

Estimating mark rate and its effect on the precision of
estimates of survival rate for a long-term study of Hector's
dolphins (*Cephalorhynchus hectori*) at
Banks Peninsula, NZ

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Hector's dolphin calf, Banks Peninsula, NZ

Abstract

An accurate and precise estimate of mark rate (the proportion of individuals with marks suitable for photo-ID) is essential for adjusting estimates of abundance from capture-recapture models to include the unmarked portion of the population. Capture-recapture analyses on marine mammals typically assume that mark rate is constant over time, but this may not be true if management has decreased the frequency of interactions with fishing gear (a known source of marks). Considering that mark rate of Hector's dolphins may have changed due to expanded set net protections around Banks Peninsula, this research had three primary aims: (1) to estimate an updated mark rate (for 2016), (2) to determine whether mark rate has changed since protection measures have expanded, and (3) to explore the implications of a low mark rate on estimating a key demographic parameter, survival rate. To determine the 2016 mark rate, several different mark rate estimation strategies were trialled and compared. Mark rate was then compared to an earlier period when set net restrictions were still relatively new (1992 – 1996). To investigate whether a decreasing mark rate affects precision of survival rates in Hector's dolphins, I simulated capture histories by resampling from the population's original capture history dataset. The comparison of different mark rate estimation strategies suggests that past studies underestimate the variance of mark rate by assuming simple random sampling of individuals, when in reality dolphins are encountered in groups (meaning observations are not truly independent). Whether a change in mark rate was detected between the two periods was method dependent. The frequentist method did not detect a statistically significant difference, but results from the Bayesian model indicated a 98% probability that the mark rate in 2016 (0.069, 95% HDI: 0.049 – 0.090) is lower than the 1992 – 1996 period (0.107, 95% HDI: 0.080 – 0.137). The simulation showed that although there was no evidence a lower mark rate would bias estimates of survival rate, it is likely to result in reduced precision. This may affect the ability to track population trends and determine whether current management is adequate.

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Chapter 1

General Introduction

Summary

Researchers commonly monitor wildlife using permanent natural marks that allow for individual identification. These natural marks can be photographed and matched to previous photos, in a technique known as photographic identification (photo-ID). Capture-recapture models can be applied to these data to estimate abundance and demographic parameters such as survival rate (Pollock et al. 1990). However, in many studies that use natural marks for individual identification, only a proportion of the population is sufficiently distinctive to be identified reliably. This proportion is known as the mark rate (Williams et al. 1993; Gormley et al. 2005). A limitation of all research applying photo-ID on a population with a mark rate of less than 100% is that information about the population as a whole is solely gained from the proportion of individuals that is marked. Additionally, abundance estimated from capture-recapture models must be scaled by the mark rate to include the unmarked portion of the population (Williams et al. 1993).

Long-term photo-ID studies only use obvious permanent marks, rather than small fin nicks or tooth rakes that can heal or be obscured by later injuries. The Hector's dolphins of Banks Peninsula have a relatively low mark rate compared to other dolphin populations. Gormley et al. (2005) estimated that the mark rate was 10.5%, while mark rates over 90% are recorded in some bottlenose dolphin populations (e.g. Nicholson et al. 2012; Mansur et al. 2012).

Since one of the ways marine mammals receive marks is through non-fatal encounters with fishing gear, fisheries restrictions in parts of Hector's dolphin habitat may have led to a decline in mark rate since it was last estimated in the 1990s. The central aims of this thesis are to estimate the current mark rate of the population, determine whether it has changed since

it was last estimated in the 1990s, and to explore the implications of a low or reduced mark rate on the ability to estimate a key demographic parameter, survival rate.

The study of marked individuals

Tagging or marking animals in order to study their ecology and behaviour has been occurring for hundreds of years. Lincoln (1921) recounts the first banded bird as a heron that was tracked between Turkey and Germany in 1710, and that birds were marked with other methods even earlier. Early studies usually relied on artificially marking individuals, a strategy still used today. Examples of artificial marks include bands on bird legs (e.g. Lincoln 1930), tags on other parts of the body such as ears (e.g. Hebeisen et al. 2008), branding (e.g. McMahon et al. 2006), or using paint (e.g. Higgins et al. 1988).

Most species have unique, stable natural markings and it is becoming more common to use photographs to track distinctive individuals through time. These marks may be individual variation in pigmentation patterns like the unique stripes on zebras (*Equus burchelli*, Foster et al. 2007) or spots on whale sharks (*Rhincodon typus*, Rowat et al. 2009), or they may be permanent scars resulting from injuries, for example tears in the ears of elephants (*Loxodonta africana*, Morley and van Aarde 2007). Photographs of unique markings make it possible to avoid physically catching and marking animals. This technique is known as photo-ID. Using natural markings is preferable to artificial marks because the tags themselves and the tagging process have been shown to change the animal's behaviour in many species (e.g. Hawaiian monk seal, *Neomonachus schauinslandi*, Henderson and Johanos 1988; bottlenose dolphin, *Tursiops truncatus*, Schneider and Baird 1998; Stellar sea lions, *Eumetopias jubatus*, Walker et al. 2010; humpback whales, *Megaptera novaeangliae*, Williamson et al. 2016).

Cetaceans have a long history of being identified by natural marks. The first cetaceans to be individually identified by natural marks on the

dorsal fin were killer whales (*Orcinus orca*) in Twofold Bay, Australia — resightings of individuals were recorded as early as the 1870s (Wellings 1944; Mitchell and Baker 1980; Würsig and Jefferson 1990). Reports of white-pigmented cetaceans have been recorded back to 1911 (harbour porpoise, *Phocoena phocoena*, McIntosh 1912), and Caldwell (1955) was the first to use a damaged dorsal fin to record the home range of an individual dolphin.

Routine photo-ID of cetaceans began with long term studies of killer whales (Bigg et al. 1987; Olesiuk et al. 1990), humpback whales (Katona and Whitehead 1981), and bottlenose dolphins (Würsig and Würsig 1977) in the 1970s (Würsig and Jefferson 1990). Photo-ID of whale and dolphin populations is usually based on distinctive pigmentation patterns or nicks on dorsal fins or flukes (e.g. Wilson et al. 1999; Calambokidis et al. 2009; Wells 2012), and it has become a cornerstone research method (see Hammond et al. 1990).

Capture-recapture analyses

In addition to investigating movement and home-range (e.g. Ingram and Rogan 2002; Calambokidis et al. 2009; Rayment et al. 2009), behaviour (e.g. Sargeant et al. 2005; Smolker et al. 2010; Deecke et al. 2011) and social structure (e.g. Whitehead et al. 1992; Slooten et al. 1993; Mann et al. 2012), photo-ID data can also be used in models to estimate population size and dynamics (e.g Hammond et al. 1990, Balmer et al. 2008, Corkrey et al. 2008). Models applied to data collected from marked individuals are called mark-recapture or capture-recapture analyses. Because photo-ID is based on photographing natural marks, interpretation of these data is usually termed capture-recapture, while interpretation of data from studies that physically capture and artificially mark animals are usually termed mark-recapture. Since this thesis relies exclusively on photo-ID methodology, the term capture-recapture will mainly be used.

Capture-recapture analyses provide a framework for answering some of the most basic questions in population biology, including: ‘how many individuals are there?’ and ‘is the population stable, increasing or declining?’ The earliest of these models, the Lincoln-Peterson model, derived abundance by marking a known number of individuals, releasing them to remix with the population, and then taking a second sample of known size to see how many marked individuals were recaptured (Petersen 1896; Lincoln 1930). Subsequent modifications to the Lincoln-Peterson model have accounted for unequal catchability of individuals (meaning some individuals are more likely to be marked or resighted than others), but an important assumption of these models is that the population is “closed”, meaning no births, deaths, immigration or emigration occur over the study period (see Otis et al. 1978; Pollock and Otto 1983; Pollock et al. 1990).

Jolly-Seber (Jolly 1965; Seber 1965) and Cormack-Jolly-Seber (CJS) models (Jolly 1963; Cormack 1964; Seber 1965) allow populations to be “open,” meaning recaptures can continue as births, deaths, and animal movements occur. CJS models and their subsequent development (see Seber 1986) have allowed additional parameters besides abundance to be estimated, including recruitment and survival rate (Pollock et al. 1990). Whereas meeting the assumption of a closed population often means data must be collected over a very short period, CJS models allow recaptures over many sampling periods. These data result in an extended capture history for each individual, representing when an individual was first seen (or “captured”) and when it was seen again (“recaptured”, see fig. 1.1 for an example). Analysis of this sequence of ‘1’s (meaning the animal was seen and photographed on that sampling occasion) and ‘0’s (meaning the individual was not photographed on that sampling occasion) allows researchers to estimate the mean survival rate of individuals in a population and potentially how it varies over time.

The ability to estimate survival rate with capture-recapture models has become a key objective in photo-ID research on marine mammals (e.g. Fearnbach et al. 2012; Gormley et al. 2012; Esteban et al. 2016). Adult

survival is typically a key driver of population trend in long-lived animals (Sæther and Bakke 2000). Additionally, survival can often be estimated with less bias and greater precision than abundance (Pollock et al. 1990). Therefore survival rates provide greater power to detect population trends (Taylor and Gerrodette 1993) partly because survival rates generated via capture-recapture are more robust to violations of assumptions than estimators of population size (Lebreton et al. 1992).

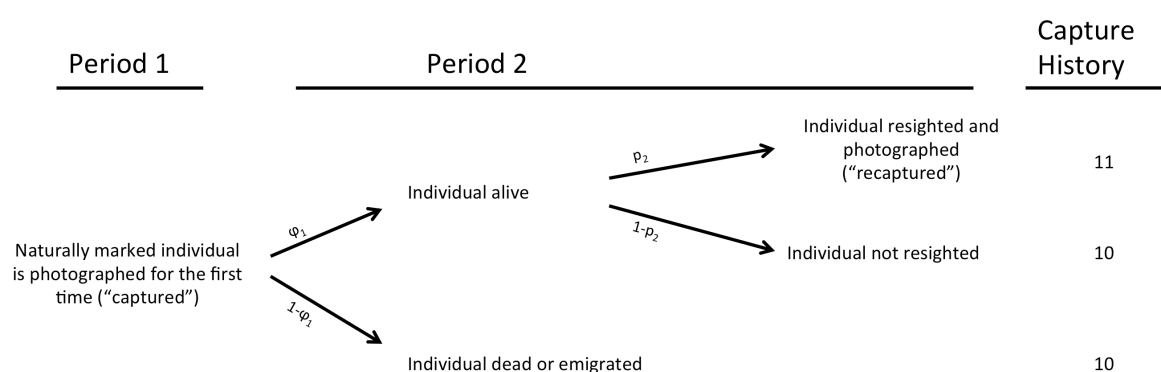


Figure 1.1: Diagram showing how capture histories are assigned under each capture-recapture scenario for two time periods. A “1” is assigned if the individual is captured or recaptured (i.e. photographed), and a “0” is given if the individual is not seen and photographed. Φ : survival rate; p : capture probability (probability that an individual is resighted/“recaptured”). Adapted from Williams et al. (2002).

The role of mark rate in analyses of marked individuals

Mark rate is defined as the proportion of the population with unique, identifiable marks (Gormley et al. 2005). Capture-recapture models estimate abundance and demographic parameters only for the marked portion of the population. Therefore, if the mark rate is less than 100%, an estimate of mark rate is necessary to scale up the estimate of abundance to include all individuals (e.g. Williams et al. 1993; Forcada & Aguilar 2000; Kuningas et al. 2013). In other words, in populations where not all individuals have unique marks, estimating abundance is a two-stage process: first, abundance of the marked population is estimated, and secondly, the estimate of mark rate is used to scale the estimate so that it applies to the entire population.

While in some marine mammal populations mark rate of adults is 100% (e.g. sperm whales, *Physeter macrocephalus*, Childerhouse et al. 1995; humpback whales, *Megaptera novaeangliae*, Barlow et al. 2011; southern right whales, *Eubalaena australis*, Carroll et al. 2011), in most others, especially dolphins, only a subset of the population is marked (e.g. Gormley et al. 2005; Nicholson et al. 2012; Tyne et al. 2014).

The first strategies for estimating mark rate were developed in the 1990s (e.g. Ballance 1990; Williams et al. 1993). Williams et al. (1993) estimated mark rate by taking the ratio of “marked” photos to total photos taken, while Ballance (1990) determined mark rate by dividing the number of identified individuals by the total known group size. Since group size is often difficult to determine accurately in the field, the use of photographs to estimate mark rate has become a more common strategy (see Wilson et al. 1999; Read et al. 2003; Gormley et al. 2005; Mansur et al. 2012).

Careful estimation of mark rate is necessary since both mark rate and its uncertainty affect final estimates of abundance determined through capture-recapture models (Urian et al. 2014). Strategies to improve the accuracy of estimates of mark rate include random photography (which means individuals are photographed regardless of whether they are marked or not) and measures to ensure photographic effort is distributed equally amongst groups of different sizes (e.g. Gormley et al. 2005; Nicholson et al. 2012).

An alternative to this two-stage approach to estimating abundance, which requires an estimate of mark rate, is the use of mark-resight models that can accommodate an unknown number of marked individuals (McClintock and White 2009; McClintock et al. 2009; McClintock and White 2012). Mark-resight models estimate abundance analogously to closed population abundance estimates using mark-recapture (McClintock and White 2012), but they have also expanded to include open demography via robust design, enabling abundance to also be estimated by modelling resighting probabilities (McClintock and White 2009; McClintock et al. 2009; McClintock and White 2012). New marks can be added between closed

periods, and models now allow for an unknown number of marked individuals and sampling with replacement (McClintock and White 2012).

To accommodate an unknown number of marked individuals, mark-resight models require the exact number of unmarked individuals observed during each sighting to be known. This requirement cannot be met for cetacean species that are typically found in very large groups, because it is difficult to determine group size and composition exactly. When group size is estimated “by eye” it is often underestimated (e.g. Mansur et al. 2012; Eguchi 2014). Additionally, if the project involves different observers, the accuracy of estimates of group size is likely to vary by observer. Issues with estimating group size may be partially resolved if using more analytical methods (e.g. Eguchi 2014), or if populations are found exclusively in very small or easily enumerated groups. For example, Ryan et al. (2011) used mark-resight models on an Irrawaddy dolphin (*Orcaella brevirostris*) population that was usually found in small groups, and they were able to differentiate all individuals within each group by subtle markings. Not only is it more difficult to estimate group size for large groups, however, but it also becomes more difficult to identify all marked individuals present. Thus, using mark-resight models may result in an overestimate of the number of unmarked individuals present when group sizes are large (Mansur et al. 2012).

Use of mark-resight models that can accommodate an unknown number of marked individuals may provide an alternative framework to the estimation of mark rate in some species. However, such models are not applicable to most cetacean populations. Instead, use of the two-stage approach to estimating abundance remains much more common (see Hammond et al. 1990; Urian et al. 2014).

Besides estimates of abundance, estimating proportions of marked individuals in a population may also be useful for other purposes. For example, researchers have documented the proportion of different types of marks to investigate the incidence of interactions with fishing gear (Baird and Gorgone 2005; Kiszka et al. 2008; Baird et al. 2014), boat strike (Wells and Scott 1997), shark predation (Corkeron et al. 1987; Heithaus 2001) and

aggressive social interactions (Marley et al. 2013). Baird et al. (2014) estimated the proportion of false killer whales (*Pseudorca crassidens*) with marks attributable to non-fatal encounters with fishing gear, which was found to differ between populations and by sex. Since marks can be attributable to social interactions, predators, or anthropogenic impacts, the proportion of marks of different origin may provide evidence for the relative significance of different threats in the population (e.g. Kügler and Orbach 2014).

Photo-ID studies on Hector’s dolphins and management history

Hector’s dolphins (*Cephalorhynchus hectori*) are an endemic New Zealand species. There are at least four genetically distinct populations, one in the North Island (the subspecies *C. hectori maui*), and three in the South Island (east, west, and south coasts) (Pichler et al. 1998). At just 1.4 m in length, *C. hectori* is the smallest dolphin in the world (Slooten & Dawson 1994). It is also one of the rarest dolphin species – the South Island populations are classified as endangered, while *C. hectori maui* is classified as critically endangered (Reeves et al. 2013a; Reeves et al. 2013b).

Photo-ID studies on Hector’s dolphins began at Banks Peninsula, New Zealand in 1984 (Slooten et al. 1992), with these surveys continuing until the present. Pigmentation patterns, nicks on the dorsal fin, and scars, are long-lasting markings used to tell individuals apart (fig. 1.2, Slooten et al. 1992).



Figure 1.2: Identifying characteristics, or “marks” on Hector’s dolphins. A: small nicks on the dorsal fin; B: pigmentation patterns; C: multiple nicks on the dorsal fin and scarring.

Photo-ID studies on Hector's dolphins have enabled analyses of individual movements and home range (Rayment et al. 2009), behaviour (Slooten 1994), and social structure (Slooten et al. 1993). For example, photo-ID research has shown that Hector's dolphins have extremely small home ranges. Average home ranges are less than 50 km and no one individual has been sighted around the whole of Banks Peninsula (Slooten and Dawson 1994; Rayment et al. 2009). Studies of associations between individuals show they have a fluid social structure and a promiscuous mating system (Slooten et al. 1993). Capture-recapture analyses of photo-ID data have been used to estimate abundance (Gormley et al. 2005), adult survival (Slooten et al. 1992; Cameron et al. 1999; Gormley et al. 2012), reproductive rate (Gormley 2010) and the impact of conservation management (Gormley et al. 2012). Indeed, research based on photo-ID has played a crucial role in the conservation management of this species (Dawson and Slooten 1993).

In response to unsustainable rates of bycatch in set net fisheries, the New Zealand government established the Banks Peninsula Marine Mammal Sanctuary in 1988 (Dawson and Slooten 1993). The sanctuary banned set netting from Sumner Head to the Rakaia River out to 4 nautical miles (see fig. 1.3). Since the sanctuary's establishment, survival rates of Hector's dolphins have increased (Gormley et al. 2012). Presumably, this change is driven by Hector's dolphins encountering set nets less often.

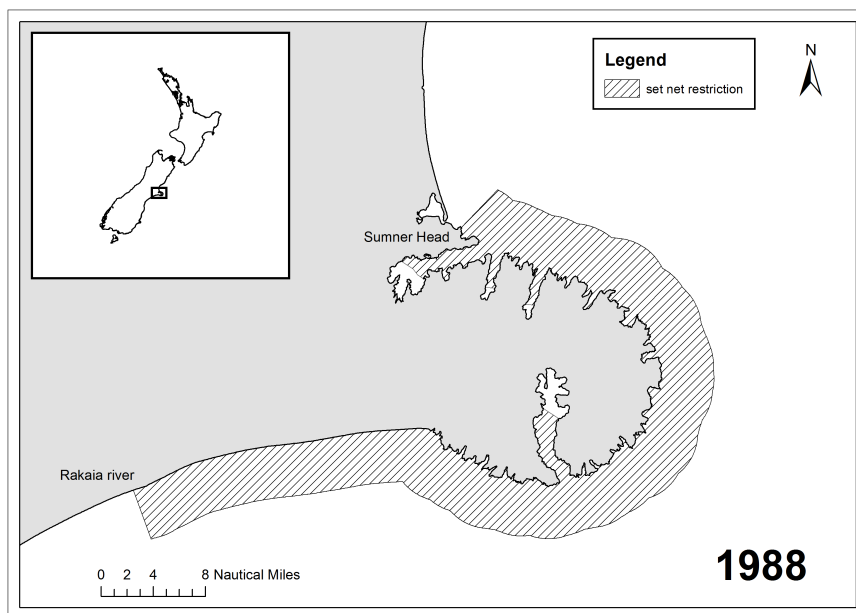


Figure 1.3: Location and extent of the Banks Peninsula Marine Mammal Sanctuary’s set net restriction when first established in 1988.

Hector’s dolphins receive marks in a variety of ways, including interactions with conspecifics (e.g. play or aggression) and predators (e.g. shark bites). However, some kinds of marks seen on Hector’s dolphins match those seen on individuals killed by entanglement in fishing gear (e.g. sharp line cuts in the dorsal fin, pectoral fins and tail flukes, fig. 1.4). Therefore, a decline in non-fatal fisheries interactions (e.g. temporary entanglement) may lead to a decline in mark rate.

Are markings on Hector’s dolphins becoming less common?

Gormley et al. (2005) estimated the first mark rate for the population of Hector’s dolphins at Banks Peninsula; 10.46% (SE=0.0057) of dolphins had features suitable for photo-ID. This mark rate was determined from methodology using random photography during the period 1992 – 1996. While mark rates are normally assumed to be relatively stable (e.g. Gormley et al. 2005; Reisinger and Karczmarski 2009; Nicholson et al. 2012; Pusineri et al. 2014), the changing environment of Hector’s dolphins (at least partly as a result of the marine mammal sanctuary) may be leading to a decline in

mark rate over time.

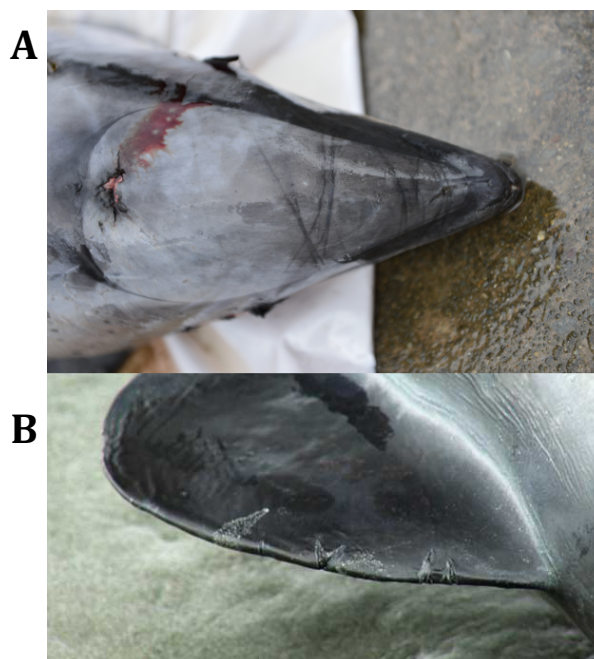


Figure 1.4 Example of parts of the body of stranded Hector's dolphins with signs of set net entanglement. 'A' shows a dorsal view of the head, while 'B' shows a lateral view of the leading edge of the dorsal fin. Depressions caused by net lines will lead to tears/nicks if severe enough.

To investigate the possibility of a decline in mark rate, an updated estimate of mark rate is needed. If analyses show a decline, this may provide additional evidence that Hector's dolphins are encountering fishing gear less frequently, thus providing further evidence for the efficacy of the sanctuary. The downside, however, is that a lowered mark rate may result in reduced precision in estimation of survival rate, a key demographic parameter that has been an important objective of the long-term research programme at Banks Peninsula (Slooten et al. 1992; Cameron et al. 1999; Gormley et al. 2012). Lower precision is expected because fewer marked individuals lead to a smaller "sampling pool" from which to estimate demographic parameters using capture-recapture models. This could mean that the very measures put in place to protect the species may make it more difficult to track the population's progress. Consequently, the Hector's dolphins at Banks

Peninsula may provide insight into a little explored issue in capture-recapture: the effect of mark rate on precision of estimates of survival rate.

Thesis objectives

The three data chapters of this thesis aim to answer three core questions:

- (i) What is the current mark rate of the Hector's dolphins at Banks Peninsula?

Chapter 2 provides updated estimates of mark rate for the population, and compares four different strategies for estimating mark rate and its precision. In addition to providing recommendations for best practice when estimating mark rate, emphasis is placed on the importance of correctly estimating the variance of mark rate so that it may be propagated into the variance of the final abundance estimate.

- (ii) Has mark rate changed since the last estimate in the 1990s?

Chapter 3 investigates whether mark rate has changed, by comparing the new (2016) estimate of mark rate with the data collected on mark rate in the 1990s (Gormley et al. 2005). Chapter 3 uses both hierarchical Bayesian modelling (see Eguchi 2014), and confidence interval approaches to detect whether the two estimates are significantly different.

- (iii) What are the consequences for the precision of estimates of survival rate when the mark rate of the population is artificially lowered?

To investigate how mark rate affects precision of survival rates in Hector's dolphins, Chapter 4 adopts a resampling approach. Instead of simulating data, a procedure was developed in which real capture histories are resampled to represent different mark rates.

Bootstrapped estimates of survival rate and its associated precision were produced for each mark rate using a Cormack-Jolly-Seber model.

Chapter 2

Estimating mark rate of Hector's dolphins: a comparison of different methods

Introduction

Accurate and precise estimation of mark rate is an essential step in estimating abundance using photo-ID methods. The last estimate of mark rate for Hector's dolphins at Banks Peninsula, 0.105 (SE=0.0057), was completed by Gormley et al. (2005) during the period 1992 – 1996. This mark rate was used to calculate an abundance estimate in 1996, but a more current estimate of mark rate is needed to produce an updated abundance estimate for this population. As discussed in Chapter 1, evolving protection measures around Banks Peninsula have the potential to affect mark rate by reducing nonfatal encounters with fishing gear, which is a potential source of some of the marks observed on Hector's dolphins. Therefore, it cannot be assumed that mark rate is the same as the estimate for 1992 – 1996. While Chapter 3 aims to detect whether a change has occurred, this chapter aims to estimate the current mark rate by trialling several different methods.

Ballance (1990) first determined mark rate of bottlenose dolphins (*Tursiops truncatus*) by dividing the number of identified individuals in a group by the total group size. This approach has continued to be used in several different populations (e.g. Silva et al. 2009; Cantor et al. 2012; and Kuningas et al. 2013). The success of this technique relies on an accurate estimate of group size, which is often difficult in the field. This problem may be mitigated by using the temporary markings present in some populations to keep track of all individuals within a group. For example, Wilson et al. (1999) used temporary markings (e.g. tooth rakes on the fin) to determine the number of unique individuals photographed in each group. Mark rate was determined by dividing the number of individuals with permanent, distinct markings by the total number of individuals observed for each survey, and then summing the mark rate for each survey over the field season (Wilson et

al. 1999). Use of this technique has continued for populations where all individuals in a group may be at least temporarily identifiable (e.g. Minton et al. 2013 and Alves et al. 2014). Since Hector's dolphins at Banks Peninsula have a relatively low rate of temporary markings, the methods in Wilson et al. (1999) are not appropriate.

Around the same time as Ballance (1990), Williams et al. (1993) estimated mark rate from a large sample of photographs taken of individual dolphins irrespective of their marking status (an approach later termed "random photography"). They then divided the number of high quality photographs showing identifiable individuals by the total number of high quality photos within a field season. This strategy does not require an estimate of group size or the number of identifiable individuals in a sighting, so it is especially useful for populations in which individuals lack temporary markings or are commonly found in large groups. The strategy of determining mark rate by using the ratio of "marked" photos to total photos is now widely used (e.g. Read et al. 2003; Reisinger & Karczmarski 2009; Tezanos-Pinto et al. 2013, and Palmer et al. 2014). The last mark rate estimate for Hector's dolphins (Gormley et al. 2005) expanded on the Williams et al. (1993) method by specifying a field protocol of attempting to obtain three times as many high quality photos per group as the estimated group size, in order to increase the chance of capturing a photo of every individual.

Eguchi (2014) built on the approach of randomly photographing individuals in each group by estimating mark rate through hierarchical Bayesian modelling. Although this technique has not yet been used for scaling up a mark-recapture abundance estimate, it provides a promising way of estimating both mark rate and its uncertainty. Except for Eguchi (2014), published techniques for estimating the variance of mark rate assume simple random sampling of individuals, when in reality individuals are usually encountered in groups. This actually constitutes a form of cluster sampling, whereby dolphins are photographed by random sampling within *groups*, rather than the entirety of the population.

In addition to the Bayesian model proposed by Eguchi (2014), there are several other options for estimating the variance of a proportion taken from groups. One option is to use the variance estimator in Cochran (1977, p. 66), which gives the variance for clusters of unequal sizes. This variance estimator is an approximation and can underestimate variance when sample sizes are low (Cochran 1977). An alternative option is to obtain an estimate of precision by bootstrapping (e.g. Nelson 2014).

Despite the importance of estimating mark rate rigorously, no studies to date have critiqued the current methods used and offered guidance for future studies. Estimating an updated mark rate for Hector's dolphins provides an opportunity to critically assess several different methods. Thus, the primary aim of this chapter was to compare four different methods for estimating mark rate and its precision (table 2.1). While the first method, from here on referred to as the "Simple Random Sample," is already a commonly used method for estimating mark rate (e.g. Williams et al. 1993, Gormley et al. 2005), the Bayesian approach by Eguchi (2014) (here called Simple Random Cluster Sample – Bayes) was only recently developed and has not been used by other studies yet. These two methods are also compared to two new approaches for estimating the precision of mark rate — using the formula for variance for clusters of unequal sizes (Simple Random Cluster Sample, Cochran 1977 p. 66) and bootstrapping (Simple Random Cluster Sample – Bootstrap).

Since the precision of mark rate should be propagated into the final abundance estimate, minimising uncertainty of the mark rate estimate is also of interest. How many photographs or groups need to be sampled for a robust, precise estimate? To explore the effect of different amounts of sampling, the datasets for mark rate collected in 1992 – 1996, as well as 2016, were subsampled and compared. Ideal sampling procedures are also discussed, with the aim of reducing bias and increasing precision in future studies.

Methods

Random photography and field methods

Photography sessions for estimating mark rate took place alongside photo-ID surveys. These surveys take place from small (5 – 6.6 m) outboard powered boats at Banks Peninsula between Rakaia River and Sumner Head. Open coasts were surveyed via a coastal strip survey method using a transect approximately 400 m offshore, while a standard zig-zag pattern was used inside Akaroa Harbour (Slooten et al. 1992). During the strip transect, larger bays were also entered to look for dolphins. Surveys were only conducted in good sighting conditions, with Beaufort sea state of 3 or less (wind speed <10 knots) and a swell of less than 2 meters. When dolphins were sighted, a GPS-linked onboard computer (HP200LX) running custom-written software was used to record the location and time of the sighting, and to allow input of data on group size, number of calves, and any other notes (e.g. behaviour). For a detailed description of survey protocol see Slooten et al. (1992).

To estimate mark rate, groups of dolphins were randomly photographed between January and March 2016 using a Nikon D3 digital camera and Nikkor 80-200 f2.8 lens. As in Eguchi (2014), the terms “photos” and “photographs” will represent photographs taken in the field, while the term “images” will be used to refer to photos of high enough quality to be used in photo-ID analysis. Photos were taken “randomly”— meaning that nearby dolphins were photographed whether or not they were obviously marked. To standardise effort and increase the chance of photographing all individuals, the photographer (L. Wickman) attempted to obtain three times as many images as the estimated group size. If group size or composition changed drastically during a photography session, or if the photographer did not think she achieved enough photographic coverage, the group was not included in the estimation of mark rate. This field protocol was modelled after the method used by Gormley et al. (2005) so that the two estimates could be compared.

Photos obtained from random photography were screened using the same techniques for the long-term photo-identification programme. Photographs were only retained if the dorsal fin was completely in focus, completely visible, and perpendicular to the camera. If multiple photos were taken of an individual's surfacing event, only one photo was chosen. Marked dolphins were classified into three categories (see Slooten et al. 1992). Category 3 contains individuals with subtle markings that may be missed in the field and may be difficult to identify in photographs. Category 2 includes individuals with obvious marks that are unlikely to be mis-identified from good quality images but may be missed in the field. Lastly, Category 1 contains individuals with obvious marks unlikely to be missed in the field or in image analysis. For this study, only individuals with Category 1 and 2 marks were considered to contribute to the mark rate.

Estimating mark rate

Four different methods of estimating mark rate were compared: (1) Simple Random Sample, (2) Simple Random Cluster Sample, (3) Simple Random Cluster Sample – Bootstrap, and (4) Simple Random Cluster Sample – Bayes. “Simple Random Sample” versus “Simple Random Cluster Sample” refers to the assumption about what sampling technique random photography of dolphin groups constitutes.

Traditionally, mark rate is estimated under the assumption of simple random sampling (SRS, e.g. Gormley et al. 2005). SRS assumes that selection of one individual (e.g. photographing one individual) does not influence the selection of another (therefore, each photograph, or “sample” is independent). Random photography of *groups* of animals, however, should actually be interpreted as simple random cluster sampling (SRCS). In SRCS the probability of photographing an individual is based on encountering and photographing the group it is found in, not the individual itself. Individuals within groups may be more similar, so assuming SRS can result in an underestimation of precision. Therefore, SRS represents a flawed assumption around the data structure, while the other three methodologies that assume

SRCS assume the correct data structure but use different estimation methodologies for variance or the parameter itself (table 2.1).

Table 2.1: Summary of similarities and differences between the four methods used for estimating mark rate and its variance.

	Data structure assumption	Parameter estimation	Variance estimation
SRS	Each image is a random sample of the population	Mark rate estimated by combining all images from all groups	“SRS” formula for a proportion
SRCS	Each image is a random sample within a <i>group</i>	Mark rate estimated by combining all images from all groups	“SRCS” formula for a proportion
SRCS–Bootstrap	Each image is a random sample within a <i>group</i>	Mark rate estimated by combining all images from all groups	cluster bootstrap
SRSC–Bayes	Each image is a random sample within a <i>group</i>	Mark rate is estimated for each group, which is linked to the population-level average	Posterior distribution of the population level mark rate

(1) SRS

Assuming simple random sampling (SRS), mark rate was estimated as the number of images showing individuals with category 1 and 2 marks, divided by the total number of images acquired, as follows:

$$\hat{\theta} = \frac{\sum_{i=1}^k I_i}{k} \tag{2.1}$$

where k =the number of photography periods (in this instance one year), I_i =the number of images showing category 1 and 2 marks for the i^{th}

photography period, and T_i =the total number of images taken for the i^{th} photography period (Gormley et al. 2005).

Precision of the proportion of marked individuals is estimated as follows:

$$\widehat{var}(\hat{\theta}) = \left(\sum_{i=1}^k \frac{\hat{\theta}_i(1-\hat{\theta}_i)}{T_i} \right) / k^2 \quad (2.2)$$

where k is the number of photography periods (in this instance one year), $\hat{\theta}_i$ is the mark rate during the i^{th} photography period, and T_i is the number of images taken in the i^{th} photography period.

(2) SRCS

When assuming simple random cluster sampling (SRCS), the number of images showing marked individuals and the total number of images for each group are noted. This process creates a set of ordered pairs as so:

Number images with marks	X ₁	X ₂	...	X _n
Total number of images	M ₁	M ₂	...	M _n

This allows a mark rate of $\frac{x_g}{M_g}$ to be computed for each group, and the average of the mark rate of each group could be estimated. However, the average of all of these groups' mark rates is not used as the mark rate of the population, as each division of $\frac{x_g}{M_g}$ produces some bias. A more accurate estimate of the mark rate of the population is achieved with as few divisions as possible (Cochran 1977). Therefore, the least biased estimator of a population ratio is simply $\frac{\sum_g^n x_g}{\sum_g^n M_g}$, which is identical to equation 2.1.

Cochran (1977, p. 66) gives the following equation for estimating variance of proportions from clusters of unequal sizes:

$$\widehat{var}(\hat{\theta}) = \frac{N-n}{N} * \frac{\sum_{g=1}^n (M_g/\bar{M})^2 (\hat{\theta}_g - \hat{\theta})^2}{n(n-1)} \quad (2.3)$$

where N =total number of dolphin groups(clusters) available for sampling, n =the number of groups photographed, M_g =the size of the g^{th} cluster

(number of images from the group), \bar{M} =the average size of all sampled clusters (groups), $\hat{\theta}_g$ =the mark rate within the g^{th} cluster (group), and $\hat{\theta}$ =the mark rate of all clusters (groups) combined.

If the ratio of the number of clusters sampled to the total number of clusters available is very large, the $\frac{N-n}{N}$ term at the beginning of equation 2.3 can be dropped. Hector's dolphins have a fission fusion social structure (Slooten et al. 1993 and Bräger 1999), meaning that group membership varies often. Therefore, it was assumed that the number of possible unique group structures, or clusters, was so large compared to the number sampled that this term could be dropped. Equation 2.3 is now then approximated as:

$$\widehat{var}(\hat{\theta}) = \frac{\sum_{g=1}^n (M_g/\bar{M})^2 (\hat{\theta}_g - \hat{\theta})^2}{n(n-1)} \quad (2.4)$$

(3) SRCS–bootstrap

The SRCS–bootstrap method uses the same estimator for mark rate as the SRCS method but provides an alternative to estimating the variance of mark rate ($\widehat{var}(\hat{\theta})$). To bootstrap the variance of mark rate, a short script was written in R (R Core Team 2015) to sample, with replacement, each “cluster” of images taken of each group. Rather than sample the individual images within clusters, resampling was done on the clusters themselves. This method, known as the “cluster bootstrap,” is considered to give reliable variance estimates for clustered data (Field and Welsh 2007). For the cluster bootstrap, n random samples were taken (again, n =the total number of clusters, or groups, originally photographed) and the mark rate estimated as the ratio of images showing marks to total images acquired (eq. 2.1). This process was repeated 10,000 times. The 95% confidence intervals were taken as the 250th and 9,750th estimates of mark rate sorted in ascending order. The standard error was calculated as the standard deviation of all 10,000 bootstrap resampled estimates of mark rate. Since the percentile bootstrap is known to be unreliable if the sampling distribution is

asymmetric (Efron 1982), the sampling distribution of the mark rate was plotted to check for normality (Appendix 2.1).

(4) *SRCS–Bayes*

An alternative to frequentist methods for estimating mark rate and its variance under the assumption of SRCS (methods 2 and 3) was developed by Eguchi (2014). This Bayesian hierarchical model also has the ability to estimate group size by estimating the number of identifiable individuals in a group and then dividing this estimate by the group’s mark rate. Only the portion of the model that estimates mark rate will be described here, however, since mark rate is the only parameter of interest. Full code for the analysis can be found in Appendix 2.1.

Similarly to the other three methods, inferences about the mark rate are taken from the number of high-quality images showing marked individuals, as well as the total number of high-quality images taken. Except in this case, data is input for each dolphin group, so that the user inputs the total number of images with marks for the g^{th} group (K_g), and the total number of images acquired for the g^{th} group (T_g). A key difference between the SRCS–Bayes method and the other three methods is that mark rate is estimated separately for each group and is linked to an overall “average” population-level mark rate. The SRS, SRCS, SRCS–bootstrap methods, in contrast, only estimate one, overall mark rate by combining the images from all groups.

Figure 2.1 illustrates the hierarchical relationship of parameters for the portion of the model that deals with mark rate. The data (K_g and T_g) are used by the hierarchical model to come up with credible values for θ_g , the mark rate of each group. This is done by modelling the number of K_g marked images out of T_g images with a binomial distribution with probability θ_g ($K_g \sim Bin(\theta_g, T_g)$). In other words, the mark rate of each group (θ_g) determines the probability of obtaining K_g “marked” images out of T_g total images.

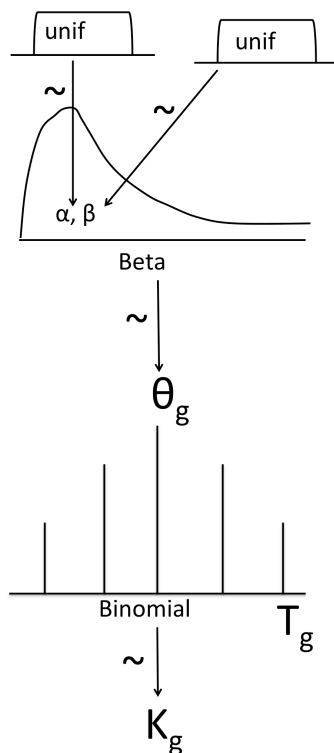


Figure 2.1: Hierarchical diagram of the Bayesian model that estimates the mark rate of each group (SRCS–Bayes). The downward arrows denote how higher-level variables generate lower-level variables. The tilde (\sim) beside each arrow indicates that a lower-level variable is generated probabilistically. The diagram should be read from the bottom up (e.g. K_g comes from a binomial distribution with a maximum value of T_g and probability θ_g). Diagram is designed in the style of Kruschke (2011).

In Bayesian data analysis, a prior distribution is required for each estimated parameter. The parameter θ_g has a beta prior distribution ($\theta_g \sim \text{Beta}(\alpha, \beta)$), which makes its value dependent on the estimated values of the α and β parameters that describe the shape of this distribution. The α and β parameters were given noninformative uniform prior distribution ($\alpha \sim U(0, 100)$, $\beta \sim U(0, 100)$). This non-committal prior represents vague prior beliefs about α and β and ensures the results for the estimated parameters are data-driven (Kruschke 2011).

As the number of groups in the dataset increase, more information on α and β becomes available. Since the beta distribution described by α and β describes the distribution of group-specific mark rates (θ_g), the population-level mark rate (θ) is taken as the mean of this distribution. Thus, the mean

population-level mark rate (θ) is estimated using the formula $\frac{\alpha}{\alpha + \beta}$ (i.e. the mean of the beta distribution).

The hierarchical Bayesian model was run in OpenBUGS (Lunn et al. 2009) via program R2OpenBUGSS (Sturtz et al. 2005) in program R (R Core Team 2015). For each model run, four independent Markov chains of 60,000 steps each were initiated at specified random values. The first 10,000 steps of each chain were considered “burn-in” samples and were not used for making inferences about the parameters. Therefore, inferences were made from 200,000 samples (4 chains of 50,000 samples each). Convergence of each of the chains was assessed visually and via the Rhat statistic (Rhat < 1.02 for all parameters) (Gelman et al. 2003). The population level mark rate (θ) was analysed by its mean and 95% highest density interval (HDI), which describes where 95% of estimates from the posterior distribution lie. Posterior distributions were plotted using the plotPost.R function, taken from Kruschke (2011).

Investigation into different sampling schemes

The 2016 random photography dataset, as well as an additional dataset from 1992 – 1996 (from Gormley et al. 2005), were analysed to determine the relative importance of the number of groups sampled and number of images per group. The 2016 random photography sessions followed the same field protocols as the earlier sessions, with a few specific exceptions. The 1992 – 1996 sessions were carried out by a different photographer (S. Dawson), separately from the routine photo-ID surveys.

Recall that for each group included in the random photography dataset, group size was estimated and the photographer attempted to obtain three times as many images as the estimated group size. Here, this “three times” multiplier will be referred to as the sampling intensity. An estimate of sampling intensity is available for each dolphin group sampled by dividing the number of images obtained by the estimate of group size. When the photos are processed the actual number of suitable photos (images) may be

above or below the target value of three times the group size. Photography sessions that do not meet a certain threshold for sampling intensity (e.g. below one times as many images as estimated group size) can be excluded from the dataset and mark rate re-estimated to see how precision is affected. Changing the sampling intensity threshold affects the number of groups included in the dataset. Therefore, the contribution of the number of sampled groups to precision can also be compared between different sampling intensities. The two datasets (2016 and 1992 – 1996) were analysed separately, in case mark rate differed between the two periods.

For the 2016 dataset, the estimate of mark rate and its precision was bootstrapped for three different scenarios: (1) all groups regardless of sampling intensity, (2) groups where sampling intensity was ≥ 1.0 , and (3) groups where sampling intensity was ≥ 1.5 .

For the 1992 – 1996 dataset, mark rate and its precision was bootstrapped for five different scenarios: (1) all groups, regardless of sampling intensity, (2) groups where sampling intensity was ≥ 1.0 , (3) groups where the sampling intensity was ≥ 2.0 , (4) groups where sampling intensity was ≥ 2.5 , or (5) groups where sampling intensity was ≥ 3.0 .

These scenarios were based on the available sampling intensities for each dataset. Lower sampling intensities were trialled for the 2016 dataset because overall, lower sampling intensity was achieved for that year (fewer photos that were suitably sharp, close and at a right angle were available for each group). For each scenario, the precision of mark rate was estimated using the nonparametric “cluster bootstrap” (identical to method 3, the SRCS-bootstrap).

Groups were resampled 10,000 times, allowing for estimates of mark rate and its precision to be bootstrapped for each sampling scheme. Resampling was done separately on the 1992 – 1996 and 2016 random photography datasets. For each scenario, a mean sampling intensity value was estimated to allow easier interpretation of the effect of sampling intensity on precision between the two datasets.

Results

Estimating mark rate

A total of 1,133 images were obtained from random photography of 163 groups of dolphins photographed in 2016. Sampling intensity varied between groups, with a mean of 1.06 (CV=0.51) times as many acceptable images as the estimated group size.

Producing an estimate of mark rate by combining all images (the SRS, SRCS, SRCS–bootstrap methods) produced a mark rate of 0.065. Assuming simple random sampling (SRS), this mark rate estimate had a SE=0.0073 and a 95% confidence interval of 0.051 - 0.078 (table 2.2). Using the SRCS method, precision was slightly lower (SE=0.0093; 95% confidence interval = 0.047 – 0.084). The SRCS–bootstrap method yielded a 95% confidence interval of 0.048 – 0.085 and SE=0.0094.

The SRCS–Bayes method (Eguchi 2014) yielded a population level mean mark rate of 0.069 and a 95% highest density interval (HDI) of 0.049–0.090 (fig. 2.2).

Estimated precision was greatest using the inappropriate SRS method and lowest using the SRCS–Bayes method (table 2.2). The SRCS–Bayes method yielded similar, although lower, precision to the estimates produced under frequentist, cluster sampling assumptions (SRCS and SRCS–bootstrap, table 2.2). The distribution of group-specific mark rates (θ_g) was skewed towards 0, rather than being normally distributed around the estimate of mark rate for either method (fig. 2.3)

Table 2.2: Summary of results for four different strategies for estimating mark rate precision.

Method	Mark rate	SE	95% CI	95% HDI
SRS	0.065	0.0073	0.051–0.078	
SRCS		0.0093	0.047–0.084	
SRCS–bootstrap		0.0094	0.048–0.085	
SRCS–Bayes	0.069	SD=0.0105		0.049–0.090

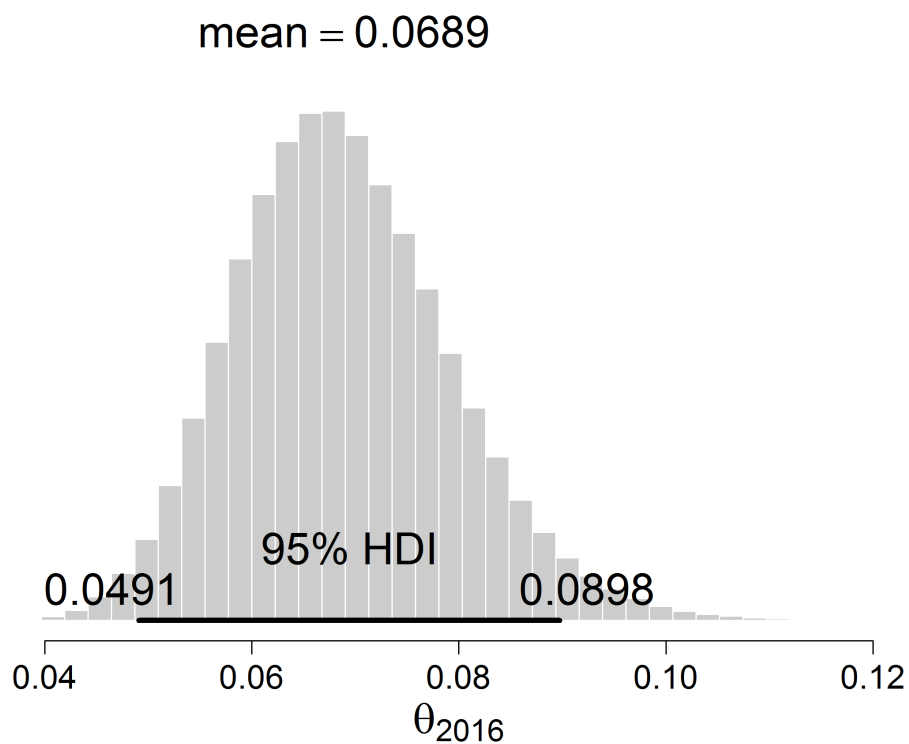


Figure 2.2: Posterior distribution of the population level proportion of marked individuals (mark rate) generated using the SRCS-Bayes method for 2016. The 95% HDI describes where the most likely 95% of estimates from the posterior distribution lie.

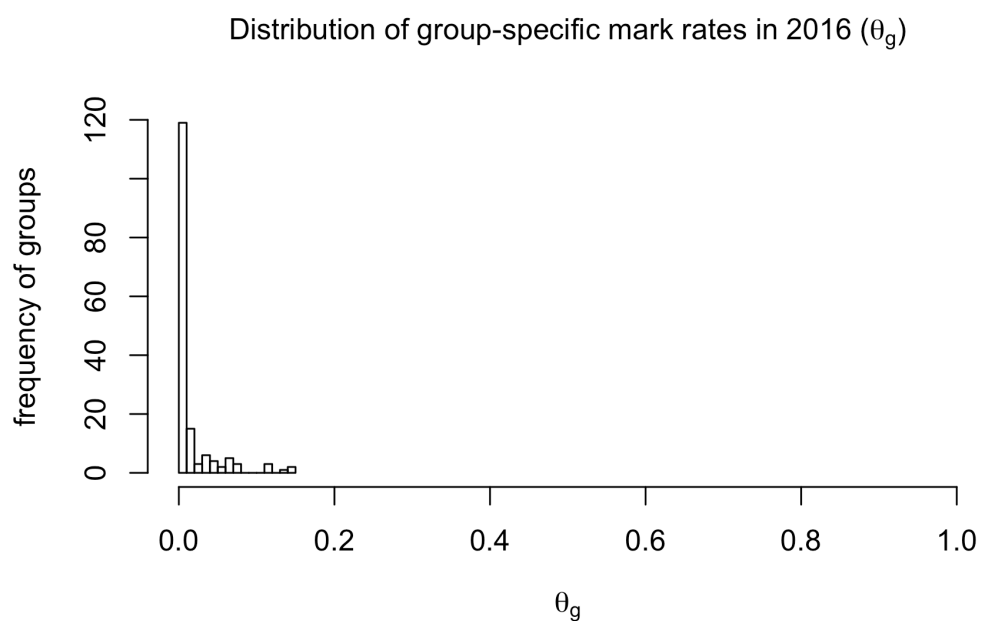


Figure 2.3: Distribution of the mark rate of each group photographed for 2016.

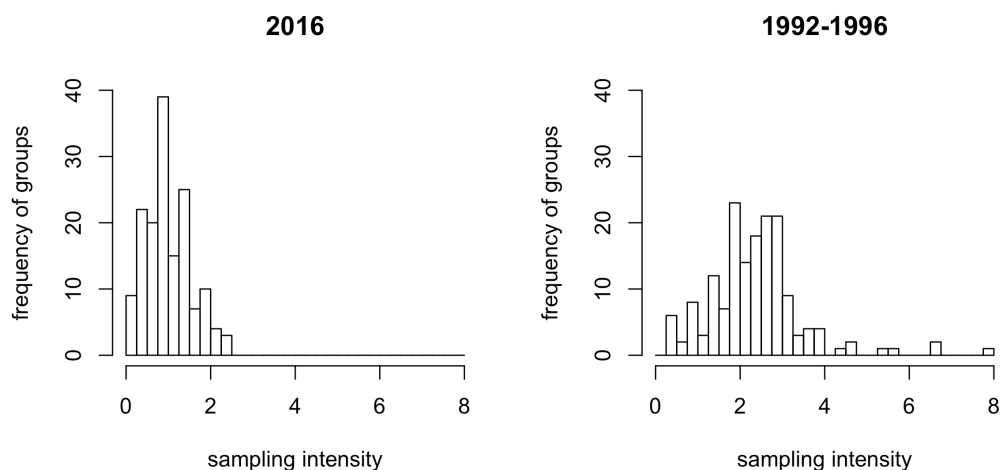


Figure 2.4: Distribution of sampling intensities for the 2016 and 1992-1996 datasets. Sampling intensity is the number of images obtained divided by the estimate of group size.

Investigation into different sampling schemes

The 1992 – 1996 dataset contained higher sampling intensity (mean of 2.43 times as many images as estimated group size, $CV=0.46$) than the 2016 dataset (mean of 1.06 times as many images as estimated group size, $CV=0.51$) (fig. 2.4). Coincidentally, both datasets contained the same number of groups sampled (163), which allowed the relative contribution of sampling intensity to number of groups sampled to be easily compared.

As must happen, the mean sampling intensity for the dataset increased as the threshold value increased (table 2.3). Choosing higher threshold values for sampling intensity reduced the number of dolphin groups included in the dataset and increased the CV (i.e. the estimate becomes less precise) in both datasets (table 2.3). The point estimate of mark rate changed little until fewer than fifty groups were sampled, and all estimates were within the confidence interval for mark rate when all groups were included (table 2.3).

Table 2.3: Total number of groups, mark rate, and CV after excluding groups from each dataset that do not meet a certain sampling intensity threshold.

Dataset	Threshold value for sampling intensity	Mean sampling intensity	Total number of groups	Total number of images	Mark rate	Bootstrapped CV of mark rate
2016	All groups included	1.06	163	1133	0.065	0.14
2016	1	1.42	89	729	0.063	0.19
2016	1.5	1.82	36	297	0.053	0.35
1992-1996	all groups included	2.43	163	2921	0.10	0.11
1992-1996	1	2.53	155	2893	0.10	0.11
1992-1996	2	2.88	117	2484	0.10	0.12
1992-1996	2.5	3.23	81	1858	0.098	0.15
1992-1996	3	3.77	41	961	0.12	0.21

The bootstrapped CV of mark rate decreased (i.e. the estimate became more precise) as the number of groups sampled increased for both datasets (fig. 2.5). This pattern held true despite a lower mean sampling intensity when more groups were included. When greater than fifty groups were sampled, the estimates of mark rate from the 1992 – 1996 dataset were slightly more precise than the 2016 dataset at similar numbers of groups sampled (a difference between CVs within 0.03 – 0.04), which may be attributable to the higher mean sampling intensities in the 1992 – 1996 dataset. The difference in CV between the two datasets was much larger when fewer than fifty groups were sampled (fig. 2.5).

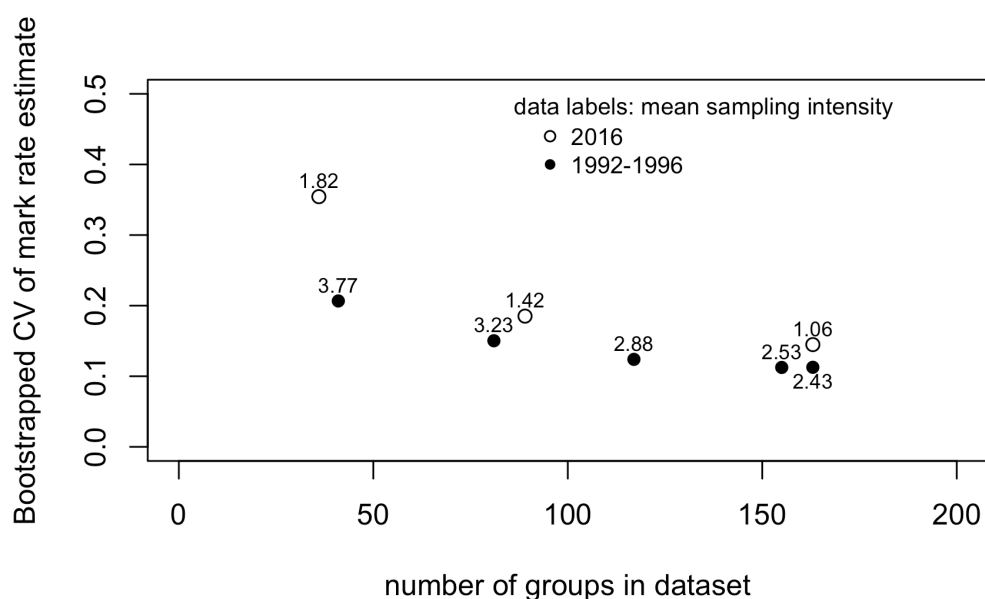


Figure 2.5: Bootstrapped CV of the mark rate estimate vs. the number of groups in each dataset. The bootstrapped CV of mark rate was calculated after excluding groups that didn't meet a given threshold value for sampling intensity (see table 2.3). Data labels represent the mean sampling intensity for each dataset after excluding groups based on the threshold.

Discussion

Estimates of mark rate for Hector's dolphins at Banks Peninsula were similar between the SRS, SRCS, and SRCS-bootstrap (point estimate of 0.065), and the SRCS-Bayes (mean estimate of 0.069). This suggests that the analysis technique for estimating mark rate appears to matter little (at least in this case using Hector's dolphin data).

However, assuming the correct sampling technique (and using the corresponding method for estimating variance) was essential for estimating precision correctly. The variance estimator based on simple random sampling (SRS; Gormley et al. 2005) led to an overly optimistic estimate of precision for this dataset. This is because SRS is known to underestimate variance when sampling individuals found in groups (e.g. Nelson et al. 2014). Because dolphins are photographed (sampled) in groups (known statistically as "clusters") each sample within the group is not independent, and therefore calculating variance assuming SRS is not recommended. Instead, the SRCS,

SRCS–bootstrap, and the SRCS–Bayes methods assume the correct sampling technique and produced larger estimates of precision for the mark rate of Hector’s dolphins.

The Bayesian model has several advantages. The model can be easily modified to include additional sources of variation, such as sea conditions or behaviour of the group. Covariates that may affect the mark rate of a group could also be added, such as age or sex (Eguchi 2014). Another advantage of this method is that the posterior distributions of all parameters in the model can be carried through in a fully Bayesian estimate of abundance (i.e. the model for estimating mark rate can be incorporated into the abundance model, allowing for simultaneous estimation of both mark rate and abundance). The Bayesian approach to abundance estimation is growing in popularity, and provides a more intuitive description of uncertainty than traditional methods (see Wade 2001; Kéry and Schaub 2011; Schofield and Barker 2011). Bayesian methods estimate the probability of different parameter values given the data. Thus, results can be communicated in more easily understandable probability statements. For this reason, Wade (2001) argues that Bayesian methods can communicate conservation research more effectively to managers and stakeholders. However, despite some clear advantages, the Bayesian framework, which is still novel to many, may deter some researchers.

In my trials, the hierarchical Bayesian model did not produce any improvement in precision when estimating the variance of mark rate (although it may if informative priors are used). Also, the point estimates of mark rate were similar to frequentist techniques assuming cluster sampling. Therefore, the SRCS–bootstrap and SRCS methods appeared to provide a good alternative. At least in the case of our dataset of Hector’s dolphins, both of these methods provided very similar estimates of precision to the Bayesian model by Eguchi (2014). In this study, both the variance estimator by Cochran (1977) and the cluster bootstrap gave the same estimate of precision. However, at smaller sample sizes, researchers should be aware the

variance estimator by Cochran might underestimate variance (Cochran 1977).

Reducing bias of the mark rate estimate

When estimating mark rate using the ratio method (Williams et al. 1993), sampling proportionately to the size of each group is recommended to reduce bias. If the same number of photos were taken of each group, regardless of size, individuals in smaller groups would have a higher probability of being sampled than individuals found in larger groups. This is of concern if there is evidence that mark rate could vary with group size. For example, Oremus (2013) observed Maui's dolphin (*Cephalorhynchus hectori maui*) calves more often in larger groups. Since calves are less likely to be marked (Urian et al. 2014), in this case over/undersampling large groups could bias an estimate of mark rate.

Many photo-ID studies do not mention field protocol (e.g. using random photography, or describing group sampling intensity) when estimating mark rate. However, if photos are not taken randomly, and instead biased towards marked individuals, the mark rate could be biased high. Spreading photographic effort over the study area, and avoiding photographic sampling in the same area on subsequent days, may also help avoid bias from resampling the same dolphin groups. Although using a strict sampling intensity of each group isn't mentioned as a requirement for estimating mark rate using the hierarchical Bayesian model, random photography of individuals is (Eguchi 2014).

Rather than choose a specific sampling intensity for each group, Nicholson et al. (2012) and Vermeulen and Bräger (2015) included groups if the researchers believed photographic coverage was "complete." Nicholson et al. (2012) used a subjective rating system for determining whether or not groups should be included. This subjective element prevented attempts to compare the performance of this approach against the methods trailed here. Nevertheless, this method will likely result in sampling proportionately to

the size of each group, as researchers will likely take more photos of large groups than small groups. However, since perception of photographic coverage is subjective, it would be difficult to incorporate samples from multiple photographers if using the SRS, SRCS, or SRCS-bootstrap method. Also, assessing how successful photographers were in capturing all individuals present is not possible when using a subjective measure. If using a measure of sampling intensity, however, completeness can be assessed by dividing the number of images by the estimate of group size. This value may then be compared to the target sampling intensity (e.g. three times as many images as the estimated group size).

Some abundance studies using photo-ID have taken a random sample of photographs from the entire dataset to estimate mark rate (e.g. Parra et al. 2006; Lukoschek and Chilvers 2008). The same concerns listed above apply to this sampling design as well. The random sample of images will only be as unbiased as the original dataset, and may only be decreasing the precision of the estimate of mark rate by decreasing sample size. Additionally, if estimating variance from a sample of photos from the dataset, the researcher still cannot assume each photograph is independent (SRS) because photos were originally gathered from groups.

By sampling proportionately to group size, theoretically each individual will have the same probability of being sampled, and an unbiased result via the SRS, SRCS, and SRCS-bootstrap methods will be achieved. However, it should be noted that due to human error, this may not always be the case. Some individuals may be photographed more than others due to variation in the photographer's perception that enough photos have been taken (which may be influenced by behaviour of the animals or sea conditions), as well as difficulty in estimating group size (especially as group size increases). As shown in fig. 2.4, sometimes intended sampling intensity is overshoot, and sometimes it is undershot. If enough groups are sampled bias caused by this variation should be low. Here, subsampling the datasets produced similar results until fewer than fifty groups were included (table

2.3). Thus, it is worthwhile to attempt to sample as many groups as possible for a robust estimate of mark rate.

Increasing precision of the mark rate estimate

This study attempted to reach acceptable precision by oversampling each group (obtaining three times as many images as the estimated group size) and by sampling as many groups as possible. Since mark rate likely changes slightly from year to year (e.g. Kuningas et al. 2013 and Silva et al. 2009), estimates where all images are taken during the same year (like the 2016 estimate from this study) may be more precise than estimates from the same number of images taken over multiple years. However, estimating a mean mark rate over multiple years may still be desirable in some settings (i.e. a gain in precision from using one year of data should not necessarily be chosen over the use of more years of data).

In the field it is helpful to know what contributes more to precision: (1) sampling as many different groups as possible or (2) obtaining as many images of each group as possible. Precision of cluster sampling is known to increase as the number of sampled groups increases, and as the similarity among groups increases (i.e. similar mark rate among groups) (Henry 1990). Because samples taken from clusters are not independent, cluster sampling schemes usually have a smaller effective sample size than simple random sampling. For example, studies in fisheries science have shown that when there is higher variation among clusters than within clusters (e.g. in length measurements) it is important to sample a relatively large number of clusters (e.g. Pennington and Volstad 1994; Bogstad et al. 1995; Zhang and Cadrin 2013; Nelson 2014). These studies showed that reducing tow duration (or number of fish caught), but collecting samples from more locations, was a more efficient design than catching more fish from fewer hauls.

As expected, as the number of sampled groups in this analysis increased, the precision of the mark rate estimate also increased for both datasets. If assessing gain in precision “per image” vs. “per group” it appears

sampling more groups is more efficient than increasing the number of images per group. For example, 1,858 images of 81 groups resulted in similar precision to 1,133 images of 163 groups (table 2.3). However, taking more photos of fewer groups is arguably an easier strategy than finding and photographing more unique groups in some populations.

In this population, increasing the number of images per group (sampling intensity) was also an important contributor to precision. The 1992 – 1996 dataset was more successful in oversampling each group (i.e. it had a higher mean sampling intensity), and the estimate of mark rate was more precise than the 2016 dataset. Also, there was a large difference in the CV of mark rate between the datasets when fewer than 50 groups were sampled. This suggests that when low numbers of groups are sampled, a higher sampling intensity may become even more beneficial for increasing precision (up to a point).

More photos of each group likely contribute so much to precision because dolphins did not appear to necessarily be clustered in groups of individuals with similar distinctiveness (i.e. some groups where no/few dolphins are marked, and some groups where all/most individuals are marked). This group organisation makes oversampling groups worthwhile. Since groups are a mixture of marked and unmarked individuals, more photographs of the same group can contribute to effective sample size more than if dolphin groups were segregated by distinctiveness.

The effective sample size may have been smaller if the mark rate of each group varied more among groups, which may happen if individuals cluster into groups of similar distinctiveness. While there is no evidence of this occurring in Hector's dolphins, it may occur in other species or populations. If one sex is more likely to become marked than another, populations that show sex-segregation may suffer this issue. For example, groups of males may have a very high mark rate, while the mark rate of groups of females may be very low compared to the population-level mark rate. In some dolphin species and populations, males are more likely to be marked than females because they participate more often in agonistic

encounters (e.g. more extensive tooth rakes in males (Scott et al. 2005) and more nicks and scarring on male fins (Rowe and Dawson 2009)). Although sex-segregation is seen in Hector's dolphins (Webster et al. 2009), there is currently no evidence that males are more likely to be marked than females. An additional reason why groups with similar distinctiveness may occur is that dolphin groups may segregate by age, which has been observed in bottlenose dolphins (Wells et al. 1987). Young dolphins are less likely to be marked, while older dolphins are more likely to be marked (Urian et al. 2014).

If it is unknown whether the population may be clustered into groups of similar distinctiveness, choosing a "strategy" for improving precision of estimates of mark rate may depend on what is more feasible — sampling as many groups as possible, or taking as many photos as possible of fewer groups. Because many unique dolphin groups may be encountered during a field season at Banks Peninsula, photographing as many unique groups as possible is a feasible option for obtaining the most precise estimate of mark rate. Attempting to obtain three times as many images as the estimate of group size may be a good compromise between having time to search for new groups and obtaining enough images of each group. However, if the population under study is only found in very large groups and/or if few groups are encountered during a survey, it may be worthwhile to increase this sampling intensity goal.

When using the model presented by Eguchi (2014), it is still recommended to oversample each group, as simulations found that the more "time" spent with each group, the more precise the posterior distribution of mark rate became (Eguchi 2014). To achieve acceptable precision, Eguchi (2014) recommended obtaining images of at least 50% of identifiable individuals in the group. This finding may not be practical for deciding how many images to obtain in the field, however. Since it is often difficult to determine the actual number of identifiable individuals in a group in the field, a decision rule like three times the estimated group size may provide better guidance for random photography protocol.

In some populations, unmarked individuals may have temporary markings that allow for short-term identification, allowing for all individuals in the group to be recognized. In this case, mark rate can be estimated using the methods described in Wilson et al. (1999). When estimating mark rate using the SRS, SRCS, and SRCS–bootstrap methods, all good quality images are included. Since some sampled groups may result in more images of certain individuals than others, the estimates for group-specific mark rates will have more variation among groups. Therefore, Wilson et al.'s (1999) method may increase precision, as the estimates of group-specific mark rates may become more similar. Like any method that samples from dolphin groups, this constitutes a form of simple random cluster sampling, and should use either the SRCS or SRCS–bootstrap methods to estimate variance.

Recommendations

Many abundance estimates of populations studied with photo-ID may be ignoring a significant amount of uncertainty in their final abundance estimate by either overestimating precision of mark rate, or ignoring its variance altogether. They may also introduce bias into the final estimate of abundance via their sampling design for mark rate. Using variance terms that incorporate the cluster-sampling element of sampling groups, as well as a non-biased sampling scheme, are therefore recommended in future studies.

Images acquired from dolphin groups should not be considered as coming from a simple random sampling design. Instead, variance of mark rate should be estimated using either the cluster bootstrap (SRCS–bootstrap), the variance estimator for cluster samples of equal sizes (SRCS, Cochran 1977), or with a hierarchical Bayesian model (SRCS–Bayes, Eguchi 2014).

Variance can be included in the final abundance estimate by:

$$\mathit{var}(\hat{A}) = \hat{A}^2 \left(\frac{\mathit{var}(\hat{A})}{\hat{A}^2} + \frac{\mathit{var}(\hat{\theta})}{\hat{\theta}^2} \right) \quad (2.5)$$

where \hat{A} is the population size estimate and $\hat{\theta}$ is the estimate of mark rate (Urian et al. 2014). Abundance may be estimated using the appropriate capture-recapture model (see equations in Pollock et al. 1990).

If using a Bayesian capture-recapture model, Eguchi's (2014) strategy for mark rate estimation incorporates an abundance estimate using the entire posterior distributions of all parameters (Eguchi 2014).

To reduce bias when estimating mark rate, groups should be sampled proportionately to group size (e.g. two or three times as many high quality photos as estimated group size), and all photos should be shot randomly.

Chapter 3

An observed decline in the mark rate of Hector's dolphins at Banks Peninsula since area-based protection

Introduction

When using mark rate to scale up an abundance estimate it is commonly assumed that this proportion remains relatively constant over the study period. In studies that have taken place over multiple years, the estimates of mark rate for each year are often either averaged or data on mark rate for all years is analysed together (e.g. Gormley et al. 2005; Reisinger and Karczmarski 2009; Nicholson et al. 2012; Pusineri et al. 2014). However, if mark rate is actually changing, assuming it is constant could bias abundance estimates. For example, if mark rate has declined over the course of a study, scaling up abundance using an estimate of mark rate from the early part of the study will negatively bias the estimates of abundance from the later part.

A few studies on cetaceans have estimated mark rates for different years or time periods, but any potential differences in mark rates have gone relatively unexplored. Poncelet et al. (2010) estimated two separate mark rates for two abundance estimates of killer whales (*Orcinus orca*; one for the period 1988-1989 and one for the period 1998-2000). These estimates of mark rate appeared to differ (0.306, SE=0.066 in 1987 – 1990 vs. 0.459, SE=0.050 in 1998 – 2000). The authors suggested that the difference might be due to differing photo-ID protocols between the two periods, or an increase in marks due to injuries from poachers repelling killer whales from longlines using explosives. Kuningas et al. (2013) also estimated separate mark rates for killer whales in different time periods, but their mark rates were more similar. In their studies of pilot whales, Verborgh et al. (2009) and Alves et al. (2014) estimated mark rates for each year and estimated abundance separately for each year. In both studies mark rates showed year-to-year variation, though Verborgh et al. (2009) could not detect a trend in

mark rate, and Alves et al. (2014) did not test for a trend. Potential reasons behind year-to-year variation in mark rate were not explored.

Researchers can sometimes categorise marks by their source, which may provide more information on why mark rate may change over time and differ between populations. For example, marks from predators (especially sharks) are often crescent shaped (Heithaus 2001) and/or show teeth marks (Heithaus 2001; Kügler and Orbach 2014), while marks from fishing gear, such as longlines, tend to appear as slices and are sometimes mirrored with marks on both the leading and trailing edge of the dorsal fin (e.g. Baird and Gorgone 2005; Baird et al. 2014). Dolphins are known to receive marks via nonfatal encounters with fishing gear (e.g. Baird and Gorgone 2005; Kiszka et al. 2008; Baird et al. 2014), other human impacts like boat collisions (Wells and Scott 1997), from play or aggressive behaviours with conspecifics (e.g. MacLeod 1998; Scott et al. 2005; Marley et al. 2013), and from predation by sharks and killer whales (e.g. Corkeron et al. 1987; Heithaus 2001; Gibson 2006).

The frequency of different types of marks may vary depending on the population or sex. For example, Kügler and Orbach (2014) discovered that the source of most marks (84%) on dusky dolphins in Kaikoura, NZ appeared to be from interactions with conspecifics, while only a few individuals (<1% of the population) had signs of fisheries interactions. In contrast, Baird et al. (2014) estimated that over 7% of marks in a population of false killer whales in Hawaii, USA were likely due to interactions with fishing gear. In Hawaii, the proportion of marks attributable to fishing gear also varied between two different populations of false killer whales with different exposure to fisheries; a lower proportion of marks caused by fishing gear were found in the area with fewer longlines (Baird et al. 2014). Incidence of fisheries-related marks was also higher in females than males, suggesting females may be more likely to have nonfatal encounters with fishing gear in that population (Baird et al. 2014).

At Banks Peninsula, it is possible that evolving management to protect Hector's dolphins from set netting could result in a decline in mark rate. The

Banks Peninsula Marine Mammal Sanctuary was established in 1988 and restricted set netting from Sumner Head to the Rakaia River (fig. 3.1A, Slooten and Dawson 2010). Within the sanctuary, commercial set netting was banned, and recreational set netting restricted to certain times of the year and day. In 2008, the fisheries restrictions within the sanctuary were expanded to prohibit recreational set netting and to include inner harbours (with an exception from 1 April – 30 September). Additional restrictions on set nets out to 4 nm and trawling out to 2 nm were also enacted in other parts of NZ waters, including an extension of these restrictions north and south of Banks Peninsula (fig. 3.1B, Slooten and Dawson 2010). Evidence for the effectiveness of the sanctuary was provided by Gormley et al. (2012), who detected an increase in adult survival rate after 1988. Presumably, this increase in survival rate means that the frequency of interactions with fishing gear has decreased since set net restrictions were imposed.

The only estimate to date of mark rate for Hector's dolphins at Banks Peninsula was conducted between 1992 and 1996 (Gormley et al. 2005). This estimate of 0.105 (SE=0.0057) applies to marks graded as quality 1 or 2 (see Slooten et al. 1992 for an explanation of mark categories). Because of the proximity of this time period to the establishment of the Banks Peninsula Marine Mammal Sanctuary, and the long lifespan of Hector's dolphins (20+ years, Slooten and Dawson 1994), this estimate may reflect a mark rate that includes more injuries from nonfatal encounters with fisheries than the present. Therefore, I hypothesised that mark rate has declined since Gormley et al. (2005)'s initial estimate. This hypothesis is investigated by comparing the dataset from 1992 – 1996 with data collected on mark rate in 2016, which should represent a population that is having fewer interactions with fisheries.

The second aim of this chapter is to compare two different analytical methods for investigating a change in mark rate. As discussed in Chapter 2, a variety of different mark rate estimation strategies have been used in photo-ID studies. The most common method involves taking the ratio of high-quality images showing marked individuals to the total number of images

taken. Recently, a Bayesian model for estimating mark rate was developed by Eguchi (2014) and has not been applied in other studies yet. While Chapter 2 compared the SRCS (simple random cluster sample) method and SRCS-Bayes (hierarchical Bayesian model) when estimating a single mark rate, this chapter aims to compare the two methods' ability to detect a change in mark rate between two different periods for this dataset of Hector's dolphins.

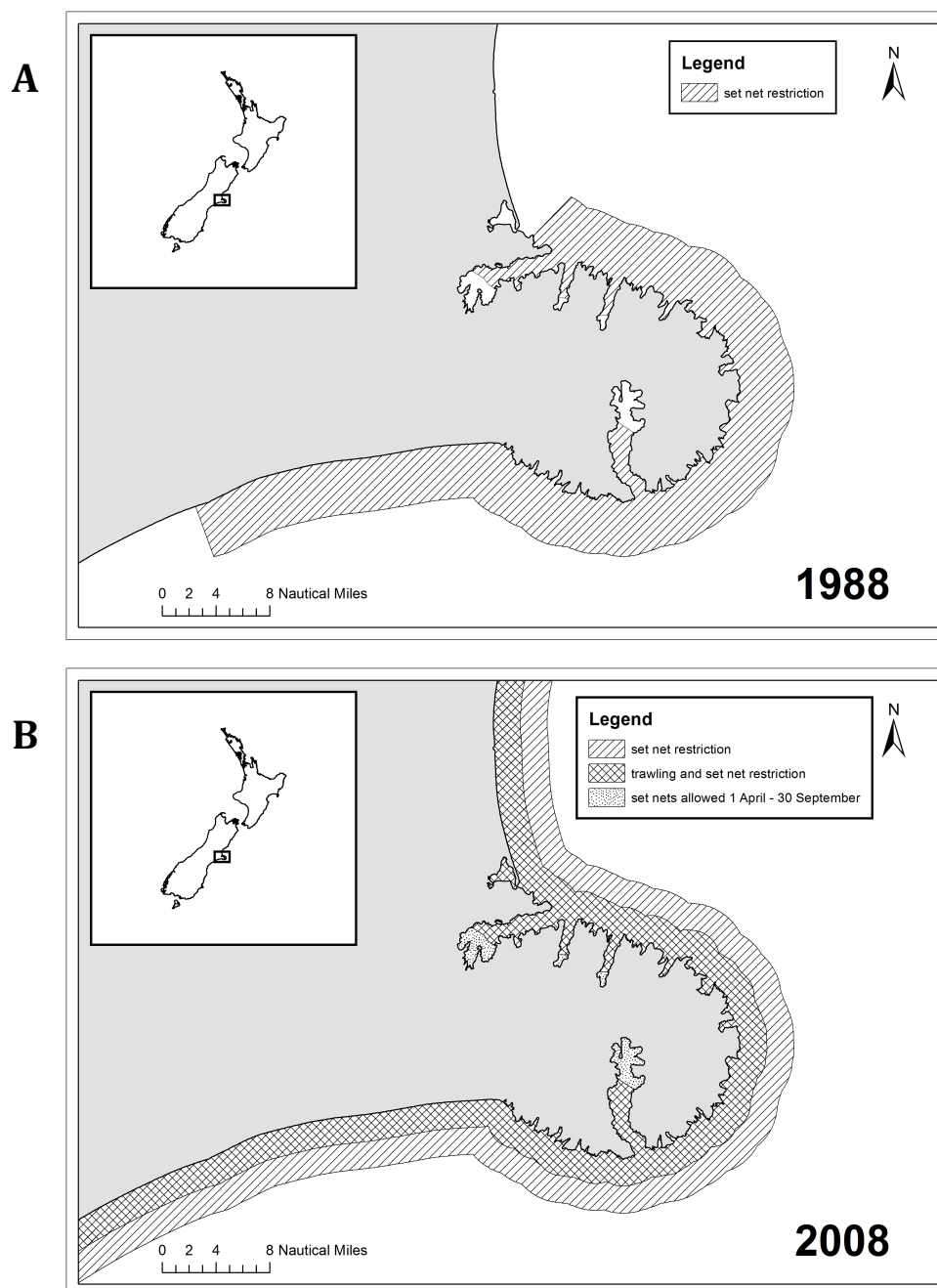


Figure 3.1: The extent of restrictions on set nets and commercial trawling to protect Hector's dolphins at Banks Peninsula in (A) 1988 and (B) 2008.

Methods

Mark rate of Hector's dolphins at Banks Peninsula was estimated for two time periods, from 1992 – 1996 and in 2016. Field methods for collecting data on mark rate during the two periods were as similar as possible. Detailed methods for the time period 1992 – 1996 are described in Gormley et al. (2005), and the methods for 2016 are described in Chapter 2. Briefly, groups of dolphins were randomly photographed during boat-based strip-transect surveys between January and March. "Randomly photographed" means that nearby dolphins were photographed regardless of whether or not they were marked, so each photography session emulated simple random sampling with replacement of individuals within each group. The 1992 – 1996 photography sessions took place separately from the routine photo-ID surveys, while the 2016 sessions took place alongside routine photo-ID surveys. As in Chapter 2, "photographs" will refer to photographs taken in the field, while the term "images" will be used to refer to photos of high enough quality to be used in photo-ID analysis.

The photographer was the same for all random photography sessions within each period (S. Dawson for 1992 – 1996 and L. Wickman for 2016). The same person (L. Wickman) screened all photographs taken during random photography sessions for both time periods, to remove the possibility of individual bias when grading photographs for quality and mark distinctiveness.

Photographs were screened by examining film negatives for the time period 1992 – 1996 and digital photographs for the period 2016. Screening of photographs for inclusion in the mark rate estimate was the same for both time periods, and used the same protocols as the long-term photo-identification programme (Slooten et al. 1992). Photographs were only retained if the dorsal fin was completely in focus, completely visible, and perpendicular to the camera. If multiple photos were taken of an individual's surfacing event, only one photo was chosen. Marked dolphins were classified into one of three categories (see Slooten et al. 1992). Category 3 contains individuals with subtle markings that may be missed in the field and may be

difficult to identify in photographs. Category 2 includes individuals with obvious marks that are unlikely to be mis-identified from good quality images but may be missed in the field. Lastly, Category 1 contains individuals with obvious marks unlikely to be missed in the field or in image analysis. For this study, only individuals with Category 1 and 2 marks were included in estimating the mark rate.

Estimating the difference between mark rates – SRCS method

For each period, 1992 – 1996 and 2016, mark rate and its variance was estimated analogously to the simple random cluster sampling (SRCS) method described in Chapter 2. Mark rate was estimated as the number of images showing individuals with category 1 and 2 marks, divided by the total number of images acquired, as follows:

$$\hat{\theta} = \frac{\sum_{i=1}^k \frac{I_i}{T_i}}{k} \quad (3.1)$$

where k =the number of years, I_i =the number of high quality photographs showing category 1 and 2 marks for the i^{th} year, and T_i =the total number of high quality photographs taken for the i^{th} year (Gormley et al. 2005). The number of k years was taken as the number of years within each time period (the period 1992 – 1996 consisted of $k = 5$ years, while the period 2016 consisted of just one year ($k = 1$)).

Variance of the mark rate was estimated using the formula for proportions from clusters (in this case, dolphin groups) of unequal sizes from Cochran (1977, p. 66). As in Chapter 2, the number of possible unique group structures, or clusters, was assumed to be so large compared to the number sampled that the $\frac{N-n}{N}$ term at the beginning of the equation was dropped.

$$\widehat{var}(\hat{\theta}) = \frac{\sum_{g=1}^n (M_g / \bar{M})^2 (\hat{\theta}_g - \hat{\theta})^2}{n(n-1)} \quad (3.2)$$

where n =the number of clusters photographed, M_g =the size of the g^{th} cluster (number of images from the group), \bar{M} =the average size of all clusters $\hat{\theta}_g$ =the mark rate within the g^{th} cluster, and $\hat{\theta}$ =the mark rate of all clusters combined.

To determine whether there was a significant difference in the estimate of mark rate between the two periods, the 95% confidence interval of the difference was estimated as:

$$(\hat{\theta}_{1992-1996} - \hat{\theta}_{2016}) \pm 1.96 * \sqrt{v\hat{a}r(\hat{\theta}_{1992-1996}) + v\hat{a}r(\hat{\theta}_{2016})} \quad (3.3)$$

where $\hat{\theta}_{1992-1996}$ is the estimate of mark rate during the period 1992 – 1996, and $\hat{\theta}_{2016}$ is the estimate of mark rate during the period 1992 – 1996.

Estimating the difference between mark rates – SRCS–Bayes method

Mark rate was also estimated using a Bayesian model developed by Eguchi (2014)(described as SRCS–Bayes in Chapter 2). As in the SRCS method, inferences about the mark rate are made using the number of high-quality images showing marked individuals, as well as the total number of high-quality images taken. Code and model structure for the analysis can be found in Appendix 3.1.

The analysis was the same as described in Chapter 2, but with a few modifications to allow for the difference in mark rate to be estimated between the two periods. For the period 1992 – 1996, θ (mark rate) was treated as time dependent and allowed to vary by year, so that $\theta_g \sim BETA(\alpha, \beta)$ became $\theta_{g,t} \sim BETA(\alpha_t, \beta_t)$. As in Chapter 2, uninformative prior distributions ($U(0,100)$) were chosen for the alpha (α_t) and beta (β_t) parameters, which describe the distribution of group-specific mark rates. The mean of this beta distribution is taken as the population-level mark rate, using the formula $\frac{\alpha_t}{\alpha_t + \beta_t}$. For each iteration of the model, the estimate of mark rate for the entire period of 1992 – 1996 was taken as the average of the population-level mark rate estimated for each year, analogously to eq. 3.1.

The difference in mark rate for each iteration of the model was the estimate of mark rate from 2016 subtracted from the estimate of mark rate during the period 1992 – 1996. This strategy is in contrast to the use of 95% confidence intervals to detect a difference in mark rate, which relies on an assumption of asymptotic normality of the estimates in both periods.

The model ran in OpenBUGS (Lunn et al. 2009) via program R2OpenBUGS (Sturtz et al. 2005) in program R (R Core Team 2015). For each model run, four independent Markov chains of 60,000 steps each were initiated at specified random values. The first 10,000 steps of each chain were considered “burn-in” samples and were not used for making inferences about the parameters. Therefore, inferences were made from 200,000 samples (4 chains of 50,000 samples each). Convergence of each of the chains was assessed visually and via the Rhat statistic (Rhat <1.02 for all parameters) (Gelman et al. 2003). The population level mark rate (θ) for each time period was analysed by its mean and 95% highest density interval (HDI), which describes where 95% of estimates from the posterior distribution lie. The probability that the mark rate in 2016 was higher or lower than the period 1992 – 1996 was taken as the percentage of model runs where the difference between mark rate of the two time periods was greater than or less than zero. Posterior distributions were plotted using the plotPost.R function, taken from Kruschke (2011).

Results

A total of 2,363 images (photographs that met screening standards) were obtained from 160 groups of dolphins for the period 1992 – 1996 (table 3.1). A total of 1,133 images were obtained from random photography of 163 groups of dolphins in 2016 (table 3.1). The un-averaged mark rates given for each year in the 1992 – 1996 period varied considerably, with the year-specific mark rates given for 1994 and 1995 much lower and more similar to 2016 than the other years (table 3.1). However, sample size of within year mark rates for the 1992-1996 period was low compared to the sample size for 2016 (table 3.1).

The ratio of images showing distinctive marks (Category 1 and 2) to total images, averaged for the entire period of 1992 – 1996 was 0.086 (SE=0.011, 95% CI=0.064 – 0.107), and in 2016 was 0.065 (SE=0.009, 95% CI=0.048-0.085) (table 3.2). The difference in mark rate between the two periods was not statistically significant (95% CI of difference= -0.008 – 0.049).

The hierarchical Bayesian model yielded a population level mean mark rate of 0.107 (95% HDI: 0.080 - 0.137) for the period 1992 – 1996 and a mean mark rate of 0.069 (95% HDI: 0.049-0.090) in 2016 (table 3.2, fig. 3.2). The posterior distribution of the difference in mark rate over the two periods (fig. 3.2) indicated that 98% of values were greater than zero. Therefore, there is a 98% probability that the estimate of mark rate in 2016 is lower than the mark rate estimated for 1992 - 1996. The mean difference between the mark rates over the two periods was estimated as 0.038 (95% HDI: 0.003 –0.074) (fig. 3.2).

Table 3.1: Summary of the number of images containing marked individuals, the total number of images, the proportion of images showing marked individuals, and the number of groups sampled for each year (k).

k (year)	1992	1993	1994	1995	1996	2016
Images with marks	40	42	35	30	56	74
Total images	328	438	502	552	543	1133
Groups encountered	19	37	32	33	39	163
Proportion of marked images	0.122	0.096	0.070	0.054	0.103	0.065

Table 3.2: Comparison of mark rate and its precision for the periods 1992 – 1996 and 2016, using the hierarchical Bayesian model and the SRCS method.

Method	1992 – 1996				2016			
	Mark rate	SE/SD	95% CI	95% HDI	Mark rate	SE/SD	95% CI	95% HDI
SRCS–Bayes method	0.107	SD: 0.015	N/A	0.080 - 0.137	0.069	SD: 0.010	N/A	0.049- 0.090
SRCS method	0.086	SE: 0.011	0.064- 0.107	N/A	0.065	SE: 0.009	0.048 - 0.085	N/A

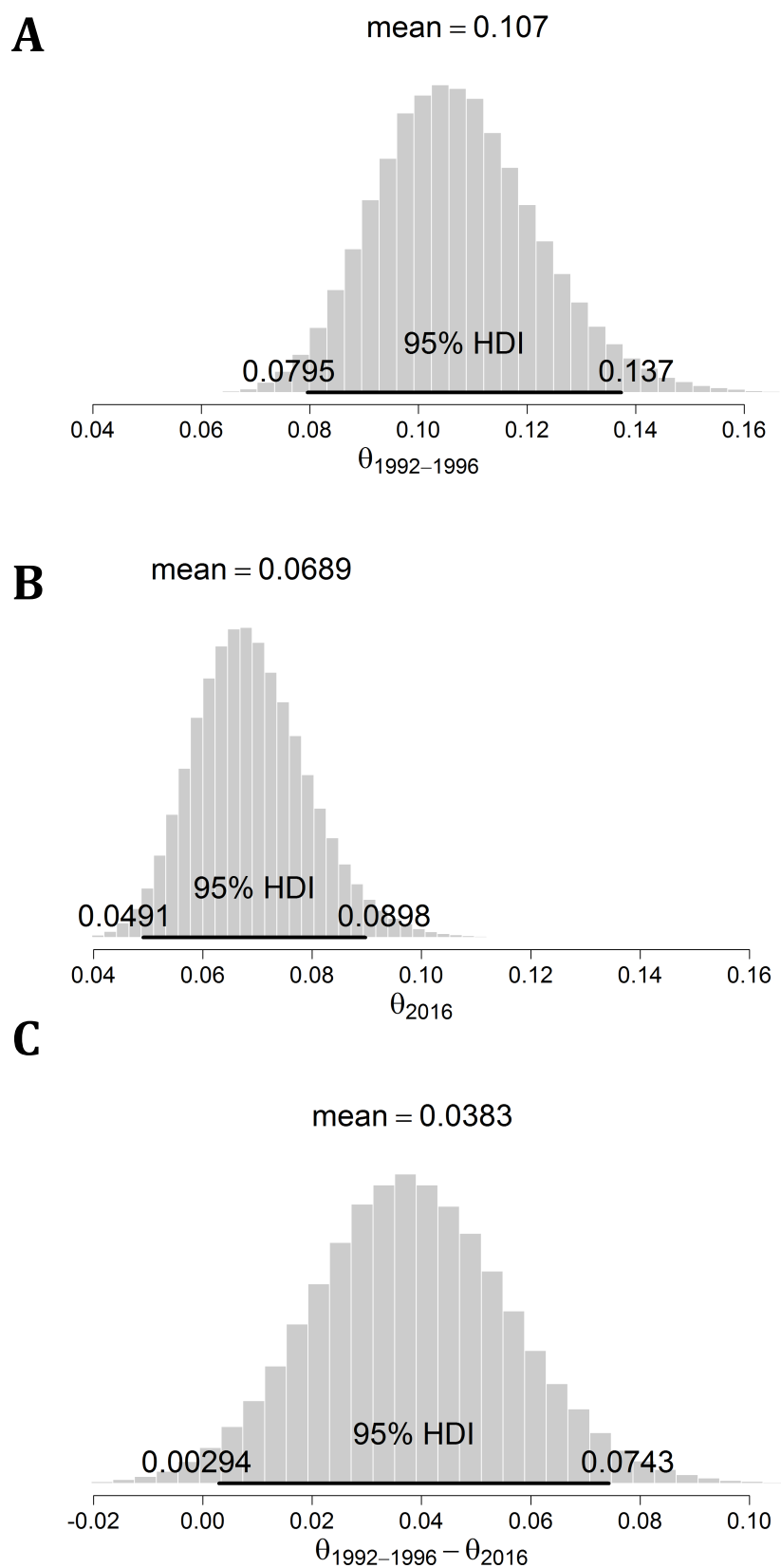


Figure 3.2 The top two histograms ('A' and 'B') represent the posterior distributions for mark rate for the two different periods (1992 - 1996 A, 2016 B). Histogram 'C' represents the posterior distribution for the difference in mark rate between the two periods.

Discussion

Mark rate was estimated from two different periods, using the same methodology: (1) the SRCS method and (2) the SRCS–Bayes method. Both methods produced evidence of a lower mark rate in 2016. The magnitude of this difference, however, depended on the method used. The Bayesian model showed that the 2016 estimate of mark rate was significantly lower than the estimate from 1992 – 1996 (with 98% probability), but the SRCS method failed to detect a difference ($p=0.16$).

The large variability observed in the 1992 – 1996 period suggests there may be a large amount of variation from year to year. Although the combined sample size of the 1992 – 1996 period was similar to the sample size for 2016 (both ~160 groups), mark rate estimates that are consistently lower beyond 2016 would strengthen the conclusion that mark rate has declined. Still, the consistency in field methods between the two periods, the same individual reviewing images for quality and marks, and the large sample size for both periods, provide strength to the conclusion that mark rate is lower than in 1992 – 1996. Rather, variations in rate of acquisition of marks on dolphins, due to predation, interactions with fishing gear, and interactions with conspecifics, will be discussed as the most likely causes for the observed decline in mark rate.

This study also emphasises the importance of reassessing mark rate regularly. Without an updated estimate of mark rate from 2016, our understanding of mark rate would be biased high and hence abundance estimates derived from capture-recapture analyses would be biased low.

Performance of SRCS vs SRCS–Bayes methods for estimating mark rate

Both methods produced a similar mark rate estimate to the 0.105 (SE=0.006) mark rate reported in Gormley et al. (2005), who used the same dataset for 1992 – 1996. The estimate from Gormley et al. (2005) lies within the 95% CI/HDI of both methods used here (SRCS and SRCS–Bayes), but is more precise since clustering (dolphins being found in groups rather than individually) was incorrectly not incorporated into the variance.

Precision of the two estimation strategies were similar, suggesting that the reason the Bayesian model detected a difference is because it estimated a slightly higher mean mark rate for 1992 – 1996 (0.107 using the Bayesian model vs. 0.086 using SRCS methods). This assumption can be illustrated by substituting the mean estimate from the Bayesian model into the equation for the 95% CI of the difference (see table 3.3), at which point the difference becomes significant.

Table 3.3: The results from substituting the mean mark rate estimating using the SRCS–Bayes method in 1992 – 1996 when estimating the 95% confidence interval of the difference. The first column shows the result when both the 1992 – 1996 mean mark rate and the 2016 mean mark rate come from the SRCS method. The second column shows the result when the 1992 – 1996 mean mark rate from the SRCS–Bayes method is used instead. The variance estimated using the SRCS method was used when estimating the upper and lower confidence limits in both scenarios.

	Means both from SRCS method	Mean from SRCS–Bayes method used for 1992 – 1996
Difference in mark rate between 1992 – 1996 and 2016	0.086 - 0.065	0.107 - 0.065
95% confidence limit of the difference	0.021	0.042
	-0.008 – 0.049	0.013 – 0.070

Which point estimate of mark rate is less biased (i.e. which estimate is more correct—the one using the SRCS method or the SRCS–Bayes method) is unclear. Not knowing the “true” mark rate, I may only compare the differences in analytical strategies here.

For both methods, the mark rate was determined using the number of images of marked individuals and the number of all images taken. While SRCS does this by pooling all photos together and taking the ratio of images showing marked individuals to total photos taken (eq. 3.1), the Bayesian method models the number of images showing marked individuals (K_g) using the mark rate and total number of images taken (T_g) for each group ($(K_g \sim BIN(\theta_g, T_g))$). More information on the mark rate of each group (θ_g) is incorporated by the use of a prior distribution ($\theta_g \sim BETA(\alpha, \beta)$), which

allows data obtained from other groups to contribute to estimating the distribution of θ_g . As more groups are included in the dataset, more information on the population level alpha (α) and beta (β) parameters become available, and this beta distribution is what ultimately provides knowledge about the population-level mark rate (θ) and its uncertainty. In other words, the model assumes dependence of group-specific mark rate on the higher-level (population-level) distribution, so that the estimates of the group-specific mark rates are influenced by the results of other groups.

For both methods, larger dolphin groups provide more information about the mark rate of the population than smaller dolphin groups, which is accounted for by sampling proportionately to group size. The SRCS method does this directly, as more images from larger groups are included in the SRCS estimate than smaller groups. The Bayesian model incorporates more information from larger groups by being more “confident” in its estimate of group-specific mark rate for groups with larger amounts of images. Therefore, groups with more images contribute more to deciding the population-level distribution of mark rate, which then affects the estimation of other group-specific mark rates.

Comparing the distribution of group-specific mark rates between the two periods, mark rates were more homogenous/less variable in 2016, with all groups having a mark rate between 0 and 0.2 (fig. 3.3). For the 1992 – 1996 period, group specific mark rates were much more variable, with group-specific mark rates spanning all the way to 1.0 (fig. 3.3). In 1992 – 1996 there was also a higher proportion of groups that contained at least one marked individual. In 2016, only 25% of encountered groups contained at least one photographed marked individual, while in 1992 – 1996, 36% of groups did. This difference is likely due in part to a higher mark rate in 1992 – 1996 (which would lead to more groups with marks being observed in 1992 – 1996). In addition, a larger number of images for each group were obtained in the early time period, which increases the chance of obtaining at least one image of any marked individuals present.

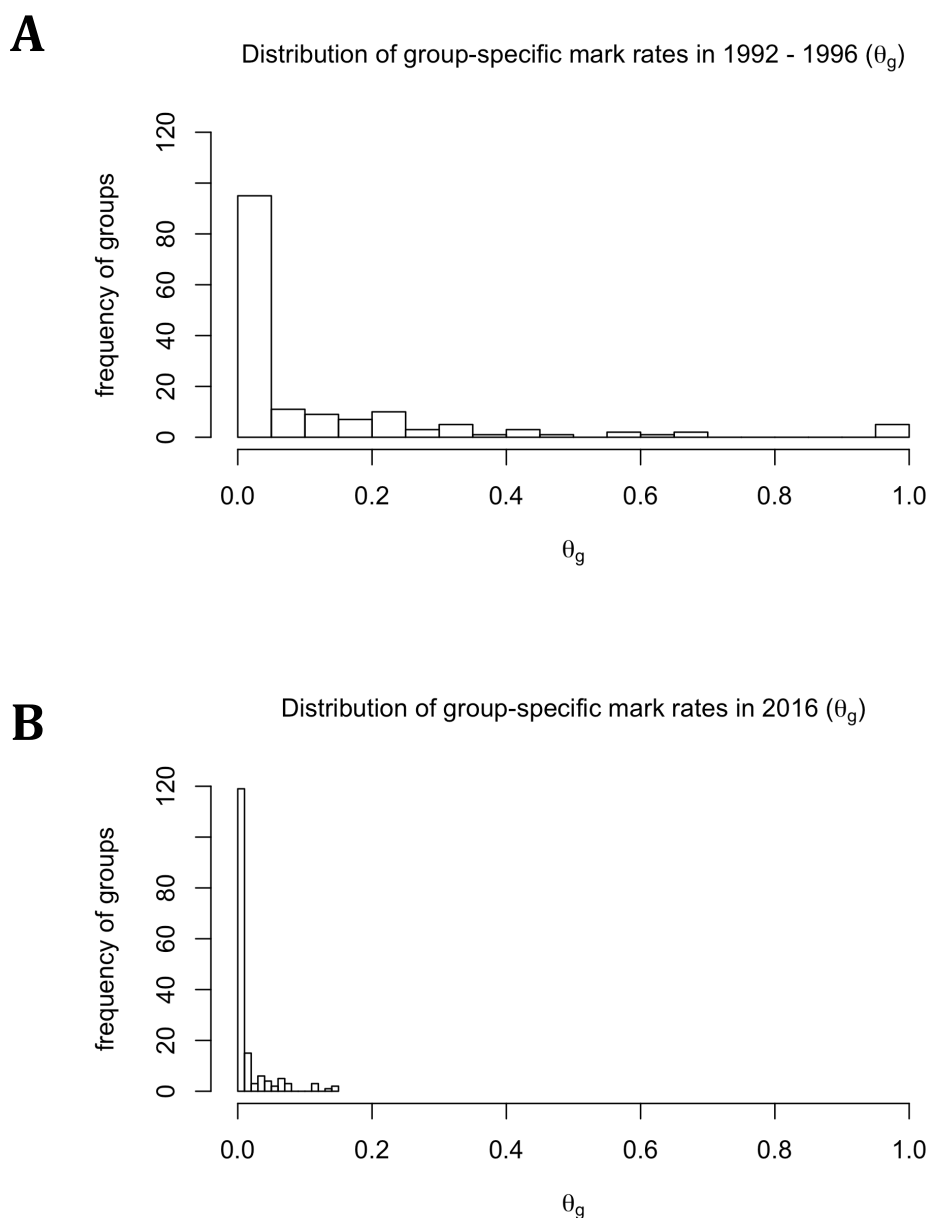


Figure 3.3: Distribution of group-specific mark rates (the mark rate of each group photographed) for each of the two periods (A: 1992 - 1996, B: 2016).

The difference in the distribution of group-specific mark rates between the two periods may explain some of the difference in the results between the SRCS and SRCS-Bayes methods for the 1992 - 1996 period. Because the SRCS method pools together all images taken, it would estimate the same mark rate whether the same number of marked images (images showing marked individuals) was spread over many groups, or if the marked images were clustered into only a few groups. However, in the SRCS-Bayes method, the mark rate of each group contributes to the estimate of the

population level mark rate. Therefore, it may consider a population with a large number of groups documented with at least one marked individual present as having a larger mark rate than if the same number of images showing marked individuals were taken but spread out over fewer groups.

Potential causes for a decline in mark rate

Permanent marks can be caused by conspecifics due to rough play and aggression, as suggested for other species (e.g. MacLeod 1998; Marley et al. 2013; Kügler and Orbach 2014). Differences in the frequency of marks from conspecifics have been observed between males and females and among different populations, but I found no studies investigating temporal changes within any dolphin population. Some research on bottlenose dolphins (*Tursiops truncatus*) and dusky dolphins (*Lagenorhynchus obscurus*) suggests that males have more conspecific-related marks, likely because of sexual competition (Rowe and Dawson 2009; Marley et al. 2013; Orbach et al. 2015). Intrasexual competition for mates, and its associated scarring, may occur less often in dolphin societies with long-term male alliances that work together to coerce females into mating. For example, less scarring was observed in bottlenose dolphins inhabiting Sarasota, FL, where male alliances are present (Tolley et al. 1995), than in Scotland where male alliances are absent (Marley et al. 2013). Marley et al. (2013) also observed a difference in tooth-rake scarring (temporary scars from conspecifics) between two populations of bottlenose dolphins. The smaller, more closed population had fewer tooth rake scars than the larger population, which was composed of two dolphin communities. Marley et al. (2013) suggested that the larger, multi-community population might have more scarring from aggressive or other social behaviours due to interactions among neighbouring communities.

However, the social processes described above do not occur in Hector's dolphins, and there are no indications that there has been a long-term shift in behaviour of Hector's dolphins that might have caused a decrease in conspecific-related scarring. Additionally, overt aggression in

Hector's dolphins is rare and there is no evidence for intrasexual competition for mates (Slooten 1994; Slooten and Dawson 1994).

A decline in the rate of non-fatal shark attacks on Hector's dolphins is another possible explanation for the decline in mark rate. Studies on bottlenose dolphins suggest that the population density of sharks affects the number of shark bite scars observed on dolphins (Heithaus 2001). Heithaus (2001) observed a greater number of fresh bites during warmer months, when tiger sharks (a known dolphin predator) were more likely to be present. As would be expected, the number of shark bite scars observed on dolphins also varies by location. For example, Heithaus (2001) observed shark attack scars on over 74% of bottlenose dolphins living in Shark Bay, Australia, compared to 31% of bottlenose dolphins in Sarasota, FL (Urian et al. 1998). Meanwhile, Bearzi et al. (1997) observed no shark bites on their study population of bottlenose dolphins in the Adriatic Sea. While these studies on shark bites refer to scars found anywhere on the body, my study refers only to marks on the dorsal fin. Kügler and Orbach (2014) found that less than 1% of individuals' dorsal fins showed signs of shark bites. They suggest this low frequency may reflect low predation pressure (low abundance of sharks in the study area and offshore movements of the dolphins at night), but also may be due to fewer shark bites found on dorsal fins. Heithaus (2001) found more shark bites on the dorsal portion of the body, suggesting dolphins may turn to protect their ventral area during an attack. The proportion of bites found on the dorsal fin (versus other parts of the dorsal surface) were not discussed, however.



Figure 3.4: Example photos of dorsal fin marks probably caused by non-fatal shark attacks.

Hector's dolphin remains have been found in blue sharks (*Prionace glauca*) and sevengill sharks (*Notorynchus cepedianus*) (Slooten and Dawson 1988), and bite marks are sometimes observed on live dolphins (see fig. 3.4 for some examples). Globally, populations of top predators, including large sharks, have undergone significant declines in the last 30 years (Stevens et al. 2000; Baum et al. 2003; Myers and Worm 2003). The IUCN classes blue sharks as Near Threatened (Stevens 2009) and sevengill sharks as Data Deficient (Compagno 2005) worldwide. Both species are susceptible to bycatch (Compagno 2005; Stevens 2009) so a reduction in set netting around the South Island (as enacted in 2008) could potentially lead to an increase in population size. Hypothetically, if shark numbers around Banks Peninsula increased, and shark bites were a significant contribution to permanent dorsal fin marks, mark rate would be expected to increase, however. To the author's knowledge, no abundance estimates or population density surveys of blue sharks or sevengill sharks have been completed around Banks Peninsula. Therefore, a decrease in shark abundance contributing to the decline in mark rate cannot be ruled out, although there is no strong evidence suggesting this would be the case.

The most parsimonious explanation is that mark rate has declined because evolving management measures (fig. 3.1) have decreased the frequency of interactions with fishing gear. Some of the marks observed on live Hector's dolphins closely resemble the types of marks seen on dead individuals recovered from set nets (see fig. 1.4, chapter 1). Therefore, it is logical that the mark rate has decreased coincident with the reduction in

overlap between distribution of dolphins and set nets. Besides a reduction in marks caused by set nets, it is also possible mark rate is lower because more young, unmarked dolphins have entered the population. This explanation may also be supported by evidence that the survival rate of Hector's dolphins has increased since the establishment of protection measures in 1988, most likely because the sanctuary reduced dolphin mortality in set nets (Gormley et al. 2012). This research showed that population decline has slowed, from about 6% per year to about 1% per year (Gormley et al. 2012).

Gormley et al. (2012) noted that although the increase in survival rate is most likely due to the sanctuary, other explanations could not be eliminated since the study had no controls or replicates. Similarly, this study provides supporting evidence that encounters with set nets have decreased; the lower mark rate in 2016, along with previous evidence of improvement of survival rate post-sanctuary, suggests encounters between dolphins and fishing gear have declined. Unfortunately, no similarly comprehensive data sets on mark rate exist for any other Hector's dolphin populations.

Studies conducted elsewhere suggest that a reduction in marks related to a decline in fisheries pressure is reasonable. False killer whales exposed to longline fisheries in Hawaii have a higher proportion of marks attributable to fisheries in areas with high fishing effort (Baird et al. 2014). The frequency of marks caused by nonfatal encounters with fishing gear has also been used in other locations to assess the amount of exposure to fishing (e.g. Kiszka et al. 2008; Bradford et al. 2009). I did not categorise marks by probable source, for two reasons; such categorisations could often be uncertain, and because Hector's dolphins have a low mark rate, the sample size of marks that could be categorised would be small. Nevertheless, to my knowledge this is the first case of an observed decline in mark rate, most likely due to management action.

Chapter 4

Decreasing mark rate affects the precision of estimates of survival rate in Hector's dolphins

Introduction

In the context of capture-recapture analysis, survival rate is defined as the probability that an individual survives from one time period (e.g. one year) to the next. Estimating survival has been an important objective of the long-term research programme at Banks Peninsula, as well as in research on other dolphin species (see Appendix 4.1). Survival rates are a key driver of population dynamics in long-lived animals (Sæther and Bakke 2000; Crone 2001; Oli and Dobson 2003; Young and Keith 2011) and are commonly used to assess risk of population decline or extinction using population viability analysis (e.g. Gaona et al. 1998; Kelly and Durant 2000; Slooten et al. 2000; Huang et al. 2014).

Another way survival rates are widely applied in conservation biology is as an ingredient in reference point estimators. These estimators produce a limit to how many individuals can be killed by human impacts and still prevent population depletion (Moore et al. 2013). For example, PBR, or Potential Biological Removal level, is a reference point estimator currently applied in the United States (through the Marine Mammal Protection Act) to prevent depletion of marine mammal populations (Wade 1998; Taylor et al. 2000; Moore et al. 2013). Computing PBR requires an estimate of population size and an estimate of the maximum population growth of the population. If available, estimates of survival along with reproductive rate should be used to estimate maximum growth rate (Wade 1998; Dillingham and Fletcher 2008).

Estimates of survival rate are also widely applied in conservation biology because they are typically less biased and more precise than abundance estimates (Pollock et al. 1990), providing a powerful tool for testing biological hypotheses (see Lebreton et al. 1992). For example,

Esteban et al. (2016) compared survival rates of killer whales with different foraging tactics in the Strait of Gibraltar. Whales that had learned to remove prey from long lines had significantly higher survival than those that exclusively hunted for prey (Esteban et al. 2016). Fearnbach et al. (2012) used a Bayesian capture-recapture model that detected an 83% probability that survival of dolphins dropped below average the year a hurricane struck their study area at Little Bahama Bank.

Hector's dolphins were one of the first species of dolphin to have an estimate of survival rate. Before the mid-1990s, very few long-term studies capable of estimating survival rates for dolphins were in place. Survival rates were available for just three species of dolphins — bottlenose dolphins (Wells and Scott 1990), killer whales (Olesiuk et al. 1990), and Hector's dolphins (Slooten et al. 1992). Now, about 15 species in over 40 different locations have estimates of survival rate (Appendix 4.1). In the majority of these studies, these estimates are derived from the analysis of photo-ID data using capture-recapture models.

Still, less than a quarter of dolphin species have estimates of survival rate, despite the importance of this parameter in demographic analyses such as risk assessments and reference point indicators. Additionally, many of these estimates are not very precise, which profoundly influences the ability to quantify differences in survival rates between populations and over time. For example, Speakman et al. (2010) mentioned comparing survival rates of dolphins <1 year old between their study site (Charleston, NC, USA) with that of another site (Sarasota, FL, USA), but their estimates were not precise enough to do so. Tezanos-Pinto et al. (2013) also discussed how there appeared to be a declining trend in survival rates in the bottlenose dolphins of the Bay of Islands, but commented that the wide confidence intervals meant they could not be sure.

Several studies of survival of Hector's dolphin have been carried out as the photo-ID dataset has grown and analytical methods have improved. The first of these (Slooten et al. 1992) estimated survival rate in the absence of protection measures as 0.85 (SE=0.083) using a modified CJS model

correcting for individuals being alive but not sighted. This survival rate, as well as survivorship curves based on other mammals, were then used to predict population outcomes in different management scenarios (e.g. Slooten and Lad 1991; Slooten and Dawson 2010).

Estimates of survival rate have also been used to assess the effectiveness of the Banks Peninsula Marine Mammal Sanctuary (Cameron et al. 1999; Gormley et al. 2012). Cameron et al. (1999) modelled survival rates by applying a multi-state capture-recapture model. Pre-sanctuary survival rate was estimated as 0.93 (SE=0.04), while post-sanctuary survival rate was estimated as 0.79 (SE=0.06), providing no evidence that survival rates increased following the sanctuary's establishment (Cameron et al. 1999). However, the power of the test used was low (Cameron et al. 1999). Gormley et al. (2012) estimated survival rates before and after the creation of the sanctuary by applying a more sophisticated model (a Bayesian random effects capture-recapture model) to a larger dataset, this time finding an increase in survival rate from 0.86 to 0.92, which is a 5.4% increase since the sanctuary's establishment. This study was the first to show significant change in a demographic parameter of any marine mammal species due to management. To detect this change, however, it was necessary to have estimates of survival that were suitably precise (as well as a suitably large difference pre/post sanctuary).

The precision of estimates of survival rate is partly determined by study design and sampling intensity. Simulations by Pollock et al. (1990) show that precision of survival rate estimates decreases with population size, low sample sizes (short study periods and/or few sampling occasions), low capture probabilities, and low true survival rates. These results have important implications for study design. For example, it may take many years until suitably precise estimates of survival rate can be obtained. Additionally, it may take an even longer time (if possible at all) to obtain suitably precise estimates of survival rate in species with very low abundance and/or with low survival rates.

In addition to fewer sampling occasions and a smaller population, mark rate (the proportion of individuals with distinct markings) will also affect the precision of estimates of survival rate by changing the effective sample size. High mark rates result in a relatively large pool of individuals from which to estimate demographic parameters, whereas lower mark rates result in fewer individuals from which to estimate these parameters. Therefore, lower mark rates may be expected to result in lower precision by lowering effective sample size.

The central limit theorem states that if the sample size is large enough, the sampling distribution of means (or proportions) will be normally distributed, with the mean of the distribution equal to the population mean and variance equal to the population variance divided by the square root of the sample size (n). Thus, we can expect that as sample size increases, so does precision, with $CV \propto \frac{1}{\sqrt{n}}$. Thus, we may also assume that $CV \propto \frac{1}{\sqrt{MR}}$, where MR = mark rate. Although this relationship between sample size and precision is known, the magnitude of the change in precision as the mark rate of different populations declines is unknown and has important implications for study design.

The results of Chapter 3 suggest that the mark rate of Hector's dolphins at Banks Peninsula has decreased, most likely due to increased area-based protection from set netting. This may be a positive sign that Hector's dolphins are encountering fishing gear less frequently. A lowered mark rate, however, is likely to result in reduced precision in survival rate estimation. This could mean the very measures put in place to protect the species may make it more difficult to track the population's progress using capture-recapture models. Consequently, the Hector's dolphins at Banks Peninsula may provide insight on a little explored issue in photo-ID studies that rely on capture-recapture models: the effect of mark rate on precision of estimates of survival rate.

Therefore, the aim of this chapter is to determine whether mark rate of Hector's dolphins has a substantive effect on precision or not. Here, I

present a method for determining the magnitude of the effect of mark rate on the precision of estimates of survival rate, using the Hector's dolphins of Banks Peninsula as a case study.

Methods

Protocols for collecting capture-recapture data on Hector's dolphins at Banks Peninsula are described in Chapter 2 and in Slooten et al. (1992). These data have been collected at Banks Peninsula since 1984, with a gap only in 1998 – 1999 due to involvement in line-transect surveys (e.g. Dawson et al. 2004). Despite a change from manual focus equipment to autofocus in 1990, and from film to digital in 2001, photographic and cataloguing methods have remained broadly consistent.

In addition to the usual photo-ID surveys, each year between 1992 and 1996, as well as in 2016, a special effort was made to estimate mark rate (see Gormley et al. 2005). Chapter 2 explains the methods used for estimating mark rate in 2016, which used random photography as input for the SRCS method and hierarchical Bayesian model. The estimate of mark rate used for this study, 0.068, comes from rounding down (to give a more conservative estimate of available sample size) the estimate of mark rate using the hierarchical Bayesian model in Chapter 2 for 2016, which gave a mark rate of 0.0689 (95% HDI: 0.0491-0.0898).

Capture-recapture data on Hector's dolphins have been collected since 1984, but this study uses data collected between 1990 and 2015. The year 1990 was chosen as a start date for two reasons: set netting regulations first established in 1988 were fully in place (Dawson and Slooten 1993), and 1990 matches the time at which Gormley et al (2012) found an increase in survival rate. Choosing this start time avoids the added complexity of incorporating a change in survival rate in the capture-recapture modelling, allowing use of a constant-survival model to be a plausible choice. The years 1998, 1999, 2010, and 2014 were also excluded from the modelling of survival rate. The years 1998 and 1999 include no photo-ID data due to the researchers carrying out

a line-transect survey during those years. The years 2010 and 2014 have yet to have all photos fully matched to the catalogue.

Simulating capture histories

To simulate datasets representing different mark rates, I randomly drew from the individuals' known capture histories (a record of whether or not an individual was sighted in a given year). The photo-ID dataset contains 518 unique individuals (each individual has its own capture history, making an effective sample size (N_{eff}) of 518). Since we know the mark rate of the population is 0.068, we can estimate there is a maximum effective sample size of 7,617 encounterable individuals ($518 \div 0.068$). This is the maximum number of capture histories we could have in our dataset (i.e. our effective sample size if mark rate was 100%).

To determine how many capture histories (N_{eff}) to simulate for each mark rate of interest, the maximum N_{eff} (7,617) is multiplied by the desired mark rate:

$$N_{eff} = 7,617 \times \theta \quad (4.2)$$

where 7,617 is a constant, representing the *maximum* N_{eff} , and θ is the mark rate of interest. N_{eff} was then rounded to the nearest integer to give the number of capture histories to be sampled from the original dataset. A table showing the number of capture histories required for each mark rate is shown in Appendix 4.2.

Capture histories vary from one individual to another. Some individuals are seen (or "recaptured") many times, while others are rarely seen. To account for this, I wrote code in program R (R Core Team 2015) to randomly draw the required number of capture histories 10,000 times for each mark rate, with replacement, from the original dataset (see Appendix 4.2). This should ensure that a realistic variety of capture-recapture histories are included in each simulated dataset.

In an effort to explore the effect of realistic mark rates for a population of Hector's dolphins, datasets were created for mark rates ranging from 5% of total dolphins marked to 15% of total dolphins marked, spaced at 0.5% intervals. These simulated data were then used to bootstrap estimates of survival rate and their associated precision (fig. 4.1).

Capture-recapture models were run using RMark, an extension of MARK for use in program R (White and Burnham 1999; Laake 2013). A suite of Cormack-Jolly-Seber (CJS) models, allowing all combinations of constant or time varying survival and recapture probability, was constructed using the original dataset (see Appendix 4.2 for the model selection results). The best model (i.e. the best compromise between fit and complexity) was chosen via AICc (Burnham and Anderson 1998). A CJS model was chosen because the long-term nature of the dataset (25 years) requires the population to be considered "open" (i.e. births, deaths are known to have occurred, and emigration and immigration were highly likely).

The model with time-varying capture probability and constant survival was chosen and then applied to each set of capture histories. This resulted in 10,000 estimates of survival rate and its associated precision for each mark rate. The estimates were ranked by magnitude; the median of survival rate was taken from the 5,000th estimate, and the upper and lower 95% confidence intervals from the 250th and 9,750th estimates, respectively.

Standard error (SE) was calculated by MARK as the square root of the estimate of survival rate variance. CV was thus calculated for each estimate of survival rate as follows:

$$CV(\hat{\phi}) = \frac{SE(\hat{\phi})}{\hat{\phi}} \quad (4.1)$$

Where $SE(\hat{\phi})$ is the standard error of the survival rate (taken from the MARK output), and $\hat{\phi}$ is the estimate itself. CV was calculated for each survival rate estimate using the MARK output. Then, to obtain a bootstrapped estimate of the CV and how it varied at each mark rate, a median estimates of CV were

taken, as well as the 2.5th and 97.5th percentiles of CV of the 10,000 estimates. An example data output is given in Appendix 4.2.

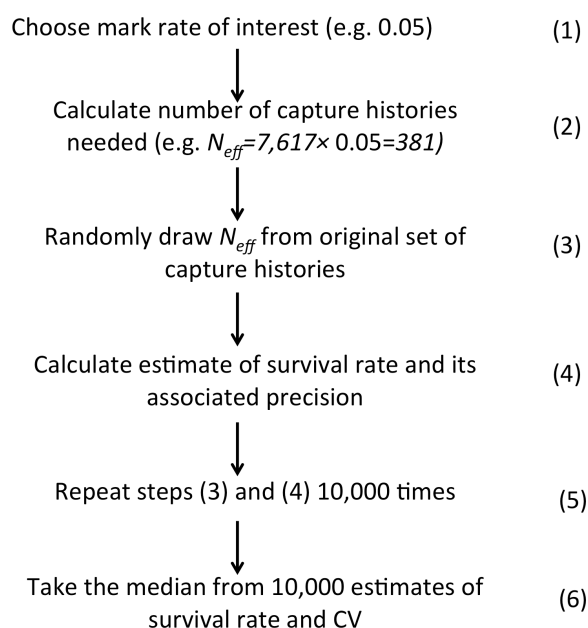


Figure 4.1: Flow chart summarising the steps for simulating capture histories and using them to bootstrap the precision of estimates of survival rate for one mark rate. In this example, a mark rate of 0.050 is chosen (meaning 5% of the animals are marked).

Results

The simulations show that as mark rate increases, the confidence interval around the estimate of survival rate narrows, indicating an increase in precision (fig. 4.2). However, no apparent bias occurred in the survival rate estimate as mark rate decreased, as all the estimates are very similar; median estimates ranged from 0.8942 – 0.8945, a 0.03% difference between the lowest and highest estimate.

The original dataset (which represents a mark rate of 0.068) produced a survival rate of 0.8940 (95% CI=0.8791 – 0.9073; SE=0.0072) (fig. 4.2). The precision of this estimate is higher than the precision of the bootstrapped dataset at a mark rate of 0.065 and 0.07 (fig. 4.2).

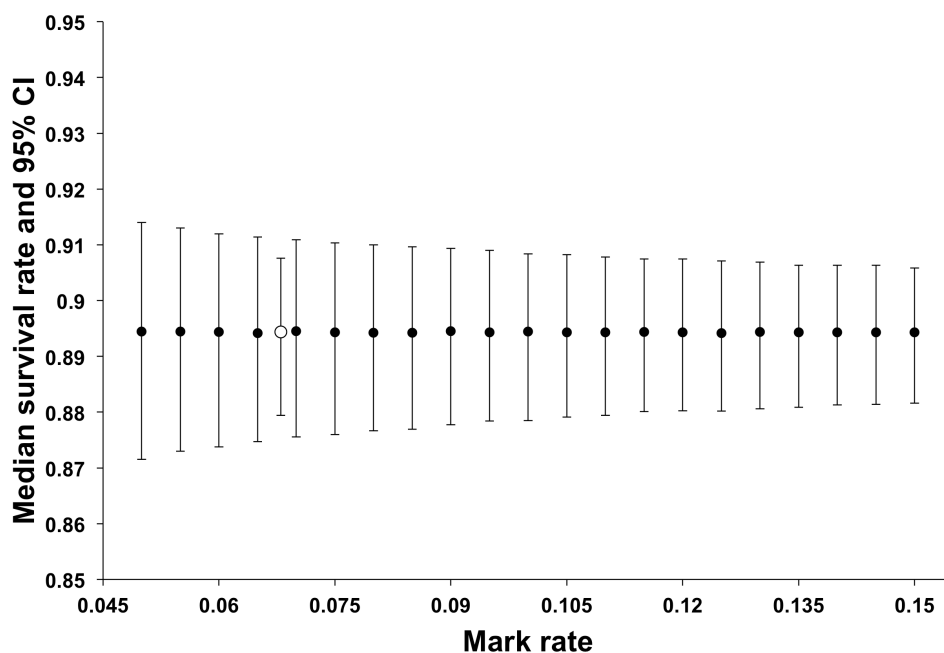


Figure 4.2: Bootstrapped median estimate of survival rate and 95% confidence interval from 10,000 simulations at each mark rate. The hollow point and its associated confidence interval represent the results of running the original dataset (not simulated).

Decreasing mark rate also clearly shows a decline in precision (fig. 4.3). Since every estimate of survival rate also produces an estimate of precision, bootstrapping survival rate also produces 10,000 coefficients of variation (CVs). Figure 4.3 plots the median of these 10,000 estimates of precision and its 95% CI (i.e. the precision of the estimate of precision). This plot shows that the variation in CV also increases with a decreasing mark rate (fig. 4.3). The median CV changed by 42% from the lowest simulated mark rate of 0.005 to the highest mark rate of 0.0165. The CV of the original dataset is about halfway between the simulated median CVs for a mark rate of 0.065 and 0.070 (fig. 4.3).

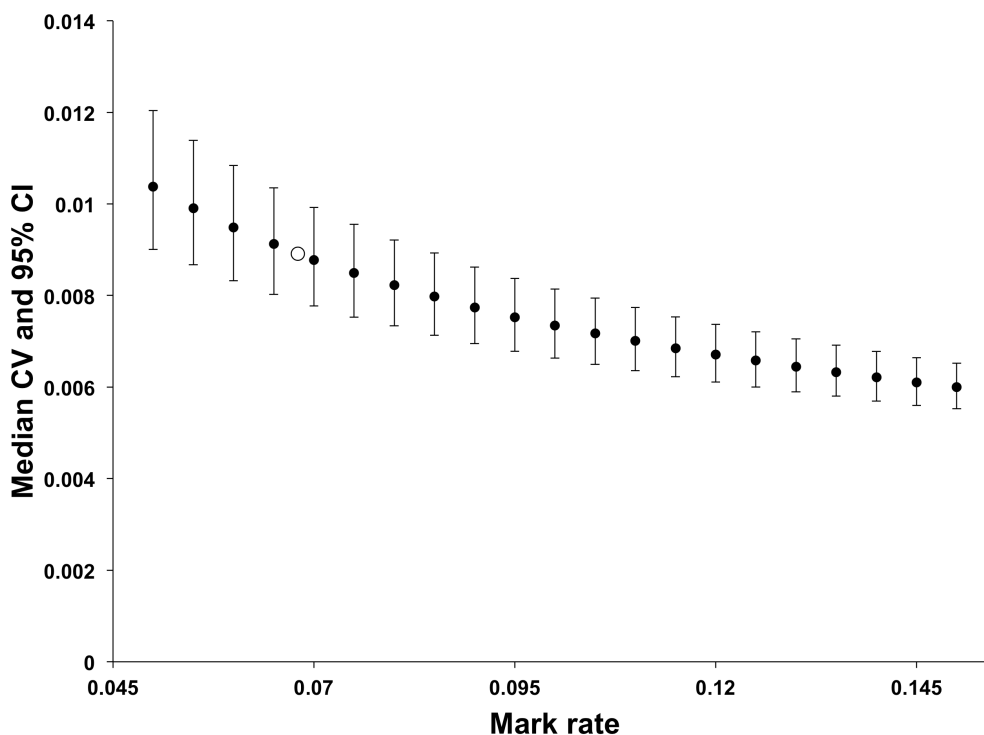


Figure 4.3: Bootstrapped median estimate of CV and its 95% confidence interval from 10,000 simulations at each mark rate. The hollow point represents the CV of running the original dataset (not simulated).

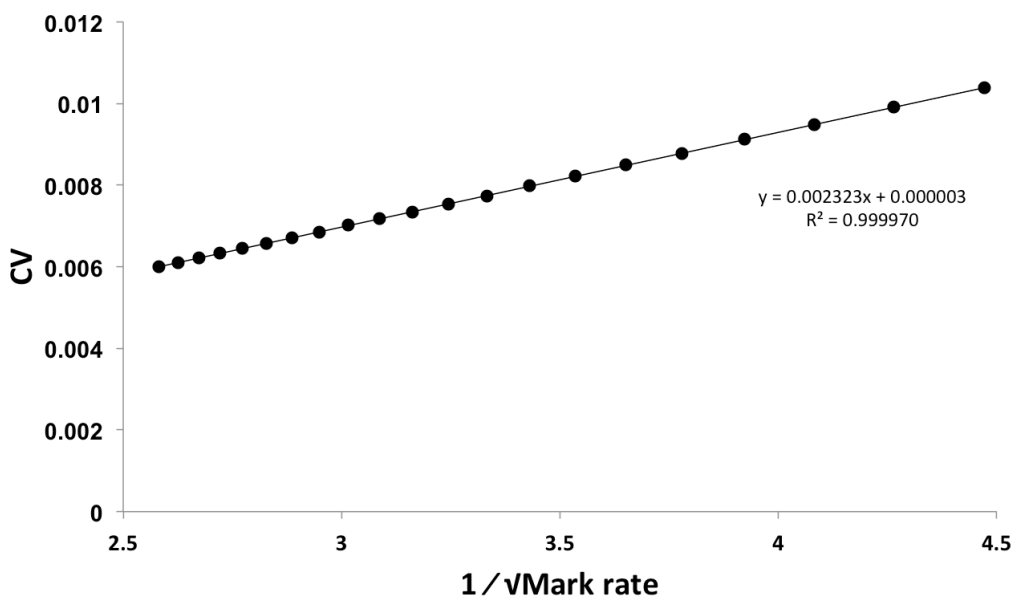


Figure 4.4: Bootstrapped median estimate of CV from 10,000 simulations at each mark rate, versus the inverse of the square root of each mark rate ($\frac{1}{\sqrt{\text{Mark rate}}}$).

Finally, the median CV is also displayed versus the inverse of the square root of mark rate. This relationship is established by the central limit theorem, which states that $CV \propto \frac{1}{\sqrt{n}}$, where n =sample size. Again, since mark rate is proportional to sample size, it may also be assumed that $CV \propto \frac{1}{\sqrt{MR}}$, where MR =mark rate. As expected, regressing CV vs $\frac{1}{\sqrt{MR}}$ led to a linear relationship (fig. 4.4, $R^2=1.00$), with a proportionality constant (slope) equal to 0.0023.

Discussion

The simulations above clearly show a decline in precision as mark rate decreases, with precision (CV) changing by 42% between a mark rate of 0.05 and 0.15. Although precision continued to increase as mark rate increased, this increase began to slow at a mark rate of about 0.11. As fig. 4.4 shows, CV is inversely proportional to the square root of mark rate. Declining precision at lower mark rates was expected given the decrease in the number of individual capture histories contributing to the estimation of survival rate. This conclusion parallels the central limit theorem, and follows other research on capture-recapture modelling that shows that as sample size decreases, so does precision.

This simulation is most analogous to the Pollock et al. (1990) simulation that shows as population size increases, so does the precision of estimates of survival rate. In both simulations, increasing the number of capture histories in the dataset improved precision. The necessary sample size for obtaining suitably precise population abundance estimates (for fin whales, *Balaenoptera physalus*, and blue whales, *Balaenoptera musculus*) has been examined by Hammond et al. (1990) and Joyce and Dorsey (1990). However, these studies looked at the number of whales that needed to be photo identified and the number of whales needing to be encountered (not the effect of mark rate explicitly).

What this study provides is a way of assessing the magnitude of the effect of mark rate on the precision of survival rate, for a specific population

of dolphins. The linear equation (from fig 4.4) can be used to determine how much CV will vary at different mark rates in our study, including at un-simulated mark rates. This is a useful tool for study planning. For example, these results could be used to determine the necessary mark rate for achieving certain precision levels, which can help to decide whether photo-ID is feasible given study aims.

In this simulation, there was no evidence that changing mark rate biased estimates of survival rate. Therefore, even at low mark rates, these results suggest that unbiased estimates can be obtained, albeit with lower precision (which is expected, as survival rate is asymptotically unbiased; Lebreton et al. 1992). This result, however, should be considered only in the context of the simulation, which simulated different but “constant” mark rates for this population. As shown in Chapter 3, there is evidence that mark rate is declining, and the process of a declining mark rate does have the potential to bias survival rate. At least for a period of time after the change in mark rate, the age-structure of individuals included in the dataset will have changed and it is likely that older individuals will be over-represented in the dataset. An age-structured population model is therefore necessary to test how this change in mark rate would affect estimates of survival rate.

Bootstrapped estimates of confidence intervals can overestimate variance (Kovar et al. 1988; Nelson 2014). This may be partly why the estimate from the un-simulated, original dataset has a lower confidence interval than the simulated, bootstrapped confidence intervals. It should therefore be noted that the confidence intervals in fig. 4.2 are most likely wider than those produced by the CJS model at a particular mark rate. The medians CVs in fig. 4.3, however, are likely a more accurate reflection of the actual precision at a particular mark rate.

A reduced ability to estimate precise survival rates as mark rate declines could have important implications for determining the effectiveness of conservation management for Hector’s dolphins at Banks Peninsula. Lowered precision decreases the ability to detect changes in survival rate, which could affect the ability to evaluate effectiveness of current

management. It is evident that current estimates of survival rate are less precise than they would have been had mark rate been higher. However, the long duration of the study and reasonably high capture probabilities may still make it possible to test hypotheses about survival. Despite a low mark rate, the survival rate estimated for this study was more precise than most other survival rates reported for dolphins (see Appendix 4.1). The survival rate estimated with the original dataset using the CJS model, 0.894 (SE=0.008; 95% CI=0.878 – 0.909) is slightly lower, but more precise than the survival rate estimated by Gormley et al.'s (2012) Bayesian capture-recapture model (0.917, 95% HDI=0.802 - 0.984), which was able to detect a change in survival rate due to area-based protection. This may be due to differences in the models used but also that the estimate here incorporates 7 years more data, which should improve precision. The lower survival rate reported here may reflect a slightly declining trend, since for this species, a 1% change in survival relates to almost a 1% change in population growth (Gormley et al. 2012). The goal of this study was only to test how precision of survival rate estimates changes with mark rate. Future research will investigate if survival rate has changed since the estimate published by Gormley et al. (2012).

In addition to a decrease in precision, as indicated by a higher CV, the estimate of the CV itself becomes more uncertain as mark rate decreases. This may be explained by variation in capture probability among individuals and sampling error as sample size decreases with a lower mark rate. Some heterogeneity of capture is expected, because some marked individuals are harder to photograph than others. Mothers with calves, for example, are typically less boat positive. The CJS model assumes that all animals have the same probability of being recaptured.

Past simulations of survival rates have shown that heterogeneity of capture causes only a very small, negative bias in survival rate estimation (Carothers 1979). However, even these small biases may impact projections of population growth rate (Fletcher et al. 2012). My results suggest that heterogeneity of capture may be expected to have a greater influence on precision of estimates of survival as mark rate declines. As mark rate declines,

fewer capture histories are available, and there is more chance of bias due to inclusion of individuals with unusually high or low capture probability. If a relatively large number of individuals with low capture probabilities are included in the sample, precision of the survival estimate will be lowered further than that caused by low mark rate (Lebreton et al. 1992).

In this study I chose to bootstrap from real capture histories, rather than artificially generate capture histories. This was done to increase realism, and ensure that all processes inherent in gathering the real data are represented in the simulations. It explores the effect of a decreasing mark rate in this population of Hector's dolphins in particular and therefore serves as a specific case study. Theory indicates, however, that the result that declining mark rate will act to decrease the precision of survival rate estimates applies generally. Specific details of the simulation, like the mark rate at which particular changes in precision are obtained and the variation in CV seen at low mark rates, should not be applied to other studies (however, the simulation methodology described here could be applied to other study populations). The main force behind the changes in precision seen here is due to the number of individuals included in the dataset. Therefore, if population size was larger, precision values at particular mark rates may be higher than reported here. Again, precision of capture-recapture studies also improves as the number of sampling occasions increases, as capture probability increases, and as abundance and survival rate increase (Pollock et al. 1990).

The simulation method described here provides a way for researchers to determine the effect of mark rate on precision in their own study populations. The results for this population of Hector's dolphins suggest that the precision of estimates of survival rate could be improved if the mark rate was higher. In addition to this method being applied to dolphin populations, it may also be useful for determining the effect of mark rate in other naturally marked wildlife populations. Considering the importance of photo-ID methodology for researching wildlife populations and the value of survival rates to

monitor population change, techniques to determine how different study elements (like mark rate) impact parameter precision will prove useful in the planning of current and future studies.

Chapter 5

General Discussion

The central aim of this thesis was to estimate the mark rate of a population of Hector's dolphins and to investigate the impact of low mark rates on the ability to estimate their survival rate. Chapter 2 highlighted that most current techniques for estimating the variance of mark rate assume simple random sampling of individuals, when in reality individuals in dolphin populations are usually encountered in groups. This means that the photographs taken of individuals within a group cannot be regarded as truly independent, and hence that variance of mark rate is likely to be underestimated. Eguchi (2014) addressed this problem via a Bayesian model that better accounts for uncertainty when estimating mark rate from dolphin groups. In Chapter 2, I compared the estimates obtained from this Bayesian method with frequentist solutions. The 2016 mark rate was estimated as 0.065 (95% CI=0.047–0.084) using the SRCS method, and 0.069 (95% HDI=0.049–0.090) using the Bayesian model (SRCS–Bayes). Mark rate was lower in 2016 compared to the average rate for the period spanning 1992 – 1996, most likely due to area-based protection measures reducing the prevalence of marks caused by nonfatal encounters with fishing gear (Chapter 3). However, whether this difference was “statistically significant” was method dependent, with only the Bayesian method indicating a strong probability of decline. In Chapter 4, the potential consequences of a low mark rate on monitoring survival rate in this population were explored through simulation. It showed that although there was no evidence for estimates of survival rate being biased, they did become less precise.

As reviewed in Chapter 2, many studies estimating abundance from photo-ID data underestimate the uncertainty in their final abundance estimate by not accounting for the variance of mark rate correctly. Photo-ID studies should be using variance terms that incorporate the cluster-sampling element of collecting data from groups. Additionally, estimates of mark rate

need to be based on an un-biased sampling protocol, such as taking photos randomly and proportionately to group size (c.f. Parra et al. 2006; Nicholson et al. 2012; Vermeulen and Bräger 2015).

The comparison of different estimation strategies for mark rate (Chapter 2) has applications for other research goals, besides adjusting estimates of abundance. Several recent studies have investigated how mark prevalence relates to environmental factors, such as predation, fisheries pressure, and aggression (Heithaus 2001; Kiszka et al. 2008; Baird et al. 2014; Kügler and Orbach 2014). Future projects could apply the recommendations in Chapter 2 to estimating the proportion of different “types” of marks in a population, and hence gain insight into impacts. Photo-ID projects could also apply similar sampling and estimation strategies to other proportions. For example, if a species is sexually dimorphic, the same estimation strategies could be applied to determine the relative proportion of males and females in a population. Similarly, if individuals can be split into different age classes from photographs, photo-ID data could also be used to estimate age structure of the population.

Although the Bayesian model can estimate group-specific mark rates, only the estimate of population-level mark rate was displayed in this work. The small group sizes and low mark rate in this population of Hector’s dolphins means that the group-specific mark rates estimated by the Bayesian model should be interpreted with caution. Because of the hierarchical structure of the model, the estimate of mark rate for a specific group is affected by two sources: (1) each group’s data, which is the number of images of marked individuals and total images obtained for that group, and (2) the higher-level distribution of population-level mark rate, which is affected by the data from all groups. Both sources affect the result for each group-specific mark rate. Therefore, if the true mark rate of a group is zero (which occurs often in this population of Hector’s dolphins due to low group sizes and a low mark rate), the estimate of group-specific mark rate will be shifted upwards towards the mark rate of the population. This is an important consideration when using the model for a population like this, where the small group sizes

and low mark rate means that many groups have a true mark rate of 0%. Since the Bayesian model uses group-specific estimates of mark rate to determine group size, the estimates of group size given by the model would also be inaccurate for many groups.

Bias in estimates of group-specific mark rates may not matter if researchers are only interested in estimating the population-level mark rate (which is used for scaling abundance estimates), as long as this estimate is unbiased. Both the SRCS method and Bayesian model produced similar estimates in 2016, but the 1992 – 1996 results differed. While it is clear that these two analysis methods produced different results, it is not yet clear which estimate is closer to the “true” mark rate of the population. The difference is relatively small. In the future, the amount of bias caused by the use of different sampling and estimation strategies for mark rate could be explored via simulation.

The evidence for a change in mark rate in Chapter 3 suggests that long-term photo-ID studies should not assume that mark rate will remain stable over time, and researchers should consider whether a change in the environment or management intervention may have influenced the mark rate of their study species. Clearly, if calculating a new estimate of abundance, recent data on mark rate should be used to adjust the estimate.

While no causal link between the decline in mark rate and a reduction in fisheries interactions could be established in this study, this is a parsimonious explanation, especially considering the increase in survival rate shown by Gormley et al. (2012). A stronger link could be established if marks were categorised by source for different time periods. A future study could examine changes in the proportion of marks likely to have been caused by fishing incidents. Mark categorisation has been done in other populations (e.g. Baird et al. 2014; Kügler and Orbach 2014). There is always a subjective element in doing so, and it is unknown at present how well this methodology would translate to Hector’s dolphins. Creating a catalogue of marks due to known causes, and a set of decision rules in allocating likely cause, would be an essential first step. It is clear, however, that the low overall mark rate of

Hector's dolphins would mean that sample size in any one category of cause would be small.

This thesis shows that mark rate should be considered, along with other elements of study design, such as number of sampling periods, population size, and capture probability, as a contributor to the precision of estimates of demographic parameters. Researchers may need to make different decisions on study design depending on the mark rate in their study population. Decreasing precision of estimates of survival rate, as observed in Chapter 4, will reduce ability to detect population trends. This could be further investigated by simulating capture histories with the same capture probabilities as the original dataset, but with a decreased survival rate. Different mark rates could be simulated as in Chapter 4, with results summarised as the proportion of model runs that correctly detect the change in survival rate.

Implications for monitoring Hector's dolphins

Although the decline in mark rate indicated in Chapter 3 provides further evidence for the efficacy of area-based protection measures (a positive sign that conservation is working), it is a catch-22 from a scientific monitoring perspective. The lower mark rate will reduce the precision of estimates of survival rate, making it more difficult to use survival rates to monitor population status (e.g. Gormley et al. 2012). Considering the low mark rate estimated in 2016, and evidence that declines in precision occur more rapidly below a mark rate of 0.11, it may be necessary to investigate alternative sampling methodologies or alternative analytical methods for estimating survival rate.

In some dolphin populations, natural marks are supplemented with artificial tags or marks (e.g. Irvine et al. 1982; Mintzer et al. 2013). This method requires temporary capture of animals and the mark itself causes injury. Since the tagged animal is not likely to remain neutral about the procedure, some behavioural response might be expected, and this could act

to increase heterogeneity of capture probability. For example, in Doubtful Sound, NZ bottlenose dolphins (*Tursiops truncatus*) showed avoidance of the research vessel (less bow-riding and surfacing further away) for more than ten days after being tagged with a suction cup (Schneider and Baird 1998). In addition, the effects of tagging might act to decrease survival and reproduction. In some populations, certain tagging techniques have not shown significant effects on survival (e.g. radio transmitters on Amazon river dolphins, *Inia geoffrensis*, Martin et al. 2006; livestock tags on Hawaiian monk seals, *Monachus schauinslandi*, Baker and Johanos 2002; and hot branding of southern elephant seals, *Mirounga leonina*, McMahon et al. 2006), but it is likely that effects of tagging on cetaceans will vary by species, and the type of artificial mark (Walker et al. 2012). Also, finding no effect of a tag on survival should not be interpreted as there being no effect on survival, as tagging studies generally have low statistical power to detect a difference (Godfrey and Bryant 2003).

Potential effects of tagging on demographic parameters have been observed in a range of species. For example, applying flipper tags to king penguins (*Aptenodytes patagonicus*) has been shown to dramatically decrease survival rate (Gauthier-Clerc et al. 2004; Saraux et al. 2011). Hastings et al. (2009) found that branding Steller sea lion (*Eumetopias jubatus*) pups contributed to 0.5 – 0.7% of mortality in the 12 weeks post branding. Gendron et al. (2015) describe swelling from implantation of a satellite tag on a blue whale (*Balaenoptera musculus*) that lasted eight years, which may have affected the whale's ability to reproduce. The whale was not seen with a calf for 15 years after being observed with swelling from the tag, but had previously reared 2 calves in 3 years (Gendron et al. 2015). Additionally, responsible capture and release of animals, especially of cetaceans (for which permanent tags may require capture and even temporary removal from water), requires expert training and specialised equipment. This process will also incur higher costs as a result. Artificial markings are normally applied to a very small portion of a population, due to cost and the practical considerations above. Therefore, this method will also

be even more strongly affected by small sample size than using natural markings.

Genetic capture-recapture does not require animals to be naturally marked. Genetic capture-recapture distinguishes among individuals by identifying unique sequences of their nuclear DNA (e.g. Baker et al. 2013). This method has been used to estimate abundance in several cetacean species, including Hector's dolphins (Hamner et al. 2017) and the subspecies *Cephalorhynchus hectori maui* (Baker et al. 2013). If the purpose of the research is exclusively to determine abundance, genetic capture-recapture can provide greater precision in the final abundance estimate than using photo-ID (Hamner et al. 2017). However, genetic capture-recapture is invasive in that small pieces of tissue need to be collected (usually from biopsy darts fired by a rifle or crossbow). Additionally, if the goal of a study is to obtain estimates of survival rate, animals need to be "recaptured" many times, meaning they would be repeatedly biopsied over many years. Again, biopsy, especially multiple biopsies, could affect behaviour and negatively bias estimates of survival rate. While most published studies do not report significant adverse behavioural or health effects in the short-term (see Noren and Mocklin 2012), the long-term, cumulative effect of multiple biopsies is unknown. Even single biopsy events are not without risk; Bearzi (2000) reported the death of a common dolphin (*Delphinus delphis*) after a biopsy. Although this is the only reported known death due to biopsy, most biopsy studies do not involve sufficient follow-up observations to accurately determine the health and behavioural impacts of the technique. Additionally, the photo-ID catalogue contains sightings from several hundred individuals, resighted over several decades. A genetic mark-recapture study with a similar sample size would be prohibitively expensive and would likely cause substantial disturbance to the population.

To reduce cost to researchers and minimise stress and ill effects to this endangered species, non-invasive methods to either increase the mark rate or develop alternative ways of estimating survival rate should be explored. The simplest approach would be to extend the capture-recapture

analyses to individuals with more subtle marks, for example by including category 3 marks (Slooten et al. 1992). This would require greater matching effort, although this may be mitigated with automated matching (e.g. Kelly 2001; Adams et al. 2006; Kniest et al. 2009). Also, additional work would be needed to determine whether inclusion of these mark types causes bias in survival estimates. In addition to nicks, notches, colouration markings and scars, Hector's dolphins also have varying fin shapes. Lasermetric photogrammetry has been successfully used on Hector's dolphins (Webster et al. 2010), and could be used to measure fin shape and size. As fin shape and size may change over the course of a dolphin's lifespan, an additional study would need to be carried out to track the permanence of this type of mark. This could be investigated by tracking change in fin size and shape in animals with additional marks (e.g. nicks in the dorsal fin). Likewise, it would be useful to track the permanence of more subtle markings (e.g. tattoo lesions caused by pox virus) on individuals who also have obvious markings known to persist over long periods of time (e.g. large fin nicks).

Looking beyond traditional Cormack-Jolly-Seber models may offer improvements in terms of data analysis. For example, Zipkin et al. (2014) developed a method for determining demographic parameters (including survival rate) using direct counts and size/age distributions. Webster et al. (2010) developed a photogrammetry technique for measuring the length of Hector's dolphins at Banks Peninsula and used these measurements to assign dolphins to different age and maturity classes. Applying Zipkin et al.'s (2014) model to Hector's dolphins might therefore be possible. Exclusive use of this method, however, would not provide the additional information that photo-ID data provide, such as movement patterns and social associations. It could be possible though, especially in a Bayesian context, to combine this sort of information with mark-recapture approaches (see Brooks et al. 2004; Wilson et al. 2016).

Another analytical alternative would be to take advantage of the fact that high capture probabilities (the probability an individual is "seen" in a year) also contribute to precision of estimates of survival rate (Pollock et al.

1990). This could be done by weighting the capture-recapture analysis according to where intensive field effort and sighting locations overlap. For example, if a dolphin normally seen near the centre of intensive field effort goes unseen for multiple years, we could be more confident of its disappearance than for an individual seen only on the outskirts of the study area. Individuals seen near the centre of field effort likely have higher recapture probabilities, which would increase precision if capture-recapture analyses put more weight on these individuals' capture histories when calculating survival probabilities. This type of analysis could be completed in a spatially-explicit capture-recapture framework (see Borchers and Efford 2008; Saracco et al. 2010).

Another option may be to modify the fieldwork schedule. Different allocations of field effort might influence precision (e.g. intensive sighting effort every 3 years, rather than a moderate level of sighting effort every year). For example, would it be best to concentrate effort at a particular time of year? Or would higher precision be obtained by smaller amounts of sampling effort spread over a longer period (e.g. sampling for 12 weeks during summer vs. 1 week every month)? These questions could be addressed via simulation. Alternatively, the effect of existing variability in the dataset could be explored, since some years have more photo-ID effort than others.

Compared to other dolphin species and populations, this population of Hector's dolphins has the lowest mark rate recorded in the literature. This mark rate is notably low compared to other well studied dolphin species like bottlenose dolphins and killer whales (e.g. Wilson et al. 1999; Kuningas et al. 2013). However, this study of Hector's dolphins deliberately focuses on very obvious markings, because estimating survival is the main focus. Expanding the dataset to more subtle markings could substantially increase mark rate. As photo-ID methods continue to be applied to more species (including non-cetaceans, such as sharks; Castro and Rosa (2005)) other research teams will also encounter low mark rates and may wish to consider the analysis alternatives presented here.

Future directions

The text above described limitations in the results of this thesis, and provided potential strategies for addressing those issues in future work. Possible solutions for studying a population with a low mark rate were also discussed, but the issue of a low or declining mark rate remains a little studied issue in photo-ID studies. A few suggestions for further research are therefore offered below.

- If the population is roughly stable, a declining mark rate implies that fewer young animals are gaining marks. In this case individuals that are marked may represent a subset of the population that is older than average. Estimating survival rate from a sample of the population that is older than average may bias survival rates, depending on the exact mix of young and old individuals. Very young as well as very old individuals have the lowest survival rates, with the highest survival achieved around the middle of life. Therefore, it would be useful to explore effects on survival rate of an aging marked population and the process of mark rate changing through time.
- Low mark rates may also have other consequences for photo-ID studies besides a decline in precision of demographic parameters, such as reduced ability to quantify social structure and associations. Presumably, as mark rate decreases, associations between individuals will become more difficult to detect. The severity of these impacts may also be explored through simulation strategies.
- Investigations of better sampling design and analysis of capture-recapture experiments to improve the precision of demographic parameters would benefit future studies. Should capture histories be weighted by capture probability? Should certain areas of a field site be concentrated on? How should the fieldwork schedule be distributed across time and space? Additionally, an investigation into further estimation strategies, such as combining photo-ID data with life

history data (e.g. frequency of maturity classes observed), could also improve estimates of demographic parameters.

Capture-recapture methods have been used to study cetacean populations for decades. Incremental improvements to these models and data collection continue to be made so that these models can be applied to a wider variety of species and populations. However, how low or changing mark rates affect the results of these models is rarely considered. This thesis stresses the importance of considering the effects of a low mark rate, and highlights the need for novel methods to gather and analyse capture-recapture data. This is especially true when the results are critical for conservation management, as is the case with Hector's dolphins.

References

- Adams, J. D., T. Speakman, E. Zolman, and L. H. Schwacke. 2006. Automating image matching, cataloging, and analysis for photo-identification research. *Aquatic Mammals* 32 (3): 374–84.
- Alves, F., A. Dinis, C. Nicolau, M. Kaufmann, C. Fortuna, and L. Freitas. 2014. Survival and abundance of short-finned pilot whales in the Archipelago of Madeira, NE Atlantic. *Marine Mammal Science* 31 (1): 106–21.
- Baird, R. W., and A. M. Gorgone. 2005. False killer whale dorsal fin disfigurements as a possible indicator of long-line fishery interactions in Hawaiian waters. *Pacific Science* 59 (4): 593–601.
- Baird, R. W., S. D. Mahaffy, A. M. Gorgone, T. Cullins, D. J. McSweeney, E. M. Oleson, A. L. Bradford, J. Barlow, and D. L. Webster. 2014. False killer whales and fisheries interactions in Hawaiian waters: evidence for sex bias and variation among populations and social groups. *Marine Mammal Science* 31 (2): 579–90.
- Baker, C. S., R. M. Hamner, J. Cooke, D. Heimeier, M. Vant, D. Steel, and R. Constantine. 2013. Low abundance and probable decline of the critically endangered Maui's dolphin estimated by genotype capture-recapture. *Animal Conservation* 16 (2): 224–33.
- Balmer, B.C., Wells, R.S., Nowacek, S.M., Nowacek, D.P., Schwacke, L.H., McLellan, W.A., Scharf, F.S., Rowles, T.K., Hansen, L.J., Spradlin, T.R., Pabst, D.A. 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *Journal of Cetacean Research and Management* 10 (2): 157–67.
- Baker, J. D., and T. C. Johanos. 2002. Effects of research handling on the endangered Hawaiian monk seal. *Marine Mammal Science* 18 (2): 500–12.
- Ballance, L. T. 1990. Residence patterns, group organization, and surfacing associations of bottlenose dolphins. In *The Bottlenose Dolphin*, edited by Stephen Leatherwood and Randall R. Reeves, 267–83. Academic Press,

References

Inc.

- Barlow, J., J. Calambokidis, E. A. Falcone, C. S. Baker, A. M. Burdin, P. J. Clapham, J. K. B. Ford, C. M. Gabriele, R. LeDuc, and D. K. Mattila. 2011. Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. *Marine Mammal Science* 27 (4): 793 - 818.
- Baum, J. K., Ransom A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299: 389–92.
- Bearzi, G.. 2000. First report of a common dolphin (*Delphinus delphis*) death following penetration of a biopsy dart. *Journal of Cetacean Research and Management* 2 (3): 217–21.
- Bearzi, G., G. Notarbartolo-di-Sciara, and E. Politi. 1997. Social ecology of bottlenose dolphins in the Kvarnerić (Northern Adriatic Sea). *Marine Mammal Science* 13 (4): 650–68.
- Beasley, I., K. Pollock, T. A. Jefferson, P. Arnold, L. Morse, S. Yim, S. L. Kim, and H. Marsh. 2013. Likely future extirpation of another Asian river dolphin: the critically endangered population of the Irrawaddy dolphin in the Mekong River is small and declining. *Marine Mammal Science* 29 (3): 226–52.
- Bigg, M.A., G.M. Ellis, J.K.B. Ford, and K.C. Balcomb. 1987. *Killer whales. A study of their identification, genealogy, and natural history in British Columbia and Washington state*. Nanaimo, BC, Canada: Phantom Press.
- Bogstad, B., M. Pennington, and J. H. Vølstad. 1995. Cost-efficient survey designs for estimating food consumption by fish. *Fisheries Research* 23 (1–2): 37–46.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64 (2): 377–85.
- Bradford, A. L., D. W. Weller, Y. V. Ivashchenko, A. M. Burdin, and R. L.

References

- Brownell. 2009. Anthropogenic scarring of Western gray whales (*Eschrichtius robustus*). *Marine Mammal Science* 25 (1): 161–75.
- Bräger, S. 1999. Association patterns in three populations of Hector's dolphin, *Cephalorhynchus hectori*. *Canadian Journal of Zoology* 77 (1): 13–18.
- Brooks, L., C. Palmer, A. D. Griffiths, and K. H. Pollock. 2017. Monitoring variation in small coastal dolphin populations: an example from Darwin, Northern Territory, Australia. *Frontiers in Marine Science* 4 (94): 1–16.
- Brooks K., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27 (1): 515–29.
- Brown, A. M., L. Bejder, K. H. Pollock, and S. J. Allen. 2016. Site-specific assessments of the abundance of three inshore dolphin species to inform conservation and management. *Frontiers in Marine Science* 3 (4): 1–18.
- Burnham, K.P., and R. Anderson. 1998. *Model Selection and Inference*. Berlin, Germany: Springer-Verlag.
- Cagnazzi, D., G. J. Parra, S. Westley, and P. L. Harrison. 2013. At the heart of the industrial boom: Australian snubfin dolphins in the Capricorn Coast, Queensland, need urgent conservation action. *PLoS ONE* 8 (2): e56729.
- Calambokidis, J., J. Barlow, J. K. B. Ford, T. E. Chandler, and A. B. Douglas. 2009. Insights into the population structure of blue whales in the Eastern North Pacific from recent sightings and photographic identification. *Marine Mammal Science* 25 (4): 816–32.
- Caldwell, D.K. 1955. Evidence of Home Range of an Atlantic Bottlenose Dolphin. *Journal of Mammalogy* 36: 304–5.
- Cameron, C., R. Barker, D. Fletcher, E. Slooten, and S. Dawson. 1999. Modelling Survival of Hector's Dolphins around Banks Peninsula, New Zealand. *Journal of Agricultural, Biological, and Environmental Statistics* 4 (2): 126–35.

References

- Cantor, M., L. L. Wedekin, F. G. Daura-Jorge, M. R. Rossi-Santos, and P. C. Simões-Lopes. 2012. Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study. *Marine Mammal Science* 28 (1): 63–83.
- Carothers, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology* 48 (3): 863–69.
- Carroll, E. L., N. J. Patenaude, S. J. Childerhouse, S. D. Kraus, R. M. Fewster, and C. S. Baker. 2011. Abundance of the New Zealand subantarctic southern right whale population estimated from photo-identification and genotype mark-recapture. *Marine Biology* 158: 2565–75.
- Castro, A. L. F., and R. S. Rosa. 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol Das Rocas Biological Reserve, Brazil. *Environmental Biology of Fishes* 72: 213–21.
- Chan, S. C. Y., and L. Karczmarski. 2017. Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong: modelling demographic parameters with mark-recapture techniques. *PLoS ONE* 12 (3): 1–28.
- Childerhouse, S. J., S. M. Dawson, and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New-Zealand. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* 73 (4): 723–31.
- Cochran, W. G. 1977. *Sampling Techniques*. 3rd ed. New York: John Wiley & Sons, Inc.
- Coimbra, Z. H., C. A. Assis, V. M. F. da Silva, and M. E. dos Santos. 2015. Mark-recapture abundance estimate of tucuxi dolphins (*Sotalia fluviatilis*) in a lake system of the central Amazon. *Marine Mammal Science*. 32(1): 241-51.
- Compagno, L.J.V. 2005. *Notorynchus cepedianus*. *IUCN Red List of Threatened Species*. www.iucnredlist.org.
- Corkeron, P. J., R. J. Morris, and M. M. Bryden. 1987. Interactions between

References

- bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquatic Mammals* 13 (3): 109–13.
- Corkrey, R., S. Brooks, D. Lusseau, K. M. Parsons, J. W. Durban, P. S. Hammond, and P. M. Thompson. 2008. A Bayesian capture–recapture population model with simultaneous estimation of heterogeneity. *Journal of the American Statistical Association* 103 (483): 948–60.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51 (3): 429–38.
- Crone, E. E. 2001. Is survivorship a better fitness surrogate than fecundity? *Evolution* 55 (12): 2611–14.
- Currey, R. J.C., S. M. Dawson, E. Slooten, K. Schneider, D. Lusseau, O. J. Boisseau, P. Haase, and J. A. Williams. 2009. Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: an information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 658–70.
- Daura-Jorge, F. G., S. N. Ingram, and P. C. Simões-Lopes. 2013. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. *Marine Mammal Science* 29 (2): 293–311.
- Dawson, S. M., and E. Slooten. 1993. Conservation of Hector’s dolphins: the case and process which led to establishment of the Banks Peninsula Marine Mammal Sanctuary. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3 (3): 207–21.
- Dawson, S., E. Slooten, S. DuFresne, P. Wade, and D. Clement. 2004. Small-boat surveys for coastal dolphins: line-transect surveys for Hector’s dolphins (*Cephalorhynchus hectori*). *Fishery Bulletin* 102 (3): 441–51.
- Deecke, V. B., M. Nykänen, A. D. Foote, and V. M. Janik. 2011. Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology* 13: 79–88.

References

- Dillingham, P., and D. Fletcher. 2008. Estimating the Ability of Birds to Sustain Additional Human-Caused Mortalities Using a Simple Decision Rule and Allometric Relationships. *Biological Conservation* 141: 1783–92.
- Dulau, V., V. Estrade, and J. Fayan. 2017. Identifying key demographic parameters of a small island-associated population of Indo-Pacific bottlenose dolphins (Reunion, Indian Ocean). *PLoS ONE* 12 (6): 1–19.
- Efron, B., 1982. *The jackknife, the bootstrap and other resampling plans*. Society for industrial and applied mathematics.
- Eguchi, T. 2014. Estimating the proportion of identifiable individuals and group sizes in photographic identification studies. *Marine Mammal Science* 30 (3): 1122–39.
- Esteban, R., P. Verborgh, P. Gauffier, J. Giménez, C. Guinet, and R. de Stephanis. 2016. Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. *Biological Conservation* 194: 31–38.
- Fearnbach, H., J. Durban, K. Parsons, and D. Claridge. 2012. Photographic mark-recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications* 22 (5): 1689–1700.
- Field, C.A., and A.H. Welsh. 2007. Bootstrapping clustered data. *Journal of the Royal Statistical Society. Series B (Statistical Methodology)* 69 (3): 369–90.
- Fletcher, D., J. D. Lebreton, L. Marescot, M. Schaub, O. Gimenez, S. Dawson, and E. Sloaten. 2012. Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. *Methods in Ecology and Evolution* 3 (1): 206–16.
- Forcada, J., and A. Aguilar. 2000. Use of photographic identification in capture-recapture studies of Mediterranean monk seals. *Marine Mammal Science* 16 (4): 767–93.
- Foster, G., H. Krijger, and S. Bangay. 2007. Zebra fingerprints: towards a

References

- computer-aided identification system for individual zebra. *African Journal of Ecology* 45 (2): 225–27.
- Fruet, P. F., F. G. Daura-Jorge, L. M. Möller, R. C. Genoves, and E. R. Secchi. 2015. Abundance and demography of bottlenose dolphins inhabiting a subtropical estuary in the southwestern Atlantic Ocean. *Journal of Mammalogy* 96 (2): 332–43.
- Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs* 68 (3): 349–70.
- Gauthier-Clerc, M., J. P. Gendner, C. A. Ribic, W. R. Fraser, E. J. Woehler, S. Descamps, C. Gilly, C. Le Bohec, and Y. Le Maho. 2004. Long-term effects of flipper bands on penguins. *Proceedings of the Royal Society* 271 (Suppl 6): S423–26.
- Gelman, A., J.B Carlin, H.S. Stern, and D.B. Rubin. 2003. *Bayesian data analysis*. 2nd ed. Boca Raton, FL: Chapman & Hall/CRC.
- Gendron, D., I. Martinez Serrano, A. Ugalde de la Cruz, J. Calambokidis, and B. Mate. 2015. Long-term individual sighting history database: an effective tool to monitor satellite tag effects on cetaceans. *Endangered Species Research* 26: 235–41.
- Gibson, Q. A. 2006. Non-lethal shark attack on a bottlenose dolphin (*Tursiops sp.*) calf. *Marine Mammal Science* 22 (1): 190–97.
- Godfrey, J. D., and D. M. Bryant. 2003. Effects of radio transmitters: review of recent radio-tracking studies. *Science for Conservation* 214: 83–95.
- Gormley, A. M. 2010. Population modelling of Hector's dolphins: a thesis submitted for the degree of Doctor of Philosophy at the University of Otago, Dunedin, New Zealand. University of Otago.
- Gormley, A. M., E. Slooten, S. Dawson, R. J. Barker, W. Rayment, S. Du Fresne, and S. Bräger. 2012. First evidence that marine protected areas can work for marine mammals. *Journal of Applied Ecology* 49 (2): 474–80.

References

- Gormley, A. M., S. M. Dawson, E. Slooten, and S. Bräger. 2005. Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* 21 (2): 204–16.
- Hammond, P. S., S. A. Mizroch, and Eds. Donovan, G. P. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Report of the International Whaling Commission*. Special Issue 12.
- Hamner, R. M., R. Constantine, R. Mattlin, R. Waples, and C. S. Baker. 2017. Genotype-based estimates of local abundance and effective population size for Hector's dolphins. *Biological Conservation* 211: 150–60.
- Hastings, K. K., T. S. Gelatt, and J. C. King. 2009. Postbranding survival of steller sea lion pups at Lowrie Island in southeast Alaska. *Journal of Wildlife Management* 73 (7): 1040–51.
- Hebeisen, C., J. Fattebert, E. Baubet, and C. Fischer. 2008. Estimating wild boar (*Sus scrofa*) abundance and density using capture–resights in Canton of Geneva, Switzerland. *European Journal of Wildlife Research* 54 (3): 391–401.
- Heithaus, R. 2001. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. *Marine Mammal Science* 17 (3): 526–39.
- Henderson, J. R., and T. C. Johanos. 1988. Effects of tagging on weaned Hawaiian monk seal pups. *Wildlife Society Bulletin* 16 (3): 312–17.
- Henry, G. T. 1990. *Applied social research methods: practical sampling*. SAGE Publications Ltd.
- Higgins, L. V., D. P. Costa, A. C. Huntley, and B. J. Le Boeuf. 1988. Behavioral and physiological measurements of maternal investment in the steller sea lion, *Eumetopias jubatus*. *Marine Mammal Science* 4 (1): 44–58.
- Huang, S. L., W. L. Chang, and L. Karczmarski. 2014. Population trends and vulnerability of humpback dolphins *Sousa chinensis* off the west coast of

References

- Taiwan. *Endangered Species Research* 26: 147–59.
- Hunt, T. N., L. Bejder, S. J. Allen, R. W. Rankin, D. Hanf, and G. J. Parra. 2017. Demographic characteristics of Australian humpback dolphins reveal important habitat toward the southwestern limit of their range. *Endangered Species Research* 32: 71–88.
- Ingram, S. N., and E. Rogan. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series* 244: 247–55.
- Irvine, A. B., R. S. Wells, and M. D. Scott. 1982. An evaluation of techniques for tagging small odontocete cetaceans. *Fishery Bulletin* 80 (1): 135–43.
- Jolly, G M. 1963. Estimates of population parameters from multiple recapture data with both death and dilution-deterministic model. *Biometrika* 50 (1/2). Biometrika Trust: 113–28.
- . 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52 (1/2): 225–47.
- Joyce, G.G., and E.M. Dorsey. 1990. A Feasibility Study on the Use of Photo-Identification Techniques for Southern Hemisphere Minke Whale Stock Assessment. *Report of the International Whaling Commission (Special Issue 12)* 12: 419–23.
- Katona, S. K., and H. P. Whitehead. 1981. Identifying humpback whales using their natural markings. *Polar Record* 20 (128): 439–44.
- Kelly, M. J. 2001. Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. *Journal of Mammalogy* 82 (2): 440–49.
- Kelly, M. J., and S. M. Durant. 2000. Viability of the Serengeti cheetah population. *Conservation Biology* 14 (3): 786–97.
- Kéry, M., and M. Schaub. 2011. *Bayesian population analysis using WinBUGS. A hierarchical approach*. Academic Press.

References

- Kiszka, J., D. Pelourdeau, and V. Ridoux. 2008. Body scars and dorsal fin disfigurements as indicators interaction between small cetaceans and fisheries around the Mozambique Channel Island of Mayotte. *Western Indian Ocean Journal of Marine Science* 7 (2): 185–93.
- Kniest, E., D. Burns, and P. Harrison. 2009. Fluke matcher: a computer-aided matching system for humpback whale (*Megaptera novaengliae* flukes). *Marine Mammal Science* 26 (3): 744–56.
- Kovar, J. G., J. N. K. Rao, and C. F. J. Wu. 1988. Bootstrap and other methods to measure errors in survey estimates. *The Canadian Journal of Statistics* 16: 24–45.
- Kruschke, J. K. 2011. *Doing Bayesian data analysis*. New York: Academic Press/Elsevier.
- Kügler, A., and D. N. Orbach. 2014. Sources of notch and scar patterns on the dorsal fins of dusky dolphins (*Lagenorhynchus obscurus*). *Aquatic Mammals* 40 (3): 260–73.
- Kuningas, S., T. Similä, and P. S. Hammond. 2013. Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. *Journal of the Marine Biological Association of the United Kingdom* 94 (6): 1–15.
- Laake, J.L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. 7600 Sand Point Way NE, Seattle WA 98115: Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv.
<http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf>.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals : a unified approach with case studies. *Ecological Monographs* 62 (1): 67–118.
- Lincoln, F. C. 1921. The history and purposes of bird banding. *The Auk* 38 (2): 217–28.

References

- 1930. Calculating waterfowl abundance on the basis of banding returns. *U.S. Department of Agriculture Circular No. 118*: 1–4.
- Lockyer, C., R.N.P. Goodall, and A.R. Galeazzi. 1988. Age and body length characteristics of *Cephalorhynchus commersonii* from incidentally-caught specimens off Tierra Del Fuego. *Reports of the International Whaling Commission Special Issue 12*: 103–18.
- Lukoschek, V., and B. L. Chilvers. 2008. A robust baseline for bottlenose dolphin abundance in coastal Moreton Bay: a large carnivore living in a region of escalating anthropogenic impacts. *Wildlife Research* 35 (7): 593–605.
- Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best. 2009. The BUGS Project: evolution, critique and future directions. *Statistics in Medicine* 28: 3049–67.
- MacLeod, C.D. 1998. Intraspecific scarring in odontocete cetaceans: an indicator of male 'quality' in aggressive social interactions? *Journal of Zoology* 244: 71–77.
- Mann, J., M. A. Stanton, E. M. Patterson, E. J. Bienenstock, and L. O. Singh. 2012. Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications* 3: 980.
- Mansur, R. M., S. Strindberg, and B. D. Smith. 2012. Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. *Marine Mammal Science* 28 (3): 561–78.
- Marley, S. A., B. Cheney, and P. M. Thompson. 2013. Using tooth rakes to monitor population and sex differences in aggressive behaviour in bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 39 (2): 107–15.
- Martin, A. R., V. M. F. da Silva, and P. R. Rothery. 2006. Does radio tagging affect the survival or reproduction of small cetaceans? A test. *Marine*

References

- Mammal Science* 22 (1): 17–24.
- McClintock, B. T., and G. C. White. 2009. A less field-intensive robust design for estimating demographic parameters with mark-resight data. *Ecology* 90 (2): 313–20.
- . 2012. From NOREMARK to MARK: Software for estimating demographic parameters using mark-resight methodology. *Journal of Ornithology* 152 (Suppl 2): 641–50.
- McClintock, B. T., G. C. White, Michael F. Antolin, and Daniel W. Tripp. 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* 65: 237–46.
- McDonald, T. L., F. E. Hornsby, T. R. Speakman, E. S. Zolman, K. D. Mullin, C. Sinclair, P. E. Rosel, L. Thomas, and L. H. Schwacke. 2017. Survival, density, and abundance of common bottlenose dolphins in Barataria Bay (USA) following the deepwater horizon oil spill. *Endangered Species Research* 33: 193–209.
- McIntosh, W.D. 1912. On a white porpoise. Notes from the Gatty Marine Laboratory, St. Andrews, No 33. *Annual Magazine for Natural History* 10: 117–19.
- McMahon, C. R., H. R. Burton, J. V. D. Hoff, R. Woods, and C. J. A. Bradshaw. 2006. Assessing hot-iron and cryo-branding for permanently marking southern elephant seals. *Journal of Wildlife Management* 70 (5): 1484–89.
- Minton, G., C. Peter, A. N. Z. Poh, J. Ngeian, G. Braulik, P. S. Hammond, and A. A. Tuen. 2013. Population estimates and distribution patterns of Irrawaddy dolphins (*Orcaella brevirostris*) and Indo-Pacific finless porpoises (*Neophocaena phocaenoides*) in the Kuching Bay, Sarawak. *Raffles Bulletin of Zoology* 61 (2): 877–88.
- Mintzer, V. J., A. R. Martin, V. M.F. da Silva, A. B. Barbour, K. Lorenzen, and T. K. Frazer. 2013. Effect of illegal harvest on apparent survival of Amazon

References

- river dolphins (*Inia geoffrensis*). *Biological Conservation* 158: 280–86.
- Mitchell, E.D, and A.N. Baker. 1980. Age of reputedly old killer whale, *Orcinus orca*, 'Old Tom' from Eden, Twofold Bay, Australia. *Report of the International Whaling Commission Special Issue 3*: 143–54.
- Moore, J. E., K. A. Curtis, R. L. Lewison, P. W. Dillingham, J. M. Cope, S. V. Fordham, S. S. Heppell, et al. 2013. Evaluating Sustainability of Fisheries Bycatch Mortality for Marine Megafauna: A Review of Conservation Reference Points for Data-Limited Populations. *Environmental Conservation* 40 (4): 329–44.
- Morley, R. C., and R. J. Van Aarde. 2007. Estimating abundance for a Savanna elephant population using mark–resight methods: a case study for the Tembe Elephant Park, South Africa. *Journal of Zoology* 271 (4): 418–27.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280–83.
- Nelson, G. A. 2014. Cluster sampling: a pervasive, yet little recognized survey design in fisheries research. *Transactions of the American Fisheries Society* 143 (4): 926–38.
- Nicholson, K., L. Bejder, S. J. Allen, M. Krtzen, and K. H. Pollock. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops sp.*) off Useless Loop in the Western Gulf of Shark Bay, Western Australia. *Marine and Freshwater Research* 63 (11): 1059–68.
- Noren, D. P., and J. A. Mocklin. 2012. Review of cetacean biopsy techniques: factors contributing to successful sample collection and physiological and behavioral impacts. *Marine Mammal Science* 28 (1): 154–99.
- Olesiuk, P.F., M.A. Bigg, and G.M. Ellis. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. *Report of the International Whaling Commission Special Issue 12*: 209–42.

References

- Olesiuk, P. F., G. M. Ellis, and J. K.B. Ford. 2005. Life history and population dynamics of northern resident killer whales (*Orcinus orca*) in British Columbia. Research Document 2005/045. Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.
- Oli, M. K., and S. F. Dobson. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161 (3): 422–40.
- Orbach, D. N, J. M. Packard, S. Piwetz, and B. Würsig. 2015. Sex-specific variation in conspecific-acquired marking prevalence among dusky dolphins (*Lagenorhynchus obscurus*). *Canadian Journal of Zoology* 93: 383–90.
- Oremus, M., R. M. Hamner, M. Stanley, P. Brown, C. S. Baker, and R. Constantine. 2013. Distribution, group characteristics and movements of the critically endangered Maui's dolphin *Cephalorhynchus hectori maui*. *Endangered Species Research* 19: 1–10.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62: 3–135.
- Palmer, C., L. Brooks, G. J. Parra, T. Rogers, D. Glasgow, and J. C. Z. Woinarski. 2014. Estimates of abundance and apparent survival of coastal dolphins in Port Essington Harbour, Northern Territory, Australia. *Wildlife Research* 41 (1): 35–45.
- Parra, G. J., P. J. Corkeron, and H. Marsh. 2006. Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: implications for conservation. *Biological Conservation* 129 (2): 167–80.
- Passadore, C., L. Möller, F. Diaz-Aguirre, and G. J. Parra. 2017. Demography of southern Australian bottlenose dolphins living in a protected inverse estuary. *Aquatic Conservation: Marine and Freshwater Ecosystems* 0: 1–

12.

- Pennington, M., and J. H. Volstad. 1994. Assessing the effect of intra-haul correlation and variable density on estimates of population characteristics from marine surveys. *Biometrics* 50 (3): 725–32.
- Petersen, C. G. Johannes. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. *Report of the Danish Biological Station* 6: 1–77.
- Pichler, F. B., S. M. Dawson, E. Slooten, and C. S. Baker. 1998. Geographic isolation of Hector's dolphin populations described by mitochondrial DNA sequences. *Conservation Biology* 12 (3): 676–82.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1–97.
- Pollock, K. H., and M. C. Otto. 1983. Robust Estimation of Population Size in Closed Animal Populations from Capture-Recapture Experiments. *Society* 39 (4): 1035–49.
- Poncelet, E., C. Barbraud, and C. Guinet. 2010. Population dynamics of killer whales (*Orcinus orca*) in Crozet Archipelago, southern Indian Ocean: a mark-recapture study from 1977 to 2002. *Journal of Cetacean Research and Management*. 11 (1): 41–48.
- Pusineri, C., C. Barbraud, J. Kiszka, S. Caceres, J. Mougnot, G Daudin, and V. Ridoux. 2014. Capture-mark-recapture modelling suggests an endangered status for the Mayotte Island (Eastern Africa) population of Indo-Pacific bottlenose dolphins. *Endangered Species Research* 23: 23–33.
- Rayment, W., S. Dawson, E. Slooten, S. Bräger, S. Du Fresne, and T. Webster. 2009. Kernel density estimates of alongshore home range of Hector's dolphins at Banks Peninsula, New Zealand. *Marine Mammal Science* 25 (3): 537–56.

References

- R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Read, A. J., K. W. Urian, B. Wilson, and D. M. Waples. 2003. Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. *Marine Mammal Science* 19 (1): 59–73.
- Reeves, R.R., S.M. Dawson, T.A. Jefferson, L. Karczmarski, K. Laidre, G. O’Corry-Crowe, L. Rojas-Bracho, E.R. Secchi, E. Slooten, B.D. Smith, J. Y. Wang, K. Zhou. 2013. *Cephalorhynchus hectori*. *IUCN Red List of Threatened Species*. www.iucnredlist.org.
- . 2013. *Cephalorhynchus hectori maui*. *The IUCN Red List of Threatened Species*. www.iucnredlist.org.
- Reisinger, R. R., and L. Karczmarski. 2009. Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay Region, South Africa. *Marine Mammal Science* 26 (1): 86–97.
- Rowat, D., C. W. Speed, M. G. Meekan, M. A. Gore, and C. J. A. Bradshaw. 2009. Population abundance and apparent survival of the vulnerable whale shark *Rhincodon typus* in the Seychelles Aggregation. *Oryx* 43 (4): 591–98.
- Rowe, L. E., and S. M. Dawson. 2009. Determining the sex of bottlenose dolphins from Doubtful Sound using dorsal fin photographs. *Marine Mammal Science* 25 (1): 19–34.
- Ryan, G. E., V. Dove, F. Trujillo, and P. F. Doherty. 2011. Irrawaddy dolphin demography in the Mekong River: an application of mark–resight models. *Ecosphere* 2 (5): 1–15.
- Sæther, B. E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81 (3): 642–53.
- Santostasi, N. L., S. Bonizzoni, G. Bearzi, L. Eddy, and O. Gimenez. 2016. A robust design capture-recapture analysis of abundance, survival and

References

- temporary emigration of three odontocete species in the Gulf of Corinth, Greece. *PLoS ONE* 11 (12): 1–21.
- Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. 2010. Modeling spatial variation in avian survival and residency probabilities. *Ecology* 91 (7): 1885–91.
- Saraux, C., C. Le Bohec, J. M. Durant, V. A. Viblanc, M. Gauthier-Clerc, D. Beaune, Y. H. Park, N. G. Yoccoz, N. C. Stenseth, and Y. Le Maho. 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469 (7329): 203–6.
- Sargeant, B. L., J. Mann, P. Berggren, and M. Krützen. 2005. Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops sp.*). *Canadian Journal of Zoology* 83: 1400–1410.
- Schneider, K., and R. W. Baird. 1998. Reactions of bottlenose dolphins to tagging attempts using a remotely-deployed suction-cup tag. *Marine Mammal Science* 14 (2): 316–24.
- Schofield, M. R., and R. J. Barker. 2011. Full open population capture-recapture models with individual covariates. *Journal of Agricultural, Biological, and Environmental Statistics* 16 (2): 253–68.
- Scott, E. M., J. Mann, J. J. Watson-Capps, B. L. Sargeant, and R. C. Connor. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142: 21–44.
- Seber, G A F. 1965. A note on the multiple-recapture census. *Biometrika* 52 (1/2): 249–59.
- . 1986. A review of estimating animal abundance. *Biometrics* 42 (2): 267–92.
- Secchi, E. R., and D. Fletcher. 2004. Estimating survival rates of Franciscana by fitting the Siler Model to data on age-at-death of beachcast and

References

- bycatch and by a modeling approach using life tables of similar species: a comparison. *Int. Whal. Commn. Scientific Committee Paper SC/56/SM16*.
- Silva, M. A., S. Magalhães, R. Prieto, R. S. Santos, and P. S. Hammond. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series* 392: 263–76.
- Slooten, E., and N. Davies. 2011. Hector's dolphin risk assessments: old and new analyses show consistent results. *Journal of the Royal Society of New Zealand* 42 (1): 49–60.
- Slooten, E. 1994. Behavior of Hector's dolphin: classifying behavior by sequence analysis. *Journal of Mammalogy* 75 (4): 956–64.
- Slooten, E., and S. M. Dawson. 1994. Hector's dolphin *Cephalorhynchus hectori*. In *Handbook of Marine Mammals, Vol V*, edited by S.H. Ridgeway and R. Harrison, 311–33. New York: Academic Press.
- Slooten, E., and S. M. Dawson. 2010. Assessing the effectiveness of conservation management decisions: likely effects of new protection measures for Hector's dolphin (*Cephalorhynchus hectori*). *Aquatic Conservation: Marine and Freshwater Ecosystems* 20: 334–47.
- Slooten, E., and S. M. Dawson. 1988. Studies on Hector's dolphin, *Cephalorhynchus hectori*: A Progress Report. *Report of the International Whaling Commission of the International Whaling Commission Special Issue* 9: 325–37.
- Slooten, E., S. M. Dawson, and F. Lad. 1992. Survival rates of photographically identified hector's dolphins from 1984 to 1988. *Marine Mammal Science* 8 (4): 327–43.
- Slooten, E., S. M. Dawson, and H. Whitehead. 1993. Associations among photographically identified Hector's dolphins. *Canadian Journal of Zoology* 71 (11): 2311–18.
- Slooten, E., D. Fletcher, and B. L. Taylor. 2000. Accounting for uncertainty in

References

- risk assessment: case study of Hector's dolphin mortality due to gillnet entanglement. *Conservation Biology* 14 (5): 1264–70.
- Slouten, E., and F. Lad. 1991. Population biology and conservation of Hector's dolphin. *Canadian Journal of Zoology* 69 (6): 1701–7.
- Smith, H. C., K. Pollock, K. Waples, S. Bradley, and L. Bejder. 2013. Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PLoS ONE* 8 (10): 2–11.
- Smolker, R., A. Richards, R. Connor, J. Mann, and P. Berggren. 2010. Sponge carrying by dolphins (*Delphinidae, Tursiops sp.*): a foraging specialization involving tool use? *Ethology* 103 (6): 454–65.
- Speakman, T. R., S. M. Lane, L. H. Schwacke, P. A. Fair, and E. S. Zolman. 2010. Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *Journal of Cetacean Research and Management* 11 (2): 153–62.
- Sprogis, K. R., K. H. Pollock, H. C. Raudino, S. J. Allen, A. M. Kopps, O. Manlik, J. A. Tyne, and L. Bejder. 2016. Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Frontiers in Marine Science* 3 (12): 1–15.
- Stevens, J. 2009. *Prionace Glauca*. *IUCN Red List of Threatened Species*. www.iucnredlist.org.
- Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (*Chondrichthyans*), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57: 476–94.
- Sturtz, S., U. Liges, and A. Gelman. 2005. R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* 12 (3): 1–16.
- Sutaria, D., and H. Marsh. 2011. Abundance estimates of Irrawaddy dolphins

References

- in Chilika Lagoon, India, using photo-identification based mark-recapture methods. *Marine Mammal Science* 27 (4): 338–48.
- Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conservation Biology* 7 (3): 489–500.
- Taylor, B. L., P. R. Wade, D. P. De Master, and J. Barlow. 2000. Incorporating Uncertainty into Management Models for Marine Mammals. *Conservation Biology* 14 (5): 1243–52.
- Tezanos-Pinto, G., R. Constantine, L. Brooks, J. A. Jackson, F. Mourão, S. Wells, and C. S. Baker. 2013. Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. *Marine Mammal Science* 29 (4): 390–410.
- Tolley, K.A., A. J. Read, R. S. Wells, K. W. Urrian, M. D. Scott, A. B. Irvine, and A. A. Hohn. 1995. Sexual dimorphism in wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, Florida. *Journal of Mammalogy* 76 (4): 1190–98.
- Tyne, J. A., K. H. Pollock, D. W. Johnston, and L. Bejder. 2014. Abundance and survival rates of the Hawai'i Island associated spinner dolphin (*Stenella longirostris*) stock. *PLoS ONE* 9 (1): e86132–e86132.
- Urrian, K., A. Gorgone, A. Read, B. Balmer, R. S. Wells, P. Berggren, J. Durban, T. Eguchi, W. Rayment, and P. S. Hammond. 2014. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science* 31 (1): 298–321.
- Urrian, K. W., R. S. Wells, A. B. Irvine, A. J. Read, and A. A. Hohn. 1998. When the shark bites: an analysis of shark bite scars on wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, FL. *The World Marine Mammal Conference, Monaco, 20-24 January, 1998 Abstracts* (139).
- Verborgh, P., R. De Stephanis, S. Pérez, Y. Jaget, C. Barbraud, and C. Guinet.

References

2009. Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* 25 (3): 523–36.
- Vermeulen, E., and S. Bräger. 2015. Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? *Plos One* 10 (3): 1–19.
- Wade, P. R. 1998. Calculating Limits To the Allowable Human-Caused Mortality of Cetaceans and Pinnipeds. *Marine Mammal Science* 14 (1): 1–37.
- Wade, P R. 2001. Bayesian methods in conservation biology. *Conservation Biology* 14 (5): 1308–16.
- Walker, K. A., A. W. Trites, M. Haulena, and D. M. Weary. 2012. A review of the effects of different marking and tagging techniques on marine mammals. *Wildlife Research* 39 (1): 15.
- Walker, K. A., J. A. E. Mellish, and D. M. Weary. 2010. Behavioural responses of juvenile steller sea lions to hot-iron branding. *Applied Animal Behaviour Science* 122 (1): 58–62.
- Wang, J. Y., S. C. Yang, P. F. Fruet, F. G. Daura-Jorge, and E. R. Secchi. 2012. Mark-recapture analysis of the critically endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins (*Sousa chinensis*): Implications for conservation. *Bulletin of Marine Science* 88(4): 885–902. doi:10.5343/bms.2010.1097.
- Webster, I., V.G. Cockcroft, and A. Cadinouche. 2015. Spinner dolphins *Stenella longirostris* off South-West Mauritius: abundance and residency. *African Journal of Marine Science* 37(1): 115–24.
- Webster, T. A., S. M. Dawson, and Elisabeth Slooten. 2009. Evidence of sex segregation in Hector's dolphin (*Cephalorhynchus hectori*). *Aquatic Mammals* 35 (2): 212–19.
- Webster, T., S. Dawson, and E. Slooten. 2010. A simple laser photogrammetry

References

- technique for measuring Hector's dolphins (*Cephalorhynchus hectori*) in the field. *Marine Mammal Science* 26 (2): 296–308.
- Wellings, C.E. 1944. The killer whales of Twofold Bay, N.S.W., Australia, *Grampus orca*. *Aust. Zool.* 10: 291–94.
- Wells, R. S. 2012. Individual dolphins as tools for conservation. *Animal Conservation* 15: 436–37.
- Wells, R. S., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Report of the International Whaling Commission of the International Whaling Commission Special Issue* 12: 407–15.
- . 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science* 13 (3): 475–80.
- Wells, R. S., M. D. Scott, A. B. Irvine, and K. H. Redford. 1987. The social structure of free-ranging bottlenose dolphins. In *Current Mammalogy*, edited by Hugh H Genoways, 247–305. Boston, MA: Springer US.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (S1): S120–39.
- Whitehead, H., S. Waters, and T. Lyrholrn. 1992. Population structure of female and immature sperm whales (*Physeter macrocephalus*) off the Gálapagos Islands. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 78-84.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. San Diego: Academic Press.
- Williams, J. A., S. M. Dawson, and E. Slooten. 1993. The abundance and distribution of bottlenosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology* 71: 2080–88.
- Williamson, M. J., A. S. Kavanagh, M. J. Noad, E. Kniest, and R. A. Dunlop. 2016. The effect of close approaches for tagging activities by small research

References

- vessels on the behavior of humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 32 (4): 1234–53.
- Wilson, B., P. S. Hammond, and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9 (1): 288–300.
- Wilson, S., K. C. Gil-Weir, R. G. Clark, G. J. Robertson, and M. T. Bidwell. 2016. Integrated population modeling to assess demographic variation and contributions to population growth for endangered whooping cranes. *Biological Conservation* 197: 1–7.
- Wursig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission Special Issue* 12: 43–52.
- Würsig, B., and M. Würsig. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198 (4318): 755–56.
- Young, K. E., and E. O. Keith. 2011. A comparative analysis of cetacean vital rates using matrix population modeling analysis of cetacean vital rates. *International Journal of Applied Science and Technology* 1 (6): 261–77.
- Zhang, Y., and S. X. Cadrin. 2013. Estimating effective sample size for monitoring length distributions: a comparative study of Georges Bank groundfish. *Transactions of the American Fisheries Society* 142 (1): 59–67.
- Zipkin, E. F., J. T. Thorson, K. See, H. J. Lynch, E. H. C. Grant, Y. Kanno, R. B. Chandler, B. H. Letcher, and J. A. Royle. 2014. Modeling structured population dynamics using data from unmarked individuals. *Ecology* 95 (1): 22–29.

Appendix 2.1

In Chapter 2, mark rate is estimated using four different methods:

Method 1. Simple random sampling (SRS, eq. 2.2); evaluated using excel

Method 2. Simple random cluster sampling (SRCS, eq. 2.3); evaluated in excel

Method 3. SRCS-bootstrap; evaluated in R

Method 4. SRCS-Bayes (Eguchi 2014); evaluated in R

R (version 3.3.2) was used for bootstrapping the variance of mark rate (*method 3*) and for estimating mark rate and its precision via *method 4*.

Bootstrapping variance for mark rate

Bootstrapping was completed separately on the 2016 and 1992 -- 1996 dataset. Below is an example using the 2016 dataset.

```
###Enter in data to be bootstrapped###
data.2016<-read.csv("Bootstrap_MR_2016.csv", header=TRUE)
#Example data
head(data.2016)

##   usable.photos Marks
## 1             7     0
## 2             4     0
## 3             4     0
## 4             4     0
## 5             1     0
## 6             6     0

groups<-length(data.2016$usable.photos) #Gives the number of
#groups in the dataset
group.list<-vector(mode="list", groups) #Creates empty list that
#the for loop will fill in
sampled<-vector(mode="list", groups)   #Creates empty list that
#the for loop will fill in
marks<-data.2016$Marks                  #Creates vector of the
#number of images showing marks per group
images<-data.2016$usable.photos         #Creates vector of
#the total number of images per group

###Create list; each element represents a group, each image is
#represented by a 0 or 1 (0 means the image is of an unmarked
#individual, 1 means the image is of a marked individual)###
for (i in 1:groups)
{
  unmarked<-rep.int(0, images[i]-marks[i])
  marked<-rep.int(1, marks[i])
  group.list[[i]]<-c(unmarked, marked)
}

#e.g.
head(group.list)
```

```

## [[1]]
## [1] 0 0 0 0 0 0 0
##
## [[2]]
## [1] 0 0 0 0
##
## [[3]]
## [1] 0 0 0 0
##
## [[4]]
## [1] 0 0 0 0
##
## [[5]]
## [1] 0
##
## [[6]]
## [1] 0 0 0 0 0 0

#Create empty list for later replicate function

bootstrap.samples<-vector("list", groups)

#Get bootstrap replicates by taking 'groups' samples from 'group.
#list' estimating mark rate, and then repeating this 10,000 times
bootstrap.reps<-replicate(10000, {
  samples<-sample(group.list, groups, replace=TRUE)
  samples.vector<-unlist(samples)
  marked<-sum(samples.vector==1) #counts number of marked photos
#in a season
  totalphotos<-sum(samples.vector<=1) #counts number of unmarked
#photos in a season
  MR<-marked/totalphotos
})

#Get standard error
sd(bootstrap.reps)

## [1] 0.009535351

#Sort bootstrap replicates from lowest to highest and get 95%
#confidence interval
bootstrap.reps.sorted<-sort(bootstrap.reps, decreasing = FALSE)
lcl<-bootstrap.reps.sorted[250]
lcl

## [1] 0.04730983

ucl<-bootstrap.reps.sorted[9750]
ucl

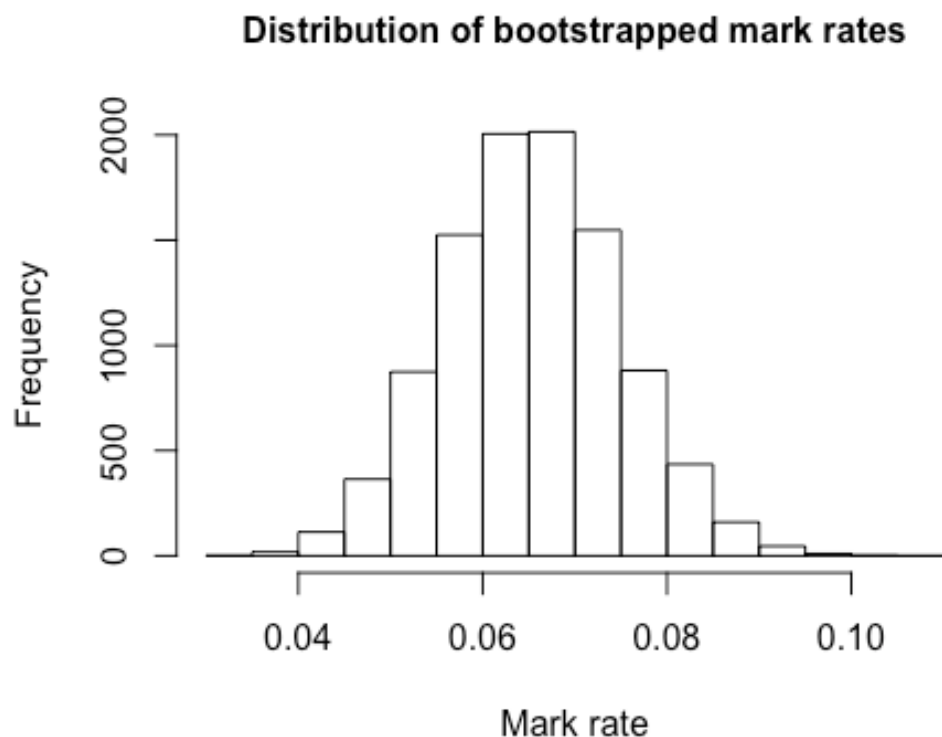
## [1] 0.08459697

#Save bootstrap replicates
write.csv(bootstrap.reps.sorted, file="Bootstrap_MR_2016_boot.csv
")

```

Checking for symmetric distribution of the bootstrap statistic

```
hist(bootstrap.reps.sorted, main="Distribution of bootstrapped
mark rates", xlab="Mark rate", ylab="Frequency", cex.lab=1,
cex.main=1, cex.axis=1)
```



Hierarchical Bayesian model for estimating mark rate and its precision

Below is the code used for estimating the mark rate of the Hector's dolphin dataset in 2016. The model was taken from Eguchi (2014). To make the Openbugs run the model in parallel, code was adapted from Petr Keil (see <http://www.petrkeil.com/?p=63>). In addition to loading the required packages, the code also requires the installation of OpenBUGS (see <http://www.openbugs.net/w/Downloads>)

Note: Uninformative prior distributions were chosen for all parameters except the number of photographs per dolphin, μ_g . Our field protocol was to take a number of photographs for each group that was three times the group size (Gormley et al 2005). Hence mark rate in a group of 6 individuals would be sampled via 18 “randomly taken” photographs. For this reason the shape and rate parameters of the gamma prior distribution of μ_g were based on the actual number of images acquired divided by the estimated group size and its variance, so that $\mu_g \sim dgamma(1.53, 2.51)$. Note that this parameter (μ_g) does not affect the estimate of mark rate, only the estimate of the number of identifiable individuals per group and group size.

```

####Load required packages for analysis###
library(coda)
library(snow)
library(snowfall)
library(data.table)
library(reshape)
library(R2OpenBUGS)
library(sirt)

####Specify parallel, number of cpus to use, and that R2OpenBUGS
#be loaded on each cpu
sfInit(parallel=TRUE, cpus=4)
sfLibrary(R2OpenBUGS)

####Create 4 folders for MCMC chains to go into within the current
#working directory###
folder1 <- paste(getwd(), "/chain1", sep="")
folder2 <- paste(getwd(), "/chain2", sep="")
folder3 <- paste(getwd(), "/chain3", sep="")
folder4 <- paste(getwd(), "/chain4", sep="")

dir.create(folder1); dir.create(folder2); dir.create(folder3);
dir.create(folder4)

####Enter in data for model###
#read in .csv file of matrix of k[ig] (number of images of each
#individual for each group)
k.df<-read.csv("k_2016.csv", header=F)
#Put k matrix into a format easily read by OpenBugs
k.melt.df<-melt(k.df)
.Data<-k.melt.df$value
k=structure(.Data,.Dim=c(38, 163))
#Enter number of observed dolphin groups
G=163
#Read in remaining model input variables from .csv and define K,
#T, and X vectors from .csv
variables.R<-read.csv("variables_2016.csv", header=T)
K<-variables.R$K..total.number.of.good.photos.of.cat.1.2
  #Total number of images of marks (category 1 and 2) per
  #group
T<-variables.R$T..total.number.of.good.photos.
  #Total number of images per group
x<-variables.R$X.number.of.cat.1.2.individuals..can.include.bad.p
otos. #Number of unique individuals photographed per group
#Put data inputs into list format
data<-list(G=163,K=variables.R$K..total.number.of.good.photos.of.
cat.1.2,T=variables.R$T..total.number.of.good.photos.,x=variables.
R$X.number.of.cat.1.2.individuals..can.include.bad.photos.,
k=structure(.Data,.Dim=c(38, 163)))

####Inserts the model text into each folder###

for (folder in c(folder1, folder2, folder3, folder4))
{

```

```

sink(paste(folder, "/Eguchi.txt", sep=""))
cat("
  model
  {

##This section of the model estimates group size (see
#Eguchi 2014)##
    for (g in 1:G){
      # Number of photos per marked indiv is Poisson
      for (i in 1:x[g]){
        k[i,g] ~ dpois(mu[g])
      }
      ##exp(-mu[g]) = Pr(not observing the jth animal) with
      #Poisson, so, probability of observing x[g] animals in m[g]
      #animals is binomial with 1-exp(-mu[g])##
      phi[g] <- 1 - exp(-mu[g])
      x[g] ~ dbin(phi[g], m[g]) #Number of identified
                                     #individuals in the gth group

      Grp[g] <- m[g]/p[g] #Group size estimated using number of
                                     #identified individuals and the mark
                                     #rate of each group

##This section of the model estimates mark rate
#Number of photos get modeled with the key parameter p, or theta
      K[g] ~ dbin(p[g], T[g]) #Sum of all k[i,g] (Number of
                                     #images of ith individual in the
                                     #gth group)

      p[g] ~ dbeta(alpha, beta)

#priors
      mu[g] ~ dgamma(1.53,2.51) #Number of images per individual
      m[g] ~ dpois(muM)
    }

    alpha ~ dunif(0, 100)
    beta ~ dunif(0, 100)
    mean.p<-alpha/(alpha+beta)
    var.p<-(alpha*beta)/((alpha+beta)*(alpha+beta)*(alpha+beta+
1))
    muM ~ dgamma(0.01, 0.01) #Poisson parameter of the number
                                     #of identifiable individuals in
                                     #group mg
  }

  )
sink()
}

###Creates function called parallel.bugs, which calls OpenBUGS to
run the model within each direcotry

parallel.bugs <- function(chain, data, params)
{

```

```

# defining directory for each CPU
sub.folder <- paste(getwd(),"/chain", chain, sep="")

# specifying the initial MCMC values
inits <- function()
{
  list(alpha=runif(1,0,100), beta= runif(1,0,100), p=runif(163,
0,1), mu=runif(163, 0.0001,5), m=sample(1:50, 163, replace=TRUE),
muM=rgamma(1,shape=.01,scale=.01))
}
# calling OpenBUGS and entering the number of iterations,
#burnin, and thinning for each chain
OpenBUGS_PATH<-"C:\'Users\'MarineMammalLab\'Program Files(x8
6)\'OpenBUGS\'OpenBUGS323\'OpenBUGS.exe"
useWINE=NULL
bugs(data=data, inits=inits, parameters.to.save=params,
n.iter=60000, n.chains=1, n.burnin=10000, n.thin=1,
model.file="Eguchi.txt", debug=TRUE, codaPkg=TRUE,
working.directory=sub.folder)
}

###Call the sflapply function that runs parallel.bugs function on
each of the 4 CPUs###
params<-c("alpha", "beta", "p", "mu", "m", "muM", "mean.p", "var.
p", "Grp") #parameters to track
sflapply(1:4, fun=parallel.bugs, data=data, params=params)

###Locate the position of each CODA chain (these contain the MCMC
iterations of each tracked parameter)
chain1 <- paste(folder1, "/CODAchain1.txt", sep="")
chain2 <- paste(folder2, "/CODAchain1.txt", sep="")
chain3 <- paste(folder3, "/CODAchain1.txt", sep="")
chain4 <- paste(folder4, "/CODAchain1.txt", sep="")

### Getting the results ###
combined.chain <- read.bugs(c(chain1, chain2, chain3, chain4))
#Summary statistics for tracked parameters
summary.combined.chain<-summary(combined.chain)
capture.output(summary.combined.chain, file="summarymcmc.txt")
#Gelman-rubin diagnostic for each parameter to assess convergence
gelman.rubin<-gelman.diag(combined.chain)
capture.output(gelman.rubin, file="gelmanrubin.txt")
#Provide plots of the four chains of each parameter to visually
#assess convergence
plot(combined.chain)

###Plot HDI of main parameter of interest, the population-level p
roportion of marked individuals###
source("plotPost.R") #from <http://www.indiana.edu/~kruschke/Doin
gBayesianDataAnalysis/Prog#rams/plotPost.R>
mark.rate.mcmc<-combined.chain[, "mark.rate"]
mark.rate.sampleVec<-c(as.matrix(mark.rate.mcmc))
plotPost(paramSampleVec=mark.rate.sampleVec, showCurve=FALSE)

```

Appendix 3.1

Hierarchical Bayesian model for comparing mark rate

This R code describes how mark rate was compared for the two different periods (1992 – 1996 and 2016) using the Bayesian hierarchical model (Eguchi 2014).

Note: Uninformative prior distributions were chosen for all parameters except the number of photographs per dolphin, μ_g . Our field protocol was to take a number of photographs for each group that was three times the group size (Gormley et al 2005). Hence mark rate in a group of 6 individuals would be sampled via 18 “randomly taken” photographs. For this reason the shape and rate parameters of the gamma prior distribution of μ_g were based on the actual number of images acquired divided by the estimated group size and its variance, so that $\mu_g \sim dgamma(1.53, 2.51)$ for 2016 and $\mu_g \sim dgamma(2.48, 3.12)$ for 1992 – 1996. Note that this parameter (μ_g) does not effect the estimate of mark rate, only the estimate of the number of identifiable individuals per group and group size.

```
###Load required packages for analysis###
library(coda)
library(snow)
library(snowfall)
library(data.table)
library(reshape)
library(R2OpenBUGS)
library(sirt)
setwd("D:/Eguchi_model_mr_comp")

###Specify parallel, number of cpus to use, and that R2OpenBUGS
be loaded on each cpu
sfInit(parallel=TRUE, cpus=4)
sfLibrary(R2OpenBUGS)

###Create 4 folders for MCMC chains to go into within the current
working directory###
folder1 <- paste(getwd(), "/chain1", sep="")
folder2 <- paste(getwd(), "/chain2", sep="")
folder3 <- paste(getwd(), "/chain3", sep="")
folder4 <- paste(getwd(), "/chain4", sep="")

dir.create(folder1); dir.create(folder2); dir.create(folder3);
dir.create(folder4)

###Enter in data for model###
##2016 data###
#read in .csv file of matrix of k[ig] (number of images of each
#individual for each group)
k.df.2016<-read.csv("k_2016.csv", header=F)
#Put k matrix into a forat easily read by OpenBugs
k.melt.df.2016<-melt(k.df.2016)
```



```

.Data.2016<-k.melt.df.2016$value
k.2016=structure(.Data.2016,.Dim=c(38, 163))
#Enter number of observed dolphin groups
G.2016=163
#Read in remaining model input variables from .csv and define K,
#T, and X vectors from .csv
variables.R.2016<-read.csv("variables_2016.csv", header=T)
K.2016<-variables.R.2016$K..total.number.of.good.photos.of.cat.1.
2
      #Total number of images of marks (category 1 and
      #2) per group
T.2016<-variables.R.2016$T..total.number.of.good.photos.
      #Total number of images per group
x.2016<-variables.R.2016$X.number.of.cat.1.2.individuals..can.inc
lude.bad.photos. #Number of unique individuals photographed per
      #group
#Put data inputs into list format
data.2016<-list(G.2016=163,K.2016=variables.R.2016$K..total.numbe
r.of.good.photos.of.cat.1.2,T.2016=variables.R.2016$T..total.numb
er.of.good.photos.,x.2016=variables.R.2016$X.number.of.cat.1.2.in
dividuals..can.include.bad.photos.,k.2016=structure(.Data.2016,
.Dim=c(38, 163)))

##1996 data###
#read in .csv file of matrix of k[ig] (number of images of each
#individual for each group)
k.df.1996<-read.csv("k_1996.csv", header=F)
#Put k matrix into a format easily read by OpenBugs
k.melt.df.1996<-melt(k.df.1996)
.Data.1996<-k.melt.df.1996$value
k.1996=structure(.Data.1996,.Dim=c(76, 160))
#Enter number of observed dolphin groups
G.1996=160
#Read in remaining model input variables from .csv and define K,
#T, and X vectors from .csv
variables.R.1996<-read.csv("variables_1996.csv", header=T)
K.1996<-variables.R.1996$K..total.number.of.good.photos.of.cat.1.
2
      #Total number of images of marks (category 1 and 2)
      #per group
T.1996<-variables.R.1996$T..total.number.of.good.photos.
      #Total number of images per group
x.1996<-variables.R.1996$X.number.of.cat.1.2.individuals..can.inc
lude.bad.photos. #Number of unique individuals photographed per
      #group
P.1996<-variables.R.1996$P..time.period.
#Put data inputs into list format

data<-list(G.2016=163,K.2016=variables.R.2016$K..total.number.of.
good.photos.of.cat.1.2,T.2016=variables.R.2016$T..total.number.of.
good.photos.,x.2016=variables.R.2016$X.number.of.cat.1.2.individu
als..can.include.bad.photos.,k.2016=structure(.Data.2016,.Dim=c(3
8, 163)), P.1996=variables.R.1996$P..time.period.,G.1996=160,K.19
96=variables.R.1996$K..total.number.of.good.photos.of.cat.1.2,T.1
996=variables.R.1996$T..total.number.of.good.photos.,x.1996=varia

```

```

bles.R.1996$X.number.of.cat.1.2.individuals..can.include.bad.photos.,k.1996=structure(.Data.1996,.Dim=c(76, 160)))

###Inserts the model text into each folder###

for (folder in c(folder1, folder2, folder3, folder4))
{
  sink(paste(folder, "/Eguchi.txt", sep=""))
  cat("
model{
  for (g in 1:G.1996){
    # Number of photos per marked indiv is Poisson
    for (i in 1:x.1996[g]){
      k.1996[i,g] ~ dpois(mu.1996[g])
    }
    # exp(-mu[g]) = Pr(not observing the jth animal) with
    #Poisson
    # So, probability of observing x[g] animals in m[g]
    #animals is binomial with 1-exp(-mu[g]).
    phi.1996[g] <- 1 - exp(-mu.1996[g])
    x.1996[g] ~ dbin(phi.1996[g], m.1996[g])

    Grp.1996[g] <- m.1996[g]/p.1996[g] # Group size estimated

    # Number of photos get modeled with the key parameter
    #p, or theta
    K.1996[g] ~ dbin(p.1996[g], T.1996[g])
    for (t in P.1996[g]:P.1996[g]){
      p.1996[g] ~ dbeta(alpha.1996[t], beta.1996[t])
    }

    # priors
    mu.1996[g] ~ dgamma(2.48, 3.12)
    m.1996[g] ~ dpois(muM.1996)
  }

  for (g in 1:G.2016){
    # Number of photos per marked indiv is Poisson
    for (i in 1:x.2016[g]){
      k.2016[i,g] ~ dpois(mu.2016[g])
    }
    phi.2016[g] <- 1 - exp(-mu.2016[g])
    x.2016[g] ~ dbin(phi.2016[g], m.2016[g]) #Number of
                                           #identified
                                           #individuals
                                           #in the gth group
    Grp.2016[g] <- m.2016[g]/p.2016[g] #Group size estimated

    K.2016[g] ~ dbin(p.2016[g], T.2016[g]) #Sum of all k[i,g]
                                           #(Number of images
                                           #of ith individual
                                           #in the gth group)
    p.2016[g] ~ dbeta(alpha.2016, beta.2016)
  }
}

```

```

    # priors

    mu.2016[g] ~ dgamma(1.53,2.51) #Number of images per
                                   #individual
    m.2016[g] ~ dpois(muM.2016)
  }

  muM.1996 ~ dgamma(0.01, 0.01) #Poisson parameter of the
                                   #number of identifiable
                                   #individuals in group mg
for (t in 1:5){
  alpha.1996[t] ~ dunif(0, 100)
  beta.1996[t] ~ dunif(0, 100)
}

  mean.p.1996.1<-alpha.1996[1]/(alpha.1996[1]+beta.1996[1])
  mean.p.1996.2<-alpha.1996[2]/(alpha.1996[2]+beta.1996[2])
  mean.p.1996.3<-alpha.1996[3]/(alpha.1996[3]+beta.1996[3])
  mean.p.1996.4<-alpha.1996[4]/(alpha.1996[4]+beta.1996[4])
  mean.p.1996.5<-alpha.1996[5]/(alpha.1996[5]+beta.1996[5])
  mean.p.1996.total<-(mean.p.1996.1+mean.p.1996.2+mean.p.1996.3
+mean.p.1996.4+mean.p.1996.5)/5
  alpha.2016 ~ dunif(0, 100)
  beta.2016 ~ dunif(0, 100)
  mean.p.2016<-alpha.2016/(alpha.2016+beta.2016)
  muM.2016 ~ dgamma(0.01, 0.01)
  mr.dif<-mean.p.1996.total-mean.p.2016
}

  ")
  sink()
}

###Creates function called parallel.bugs, which calls OpenBUGS to
run the model within each direcotry

parallel.bugs <- function(chain, data, params)
{
  # defining directory for each CPU
  sub.folder <- paste(getwd(),"/chain", chain, sep="")

  # specifying the initial MCMC values
  inits <- function()
  {
    list(alpha.2016=runif(1,0,100), beta.2016= runif(1,0,100), p.
2016=runif(163, 0,1), mu.2016=runif(163, 0.0001,5), m.2016=sample
(1:50, 163, replace=TRUE), muM.2016=rgamma(1,shape=.01,scale=.01),
alpha.1996=c(runif(1,0,100), runif(1,0,100), runif(1,0,100), runi
f(1,0,100), runif(1,0,100)), beta.1996= c(runif(1,0,100), runif(1,
0,100), runif(1,0,100), runif(1,0,100), runif(1,0,100)), p.1996=r
unif(160, 0,1), mu.1996=runif(160, 0.0001,5), m.1996=sample(1:50,
160, replace=TRUE), muM.1996=rgamma(1,shape=.01,scale=.01))
  }
  # calling OpenBugs and entering the number of iterations,

```

```

#burnin, and thinning for each chain
OpenBUGS_PATH<-"C:\\Program Files (x86)\\OpenBUGS\\OpenBUGS3
23\\OpenBUGS.exe"
useWINE=NULL
bugs(data=data, inits=inits, parameters.to.save=params,
      n.iter=60000, n.chains=1, n.burnin=10000, n.thin=1,
      model.file="Eguchi.txt", debug=TRUE, codaPkg=TRUE,
      working.directory=sub.folder)
}

###Call the sflapply function that runs parallel.bugs function on
#each of the 4 CPUs###
params<-c("alpha.2016", "beta.2016", "p.2016", "mu.2016", "m.2016",
          "muM.2016", "mean.p.2016", "mean.p.1996.total", "mean.p.1996.1",
          "mean.p.1996.2", "mean.p.1996.3", "mean.p.1996.4", "mean.p.1996.
          5", "alpha.1996", "beta.1996", "p.1996", "mu.1996", "m.1996", "mu
          M.1996", "mr.dif") #parameters to track
sflapply(1:4, fun=parallel.bugs, data=data, params=params)

###Locate the position of each CODA chain (these contain the MCMC
#iterations of each tracked parameter)
chain1 <- paste(folder1, "/CODAchain1.txt", sep="")
chain2 <- paste(folder2, "/CODAchain1.txt", sep="")
chain3 <- paste(folder3, "/CODAchain1.txt", sep="")
chain4 <- paste(folder4, "/CODAchain1.txt", sep="")

### Getting the results ###
combined.chain <- read.bugs(c(chain1, chain2, chain3, chain4))
#Summary statistics for tracked parameters
summary.combined.chain<-summary(combined.chain)
capture.output(summary.combined.chain, file="summarymcmc.txt")
#Gelman-rubin diagnostic for each parameter to assess convergence
gelman.rubin<-gelman.diag(combined.chain)
capture.output(gelman.rubin, file="gelmanrubin.txt")
#Provide plots of the four chains of each parameter to visually
#assess convergence
plot(combined.chain[, "mean.p.2016"])

###Plot HDI of main parameter of interest, the population-level
#proportion of marked individuals for each period and their
#difference###
source("plotPost.R") #from <http://www.indiana.edu/~kruschke/Doing
gBayesianDataAnalysis/Programs/plotPost.R>
mr.dif.mcmc<-combined.chain[, "mr.dif"]
mr.dif.sampleVec<-c(as.matrix(mr.dif.mcmc))
mr.dif.vector<-as.vector(as.matrix(mr.dif.mcmc))
mr.2016.mcmc<-combined.chain[, "mean.p.2016"]
mr.2016.sampleVec<-c(as.matrix(mr.2016.mcmc))
mr.1996.mcmc<-combined.chain[, "mean.p.1996.total"]
mr.1996.sampleVec<-c(as.matrix(mr.1996.mcmc))
plotPost(paramSampleVec=mr.2016.sampleVec, xlab=expression(theta
[2016]), col="gray80", cex=1.5, xlim=c(0.04, 0.16))
plotPost(paramSampleVec=mr.dif.sampleVec, xlab=expression(theta[1
992-1996]-theta[2016]), col="gray80", cex=1.5, xlim=c(0, 0.10))

```

Appendix 3.1

```
plotPost(paramSampleVec=mr.1996.sampleVec, xlab=expression(theta  
[1992-1996]), col="gray80", cex=1.5, xlim=c(0.04, 0.16))
```

Appendix 4.1

Table of current estimates of survival for delphinids

Survival rates estimated for dolphin species thus far. SE=standard error, 95% CI=95% confidence intervals, SD=standard deviation, UNK=unknown. Some studies include different survival rates for different time periods; in these cases only the most recent estimates of survival rate were included. Note that mortality rate estimates from capture-recapture models represent mortality and permanent emigration. Additional research is needed to estimate permanent emigration, in order to correct the survival estimate. Refer to each paper for a discussion on whether the quoted survival rate most likely represents “apparent” survival or “true” survival.

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
Amazon river dolphin (<i>Inia geoffrensis</i>)	Mamirauá Lake System, Brazil	UNK	2000 - 2011 (12 years)	0.899	0.007		capture-recapture	Mintzer et al. 2013
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Sarasota FL, USA	>1 year old	667 animal-years (1980 - 1987)	0.961			capture-recapture/age-distribution data	Wells and Scott 1990
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Charleston NC, USA	adults and juveniles	2004 - 2006 (3 years)	0.951	0.035	0.882 - 1	capture-recapture	Speakman et al. 2010
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Doubtful Sound, NZ	adults	1990 - 2008 (18 years)	0.9374		0.9170 - 0.9530	capture-recapture	Currey et al. 2009
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Azores	adults	1999 - 2004 (6 years)	0.97	0.029		capture-recapture	Silva et al. 2009

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Moray Firth, Scotland	adults and subadults	1990 - 2002 (13 years)	0.93		0.861 - 0.979	capture-recapture	Corkrey et al. 2008
Bottlenose dolphin (<i>Tursiops truncatus</i>)*	Shark Bay, Australia	adults	2007 - 2011 (5 years total)	0.95	0.02	0.87 - 0.98	capture-recapture	Nicholson et al. 2012
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Bay of Islands, NZ	UNK	2 periods: 1997 - 1999, 2003 - 2006; 7 years total	0.928	0.008	0.911 - 0.942	capture-recapture	Tezanos-Pinto et al. 2013
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Barataria Bay LA, USA	adults	2011 - 2013 (3 years)	varied between 0.80 - 0.85, upper credible interval at or below 0.90			capture-recapture (SERD model)	McDonald et al. 2017
Bottlenose dolphins (<i>Tursiops truncatus</i>)	Patos Lagoon Estuary, Brazil	adults (males and females) and juveniles	2005 - 2012 (8 years)	adult(female): 0.97; adult (male): 0.88; juveniles: 0.83		adult(female): 0.91-0.99; adult (male): 0.75-0.94; juveniles: 0.64-0.93	capture-recapture	Fruet et al. 2015
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Little Bahama Bank, Bahamas	adults	1992-2010 (19 years)	average ~0.94		95% HPDI: 0.82–0.99	capture-recapture	Fearnbach et al. 2012
Bottlenose dolphin (<i>Tursiops truncatus</i>)	St. Antonio, Imarui, and Miram Lagoons, southern Brazil	adults	1989-1991; 2007-2009 (3 years each)	1989-1991: 0.941; 2007-2009: 0.917		1989-1991: 0.888–0.998; 2007-2009: 0.876–0.961	capture-recapture	Daura-Jorge et al. 2013

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
bottlenose dolphins (<i>Tursiops sp.</i>)	Coffin Bay, Australia	males, females, unknown sex	2013-2015 (3 years)	males: 0.98 ; females: 0.98; unknown: 0.67	males:0.04; females: 0.05; unknown: 0.06	males:0.17-1; females:0.28-1; unknown: 0.54-0.78	capture-recapture	Passadore et al. 2017
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Bahia San Antonio, Argentina	adults	2006 - 2011 (6 years)	0.97 - 0.99	0.010 - 0.037			Vermeulen and Bräger 2015
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)*	Bunbury, Western Australia	adults and juveniles	2007 - 2009 (3 years)	0.95	0.02		capture-recapture	Smith et al. 2013
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)	Mayotte Island, East Africa	adults	2004 - 2009, 6 years	0.937	0.059	0.678 - 0.990	capture-recapture	Pusineri et al. 2014
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)	Swatch-of-No-Ground, Bangladesh	adults	2005 - 2009 (5 years)	0.976	0.022	0.860 - 0.996	capture-recapture	Mansur et al. 2012
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)	Bunbury, Western Australia	adults and juveniles (combined), adult females, adult males	2007 - 2013 (7 years)	adults and juveniles: 0.99; adult females: 0.98; adult males: 0.99	adults and juveniles:0.002; adult females:0.004; adult males: 0.003	adults and juveniles: 0.98 - 0.99; adult females: 0.97-0.99; adult males: 0.98 - 1.0	capture-recapture	Sprogis et al. 2016
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)	Algoa Bay, South Africa	adults	1991 - 1994 (4 years)	0.992 - 1.00	0.002 - 0.010		capture-recapture	Reisinger and Karczmarski 2009

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>)	Reunion Island, Indian Ocean	adults (males and females)	2009 - 2014 (6 years)	0.93	0.018	0.886-0.958	capture-recapture	Dulau et al. 2017
Commerson's dolphin (<i>Cephalorhynchus commersonii</i>)	Argentina	adults	136 individuals stranded/by-caught	0.914			age distribution data	(Lockyer, Goodall, and Lockyer et al.1988)
Franciscana (<i>Pontoporia blainvillei</i>)	Southern Brazil/Uruguay	adults	184 beachcast from S Brazil, 102 by-caught off Uruguay, 115 by-caught S Brazil 1994/97	0.854	0.015		age distribution data	Secchi and Fletcher 2004
Guiana dolphin (<i>Sotalia guianensis</i>)	Caravelas River estuary, Brazil	likely adults only	2002 - 2009 (8 years)	0.88	0.07	0.67 - 0.96	capture-recapture	Cantor et al. 2012
Hector's dolphin (<i>Cephalorhynchus hectori</i>)	Banks Peninsula, NZ	adults and juveniles	1990 - 2006 (16)	0.917		0.802 - 0.984	capture-recapture	Gormley et al. 2012
Short-finned pilot whales (<i>Globicephala macrorhynchus</i>)	Madeira, NE Atlantic	adults	2005 - 2011 (7)	0.96	0.028	0.853 - 0.990	capture-recapture	Alves et al. 2014
Long-finned pilot whales (<i>Globicephala melas</i>)	Strait of Gibraltar	adults	1999 - 2005 (7 years)	0.982	0.008	0.955 - 0.993	capture-recapture	Verborgh et al. 2009
Orca (<i>Orcinus orca</i>)	Crozet Archipelago, Indian Ocean	adults	1964 - 2002 (20 capture occasions)	0.894		0.84 - 0.93	capture-recapture	Poncelet et al. 2010

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
<i>Orca (Orcinus orca)</i>	northern Norway	adults	1986 - 2003	0.981	0.006	0.965 - 0.990	capture-recapture	Kuningas et al. 2013
<i>Orca (Orcinus orca)</i>	British Columbia	adults	1996 - 2004; 286 male animal-years, 552 female animal-years	females: 0.9705; males: 0.9089	females: 0.0072; males: 0.017		capture-recapture/age distribution data	Olesiuk et al. 2005
<i>Orca (Orcinus orca)</i>	Strait of Gibraltar	adults and juveniles (interacting with fishing gear INT, and not interacting with fishing gear, NOT)	1999 - 2011 (13 years)	adult (INT): 0.991; adult(NOT): 0.901; juveniles (INT): 0.966	adult (INT): 0.014; adult(NOT): 0.067; juveniles (INT): 0.031	adult (INT): 0.837-1.0; adult(NOT): 0.672-0.980; juveniles (INT): 0.819-0.994	capture-recapture	Esteban et al. 2016
Spinner dolphin (<i>Stenella longirostris</i>)	Kona Coast, Hawai'i Island	UNK	2010 - 2011 (2 years)	0.97	0.05		capture-recapture, "apparent" survival	Tyne et al. 2014
Spinner dolphin (<i>Stenella longirostris</i>)	SW Mauritius	adults	2008 - 2010 (3 years)	0.99	0.02		capture-recapture	Webster et al. 2015
Australian humpback dolphins (<i>Sousa sahulensis</i>)	North West Cape, Western Australia	adults	2013-2015 (3 years)	ranged from 0.86 - 0.96 over each sampling period		0.05-1.00	capture-recapture	Hunt et al. 2017

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
Indo-Pacific humpback dolphins (<i>Sousa chinensis</i>)	East Taiwan Strait	UNK	2007 - 2010 (4 years)	0.985	0.018	0.832 - 0.998	capture-recapture	Wang et al. 2012
Indo-Pacific humpback dolphins (<i>Sousa chinensis</i>)	Hong Kong	adults	2010-2014 (5 years)	0.98	0.034		capture-recapture	Chan and Karczmarski 2017
Irrawaddy dolphin (<i>Orcaella brevirostris</i>)	Mekong River, Cambodia	likely adults only	2007 - 2010 (3 years)	0.977	0.04		capture-recapture	Ryan et al. 2011
Irrawaddy dolphin (<i>Orcaella brevirostris</i>)	Mekong River (5 km north of Laos/Cambodian border to Vietnamese Delta	adults	2001 - 2005; limited surveys 2005 - 2007	0.88			capture-recapture	Beasley et al. 2013
Irrawaddy dolphin (<i>Orcaella brevirostris</i>)	Chilika Lagoon, India	adults	2004 - 2006 (3 years)	0.98	0.06		capture-recapture	Sutaria and Marsh 2011
Australian snubfin dolphin (<i>Orcaella heinsohni</i>)	Fitzroy River, Queensland, Australia	adults	2006 - 2011 (6 years)	0.9	0.02	0.84-0.94	capture-recapture	Cagnazzi et al. 2013
Australian snubfin (<i>Orcaella heinsohni</i>), humpback (<i>Sousa sp.</i>) and bottlenose (<i>Tursiops sp.</i>) dolphins	Port Essington, Australia	adults	2008 - 2010 (3 years)	snubfin: 0.81 , humpback: 0.59, bottlenose: 0.51	snubfin: 0.11, humpback:0.12, bottlenose: 0.17		capture-recapture	Palmer et al. 2014

Appendix 4.1

Species	Location	demographic included	number of years used to produce estimate (or number of individuals examined)	estimate of survival rate	SE	95% CI	method	citation
Striped (<i>Stenella coeruleoalba</i>), short-beaked common (<i>Delphinus delphis</i>), and bottlenose (<i>Tursiops truncatus</i>) dolphins	Gulf of Corinth, Greece	adults	2011 - 2015 (5 years)	striped and common dolphins: 0.94, bottlenose: 0.85 (average, year-dependent)		striped and common dolphins: 0.92–0.96; bottlenose: 0.76–0.95	capture-recapture	Santostasi et al. 2016
Australian humpback (<i>Sousa sahulensis</i>), bottlenose (<i>Tursiops sp.</i>) and Australian snubfin (<i>Orcaella heinsohni</i>) dolphins	Darwin, Australia	adults	3.5 years	varied between sites, species and season (0.46 - 0.98)		varied between sites, species and season; wide confidence intervals for all estimates	capture-recapture	Brooks et al. 2017
Indo-Pacific bottlenose (<i>Tursiops aduncus</i>), Australian humpback (<i>Sousa sahulensis</i>), and Australian snubfin (<i>Orcaella heinsohni</i>) dolphins	Kimberly region, north-western Australia	adults	2012 - 2014 (3 years)	bottlenose: 0.86; humpback: 0.62; snubfin: 0.95	bottlenose: 0.09; humpback: 0.12; snubfin: 0.05		capture-recapture	Brown et al. 2016

Appendix 4.2

CJS model comparison

Notation: Phi represents survival while p represents recapture probability. A (~1) indicates a model where the parameter is kept constant while a (~time) indicates a model where the parameter varies.

```
capturehistory <- read.csv("ch2015.csv", header=TRUE, colClasses=
c("character"))
library(RMark)

phi.dot<-list(formula=~1)
p.dot<-list(formula=~1)
p.time<-list(formula=~time)
phi.time<-list(formula=~time)
model.phi.dot.p.t <- mark(capturehistory,model.parameters=list(Phi
=phi.dot, p=p.time), time.intervals=c(1,1,1,1,1,1,1,3,1,1,1,1,1,
1,1,1,1,2,1,1,2), begin.time=1990)

model.phi.dot.p.dot <- mark(capturehistory,model.parameters=list
(Phi=phi.dot, p=p.dot), time.intervals=c(1,1,1,1,1,1,1,3,1,1,1,1,
1,1,1,1,1,2,1,1,2), begin.time=1990)

model.phi.t.p.t <- mark(capturehistory,model.parameters=list(Phi=
phi.time, p=p.time), time.intervals=c(1,1,1,1,1,1,1,3,1,1,1,1,1,1,
1,1,1,2,1,1,2), begin.time=1990)

model.phi.t.p.dot <- mark(capturehistory,model.parameters=list(Phi
=phi.time, p=p.dot), time.intervals=c(1,1,1,1,1,1,1,3,1,1,1,1,1,
1,1,1,1,2,1,1,2), begin.time=1990)

cjs.results=collect.models(type="CJS")
cjs.results

##              model npar      AICc DeltaAICc      weight Devia
nce
## 2      Phi(~1)p(~time)    22 3714.963   0.00000 0.997770339 1552.
454
## 4 Phi(~time)p(~time)    42 3727.170  12.20735 0.002229661 1522.
536
## 3      Phi(~time)p(~1)    22 3811.335  96.37180 0.000000000 1648.
826
## 1          Phi(~1)p(~1)     2 3879.815 164.85159 0.000000000 1758.
105
```

Table of capture histories required for each mark rate

```
## -----  
-  
## mark.rate    number.of.capture.histories  
## -----  
-  
##    0.15                1143  
##  
##    0.145               1105  
##  
##    0.14                1066  
##  
##    0.135               1028  
##  
##    0.13                990  
##  
##    0.125               952  
##  
##    0.12                914  
##  
##    0.115               876  
##  
##    0.11                838  
##  
##    0.105               800  
##  
##    0.1                 762  
##  
##    0.095               724  
##  
##    0.09                686  
##  
##    0.085               648  
##  
##    0.08                609  
##  
##    0.075               571  
##  
##    0.07                533  
##  
##    0.065               495  
##  
##    0.06                457  
##  
##    0.055               419  
##  
##    0.05                381  
## -----  
-
```

Simulation to determine the effect of mark rate on estimating survival rate

To speed up analysis, multiple R sessions may be opened, each evaluating a different set of mark rates.

```

setwd("C:/mark_rate_simulation_2017")
#Load required packages
library(RMark)
library(data.table)
capturehistory <- read.csv("ch2015.csv", header=TRUE, colClasses=
c("character")) #Read in CSV of capture histories
clean.output<-NULL #clears any previous simulation runs
mark.output<-NULL

##enter number of cores for computer to use
#####-----Global variables-----#####
simulationNumber = 10000 # Number of simulations to run for a
#given mark rate
totalmarkedDolphins = 518 # Number of marked dolphins in the
#catalogue
currentMarkRate = 0.068 # Current, measured mark rate of the
#population
minMarkRate = 0.05 # Minimum mark rate of interest
maxMarkRate = 0.15 # Maximum mark rate of interest

#####-----#####
directory for this script run; makes a file with time stamp where
final data goes in
setwd(workingDir) # Go into the overall directory
markRateRange <- seq(minMarkRate, maxMarkRate, by = 0.005) #Gen-
#erates a range of hypothetical mark rates, spaced by 0.5%
print(paste0("*** Starting script in '",workingDir,'" for mark ra
tes ",paste(markRateRange, sep=", "))) # Announce the overall
#start, tell use what mark
#rates will be tested

#setting model parameters; ~1=constant, ~time=time varying
phi.dot<-list(formula=~1)
p.time<-list(formula=~time)

for (markRate in markRateRange)
{
# Number of rows to grab from sample data per simulation

sizeOfSamples = round((markRate * totalmarkedDolphins)/currentMar
kRate)
print(paste0("** Beginning simulation at mark rate of ",markRat
e))
# Make data frame containing 'sizeOfSamples' number of sighting
#histories
globalData <- as.data.frame(replicate(simulationNumber, {matrix(u
nlist(sample(capturehistory$ch, size = sizeOfSamples, replace=T,
prob=NULL)),nrow=sizeOfSamples, byrow=T)}),stringsAsFactors=F)

```

```

for (i in 1:simulationNumber)
{
  # Grab the i'th row from globalData as a 1 column data- frame
  #with sizeOfSamples rows (each a sighting history)
  simData <- globalData[i]
  # Give this column the heading "ch" to keep Mark happy
  colnames(simData) <- c("ch")
  model.phi.dot.p.t <- mark(simData,model.parameters=list(Phi=p
hi.dot, p=p.time), time.intervals=c(1,1,1,1,1,1,1,3,1,1,1,1,1,1,
1,1,2,1,1,2), begin.time=1990, threads=1) # Run model and return
#data matrix, threads=number of processor cores to calculate
#model
  #turn matrix into a data frame
  mark.output[[i]]<-as.data.frame(model.phi.dot.p.t$results$rea
l, row.names=NULL)
}
print("* Done! Processing data..")
for (j in 1:simulationNumber)
{
  clean.output[[j]] <- mark.output[[j]][1,1:4]
}
print("* Binding list..")
FinalResult <- rbindlist(clean.output, use.names=T, fill=T)
print(paste0("* Writing mark_rate",markRate,".csv"))
write.csv(FinalResult, file = paste0("mark_rate",markRate,".csv
"))
#Announce finished for this mark rate
print(paste0("* Done for mark rate ", markRate))
}

print('*** END')

```


Example output of simulation

Below are the first 20 entries of a data output to illustrate what the product of the simulation looks like at each mark rate (this particular output was taken from a mark rate of 0.12); estimate=estimate of survival rate, lcl=lower confidence limit, ucl=upper confidence limit, CV=coefficient of variation.

```
##
## -----
## X estimate se lcl ucl
## ---
## 1 0.8923 0.005952 0.8801 0.9034
##
## 2 0.8858 0.006292 0.8729 0.8976
##
## 3 0.89 0.006101 0.8774 0.9014
##
## 4 0.8888 0.006038 0.8764 0.9001
##
## 5 0.8833 0.006555 0.8698 0.8955
##
## 6 0.9007 0.005687 0.889 0.9113
##
## 7 0.9019 0.0057 0.8901 0.9125
##
## 8 0.8937 0.006161 0.881 0.9052
##
## 9 0.8977 0.005787 0.8858 0.9085
##
## 10 0.8846 0.006519 0.8712 0.8968
##
## 11 0.8883 0.006064 0.8759 0.8997
##
## 12 0.8927 0.005982 0.8804 0.9039
##
## 13 0.8853 0.006265 0.8725 0.8971
##
## 14 0.8917 0.006052 0.8792 0.903
##
## 15 0.8951 0.005935 0.8829 0.9061
##
## 16 0.896 0.005705 0.8843 0.9067
##
## 17 0.8789 0.006323 0.866 0.8908
##
## 18 0.8849 0.006275 0.872 0.8966
##
## 19 0.8955 0.005753 0.8837 0.9063
##
## 20 0.9018 0.005725 0.89 0.9124
## -----
```