	3	1
15-Apr-11	A	D721	4	3	1	2
14-Sep-10	A	D029, D074, D422	5	5	2	3
12-Sep-10	A	D029	7	2	1	1
29-Jul-13	B	NA	4	2	1	1
13-Apr-11	B	NA	16	9	8	1
16-Oct-10	B	NA	9	3	2	1
16-Nov-10	B	NA	2	1	0	1
20-Jul-13	B	NA	7	1	0	1

5.3.2 Between group differences in calls

After processing data from Group A and Group B using the PAMGuard whistle and moan detector, the training data resulted in 2,007 contours from Group A and 1,818 contours from Group B. Classification was optimised at a fragment length of 31 and a section length of 50, after evaluating multiple values for fragment length and section length. At these levels, bootstrapped 50 times, the probability of correct classification was maximised at 0.715 (Table 5.2). When other values of fragment length or section length were considered, classifier performance fell as low as 50%.

For the randomly chosen data, the training data resulted in 1,465 contours from Group A_random and 980 contours from Group B_random. Classification was optimised at the same fragment and section lengths and same number of bootstraps as the non-random data. The

probability of correct classification was maximised at 0.602. Similarly, when other values of fragment length or section length were considered, classifier performance fell as low as 50%.

A t-test was carried out on the classification rates of the non-random and random classifier. Only the non-random data showed a significant difference in classification rates between Group A and Group B (P=0.02). Therefore, only the non-random classifier was used to classify the recordings withheld for ‘testing’ the classifier.

During testing (called “classification” in PAMGuard terminology), the whistle classifier correctly identified 60% of naive Group A data as Group A and 55% of naive Group B data as Group B. The difference in classification rate for both Group A and Group B classification rates were statistically significantly different (Table 5.3).

Table 5.2: Whistle classifier confusion matrix with correct classification of groups at 0.715 from a fragment length of 27 and a section length of 50.

	Group A	Group B
Group A	0.71	0.29
Group B	0.28	0.72

Table 5.3: Classifier performance when given ‘testing’ data from Group A and Group B recordings.

	No. Classified as A	No. Classified as B	Total No. fragments	P-value
Group A	103	70	173	0.002
Group B	12	22	34	0.008

5.3.3 Between-group differences in echolocation click rate

Echolocation click rates were similar for both Group A and Group B (Table 5.4). Group A rates were between 5 and 121 clicks s^{-1} and Group B between 4 and 123 clicks s^{-1} . To test the null hypothesis of no difference in click rate between Group A and Group B, an unpaired t-test (unequal variance) was carried out. The test failed to reject the null hypothesis at the 0.05 probability level ($t = 1.1154$, $df = 58$, $p = 0.2693$).

Table 5.4: Summary of click rate for Groups A and B

	Min	Max	Ave
Group A	5	121	44
Group B	4	123	54
Combined	4	123	47

5.3.4 Social analysis results

A total of 1,152 sighting records of 879 unique individuals collected on 175 sampling days were used in this analysis. On average, 6.6 IDs (i.e., high-quality photographs of distinctive animals) were taken each day; including recaptures, this translates to a mean of 5.9 unique individuals identified in each encounter. Figure 5.1 shows the rate of discovery of new individuals plotted against the cumulative number of all identified animals. Similar to the discovery curve in Chapter 3 which shows the rate of discovery plotted against time, the rate of discovery does not currently show any sign of levelling off.

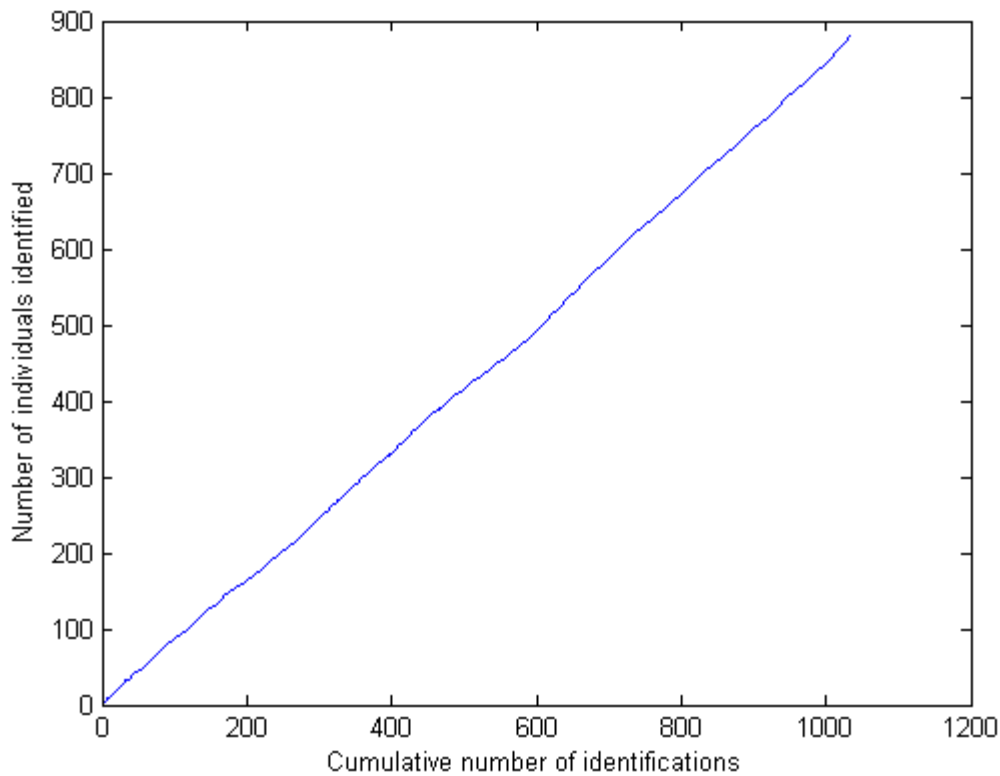


Figure 5.1: Rate of discovery of new individuals made in the Broughton Archipelago study area 1987-2012.

5.3.5 Social differentiation

When restricting inference to the sample of dolphins that were seen on three or more occasions (3+ dataset), the estimate of social differentiation (S) was 0.749 (SE = 0.494), which suggests a moderately differentiated society (Table 5.5).

The correlation coefficient (r) was estimated at 0.265 (SE = 0.113), which is lower than the guideline of 0.4 that indicates a “somewhat representative” view of a social system (Whitehead 2008a, b). Similar results were obtained with individuals observed during the winter months at least two times. A social differentiation estimate of 0.711 (SE=0.421) was estimated for the “winter dolphins” with a correlation coefficient of 0.196 (SE=0.077). Social differentiation was re-calculated for individuals observed two or more times (2+ dataset) and four or more times (4+ dataset), to gauge how sensitive this metric was to different cut-offs for inclusion in the analysis. Some degree of social differentiation was suggested at both levels, with a significantly higher level of differentiation for the best-studied individuals that were seen four

or more times during the study. Social differentiation was not estimable for “summer” dolphins at any level nor for “winter dolphins” at the three or more level due to small sample size.

Social differentiation and the correlation coefficient increased with increasing restriction of the dataset to animals seen more times (Table 5.5). Using the most restricted dataset (4+), social differentiation was estimated to be high ($S = 3.16$) and accurate ($r = 0.698$), providing a better representation of the social system (Table 5.5). However, as described above, when restricting the data to those individuals seen four or more times (4+ dataset), the number of individuals included was only seven, and restricting the data to animals seen at least four times is still low by the standards of most sociality studies (Bejder et al. 1998; Whitehead 2009).

Using the HWI as a measure of the strength of associations, this dolphin society is characterised by a mean association index of 0.07 - 0.18 per dyad or 0.57 – 7.18 associations per individual, depending on the dataset used (Table 5.5). Some of the associations observed in the study also spanned considerable time periods. The longest confirmed association observed exceeded 16 years: D184 and D193 were seen together on 2 April 1993 and 11 September 2009 (5,975 days, or 16 years, 4 months and 9 days apart).

Permutation tests offered support for concluding that the observed associations were more structured than one would expect from a random association pattern of the same number of individuals. Generally, P-values stabilised after approximately 5000 randomisations and 1000 trials.

For the 2+, 3+ and 4+ datasets, and the summer (2+) and winter (2+) dolphins, permutation tests rejected the null hypothesis that observed associations were different from random (Table 5.6), indicating support for a non-randomly associating dolphin society at all levels evaluated.

Table 5.5: Estimates of social differentiation (S), correlation coefficient (r), mean association index per dyad and per individual for all individuals, for individuals seen at least twice (2+), three times (3+), and four times (4+) during the course of the study and for individuals seen during winter and summer months at least twice (2+) and three times (3+).

Restriction	S	SE of S	r	SE	No. Individuals	No. Sampling Periods	No. IDs	Mean	Mean
								assoc. per dyad	assoc. per individual
All	0		0		879	175	1152		
2+	0.784	0.408	0.202	0.066	105	109	298	0.07	7.18
3+	0.749	0.494	0.265	0.113	40	81	146	0.13	5.25
4+	3.16	1.696	0.698	0.375	7	28	35	0.1	0.57
Winter 2+	0.711	0.431	0.196	0.077	59	63	2.44	0.08	4.58
Winter 3+	0	NA	0	NA	12	33	1.33	0.06	0.67
Summer 2+	0	0.0463	0	0.144	34	32	2.75	0.18	6.06
Summer 3+	0	1.244	0	0.38	10	25	37	0.13	1.2

Table 5.6: Summaries of associations and P-values for the CV of the mean for testing the hypothesis of random association. Based on 1000 replicates of 5000 randomisations.

	3+	4+	summer	winter	
	2+(>1)	(>2)	(>3)	2+(>1)	2+(>1)
Mean of all observed HWI for all individuals sighted	0.0269	0.0413	0.0191	0.08093	0.0355
Mean of observed HWI values (>0) for all individuals sighted (non-zero elements)	0.652	0.121	0.048	0.48298	0.47822
P-value for CV of the mean	0.003	0.002	0.034	0.003	0.004

5.3.6 Hierarchical cluster analysis

Based on the results of the permutation tests (Table 5.6), dendrograms were produced for all individuals in the 3+ and 4+ datasets. The dendrogram (Figure 5.2) was found to be representative of the structure for individuals three or more times during the course of the study (cophenetic correlation coefficient, CCC=0.83, with CCC>0.8 generally used to indicate a

reliable result). Using this 3+ dataset, 40 individuals were included in three significant clusters (shown in black, blue and red).

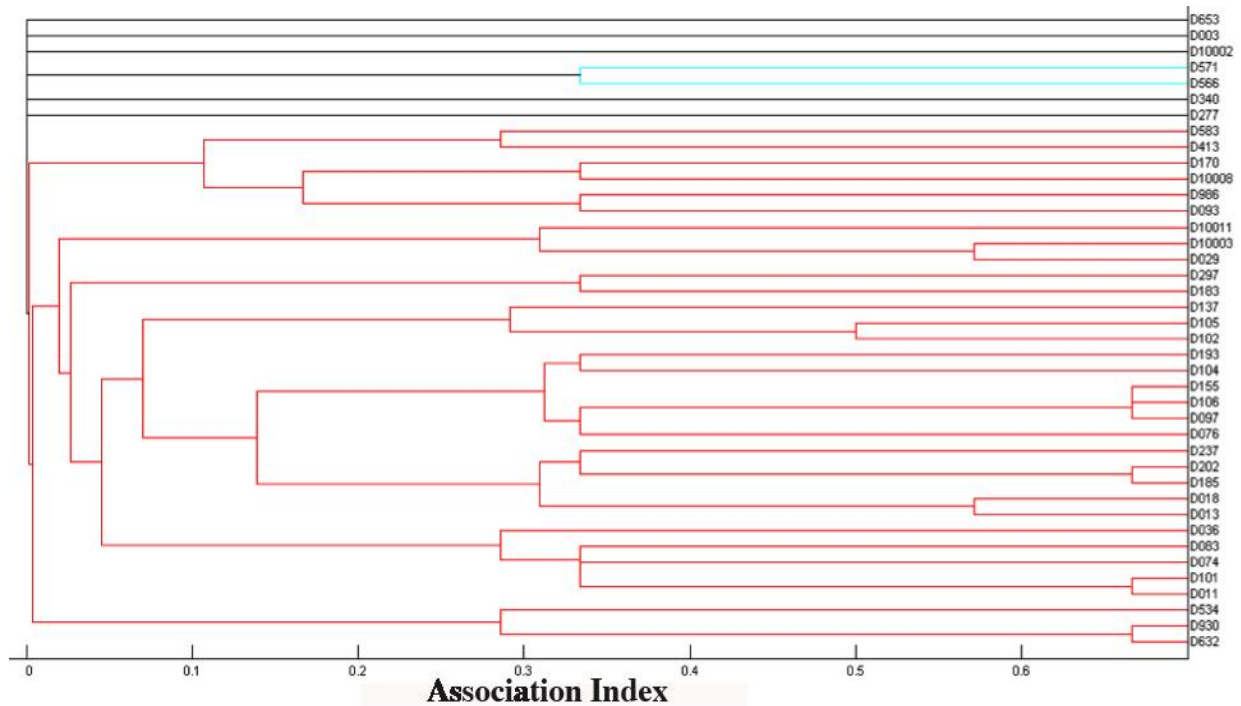


Figure 5.2: Dendrogram of individuals seen three or more times during the course of the study (CCC=0.83).

5.3.7 Network analysis

For illustrative purposes, the network of dolphins seen on three or more occasions (i.e., the dendrogram shown in (Figure 5.2) is represented in Figure 5.3. As a visual check for obvious patterns of summer versus winter associates, dolphins were colour-coded in the network (blue=seen only in winter; red=seen only in summer; purple: seen in both summer and winter).

The network diagram (Figure 5.4) shows one cluster of associated individuals as well as an outgroup of individuals that has no links to the core group of associated dolphins. The network in Figure 5.3 highlights many of the same individuals that are shown clustered in red (Figure 5.2), but the two figures do not show identical results. The network was drawn to facilitate ease of identifying key dolphins in the social network, but no statistical analyses were conducted to choose the best way of illustrating or quantifying properties of the dolphin social network.

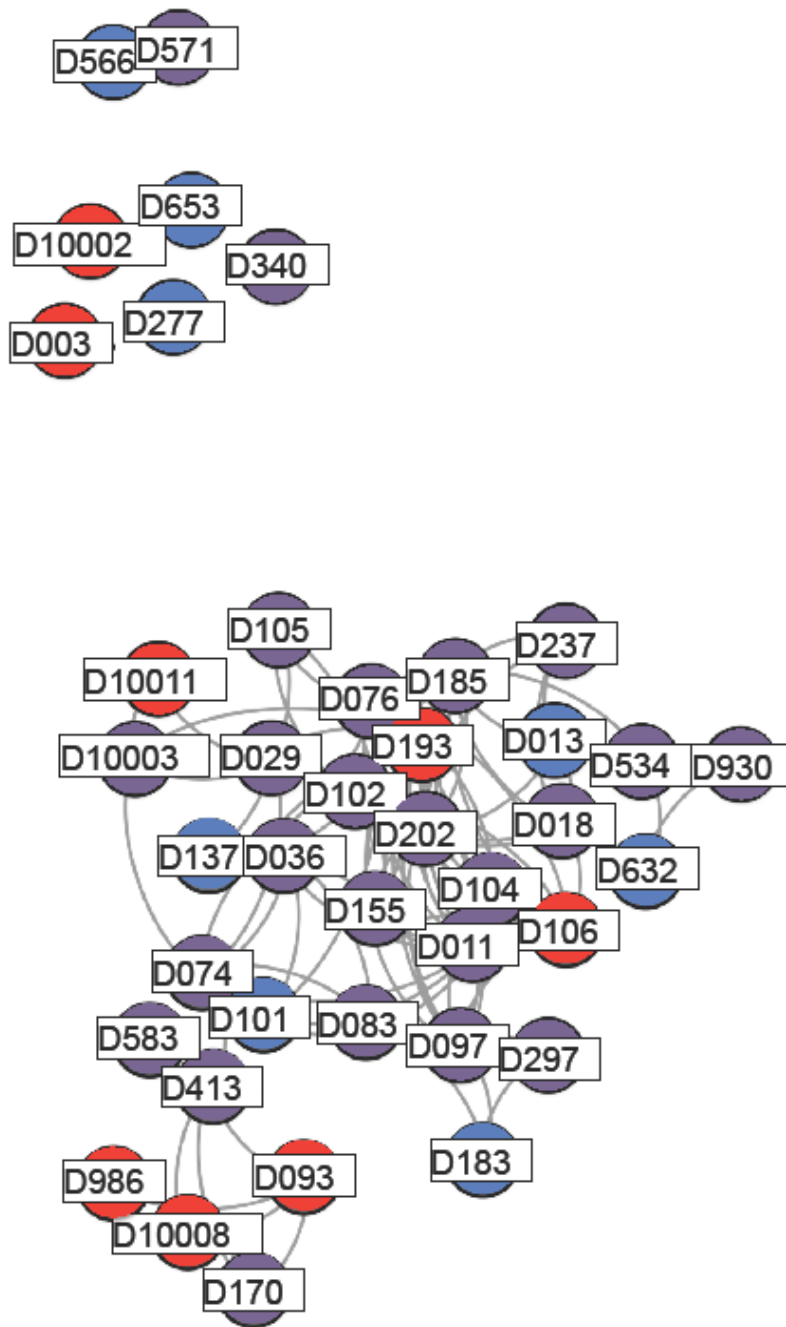


Figure 5.3: Network of dolphins (nodes, in circles) seen on three or more occasions in the study area, with edges (significant attractive associations) shown in grey lines. The blue individuals were seen during winter months only, the red during summer only, and the purple during both winter and summer months.

5.3.8 Reproduction

The estimated proportion of YOTY *per capita* was 0.0595 (CV=23.8%). There was insufficient coverage to provide quantitative analyses of timing of reproduction, but it is worth noting that all of the newborn calves that were observed were seen in July and August. Assuming half of the individuals are adult, and half of the adults are female, this translates to a fecundity rate of 0.238 per adult female. The inter-birth interval is approximately equivalent to the reciprocal of the fecundity rate (Perrin and Reilly 1984), which is therefore ~4 years.

A GLM with school size as a covariate was strongly preferred over an intercept-only model ($\Delta AIC=32.5$). The estimated proportion of YOTY per adult decreased as group size increased (Figure 5.4).

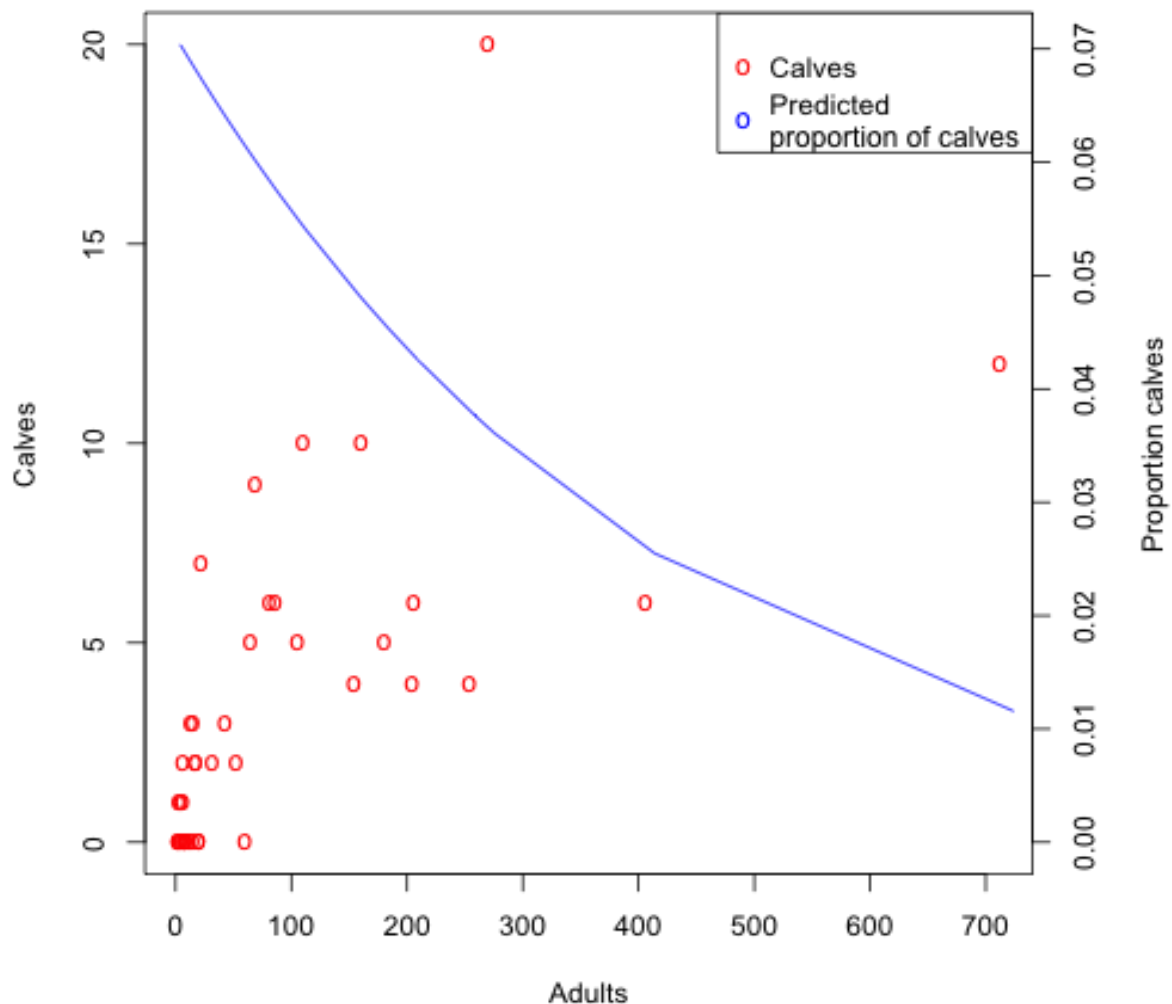


Figure 5.4: Proportion of calves (i.e., young of the year per adult) as a function of the best estimate of group size. The raw counts are shown as red dots, and the predicted proportion of calves from the GLM is shown as a blue line.

5.4 DISCUSSION

5.4.1 Evidence of population structure from acoustics

The confusion matrix (Table 5.2) resulting from the whistle classifier suggests that there is some acoustic differentiation in Pacific white-sided dolphins that is worth pursuing with future research. The classifier classified Group A vocalisations with 71% certainty, but did not perform as well with Group B. This could mean that some of the putative “transient” groups were actually misidentified “resident” groups, or that only one population is in the study area. Alternatively, it could mean that the classifier was trained on burst pulse calls when the difference between groups is best detected using echolocation clicks. For example, (Soldevilla et al. 2008) examined echolocation clicks for spectral peaks and notches and found an acoustic difference that supports the genetic and morphological lines of evidence for the presence of two populations off Southern California. It is not known whether the two populations are sympatric. Also, it is important to note that the echolocation clicks were not collected on-axis (recorded directly in front of the animal vocalising), possibly distorting the clicks and introducing variability that could account for the difference in spectral peaks between the two groups. With respect to burst pulse calls, (Henderson et al. 2011) found that variability in call attributes was context-dependent and linked to the dolphins’ behavioural state.

The PAMGuard detector is sensitive to signal to noise ratios (Caillat 2013; Gillespie et al. 2013; Watkins 1968). Although I accounted for this by using only boat-free recordings in quiet conditions, it became apparent that some dolphins approached the hydrophone to echolocate on it. This meant that the received level of the echolocation clicks was much higher than the received level of burst pulse calls of distant animals. This may have reduced the statistical power to detect real differences in burst pulse calls. This observation also provides a suggestion for directions for future research. We know from Southern California that some features of the echolocation click, rather than burst pulse calls, can be used to discriminate putative stocks (Soldevilla et al. 2008). These features of the click are less variable than the contours of burst-pulse calls and may be a more reliable indicator in future. Knowing that Pacific white-sided dolphins in BC tend to echolocate on hydrophones suggests that studying echolocation patterns rather than burst pulse calls may be a powerful tool for stock definition studies but such studies require calibrated hydrophone arrays that were not available during this study (Kyhn et al. 2013).

5.4.2 Evidence for sociality

For the first time, evidence for true sociality, rather than random associations or ephemeral aggregations, was found for this species. The point estimate of social differentiation in the best-studied dolphins (4+ dataset) was 3.16, which is consistent with a social structure that is as highly differentiated as pilot whales ($S=1.3$; Mahaffy 2012) or sub-Antarctic killer whales ($S=1.3$; Tosh et al. 2008). For the larger group of animals that were seen less frequently (2+ or 3+ datasets), social differentiation was estimated at ~ 0.8 , which is similar to that observed among adult female sperm whales and their calves (Gero 2006). In visual terms, this looks like a core group of 40 individuals with a peripheral group that rarely associates with the core group (Figure 5.3). Permutation tests revealed evidence for non-random association for dolphins seen more than once, twice and more than three times (Table 5.6). The long-term, although infrequently detected, associations are evidence for long-term social bonds. For example, one dyad associating in 1993 was also photographed associating in 2011. As the study matures, more long-term associations like these may be detected.

Future social analyses could benefit from increasing capture probability through an increase in field effort. As the study matures with additional effort, capture probability is likely to increase. Analytical methods that account for imperfect detection could also be explored (Klaich et al. 2011). It is possible that including “likely” identifications, rather than “certain” ones (Chapter 2) would reveal additional long-term associations. The level of social differentiation suggests strong heterogeneity in the social structure and, notwithstanding the sparseness of the data, the statistical support for that conclusion is high (Table 5.5, $P=0.002$).

There is some evidence to support social differentiation in winter, but it is unknown how the level of differentiation compares to summer due to sample size restriction. However, some of the long-term associations (>10 years) were observed during summer months. Summer is the season in which dolphins come together for calving and reproduction (Ferrero and Walker 1993; Harrison 1972; Robeck et al. 2009). Although the sample size was too small to explore how associations may vary seasonally in a quantitative way, it is noteworthy that most of the most frequently seen dolphins have been seen in the study area in both winter and summer (Figure 5.3).

5.4.3 Reproduction and population structure

The proportion of YOTY *per capita* was estimated as 0.0595 (CV=23.8%). Group size is extremely difficult to estimate when groups are large (Gerrodette et al. 2002). In extremely large groups, the number of adults could be overestimated or underestimated, but Figure 5.4 suggests either that (a) mothers with calves were much less likely to be present in the largest groups, or (b) it is more difficult to detect calves in very large groups.

In very large groups, calves may be more difficult to detect because of the sheer number of dolphins, but this may also be a result of the “dilution effect” (Foster and Treherne 1981) where mothers and calves remain in a less-vulnerable location (in the centre or close to shore) in large groups to avoid predation. Both male and female Pacific white-sided dolphins have a well-defined (~3 month) reproductive seasonality (Ferrero and Walker 1993; Harrison 1972; Robeck et al. 2009) during which there is oestrus synchronisation among females and a peak in semen production among males (Robeck et al. 2009). Synchronization of births may lend some protection from predators via the dilution effect if there are other calves of similar age in the group (Whitehead and Mann 2000).

Differences in reproductive seasonality among putative populations may provide further insight into population structure. Off California, calves first appear during June (Black 1994) and off Japan during May (Iwasaki and Kasuya 1997), whereas I first observed newborn calves during July.

The estimate for the proportion of YOTY *per capita* of 0.0597 (SE=0.0083, 95% CI: 0.045-0.079; Figure 5.4) is consistent with existing information for Pacific white-sided dolphins. Fecundity rate (i.e., YOTY per mature female rather than *per capita*) is approximately the reciprocal of inter-birth interval (IBI) (Perrin and Reilly 1984). Assuming a 1:1 sex ratio and that half of all females were mature (based on life table data for bottlenose dolphins; Stolen and Barlow 2003), a YOTY *per capita* of 0.0597 would translate into a fecundity rate of 0.24 and an IBI of 4.2 years. Heise (1996b) reported an IBI in stranded and bycaught animals of approximately 4 years. This is an important parameter in any population model, and warrants

additional research to improve the accuracy and precision of this estimate.

Although Figure 5.4 shows that there is potential to generate biased estimates of fecundity in this species from field observations of calves and adults, the rates I observed are consistent with what one would predict from pregnancy rates of recovered carcasses (Heise 1996b). A relatively long (4-year) inter-birth interval in odontocetes (Taylor et al. 2007a) is present in highly social populations (e.g., sperm, pilot and killer whales; Whitehead and Mann 2000). This is consistent with the sociality metrics I report here.

5.4.4 Future research

Given the need for a population-level assessment, I suggest the following directed and focused research:

5.4.4.1 Genetics

The last comprehensive genetic analysis for this species (Lux et al. 1996) in North America suffered from low sample size from BC. This study provides evidence for population structure that could provide hypotheses and impetus for a dedicated genetics study.

5.4.4.2 Assessing age-sex class of dolphins using the study area

Genetic studies would also have the benefit of revealing the sex of individuals. It has been suggested that dolphins with a “drooping” fin, that is fin tips that are round and whose tip curves $>3\text{cm}$ below the maximum fin height, are sexually mature males (Kasuya 1995; Morton 2000). Such animals are referred to in my database as putative males. Animals with falcate dorsal fins whose tips curve only slightly ($<3\text{cm}$) below maximum fin height are suggested to be females or sexually immature animals (Kasuya 1995; Morton 2000). Given the tentative and somewhat subjective nature of this observation and the small sample size in my data, I have not tested for differences in survival (Chapter 2) or sociality (this chapter) by presumed sex, but it should be noted that 17 of the core group of 40 individuals (42.5%) possess fins that could be classed as lobate/drooping. If genetic markers reveal that these animals could be sexed reliably from dorsal fin marks, laser photogrammetric methods could be added easily to my field protocols (Durban and Parsons 2006; Rowe et al. 2010) so that such differences can be

tested in future as sample size increases. Other authors have observed a variety of fin shapes in both males and females, but admitted that standard measures of cetacean morphology may not have been adequate to test a difference. (Walker et al. 1986) hypothesized that the variability in fin shape was age-related and the fin becomes more lobate and droops with the onset of physical maturity. This remains a priority item for future research to refine estimates of reproductive rate, estimate age- and sex-specific survival rates, and to understand which mothers are related to which offspring.

5.4.4.3 Acoustics

A next step to assess population structure from an acoustics perspective would include using a calibrated hydrophone array to collect on-axis echolocation clicks over their full frequency range as well as burst pulse calls (Kyhn et al. 2010; Kyhn et al. 2013). Acoustic data combined with detailed data on group size and behaviour within the range of the hydrophone would aid in identifying whether acoustic variability exists among groups in the study area. Acoustic analyses at a much larger spatial scale may reveal differentiation that my study was unable to detect within a single site. In studies of vocal behaviour of killer whales since the 1980s, Pacific white-sided dolphins have been observed off the central coasts of BC and California, and animals from these regions sound different enough to distinguish by ear without the aid of spectrograms or statistical measurements, just as resident and transient killer whale calls (or calls from different resident clans) sound quite different to a trained ear (David Bain, pers. comm., Dec 2013).

5.4.5 Conclusions

The results of the acoustic analysis lend some support to the idea that two populations exist within the study area, but do not completely rule out the possibility of one population. Resident killer whale clans in the area have call repertoires specific to their family groups, but are part of one population (Ford et al. 2000). Whistles among bottlenose dolphins (*Tursiops truncatus*) may indicate population structure and social differentiation (May-Collado and Wartzok 2008). Social organisation accompanied by stereotyped acoustic repertoires could exist among dolphins in this study area. The sociality analysis suggests that Pacific white-sided dolphins are social and long-term (at the scale of decades in some cases), non-random associations have

been observed between dolphins in the study area. The reproductive rate and pattern imply sociality and lend support to the idea of a strongly structured population.

Although the acoustic analysis did not provide definitive proof of population structure within the study area, other lines of evidence suggest that population structure may exist between the study area and other regions such as Japan, California or perhaps even other parts of BC (e.g. offshore). Anomalous colour patterning has been reported in California (Black 1994; Brownell 1965; Hain and Leatherwood 1982; Stacey and Baird 1991; Walker et al. 1986), Mexico (Brown and Norris 1956), Japan (Tsutsui et al. 2001) and off the west coast of Vancouver Island, BC (unpublished photographs presented at BC Marine Mammal Symposium, Dec 2013), but has never been photographed or reported in the Broughton Archipelago study area or adjacent regions where whale-watching and other recreational boat tours observe and photograph dolphins regularly.

Population structure has implications for conservation and management. The last status assessment in Canada designated the population as “Not At Risk”. However, this relied heavily on a presumed rescue effect such that if the Pacific white-sided dolphin population in Canada were threatened in any way, a large offshore population (Buckland et al. 1993) would replace dolphins in Canada’s Pacific waters. Given the new hints about site fidelity and finer scale population structure revealed by this study, perhaps a conservation status assessment should be revisited. It is not precautionary to manage several small populations as though they form one large one (Taylor 2005). It may be time to reconsider the population structure of Pacific white-sided dolphins in the region, and assess the status at the level of the population. This will require additional resources.

The results presented here, although preliminary, do contribute to our understanding of Pacific white-sided dolphins. In an essay about the development of our understanding of wild dolphins, Ken Norris wrote, “Though these notations may clutter the story line, they provide the most precious scientific treasures – little truths on which future understandings of the dolphins may be anchored” (Norris 1998). Many “little truths” were uncovered in this study. While some of the results are more tentative than others, collectively they increase our

knowledge of the basic biology of this species, inform the discussion about priority topics for future research, and provide a foundation on which those future research projects may be based.

Chapter 6

POPULATION VIABILITY ANALYSIS

6.1 INTRODUCTION

The conservation status of Pacific white-sided dolphins has not been assessed in Canada since 1989 (Stacey and Baird 1991). Although the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) concluded in 1989 that this species was not at risk in Canadian waters, it is important to note that this was a problematic determination. Until 1984, COSEWIC maintained a list of species for which there was “Insufficient Scientific Information on which to Base a Designation” (pers. comm., Professor Rick Taylor, UBC, and current Chair, COSEWIC, 18 November 2014). COSEWIC is made up of subcommittees with different taxonomic focus areas. Different subcommittees apparently have used that category in inconsistent ways, over the years, owing to the different standards of qualitative and quantitative measures used to assess status of plants, invertebrates, birds, fish, terrestrial or marine mammals. This gradually and unevenly shifted toward the formation of an “Indeterminate” category, which pooled populations known to be healthy and populations that were poorly studied. By 1998, COSEWIC had clear guidelines on designating species either “Not at Risk” or “Data Deficient” (pers. comm., Professor Rick Taylor, UBC, and Chair, COSEWIC, 18 November 2014).

Viewed in this historical context, it is unclear whether COSEWIC believed, in 1989, whether Pacific white-sided dolphins were Data Deficient or Not at Risk. The status report appears to conflate the two when it concludes, “With the presumed lack of serious threats, however, and until further studies elucidate population numbers and trends, the Pacific white-sided dolphin should be considered not in jeopardy and therefore not in any COSEWIC category” (Stacey and Baird 1991). It is not my intention to question the previous assessment. I raise the historical context simply to point out that COSEWIC’s stated intent was to revisit the status assessment

when quantitative demographic information became available. Now that I have generated parameter estimates, it is timely to revisit a status assessment.

The motivation of the population viability analysis (PVA) presented here was to explore the future viability of Pacific white-sided dolphins in my study area with the first estimates of many population parameters (see Chapters 3, 4 and 5). Given the new demographic estimates and associated measures of uncertainty, I wanted to assess the likelihood that the dolphins in the study area would increase, decrease or remain stable over the next several decades.

The demographic analyses presented in this thesis have attempted to describe how the Pacific white-sided dolphin “population” in the Broughton Archipelago and adjacent waters has behaved over the last few decades. Conservation decisions often require forecasting how a population is likely to behave in future, either naturally or under various management scenarios. Many of the demographic parameter estimates presented in this thesis are new for this species and this allows conducting population viability analyses to make predictions about population growth rate and assess extinction risk (Coulson et al. 2001). A PVA is a deliberately simplistic representation of reality, so it is important to have reasonable expectations and interpret the outputs with caution (Lacy 2000). Traditionally, PVA is used to model risk of extinction (i.e. either of the population as a whole falling below some level, or losing all members of one sex), but quantifying extinction probability has been criticized as the least reliable use of PVA (Harwood 2000). I conducted PVA to accomplish three objectives:

- i. Estimate the probability that the population is either increasing or decreasing under a natural mortality scenario;
- ii. Estimate the probability that the population is either increasing or decreasing under two “harvest” scenarios: human-caused mortality and increased killer whale predation; and
- iii. Explore sensitivity of the forecast to uncertainty in various input parameters.

Using the conventional notation in the PVA literature (Lacy 2015), the first two objectives are called “scenario testing,” whereas the third is called “sensitivity testing.” In scenario testing, the best point estimates (and their standard deviation) are used to model stochastic population growth under that scenario. One scenario, representing either the most optimistic or the “best available evidence” case, is referred to as the baseline scenario, and other scenarios are

interpreted in relation to this baseline case. In contrast, sensitivity testing through simulation evaluates how robust predictions from the baseline model are to variations in parameter values, which may come from different models or studies. My third objective was therefore to conduct sensitivity testing to gauge the extent to which uncertainty in input parameters affects the probability that the population is either increasing or decreasing. Conventionally, sensitivity analyses are done by varying one parameter at a time to quantify how a proportional change in one demographic parameter (e.g., adult mortality) affects the response value (e.g., population growth rate or extinction probability; Lacy et al. 2015). My aim was to integrate uncertainty in all parameter values simultaneously, across the entire range of scenarios tested (above) and evaluate, given all sources of uncertainty, the probability that the population would increase or decrease over a specified period. The sensitivity testing considered a wider range of potential killer whale predation than the scenario testing, in light of the anecdotal evidence that killer whale predation of Pacific white-sided dolphins is more common in recent years than it was since the photo-ID study began.

In this PVA, estimates of abundance and mortality/survival rate are taken from Chapter 3 and reproductive rate from Chapter 5. Mariners interviewed in Chapter 4 believed that Bigg's (also known as transient, or mammal-eating) killer whale predation on Pacific white-sided dolphins had increased over their careers (coinciding with the decades from which photo-ID data are available on Pacific white-sided dolphins). Normally, killer whale predation would be subsumed within the natural mortality estimates provided in Chapter 3. But if killer whale predation on dolphins is truly increasing in frequency of occurrence in recent years, then the mortality rates presented in Chapter 3 (i.e., derived from data dating as far back as 1988) may be lower than we can expect to see in future years. Therefore, the killer whale injury/scar rate analysis presented in Chapter 4 was used to outline a scenario in which killer whales "harvest" more dolphins from the population in future than they did in the scenario testing.

The PVA was conducted using the program Vortex 10.0.8.0 (Lacy 2015), which is commonly used for modelling populations of long-lived, slowly reproducing mammals. Many cetacean populations have been assessed using these methods, including southern resident killer whales (Taylor and Plater 2000), bottlenose dolphins (Currey et al. 2009a; Thompson et al. 2000), and Hector's dolphins (Burkhardt and Slooten 2003). Projections of future population size were

used to assess whether population growth rates were likely to be positive or negative, and how these predictions of growth rate varied given uncertainty in adult mortality, reproductive rate and plausible increases in killer whale predation.

6.2 METHODS

Program Vortex (version 10.0.8.0; Lacy 2015) is an individual-based population simulation model that uses user-specified population parameters and associated measures of uncertainty (either due to sampling error or environmental variability). In Vortex, demographic stochasticity from individual variability in mortality rates, proportion of females that are pregnant, and calf sex ratio, is modelled as a binomial distribution. Environmental variability and probability of a catastrophe are modelled as a normal distribution (Lacy 2000b). The new demographic parameter estimates reported in this thesis (Chapters 3, 4 and 5) were used wherever possible. In cases where empirical parameter estimates were not available, they were taken from literature reviews or model predictions (Taylor et al. 2007).

6.2.1 Scenario testing

6.2.1.1 Model parameters

Parameters relating to the reproductive system, mate monopolization and initial population size were the same for all modelled scenarios (Table 6.1). Reproduction was specified as being polygynous (Connor et al. 2000). Age of first reproduction was set to 10 years for both females and males (Taylor et al. 2007). Reproductive senescence was specified to occur at 46 years, based on the oldest known pregnant female (Taylor et al. 2007).

The initial population size of 1,000 individuals was chosen as a plausible starting value from the results of the mark-recapture models presented in Chapter 3. The estimate of population growth rate, r , is somewhat insensitive to this initial starting value, and the goal was not to predict abundance in any given year. Population growth rate, r , is defined as stochastic population growth rate (Lacy 2015) which: (1) incorporates the estimated variability in all demographic parameters, and; (2) is the average population growth rate in all simulations across the entire 50 year simulation period. The initial age distribution was set to be stable.

Density dependence and inbreeding were not included in this analysis, due to lack of quantitative information. Environmental variability (EV) was set to be concordant between reproduction and survival, such that favourable prey conditions were considered to be good for both survival and fecundity.

Table 6.1: Parameters used as inputs to program Vortex for the “Baseline” scenario.

Parameter	Value	Source
Age at first reproduction	10	Taylor et al. (2007)
Age of senescence	46	Taylor et al. (2007)
Sex ratio at birth	50:50	Taylor et al. (2007)
Males in breeding pool	100%	Connor et al. (2000)
Maximum number of broods per year	1	Taylor et al. (2007)
Maximum number of progeny per brood	1	Taylor et al. (2007)
% adult females that breed each year	23.8%	Chapter 5
EV in breeding	5.60%	SD on percent pregnant females (Chapter 5)
Adult mortality rate	1.10%	robust design, “winter-only” (Chapter 3)
Calf mortality rate	20.2%	Taylor et al. (2007)
Initial population size	1,000	Illustrative starting value (Chapter 3)
Carrying capacity	10,000	Largest abundance estimate calculated (Chapter 3)

The reproductive and mortality rates used in the baseline model are given in Table 6.1. The percentage of adult females breeding and its standard deviation were set to be 23.8% and 5.6%, respectively, based on modelled proportion of young of the year seen in groups of various sizes (Chapter 5). Male and female dolphins were assumed to have the same annual mortality rates. The baseline mortality rate was calculated by taking the average of the mortality rates equivalent to the two survival rates estimated in the robust design analyses in Chapter 3. The “winter only” survival estimate was 98.9% (1.1% mortality) and 90.2% (9.1% mortality) was the “year-round” survival estimate. The average adult mortality used for the adult mortality was thus 5.1%. Mortality rates were assumed to be constant in all non-calf (>1 year) age classes, because there is no reliable way to age Pacific white-sided dolphins in the current study. Calf mortality was taken to be 20.2%, i.e., 100% minus the assumed calf survival estimate of 79.8% (Taylor et al. 2007), for both males and females.

6.2.1.2 Specification of scenarios

The number of iterations used in all simulations was 100. The population size projection was evaluated over a 50-year period, in order to exceed the 46-year age of the oldest female (Taylor et al. 2007), but not to exceed the 3-generation ($21.8 \times 3 = 65.4$ years) period used in IUCN risk assessments (Taylor et al. 2007). Extinction was defined as having no members of either sex. Carrying capacity was set to 10,000, to correspond roughly to the upper confidence interval of the highest abundance estimate observed in the study (Chapter 3).

Including the “Baseline” scenario, three scenarios were initially run in program Vortex (Table 6.2). The Baseline scenario (Scenario A) was populated with the average of the “winter-only” Robust Design (RD) model and the “RD-year round” estimates of mortality. In the “RD average + Human Injury” scenario (Scenario B), the baseline mortality rate was increased by a proportion corresponding to the human-injury rates estimated in Chapter 4 (namely 0.5% divided by the 6-year study period). This very small increase in mortality is used as a proxy for serious injury that could cause a prolonged death. The “RD average + increased killer whale predation” scenario (Scenario C) projects higher rates of killer whale predation in future, based on the suggestion from local mariners that killer whale predation has increased in recent years since the last transient diet study was published (Ford et al. 1998). In this scenario, killer whale predation was predicted to increase in a manner consistent with the proportion (3.5%) of dolphins in a recent sample of photographs (2008-2013) that had killer whale injuries (Chapter 4), divided by the 6-year duration of the sampling period, to get a per capita, per annum rate of risk of killer whale predation.

Table 6.2: Specifications and parameter values used in the three scenarios modelled in program Vortex. Scenario A used the average of the “year-round” and “winter only” robust design analysis, Scenario B includes the addition of human injury, and Scenario C includes an increase in killer whale predation.

Scenario	% mortality rate	Harvest	
		Human injury	Killer whale predation
Scenario A	5.1		
Scenario B	5.1	0.08% of N	
Scenario C	5.1		0.58% of N

6.2.2 Sensitivity testing

Sensitivity testing was conducted to consider simultaneously the effects on population growth rate of the widest plausible ranges of input parameters, namely: uncertainty in reproductive rates (based on young of the year analyses in Chapter 5); estimates of mortality rate from both robust design models (winter and year-round; Chapter 3) during the period of the current study (1987-2013); and potential increases in harvest if killer whale predation increased over rates observed between 1987 and 2013 (i.e., the highest and lowest estimates from energetics calculations in Chapter 4). These variables are referred to below as “reproduction”, “mortality” and “harvest”.

Sensitivity testing was conducted in Vortex 10.0.8.0 using the Latin Hypercube Sampling (LHS) option with 100 iterations, which is considered appropriate for PVAs with four independent variables and relatively imprecise parameter estimates (Lacy et al. 2015). The LHS sampling option allows users to cover evenly the entire parameter space from the lowest to the highest plausible values of every input parameter, and is more computationally efficient than random sampling. The process works in Vortex in the following way. The LHS algorithm divides the specified range of each input parameter to obtain 100 evenly spaced values of each input variable (i.e., reproduction, mortality and harvest). A value is sampled randomly, without replacement, for each parameter, such that each value of each parameter is chosen once. This sampling is conducted independently for each parameter, such that the 100 iterations include random values of each of 3 input parameters that collectively cover the entire range of the specified, plausible values of the 3 input parameters (Lacy & Pollak 2015). The sensitivity test requires specification of a reference value to serve as a baseline. In sensitivity plots, this baseline value is plotted at the 50% mark on the x-axis. The lowest and highest plausible values of any given input parameter are plotted at 0% and 100%, respectively, along the x-axis.

Input values used in the sensitivity analysis (Table 6.2) were derived as follows. Adult male and female survival were permitted to range from the best-case scenario (Robust-Design:Winter; 0.989) to the worst-case (Robust-Design:Year-Round; 0.902) scenario, with a middle value derived by taking the average of the two robust design estimates (Chapter 3). This corresponds to a sensitivity test with lower and upper bounds on mortality rates of 1.1-

9.8% and a baseline value of 5.1%. A mortality rate of 1.1% is very low and inconsistent with increasing predation (see below). This value was obtained from analysis of data from 1991-2002, a period of relatively low killer whale predation compared to later years. It may not be a realistic value but was included as an extreme lower limit for the purposes of sensitivity testing.

Table 6.3: Highest and lowest reproduction, non-calf mortality, and harvest (projected increases in killer whale predation) parameter values used for sensitivity analysis.

Parameter	Low	Baseline	High	Source
% 1+ age class mortality	1.1	5.1	9.1	Chapter 3
Annual % of adult females reproducing	18.0	23.8	31.6	Chapter 5
Harvest: number of dolphins killed by killer whales	1	8	71	Chapter 4
Harvest: additional human-caused mortality	0.83	2	7.2	Chapter 4

Killer whale predation is subsumed within these historical mortality rates (when killer whale predation was rare) but a “harvest” is included in the sensitivity testing to explore the consequences of interview respondents’ perception that killer whale predation has been increasing in recent years (Chapter 4). Using the lowest estimate of killer whale predation (based on lowest mean body mass, lowest mass-specific metabolic rate, lowest number of killer whale-days observed by Orcalab between 1987 and 2012, and previous estimates (Ford et al. 1998) of the proportion of transient killer whale diet that is composed of dolphins) equates to an annual harvest of 1 dolphin. The best estimate of additional killer whale predation is 8 dolphins per year (based on best estimate of body mass, mass-specific metabolic rate, median killer whale-days in the Orcalab database; and the best estimate (9.5%) of the proportion of dolphins in the transient killer whale diet), and is considered the baseline case in the sensitivity tests. The maximum estimate of additional killer whale predation is 71 dolphins per year (based on the highest estimate of body mass and mass-specific metabolic rate, the year with the highest number of killer whale-days in the Orcalab database; and the best estimate (9.5%) of the proportion of dolphins in the transient killer whale diet). Therefore, the sensitivity testing considered population-level effects on dolphins of an increase in killer whale predation from 1 to 71 dolphins per year.

The values for the additional human-caused mortality were derived from the injury-rate reported in Chapter 4. The results from the survey of experts on human-injury informed the “high” and “low” values (Chapter 4), namely by attributing all or none of the “unknown” injuries to human activities.

Uncertainty in the proportion of females pregnant was incorporated in the scenario testing by considering a best estimate from the young of the year calculations (Chapter 5). The best estimate (23.8% of adult females being pregnant on average) served as the baseline reference point for this parameter. The low and high values for sensitivity testing were taken as the 95% confidence limits estimated in Chapter 5, namely 18.0 % and 31.6%. All other parameters were fixed (Table 6.2).

6.3 RESULTS

6.3.1 Scenario testing

All three scenarios predicted a small negative population growth rate (Table 6.4). In these three scenarios, the population is predicted to decline, on average, at 0.3% per year over the next 50 years, depending on the magnitude of human injury and additional killer whale mortality. No scenario predicted extinction over 50 years.

Table 6.4. Results of scenario testing, with stochastic growth rate (r) together with standard deviation (SD).

Scenario	r	SD
A. RD Average	-0.0008	0.021
B. RD Average + Human Injury	-0.0014	0.022
C. RD Average + Increased Killer Whale Predation	-0.0067	0.022

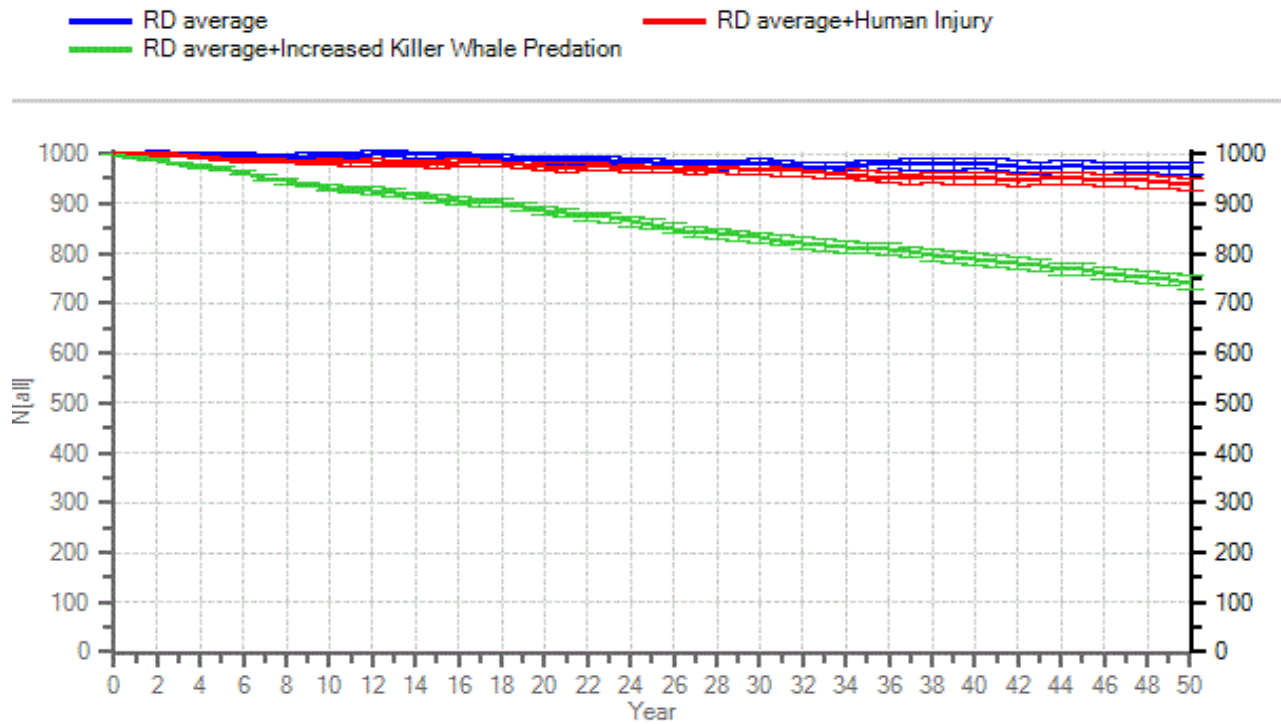


Figure 6.1: Predicted population trajectories (with SE bars from 100 iterations at each annual time step) for each of the three scenarios described in Table 6.2. Scenario A (blue) is referred to as the Baseline scenario. Scenario B (red) considers “harvests” from serious human injuries (boat propellers and fishing gear) and and Scenario C (green) considers potential increases in killer whale predation.

6.3.2 Sensitivity testing

With 100 model runs, a plot showing all trajectories is difficult to visualise. Trajectories for the first 20 runs are shown in Figure 6.2.

— survival harvest and calving uncertainty(Base):5.1; 8; 23.8; 5.1	— survival harvest and calving uncertainty(1):8.0495; 11.6061; 26.7919; 4.3323
— survival harvest and calving uncertainty(2):4.9788; 54.0303; 18.9616; 3.9283	— survival harvest and calving uncertainty(3):6.1909; 32.1111; 26.2424; 4.5747
— survival harvest and calving uncertainty(4):3.4434; 65.3434; 23.4949; 5.0596	— survival harvest and calving uncertainty(5):4.2515; 3.1212; 28.0283; 7.6455
— survival harvest and calving uncertainty(6):1.1808; 44.8384; 24.8687; 7.403	— survival harvest and calving uncertainty(7):1.5848; 58.2727; 24.1818; 8.9384
— survival harvest and calving uncertainty(8):2.8778; 10.1919; 24.7313; 3.1202	— survival harvest and calving uncertainty(9):4.0091; 17.9697; 21.8465; 8.3727
— survival harvest and calving uncertainty(10):3.9283; 25.7475; 29.402; 4.4939	— survival harvest and calving uncertainty(11):5.5444; 33.5253; 20.6101; 6.7566
— survival harvest and calving uncertainty(12):6.0293; 22.2121; 19.3737; 2.1505	— survival harvest and calving uncertainty(13):2.2313; 20.0909; 25.9677; 1.9081
— survival harvest and calving uncertainty(14):1.8273; 61.8081; 25.5556; 2.8778	— survival harvest and calving uncertainty(15):6.5949; 61.101; 22.5333; 6.5141
— survival harvest and calving uncertainty(16):3.5242; 7.3636; 19.7859; 5.2212	— survival harvest and calving uncertainty(17):8.696; 25.0404; 18.6869; 1.504
— survival harvest and calving uncertainty(18):6.2717; 37.7677; 20.0606; 1.4232	— survival harvest and calving uncertainty(19):2.797; 22.9192; 22.1212; 5.7869

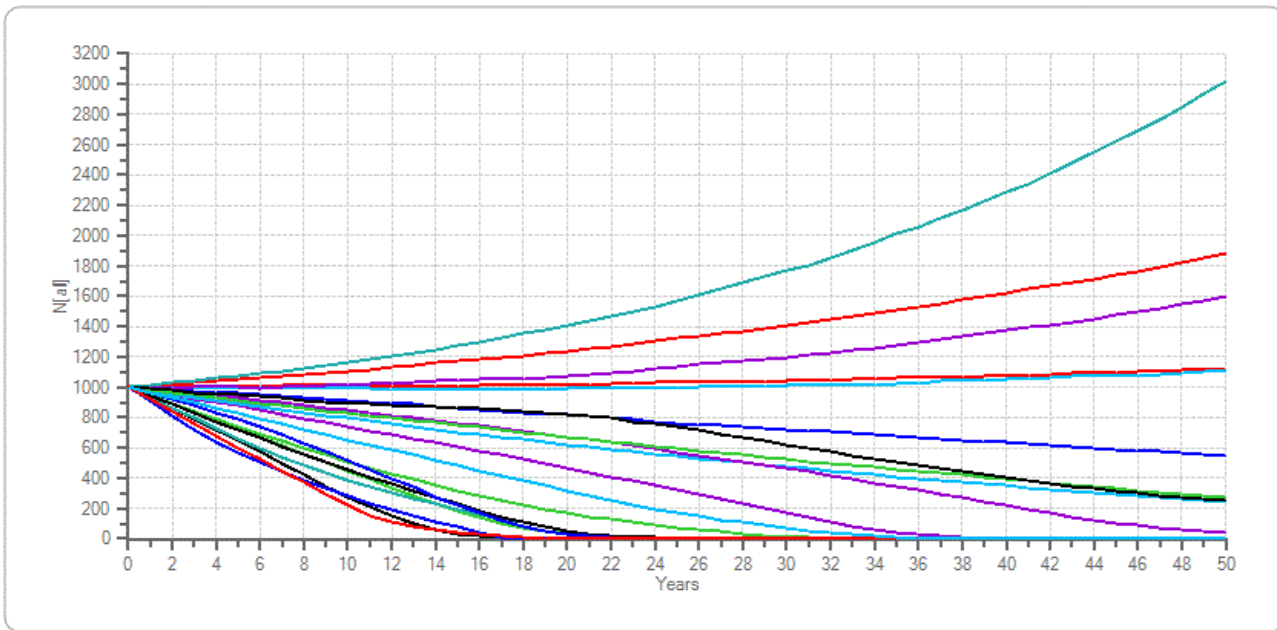


Figure 6.2: For illustrative purposes only, the first 20 scenarios (randomly sampled combinations of 100 evenly spaced samples across the range of input values for mortality, reproduction and harvest from Table 6.3) are shown as 20 lines. The legend shows the randomly sampled values in that iteration for each of the four input variables in the following sequence: % annual mortality rate for non-calf males; # of dolphins harvested annually by killer whales; % calving probability of adult females; and % annual mortality rate for non-calf females.

A new option in Vortex 10 is to plot sensitivity of outputs to uncertainty in inputs in the form of “spider plots”. Spider plots were used to show predicted values of population growth rate, r (Figure 6.3), given random combinations of systematically sampled values across the plausible ranges (Table 6.3) of the four explanatory variables (% annual mortality of adult males and females; % of pregnant females; and absolute number of dolphins killed via increased predation by killer whales, which is treated as a harvest in Vortex). Note that the simulations are centred on the baseline value (Table 6.3), such that $x=50$ corresponds to the baseline values of reproduction (calving probability, purple line), mortality (male mortality shown as a red line and female mortality as a black line) and harvest (increased killer whale predation, shown as a

green line). Each line represents one iteration of the simulation. Values <50 on the x-axis correspond to values lower than the baseline, with $x=0$ corresponding to the lowest case and $x=100$ the highest case (Table 6.3).

Figure 6.3 shows example trajectories when predicting stochastic population growth rate, r , after 50 years, by sampling across the entire parameter space in all four input parameters (shown in Table 6.3). Population growth rate, r , is plotted on the y-axis. Of the 100 simulations, 89 resulted in negative values of population growth, and 11 resulted in positive values of population growth. Visually, this can be seen by the few spikes in Figure 6.3 that are above the value of 0 on the y-axis. A few iterations with high (i.e., with x approaching 100, corresponding to highest mortality limits in Table 6.4) male mortality (red line; Figure 6.3) still resulted in positive population growth. These iterations presumably sampled cases when calving probability was high and female mortality and killer whale predation were low. In contrast, populations always declined when killer whale harvest (green line) was much greater than $x=65$. If the upper limit on killer whale harvest ($x=100$) were true, the dolphin population could not persist for 50 years. With few exceptions, populations failed to persist at initial abundance when values of calving probability (purple line) were below the baseline scenario ($x=50$, corresponding to 23.8% of adult females being pregnant in a given year). Populations failed to persist when female mortality rates fell below the baseline value (i.e., no black lines are seen at values of $x < 50$).

The proportion of variance in stochastic r explained by each variable in the sensitivity testing is shown in Table 6.5. The sensitivity analysis with five state variables includes a harvest from human injury and from an increase in killer whale predation in recent years. In this analysis, the proportion of the variance in r is primarily explained by killer whale predation followed by female mortality. When the harvest variables are removed entirely from the sensitivity analysis, female mortality is the primary factor that explains variation in r (Table 6.5).

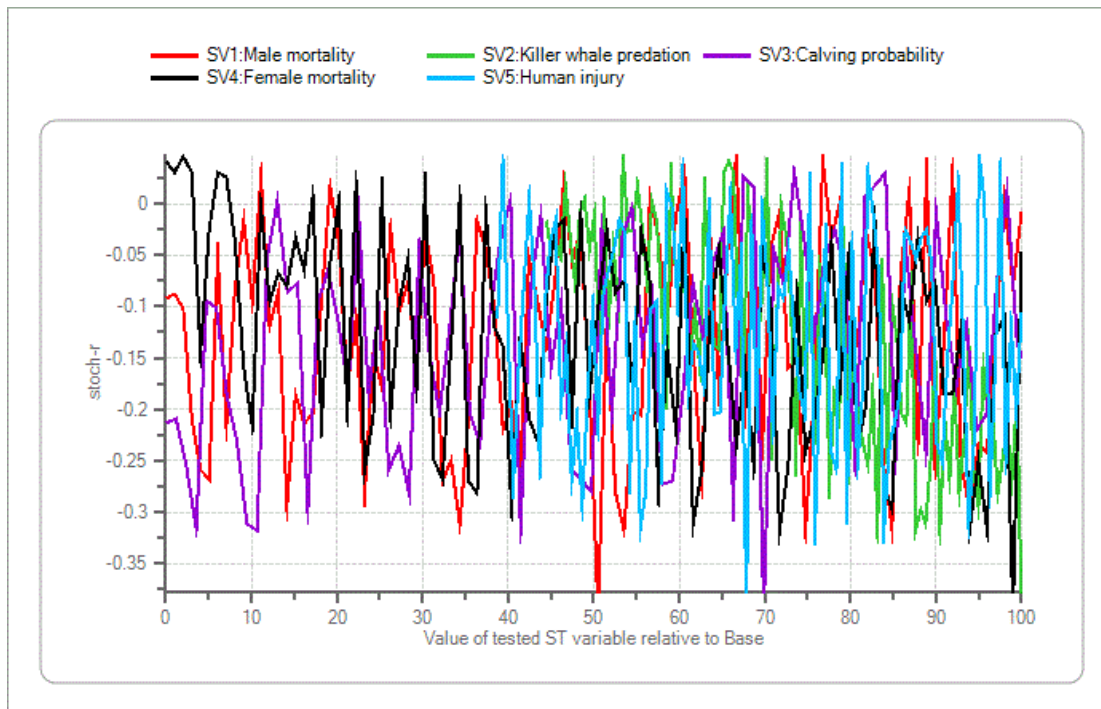


Figure 6.3: A spider plot of scenarios tested to explore effects of uncertainty in mortality, reproduction and “harvest”. Stochastic population growth rate, r , is shown on the y-axis and the range of tested values of the state variables is shown on the x-axis. Only the first 10 of 100 lines are shown. The spider plot is centred ($x=50$) on the baseline values for each of the four input values (Table 6.3). The lowest value (Table 6.3) is plotted at $x=0$ and the highest value at $x=100$. Variation is shown proportional to the baseline value for that variable. Unexpected values occur when pessimistic values for one variable happen to be sampled with optimistic values for the other variables (see Figure 6.2 for detailed examples).

Table 6.5: The proportion of variance in stochastic r explained by each state variable included in a sensitivity analysis.

State Variable	Proportion of variance in r explained by 5 state variables	Proportion of variance in r explained by 3 state variables
Male Mortality	<0.001	0.185
Female Mortality	0.260	0.556
Calving Probability	0.016	0.091
Killer Whale Predation	0.647	-
Human Injury	0.002	-

6.4 DISCUSSION

All three scenarios tested here predicted a small (0.5%) annual population decline over 50 years. The baseline scenario (Scenario A) predicted a population decline ($r = -0.007$ in the absence of any additional sources of mortality). The baseline adult mortality rate of 5.1% used in Scenario A was derived from the two survival rate estimates calculated in Chapter 3 and it is not known how realistic it is. However, the baseline mortality rate used in Scenario A is close to the 5% mortality rate calculated by Taylor et al. 2007 and much lower than mortality rate derived from the best estimate of survival rate from the year-round robust design analysis (0.902) (Chapter 3). Future research should focus on improving the robustness of the survival rate estimates. Trends in cetacean populations are challenging to predict due to low statistical power (Taylor and Gerrodette 1993; Taylor et al. 2007b; Thompson 2000), and this study is no exception. In addition, the ability to predict extinction risk using PVA can be sensitive to precision of parameter estimates (Ellner et al. 2002). PVA is useful for assessing the relative risk of extinction (Beissinger and Westphal 1998) and to assess the potential efficacy of different management scenarios (Thompson 2000). Here, the relative difference between the baseline and harvest scenarios and the sensitivity analyses can be used to inform management and research priorities.

The difference between the population decline due to stochasticity (*i.e.*, the baseline scenario) and the decline due to the removal of 0.8% of the dolphin population due to human injury over a 50-year period of harvest was small, but still warrants monitoring and consideration in management plans. The ability to detect this low-level threat is small, but continued monitoring using photo-ID, and increase in response to strandings, and any additional monitoring of fisheries interactions could improve estimates. Bycatch of Pacific white-sided dolphins in British Columbia is thought to be very low, however not all fisheries are monitored (Hall et al. 2002; Williams et al. 2008).

The harvest scenario resulting from killer whale predation (Scenario C) predicted a larger difference in population decline relative to the baseline over a 50-year period than the human injury scenario (Scenario B). The sensitivity analysis including harvest variables shows that killer whale predation could be influencing population growth rate (Table 6.5). The range of

potential dolphin removals due to killer whale predation is quite large, however (Table 6.3). If killer whale predation increases and raises mortality rates, the sensitivity analysis predicts a much more pessimistic outcome for the future of the dolphin population. This range may be a robust representation of the range of dolphin removals if killer whale diet composition follows a variable pattern from year to year. Given the evidence in Chapter 4 that killer whale numbers (Figure 4.2) and attacks (Tables 4.2 and 4.3) may be on the rise, and a prediction from the population viability analysis that increased predation would have a strong influence on population growth rate (Table 6.5), this is an area of research that warrants closer attention.

Not surprisingly, female mortality rate strongly influenced population growth rate in the three-state-variable sensitivity analysis (Table 6.5). Future research should include methods such as dorsal fin photogrammetry (Kasuya 1995; Webster et al. 2010), biopsy or skin-swabbing (Harlin et al. 1999), or analyses of hormones from exhaled breath (Hunt et al. 2014) in combination with photo-ID to determine the sex of individual dolphins and allow estimation of sex-specific survival rates. Differences in mortality rates between males and females have been found in killer whales (Bigg et al. 1990; Kuningas et al. 2014) and pilot whales (Kasuya and Marsh 1984).

Integrating all of the sources of uncertainty into 100 simulations allows for some general conclusions to be drawn from the sensitivity testing. Based on the best parameter estimates and their associated uncertainty, the best prediction is that the population in the area will experience an annual decline of -0.122 (95% CI: -0.143 to -0.101) over the next 50 years. The confidence intervals on that rate do not span zero, and it is far more likely to expect a decline than an increasing or stable population, given no additional information and assuming that this population is geographically closed and that the sensitivity tests correctly span plausible ranges of the input variables. The assumption of geographic closure may have been violated. The results of the robust design analysis suggest movement in and out of the study area (Chapter 3), but the robust design analysis of the winter-only data gave most support to a 'no-movement' model, suggesting site-fidelity. Future work should focus on estimating the proportion of dolphins resident to the area to improve our ability to forecast population trajectories.

The sensitivity testing results in a wide range of uncertainty in the predictions, as illustrated in Figure 6.3. Improving predictive power will require improving the accuracy and precision of all of the input variables, to narrow the range of plausible values. This will require increasing photo-ID effort, but new methods may be needed to estimate calving probability, because the PVA showed that it is exceedingly unlikely that this population can persist if the lower bound on the calving probability variable is correct.

Chapter 7

GENERAL DISCUSSION

7.1 General summary of findings

The protected, inshore waters of British Columbia (BC), Canada offer a rare opportunity to study a typically pelagic species, Pacific white-sided dolphins, using cost-effective, small-boat methods usually only tenable for coastal species. During the last major review of studies of odontocete sociality, it was noted that few species had been studied as “living individuals” (Connor et al. 1998); by doing so for Pacific white-sided dolphins, the current study has advanced ecological knowledge of this species. One of the most difficult decisions to make in conservation biology is how to prioritise species on which conservation efforts should be focussed (Mittermeier et al. 1998). There are many important data gaps on demography, threats and population structure of Pacific white-sided dolphins; this study presented an opportunity to be the first to explore a number of scientific questions, offer valuable insights into the ecology of this species and pelagic dolphins generally, and inform conservation and management.

New population parameters, namely survival rate, fecundity rate and abundance, were estimated from photo-ID data for the first time in this species (Chapter 3). The analysis of the effect of uncertainty in matching photos of marked individuals for photographic identification showed that as less certain matches were included in the abundance estimation analysis, estimates of abundance had increased negative bias but an improvement in precision (Chapter 2). The results of the simplest two-sample estimators indicate that dolphin abundance in the area is highly variable from year to year, ranging from around 500 to around 3,000. Province-wide, systematic line transect surveys estimated 25,000 (95% CI: 12,900-52,100) dolphins in BC continental shelf waters (Williams and Thomas 2007). The number of dolphins using the waters of the Broughton Archipelago therefore comprises anywhere from approximately 0.2 to 12% of the point estimate of the total number of dolphins in BC.

The dolphins of the Broughton Archipelago are a demographically and geographically open population. Two robust design mark-recapture analyses revealed a random temporary emigration movement pattern (Chapter 3). Apparent survival from the CJS model was 0.924 (95% CI: 0.881-0.969), but this is confounded with temporary emigration. A robust design model, accounting for temporary emigration, generated a survival estimate of 0.907 (95% CI: 0.843-0.972) when using year-round data, and 0.989 (95% CI: 0.866-1.000) when restricted to winter months. A Pradel model with cohorts for transients and non-transients estimated survival of the non-transient group to be 0.942 (95% CI: 0.871-0.975). These mark-recapture estimates are the first empirical estimates of survival for this species, and to the best of my knowledge, the first for *Lagenorhynchus* as a whole. They also correspond with the predicted survival estimate (0.95) from life-history tables (Taylor et al. 2007).

Individuals were resighted in the area over periods of up to 19 years. An inter-birth interval of 4.2 years was estimated from the data (Chapter 4), which is consistent with a 4.5-year inter-birth interval predicted from life-history tables (Taylor et al. 2007). Dolphin presence may well be influenced by the number of days that mammal-eating killer whales were observed in the study area (Chapter 4), and 3.9% of dolphins carry scars from killer whale attacks. From a simple bioenergetic model, it is estimated that, in some years, the number of killer whales using the area was high enough to account for the entire estimated dolphin mortality in the local population if killer whales consumed dolphins exclusively (Chapter 4). However, the best estimate indicates that dolphins comprise less than 10% of killer whale diet in the study area. Interviews with local scientists and mariners revealed that the frequency of transient attacks on Pacific white-sided dolphins may comprise 9.5% of observed transient killer whale kills in recent years (Chapter 4), whereas Pacific white-sided dolphins were only observed to be killed once (<1% of observed kills) in the period 1973-1996 in BC (Ford et al. 1998).

Acoustic evidence for population structure was equivocal. There is a strong signal in the recordings that there are two acoustically dissimilar groups using the study area, but the discriminatory power is low. Assigning recordings into groups corresponding roughly to “resident” and “non-resident” groups offered more discriminatory power than assigning groups randomly to two groups. Given the potential for acoustic methods to define stocks, this aspect of the study warrants additional, targeted research (Chapter 5). A social analysis revealed

statistically significant support for concluding that there is a high degree of non-random associations and social differentiation in Pacific white-sided dolphins. This fits with expectations from studies of comparative anatomy and mating systems in cetaceans (Connor et al. 2000).

The Population Viability Analysis (Chapter 6) showed what would be expected from the parameter estimates themselves presented in Chapters 3, 4 and 5. The ability to predict whether the population is likely to decrease or increase over the next 50 years is largely contingent on whether adult survival, especially for females, is closer to 0.91 or to 0.99 (RD Year-round or RD Winter-only, respectively; Chapter 3). Many simulations showed positive population growth even when adult male mortality was at the highest end of the estimates (Table 6.4, Figures 6.3 and 6.4), as long as adult female survival and calving probability are high and killer whale predation does not increase. In general, if killer whale predation does not increase in the next 50 years (i.e., if the highest plausible values of killer whale predation are already subsumed within the existing best estimates of adult survival), the population should persist and grow; if killer whales start to meet a higher percentage of their energetic requirements (Chapter 4) by preying on dolphins, the dolphin population will likely decrease. However, population structure is not defined for these animals and the results of the robust design analysis show a 0.14 rate of temporary emigration, suggesting that the assumption of geographic closure was likely violated. It is plausible that dolphins immigrating from outside the study area could slow or prevent a local decline. However, the mortality rate and threat exposure to this population outside the study area is unknown. The “no-movement” model was preferred in the robust design analysis of the winter data suggesting a geographically closed population (at least seasonally). Taken together, this suggests a small, core group of dolphins using the study area year round, with other dolphins showing less site fidelity to the area. Going forward, defining the proportion of resident and transient dolphins would be informative when interpreting these population predictions and setting management priorities.

The best estimate of the average percentage of adult females being pregnant annually (23.8%) is low, and translates into a long inter-birth interval (4.2 years; Chapter 5). The PVA showed that if the lower bound on that estimate (18.0%) were real, the population could only persist if adult survival were high (especially for females) and killer whale predation were low.

7.2 Improving accuracy and precision of estimates

7.2.1 Abundance estimation using mark-recapture and line transect methods

It is more common to estimate population size of abundant odontocete populations, including Pacific white-sided dolphins, using line-transect surveys (e.g., Barlow and Forney 2007; Forney et al. 1995). This is because oceanic dolphins typically occur in large areas in which it is more effective to sample space rather than individual animals. Line transect surveys can also give large CVs (Buckland et al. 1993), and they may be biased due to responsive movements (Buckland et al. 1993; Palka and Hammond 2001). In many cases, high CVs on abundance estimates of pelagic dolphins are actually underestimates of variance, because they fail to incorporate school size uncertainty (Gerrodette et al. 2002). Field estimates of group size can range by an order of magnitude, with uncertainty in school size estimation increasing as groups get larger (Thomas et al. 2010). Typically, this uncertainty is ignored in line transect surveys, because standard approaches generally use only the best estimate of school size, rather than incorporating low, best and high estimates in a robust variance estimate (Thomas et al. 2010). While line transect surveys are undoubtedly valuable, a line transect survey would not have yielded any of the information I generated on survival, reproduction, killer whale predation or sociality, or allowed me to make use of the long-term data from the historical catalogue.

We recently carried out a small-boat line transect survey to estimate abundance of dolphins in the study area and are eager to compare density and mark-recapture based estimates of abundance of this species (Calambokidis and Barlow 2004; Williams and Thomas 2009). Analyses are underway, but the largest challenge was generating reliable estimates of school size from a small boat. Aerial surveys or inexpensive unmanned autonomous vehicles (Sutherland et al. 2012; Vermeulen et al. 2013) could help obtain aerial photographs to estimate school size and would eliminate the issue of any responsive movement to survey vessels. Calculating sex-specific survival rates would greatly inform the PVA. Photogrammetric measurements of dorsal fin size using lasers mounted on photo-identification would help identify males and females in this population. Additional photo-identification effort would improve the precision of the survival estimates.

7.2.2 Sustainable limits to bycatch

One precautionary approach to prevent undetected depletions of species for which we have sparse data is to ensure that human-caused mortality is kept below a limit that could be withstood by some precautionary, lower estimate of population size (Winship 2009). Abundance estimates are essential for setting sustainable limits to human-caused mortality (e.g., fisheries bycatch, ship strikes) such as in the Potential Biological Removals (PBR) method used in the United States under the Marine Mammal Protection Act (Read and Wade 2000; Wade 1998). Williams et al. (2008) used province-wide estimates of dolphin abundance in BC to estimate a PBR of 388 dolphins.

The robust design analysis (Chapter 3) provided new insight into temporary emigration rates, and conversely, some measure of residency of this species in the study area. The 14% random movement rate in and out of the Broughton Archipelago study area is lower than that found for bottlenose dolphins in Shark Bay, Australia (33%; Nicholson et al. 2012a), bottlenose dolphins in the Azores (42-76%; Silva et al. 2009b), and the same as the lower range of movement rates for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) off Western Australia (0.14-0.56; Smith et al. 2013). Smith et al. (2013) estimated movement rates seasonally, which revealed a “no movement” pattern during winter months. Movement rates can provide insights into population structure. From a conservation and management perspective, the degree to which these animals are resident to the region will affect the degree to which they are exposed to anthropogenic and natural threats in this area. The results of the PVA show that a population of dolphins resident to the study area is predicted to decline over the next 50 years; however, there is evidence from mark-recapture data for a geographically open population (Chapter 3). Finer scale data on movement patterns and rates could be estimated from tags to track movements of dolphins in and out of the study area (Elwen et al. 2006; Hooker and Baird 2001) and inform both the survival estimates and population structure. Similarly, expanding photo-ID efforts north and south of the study area could provide useful information on movement rates.

7.2.3 Improving estimates of survival rate

The estimate of survival rate could be improved by an increase in recapture probability through increased effort (Hammond 1986; Seber 2002) which hinges to a large degree on funding and

logistics. However, statistical approaches are also available that may effectively increase capture probability by including photographs of dolphins that could only be detected from one side (e.g., marks only on one side of the dorsal fin, rather than outline (nicks and notches) of the dorsal fin, which is symmetrical). Recent approaches have developed methods to incorporate photographs of animals that are recognisable or photographed from one side only (Bonner 2013; Hiby et al. 2012; McClintock et al. 2013). This approach of combining information from left and right sides of animals (Bonner 2013; McClintock et al. 2013) is an integrated modelling approach that builds on an extension of the Jolly-Seber model. Additionally, mark-resight models (McClintock et al. 2009a; McClintock et al. 2009b) incorporate information from high-quality photographs of the number of times that marked and unmarked individuals were seen, such that the input data are Poisson distributed rather than binomial.

Mark-resight models may hold the greatest promise for improving my parameter estimates, because they are robust to over-dispersion (most dolphins in this study were seen only once) and would thus reduce the variance by integrating information on mark rate into the maximum likelihood estimator (McClintock et al. 2009a). The mark-resight models can be built in a robust design framework, which would eliminate the need to choose among models that prioritise precision versus accuracy (McClintock et al. 2013).

Alternatively, for most of the models used in this study, a Bayesian option exists (Gimenez et al. 2009; Kery 2010; King et al. 2010). A simulation study has found that, all other things being equal, Bayesian estimators provide similar point estimates of survival to their frequentist counterparts, but with better precision (Poole 2002). Importantly, Bayesian methods are particularly useful in cases where there are years in which data are missing. Although it is reasonable to keep these alternative methods in mind as sample size grows, the top priority for improving inference is to increase capture probability and consequently sample size.

7.2.4 Match uncertainty in photo-identification

Photo-identification studies generally assume that all matches are identified with certainty (Hammond 1986; Pollock et al. 1990; Seber and Schwarz 2002), but it is likely that misidentifications occur in most studies and that the impact of mismatches on estimates of

abundance is especially pronounced in studies with low rates of recapture (Yoshizaki et al. 2009). Methods are needed to quantify the degree to which parameter estimates are sensitive to uncertainty in the matching process (Urian et al. 2015). The effect of match uncertainty on estimates of abundance and survival of Pacific white-sided dolphins was explored in Chapter 2. The direction of the findings was as expected: as one allows increasingly uncertain matches to be called a match, the number of resightings increases; consequently, abundance estimates decrease, survival rate estimates increase, and the estimated precision of both is improved. The magnitude of these effects was found to be modest. Treating “certain” matches as truth, as matches became less certain there was a ~33% negative bias in abundance and little improvement in precision (Chapter 2). I could not use the data from the historical study to explore this, and the small sample of suitable data hindered efforts to investigate these impacts fully.

This chapter points the way toward an important area of additional research, both for this study and for other studies of wildlife populations, because the potential bias introduced at the photo-matching stage could carry implications for conservation and management. In practical terms, this chapter begs the question: Is it better to include dubious matches to increase sample size to get a more precise (albeit negatively biased) abundance estimate, or to aim for accuracy and make decisions with poorer precision? It is a case-specific decision whether to err on the side of accuracy or precision, or to try to strike a balance. If one is studying a species that is new to science, or a critically endangered species (e.g., with small sample size) facing imminent threats, one may need to generate an abundance estimate quickly; in that case, a biased estimate may be better than none. Alternatively, one may strive for accuracy, and use management models that are robust to uncertainty (but not bias) (Taylor et al. 2000).

Collaborations between quantitative ecologists and statisticians could result in development of new analytical methods to incorporate match uncertainty in resulting parameter estimates. As this study progresses, it is my intention to ensure that photo matching protocols continue to provide an honest reflection of the degree of certainty in a match. If the photo-ID matching routinely includes a certainty level, Bayesian or resampling methods could be developed to integrate that source of uncertainty in the resulting parameter estimates. The matching process

inherently includes some degree of subjectivity that is ignored when we force photo-ID data into a binary framework.

The main problems found in this study, namely low capture probability, imperfect match identification, and inadequate sample size to select quantitatively among as many models as one might like, are not unique. Researchers faced with similar problems have developed tools to address these problems, including a method to estimate the rate of mismatches in photo-identification data using genetic ID as an additional, independent source of information (Stevick et al. 2001). Conducting double-tagging experiments to estimate mark loss is common practice in tagging studies (Bradshaw et al. 2000; Pistorius et al. 2000; Stobo and Horne 1994), but it is not commonly practiced in photo-ID studies. Future work in the current study will consider partnerships with geneticists, to see if that might address the problem of mark uncertainty. Adding a biopsy component to collect skin and blubber would also improve understanding of population structure, provide information on sex of known individuals, and potentially result in measures of contaminant loads of known individuals (see *Threats*).

7.3 Killer whale predation

The current study has generated some information that is directly relevant to the controversial and contentious discussions around the role of top-down forcing in shaping marine mammal population dynamics (DeMaster et al. 2006; Estes et al. 1998; Springer et al. 2003; Taylor et al. 2000; Trites et al. 2007; Wade et al. 2007a). Pacific white-sided dolphins are frequently exposed to the risk of predation. Integrating several data sources since the 1980s, Chapter 4 outlines direct and indirect lines of evidence to suggest that killer whales are involved in successful and unsuccessful attacks on Pacific white-sided dolphins in BC far more often than one might expect from previous studies of the diet of mammal-eating killer whales (Baird and Dill 1995; Ford et al. 1998).

In interviews with mariners and researchers, I found that killer whale attacks on Pacific white-sided dolphins follow a common narrative: killer whales split large groups of dolphins into smaller subgroups and chase the small group of dolphins into shallow water or a confined area. Typically, some dolphins attempt to evade predators through high-speed chases that can succeed (e.g., when dolphins reach open water) or fail (e.g., when dolphins are eaten or beach

themselves in an attempt to avoid capture). This new information leads to some intriguing directions for studies of behavioural ecology, namely to explore how Pacific white-sided dolphins make decisions with respect to foraging and mating under risk of predation (Lima and Dill 1990). Behavioural studies of human disturbance in wildlife have often treated human activities as predation-free predators (Beale and Monaghan 2004; Frid and Dill 2002; Williams et al. 2002c). The dolphin-killer whale system may provide a real-world opportunity to test how well the evasive tactics marine mammals use to avoid human activities fit with what is observed during actual predation attempts. Perhaps more refined studies of anti-predatory tactics of Pacific white-sided dolphins could be used to guide more effective mitigation measures to reduce impacts of human-caused disturbance on sensitive species (Frid and Dill 2002).

Although I have compiled observations of short-term responses of dolphins to acute predation attempts, there is a need to expand this work to consider the effects of chronic, low-level vigilance associated with living in regions in which predators are ubiquitous. Small changes in the anti-predatory behaviour of prey species (Gerrodette and Gilmartin 1990) and even the threat of predation alone can affect demography (Laundre et al. 2001). During years when killer whales were scarce, Pacific white-sided dolphin survival rate was as high as predicted from life history calculations; but in the years of peak transient killer whale usage of the area, dolphin survival rates were lower (Chapter 4). Due to data sparseness, the confidence intervals on survival rate are wide but there is weak support from the data for including killer whale presence as a covariate in the CJS model, and both first hand and circumstantial evidence that the killer whales are an important predator of Pacific white-sided dolphins. The dolphin demographic data suggest that killer whale predation is not rare but, rather, rarely witnessed by any one observer.

Simple bioenergetics calculations show that killer whales are unlikely to account for all of the natural mortality in the group of dolphins using the area. For killer whales to account for all of the observed mortality, observed killer whale usage would have to be markedly underestimated (e.g., spending time in the area without being vocal or detected by whalewatchers), or dolphins would have to make up a much larger proportion of the whales' diet than previously estimated (Baird and Dill 1995; Ford et al. 1998).

7.4 Population structure

While Chapter 3 provides new demographic parameter estimates for Pacific white-sided dolphins in the study area, Chapter 5 explores the extent to which we can identify the biological unit to which these estimates apply. Unfortunately, the use of genetic methods to discriminate stocks (Baker et al. 1998; Hoelzel et al. 2007; Mendez et al. 2011) was beyond the scope of this study. Acoustic and sociality data offer hints that there is a core group of dolphins that shows some degree of residency to this study area. Whether such a social unit represents a biological “unit to conserve” remains an open question but, if that is the case, threats should be evaluated at the level of the population. One can define stock boundaries from data on dispersal rates (Aschettino et al. 2012), migratory destinations (Sremba et al. 2012) or movement data (Baird et al. 2011). There is one case where two dolphins photographed in the study area were matched to dolphins photographed off Victoria, British Columbia (approximately 400 km away) over a 6-week period. Additional effort outside the study area combined with matching opportunistically collected photographs may reveal more information about movement patterns and rates. As noted in Section 7.2, such better information would also improve demographic estimates.

7.5 Sociality

Analyses of associations between dyads suggest a strong degree of social differentiation in Pacific white-sided dolphins that differs significantly ($P < 0.01$) from a randomly associating society. The point estimate of social differentiation puts Pacific white-sided dolphins on a par with pilot whales when it comes to sociality, but the statistical power to explore that differentiation is low. This evidence for sociality is new for this species but it is consistent with predictions from ecological theory and from large testes size and a long (4.2 years) inter-birth interval (Connor 2000). Some pairs of dolphins were seen together repeatedly over periods spanning 15 to 19 years. Few animals were seen more than 5 times, so the effect size must have been high for the study to have generated statistically significant results. Similarly, the odds of seeing pairs of dolphins together by chance, more than a decade apart, are slim.

The sociality analyses would benefit from additional work to explicitly incorporate estimates of capture probability, to mitigate the chances that low capture probability is not causing

SOCPROG to mistake lack of association of dyads for active avoidance (e.g., Klaich 2011). Methods to incorporate uncertainty in association indices have not yet been integrated in SOCPROG. As a result, some methodological development and/or more sophisticated social analyses are needed before I can provide a more reliable picture of the social structure of Pacific white-sided dolphins, given my small sample size and allowing for uncertainty. Until then, the number of and time span between resightings suggest a degree of site fidelity and long-term associations that have not been reported previously in this species. The permutation tests indicate a well-differentiated society ($P < 0.01$; Chapter 5). The evidence for sociality is compelling and warrants additional research.

To some extent, the presence of sociality is expected. In a previous review, Pacific white-sided dolphins clustered with killer whales and pilot whales with respect to testes mass, given predictions from body size and presence or absence of sexual dimorphism (Connor 2000) and the authors predicted that Pacific white-sided dolphins should have a social structure more similar to killer whales or pilot whales than to bottlenose dolphins. At that time, Connor (2000) was unable to make predictions about female reproductive strategies in Pacific white-sided dolphins, due to lack of individual association data on sociality or empirical demographic estimates. Notably, the current study's estimate of an average inter-birth interval of 4.2 years is long compared to the 2.5-year inter-birth interval reported for dusky dolphins and Atlantic white-sided dolphins (Taylor et al. 2007a; Whitehead and Mann 2000). It is similar to that of long-finned pilot whales (*Globicephala macrorhynchus*; 3.3 years) and short-finned pilot whales (*Globicephala melas*; 5 years; Whitehead and Mann 2000), and approaches the 4.9-5.5 year calving intervals of resident killer whales (Olesiuk et al. 1990).

7.6 Timing of reproduction

Although seasonal coverage in my study was not uniform, most newborn calves were observed in July and August. There has been a suggestion that calving takes place in inlets where warmer water temperatures lower energetic costs to calves (Morton 2000), which has also been postulated for beluga mothers and calves near river mouths (Connor 2000). This is consistent with my observations of Pacific white-sided dolphins. During July and August, groups of mothers and newborn calves were found at the head of inlets in warm, shallow water. This warrants additional research, because timing of reproduction can be used to inform studies of

population differentiation. In California, newborn Pacific white-sided dolphins are observed beginning in June and throughout the summer months (Black 1994). No newborn calves were seen in June in any year of the current study. This could reflect geographic differences relating to prey abundance or physical oceanographic conditions, rather than a stock boundary, but in the absence of genetic data or movement patterns, any information that can guide stock structure hypotheses is potentially useful.

My future work in this field will try to integrate emerging information on sociality with the predator-prey interactions described in Chapter 4. Pelagic dolphins are distributed at large spatial scales and can occur in groups of thousands. Predator (killer whales and sharks) avoidance and efficient prey acquisition in a patchy ocean (Martin et al. 2002) are two hypotheses, not mutually exclusive, to explain the formation of long-term, socially bonded groups (Rubenstein 1978). How do these various selective pressures work to increase an individual's chance of survival or reproductive success (Rubenstein 1978)?

Infant mortality from predators can be important (Jefferson et al. 1991). The need to guard infants from predation may influence female reproductive success and the investment in parental care. A shared interest in protecting calves from predation supports female-female bonds (Connor et al. 1998). The idea that predation is at least one factor determining the benefits of group living in this pelagic dolphin is consistent with the finding that females with calves were first detected up to 7 years after dolphins first appeared. A delayed appearance of mothers and calves is consistent with ecological theory in which dolphins rely on a dilution effect (Foster and Treherne 1981) to avoid predation. If killer whale predation is driving group decision-making (Conradt and Roper 2003), then one would expect to see evidence of sentinel behaviour (*discussed below*).

Alternatively, group formation may be driven largely in response to a shared need to find patchy prey in a vast ocean. The simplest test for the cooperative foraging hypothesis is to see how dolphins behave when one member finds food. If dolphins happen to have aggregated in a productive feeding area that they each found independently, then individuals should maintain spacing when a prey patch is found; cooperative foraging is evidenced by other individuals approaching when an individual finds a prey patch (Connor et al. 1998). In my study, groups

did coalesce when feeding, which suggests some degree of cooperative foraging but this process may be a predator avoidance tactic as well. If prey acquisition is driving group behaviour in these dolphins, then we might expect to see acoustic sharing of information on prey patches, such that larger groups may be noisier than smaller groups. Larger, noisier groups may be more vulnerable to predation, because their calling would make it easier for killer whales to find them: the so-called *encounter effect* (Turner and Pitcher 1986). Testing these hypotheses will be an interesting future area of research. My expectation is that group living may prove to offer costs and benefits, that is, the dolphins may behave in ways that conform to both hypotheses.

7.7 Acoustic methods to discriminate groups

The acoustics work is in its very early stages. The training step in the data analysis offered a hint that there is a core group (Group A) that can be differentiated acoustically from some “putative transient” groups (Group B) that differ acoustically. During training, the Bayesian whistle classifier was able to discriminate between Group A and B recordings with 71% accuracy (Chapter 5). Specifically, recordings from groups containing at least one dolphin that was resighted at least once previously (>7 years earlier), sounded different from groups containing only “new” dolphins (Chapter 5). The discriminatory power of this test was better than placing the recordings in two random groups. There is enough between-group difference in characteristics of burst pulse calls to warrant pursuing this line of inquiry, and to expand it to include characteristics of higher-frequency echolocation clicks (Henderson et al. 2011; Soldevilla et al. 2008). Ideally, a calibrated hydrophone array would be used to give an estimated source level in addition to high-quality recordings of click characteristics (Kyhn et al. 2013). The combination of genetic and acoustic evidence will be useful for placing the demographic data (Chapters 3 and 5) in the context of biological populations. In some cetaceans, there is a strong link between within-species call variation and social structure (Tyack 1986).

7.8 Broader research needs

My study has filled some knowledge gaps but many remain. Most importantly, information on population structure would place the demographic estimates, threats, social analysis, and population viability in a context that would both advance our biological understanding of

Pacific white-sided dolphins and provide key information to inform conservation status assessments in Canada, the USA, and under IUCN. This could be achieved through additional research into genetics (Baker and Palumbi 1996; Hayano et al. 2004; Hoelzel 1998), implementing a tagging study to track movements (Patterson et al. 2008; Wells et al. 1999), and continued photo-identification (Baird et al. 2008; Calambokidis et al. 2001), acoustic investigation (including passive acoustic monitoring (Oleson et al. 2009; Soldevilla et al. 2008) and social analyses (Lusseau et al. 2006; Sugg et al. 1996). Each of these lines of inquiry represents a worthy topic in its own right. Given the logistical challenges of studying Pacific white-sided dolphins, it will no doubt take an international, collaborative effort to provide enough information at appropriately large spatial scales to resolve questions of population structure and conservation status. A basin-wide study of Pacific white-sided dolphins at the scale of previous efforts to study humpback whales: e.g., the SPLASH project in the North Pacific (Calambokidis et al. 2008) and the YONAH project in the North Atlantic (Smith et al. 1999) could fill in many of these remaining data gaps.

7.8.1 Threats

In the absence of definitive information on population structure and trends, one practice in conservation status assessment is to use information on anthropogenic threats to guide decision-making (Mace and Lande 1991). The high-seas driftnet fishery that killed ~100,000 Pacific white-sided dolphins in the North Pacific in the 1980s is now illegal, although some illegal fishing may continue to take place (NMFS 2012). The current study has provided new data to update the previous assessment of known and potential threats (Stacey and Baird 1991).

Results from previous questionnaire surveys of the salmon gillnet fishing fleet suggest that bycatch of Pacific white-sided dolphins in gillnets is too rare to pose a population-level impact (Williams et al. 2008), but because that study was focussed on harbour porpoise in BC's south coast waters (where dolphins are rare; Williams & Thomas 2007), it failed to include the most important habitats for dolphins and did not cover the fleets using other gear types that can harm dolphins. The evidence of fishing interactions found in this study suggests that we should not be complacent about anthropogenic threats in this region, but that it is unlikely to be a conservation concern at present.

One respondent noted that determining cause of death in marine mammals is difficult enough from necropsies; it can rarely be accomplished from a photograph (Moore et al. 2013). That respondent observed that photographs of injuries in living animals can offer hypotheses about what stressors animals are exposed to, but photographs alone will not allow us to rank or quantify magnitude of threats. Funding for necropsies of stranded animals is scarce in many regions and in Canada the allocation of that funding is prioritised by conservation status². Because Pacific white-sided dolphins are currently considered not at risk in Canada, stranded dolphins are a low priority for full necropsies to determine (natural or anthropogenic) cause of death. If these animals were subject to an anthropogenic stressor causing declines, we would be hard-pressed to detect that from either current marine mammal response plans or declines in abundance.

7.8.2 Potential anthropogenic threats

Pacific white-sided dolphins rely heavily on burst-pulse calls for communication and echolocation for finding prey (Dawson 1991; Lammers et al. 2003; Richardson et al. 1995). Anthropogenic ocean noise is an obvious threat to consider. A recent empirical study found that the Broughton Archipelago is among the quietest sites along the BC mainland coast in the frequency bands that dolphins use to communicate – far quieter than urbanised areas off Vancouver and Victoria (Williams et al. 2013). This was not always the case. In the 1990s (1993-1999), acoustic harassment devices (AHDs) introduced high-amplitude (a 10 kHz signal at 194 dB re 1 μ Pa @ 1 m) sounds to deter seals from fish farms; they failed to keep the seals away, but did displace dolphins, killer whales and harbour porpoise (Morton 2000; Morton 2002; Olesiuk et al. 2002). AHDs were banned from the region immediately after this unintended side effect came to light. No study to date has measured or modelled how chronic ocean noise could affect the loss of communication space, foraging efficiency or efficacy of predator-avoidance tactics in Pacific white-sided dolphins.

Pacific white-sided dolphins have reportedly become entangled and died in salmon aquaculture anti-predator nets in the study area (A. Morton, personal communication) but there is no

² <http://www.dfo-mpo.gc.ca/fm-gp/mammals-mammiferes/prog-eng.htm>

obligation for fish farmers to monitor their net cages for entangled dolphins and reporting is incomplete. Similarly, with little to no monitoring or public reporting of diseases around fish farms, it is unknown if pathogens from fish farms are affecting dolphins via indirect effects on prey species (Krkosek et al. 2006). Poor water quality around fishmeal factories has been linked to skin lesions in cetaceans, and the tendency for salmon farms to use antibiotics prophylactically may expose dolphins to fish pathogens including *Vibrio cholerae* and *Aeromonas hydrophila* (Van Bresseem et al. 2009). The failure to consider disease transfer from aquaculture to wildlife is inconsistent with cetacean emerging infectious diseases being considered a priority for conservation action internationally (Van Bresseem et al. 2009).

7.8.3 Trade-offs between feeding and avoiding predation

Large knowledge gaps remain in our understanding of how dolphins detect and avoid predators. The hydrophone system at Orcalab allows human detection of both dolphins and mammal-eating killer whales at scale of kilometers. For killer whales, prey detection is likely to be made acoustically (Barrett-Lennard 2000; Deecke et al. 2010; Morton 1990). Despite theoretical discussions of the acoustic arms race between marine mammal predators and prey (Tyack and Clark 2000), we lack source level data to parameterise models of the range at which a Pacific dolphin is audible to a mammal-eating killer whale, and *vice versa*. A component of this line of research would be to compare whether activity budgets of Pacific white-sided dolphins change when mammal-eating killer whales are nearby, even if the latter are not hunting (Lima and Dill 1990; Srinivasan et al. 2010). An opportunity to measure dolphin stress hormones in the presence and absence of killer whales may offer valuable insight into how pelagic dolphins respond to stressors, such as sonar, that animals may interpret in the context of predation risk, and improve our understanding of mechanisms for how stress in individuals can lead to population consequences (Hunt et al. 2012; Rolland et al. 2012).

Given the continuing increase in anthropogenic noise to the ocean, there is an urgent need to explore the extent to which human-generated noise could be disrupting acoustically mediated predator-prey interactions. Assuming the dolphin-killer whale predator-prey relationship evolved in a quiet ocean over previous millennia, anthropogenic noise may make it harder for prey to hear predator, or *vice versa* (Tyack 2008).

7.9 Conservation and management

The current study has advanced our knowledge considerably of the ecology of Pacific white-sided dolphins in BC. There are a number of future research directions that have arisen from these results, but three of them are particularly important for conservation and management.

7.9.1 Conservation status assessment of Pacific white-sided dolphins in Canada

Given other demands for assessment, Pacific white-sided dolphins have not been reassessed since 1989 (Stacey and Baird 1991). Although the species may never again become a sufficiently high conservation priority to cause the Committee on the Status of Endangered Wildlife In Canada (COSEWIC) to find funding to commission a status report, anyone can submit an unsolicited report to be considered when the Committee has time to review it³. COSEWIC status reports are supposed to be updated at least every 5 years but in practice they are most often triggered by the appearance of new information on status or threats.

7.9.2 Rethinking *Lagenorhynchus*

There is an imperative to assess the taxonomic status of the members of *Lagenorhynchus*, using genetic and acoustic data, to inform conservation priority-setting exercises (Harlin-Cognato 2009; LeDuc et al. 1999; May-Collado and Agnarsson 2006; Perrin et al. 2013). As one of only two species in the putative new genus *Sagmatius* (Chapter 1), Pacific white-sided dolphins may come to be seen as a species that deserves more scientific scrutiny than as one of six species in *Lagenorhynchus*. Such a shift in perception would be similar to what happened when Maui's dolphins were given the status of a subspecies (Slooten et al. 2006). When previously considered as a discrete population of Hector's dolphin, conservation status was known to be poor but the taxonomic reassessment caused a reconsideration of what the extinction of this unit might mean. Similarly, taxonomic recognition of the Australian snubfin dolphin (*Orcaella brevirostris*; Beasley et al. 2005) and the coastal form of *Sotalia* (*Sotalia guianensis*; Caballero et al. 2007) appears to have revitalised research efforts on these previously neglected dolphins. Perhaps reclassification of *Lagenorhynchus* into “new” species

³ http://www.cosewic.gc.ca/htmldocuments/Instructions_e.htm

will raise the profile of these dolphins that would allow us to take a closer look at their biology and conservation status.

7.9.3 Conservation beyond crisis: routine monitoring, new methods and approaches

One of the clearest lessons in the last few decades of marine mammal conservation is that we need to avoid crises and crisis-driven reactions, and instead move toward proactive management frameworks that will require a shift in our policies, regulations and incentives (Reynolds III 2005). In many cases, marine mammal conservation has involved a process of triage, such that only the populations at most imminent risk of extinction receive attention, until previously abundant stocks have declined to the point at which they can no longer be ignored. Although this priority-setting approach is understandable on one level, it has not been effective: it failed to prevent the extinction of baiji (*Lipotes vexillifer*; Turvey et al. 2007), and does not seem to be preventing the slide towards extinction of vaquita or Maui's dolphins (D'Agrosa et al. 2000; Slooten et al. 2006).

To maintain ecosystem function and ecosystem services, it is essential that we maintain the common species along with the rare ones (Gaston 2010; Gaston and Fuller 2008). Doing so requires a commitment to funding basic monitoring of abundance to ensure that there are no silent losses in biodiversity over time. In terms of single-species management, this means that we should avoid allowing populations to fall so low that their long-term viability becomes questionable (Gilpin and Soulé 1986)

In practical terms, this may mean funding coarse-scale, multi-species surveys periodically (e.g., Hammond et al. 2002; Hammond et al. 2013). These broad-scale surveys give abundance estimates that can be used to set sustainable limits to wildlife mortality incidental to human activities (e.g., fishery bycatch). As long as we keep human-caused mortality below those limits, it is unlikely that populations will ever become so heavily depleted that declines become irreversible. If these monitoring efforts suggest sufficient decline that a species warrants an endangered listing, either in terms of the small population or the declining population paradigm (Caughley 1994), it would warrant more precautionary measures and more focused research efforts designed to understand management tools that could promote recovery.

Canada is not alone in ignoring common species like Pacific white-sided dolphins. Many countries drive research funding priorities by endangered species status (Mooers et al. 2007; Taylor 2013; Taylor and Pinkus 2013). Most countries use science that becomes available on non-listed species, but many countries fail to fund routine monitoring to ensure that all species have an equal chance of being listed when necessary. Moving beyond crisis management would require Canada to shift from a passive (i.e., “best available science will be used”) mandate to one that actively funds research on all species (including data-deficient ones) and aims to provide abundance estimates every 5-10 years (e.g., Hammond et al. 1995; Hammond et al. 2002b; Moore 2011).

For regulatory frameworks that set minimum data standards on the use of abundance estimates in decision-making, there is an explicit recognition that lack of information should not be mistaken for a lack of threat (Moore 2011). In practice, commonness is often equated with “not at risk”, and species that are not at risk are a very low priority for research funding (Reynolds III 2005).

Some environmental foundations explicitly restrict research funding to the most critically endangered populations. But this approach, while understandable in one way, can create a situation in which declines of common species are never detected. Taking funds away from research on species at imminent risk of extinction is an untenable situation (Possingham 2001; Possingham et al. 2002). A tractable solution, consistent with good practice in conservation biology, would be to mandate certain minimum research standards (e.g., Moore 2011) that must be met for both common and rare species. Until then, in the absence of adequate funding, scientific advice to resource managers must explicitly account for uncertainty, so that human activities can be managed to prevent depletion of abundant marine mammal populations, rather than solely focusing on recovery of rare ones (Taylor et al. 2007b).

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{Photo Quality Grading Flow Chart}

1. **Fin image size:** does the fin take up >10% of the photo?

Yes



2. **Focus:** Is the fin in focus?

Yes



No →



No →



3. **Angle:** Is the fin angle...

Perpendicular (0°-5° angle)



Yes



Slight (5° -20° angle)



Oblique (20°-90° angle)



4. **Part of fin:** Is most of the fin showing?

Yes



No →



No →



5. **Lighting**



Appendix 1

Dolphin Distinctiveness Score Chart, v. 1 | August 11, 2013

D1



D1-Highly distinctive

Major nicks, notches that make the dolphin identifiable from **both** sides of the fin.

Features that appear constant and that are identifiable over a period of several years.

D2



D2- Moderately distinctive

Intermediate features such as a small nick, or many small nicks that are detectable from **both** sides.

D3



D3- Somewhat distinctive

Subtle features such as black scratches or other long-lasting distinguishing marks that are **only identifiable from one side**. This category does not include nicks and notches.

D4



D4-Not distinctive

Unmarked, generic, clean fin or with faint scratches that are not traceable over time.

Features that may be distinctive within an encounter or over several months, but not consistently identifiable over years.