

**Using photo-ID data to investigate population parameters and
social structure of sperm whales visiting Kaikōura**

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Abstract

In order to effectively manage and protect populations, it is crucial that long-term trends in abundance and population structure are understood. Kaikōura is one of the few places worldwide where sperm whales can be found only a few miles offshore. Although whales are present nearly all year round, individuals come and go from the study area, and hence none are truly resident. They are the focus of an economically important whale watching industry and may also indicate changes in the ecosystem, driven by climate change or other human impacts. Previously, a decline in individuals using the study area had been detected from 1991-2007. My research used photo-ID capture-recapture techniques to: 1) Investigate long-term trends in abundance of sperm whales at Kaikōura with Cormack-Jolly-Seber (CJS) modelling to determine if the previously detected decline has continued, 2) Contrast these analyses with an alternative, and potentially more appropriate, approach to modelling abundance (the Robust design), which allows for temporary emigration of whales from the study area, and 3) Explore the social structure of male sperm whales visiting Kaikōura by investigating ways to define associations and testing for preferred associations between individuals. The CJS modelling showed that there was a significant decline in the number of individuals using the study area, from 89 (95% CI: 60-131) individuals in 1991 to 40 (95% CI: 33-49) in 2017. The Robust design analysis indicated that this decline was driven by summer abundance with a significant decline from 43 individuals (95% CI: 12-148) in 1990 to 23 individuals (95% CI: 16-32) in 2017. There was no significant trend in winter abundances over time. Preferred and/or avoided companions, and the temporal patterning of associations were investigated using the program SOCPROG. Potential associations among individual whales were investigated over three time-spans; associated if seen on the same day, associated if seen within two consecutive days, and associated if seen over a four day time-span. Preferred associations were detected in all three scenarios, with preferred associations lasting approximately four years. This is the first statistical evidence of preferential associations in male only groups of sperm whales. Continued research on this population and the potential causes of the decline will aid in determining appropriate management for this economically, ecologically and culturally important population.

Keywords: photo-ID, capture-recapture, Cormack-Jolly-Seber, Robust design, sperm whale, Kaikōura, abundance, social organisation.

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This thesis is dedicated to Eko and Igor

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Chapter 1

Introduction

A central challenge in research on animal ecology is that many of the processes influencing populations occur over long temporal scales, such as multiple years or decades (Clutton-Brock & Sheldon, 2010). Studies with long-term datasets extending over decades are therefore essential for understanding abundance and population dynamics, and supporting management decisions (Clutton-Brock & Sheldon, 2010). Population parameters, such as abundance, survival and recruitment, can be better understood if individuals are recognisable and trackable through time and space (Hammond et al., 1990; Würsig & Jefferson, 1990). Historically, individual-based field studies involved capturing individuals and physically marking them (e.g. Kluijver, 1951; Schwartz et al., 1998). Many taxa, however, have natural markings which are unique to each individual and remain relatively unchanged over time, including beetles (Caci et al., 2013), cetaceans (Hammond et al., 1990), cheetahs (Kelly, 2001), frogs (Bradfield, 2004), octopuses (Huffard et al., 2008), manta rays (Barker & Williamson, 2010), and lizards (Treilibs et al., 2016).

As an alternative to physical marking, animals that are individually distinctive due to unique natural marks can instead be photographed, a process called photographic identification, or photo-ID (Hammond et al., 1990). Photo-ID has several advantages over tagging or marking, including eliminating the risk of behavioural change or physical harm to animals caused by capture and handling (Hammond et al., 1990). Estimating abundance has been the focus for many individual-based studies (Hammond, 1990). This is because understanding abundance is essential for assessing the severity of threats and for supporting conservation and management decisions (Taylor & Gerrodette, 1993). Photo-ID data are commonly used in capture-recapture models, which use resightings of known individuals to estimate population parameters (Seber, 1982). Capture-recapture methodology is often employed for estimating abundance (Cerchio, 1998; Silver et al., 2004; Gormley et al., 2005; Cantor et al., 2012), but depending on the models used, survival rates, temporary emigration and recruitment can also be estimated (Seber, 1982; Kendall, 1990). Photo-ID data are also used in assessments of fecundity (Thompson & Wheeler, 2008; Kuningas et al., 2014), home-range (Crawshaw & Quigley, 1991; Rayment et al., 2009), site fidelity (Gowans et al., 2000; Fox et al., 2013), migration pathways (Barker & Williamson, 2010; Morrison & Bolger, 2014), social organisation (Lettevall et al., 2002; Karczmarski et al., 2005), and stock

structure (Dufault et al., 1999; McConkey et al., 2002). Photo-ID data are therefore applicable to a wide range of biological concepts, and can be used to answer fundamental ecological questions.

Photo-ID methods are commonly used in studies of cetaceans in particular, most of which are not amenable to traditional capture and marking methods (Hammond et al., 1990; Stevick et al., 2001). Historically, studies of marine mammal populations used catch-per-unit-effort data gathered by whaling operations. However, these data proved unreliable due to misreported catch numbers and the wide-ranging nature of many populations (Cooke, 1986). The need for a reliable way to track live individuals led researchers to investigate the use of natural markings (Hammond, 1990). The success of photo-ID, and the analyses of the resulting data, mean that today we have an improved understanding of population parameters, movement, behaviour and abundance of many whale populations (Gormley et al., 2005; Foster et al., 2012; Gero & Whitehead, 2016).

In capture-recapture studies, a population is sampled and individuals are marked or captured via natural markings (Seber, 1982; Hammond, 1986). The population is then resampled at subsequent sampling periods, and all new and previously identified individuals are recorded each time. The specific capture-recapture method used to analyse photo-ID data depends on the type of population being assessed. The most basic capture-recapture model is the Lincoln-Peterson model, which can be used to estimate abundance of a closed population (Pollock et al., 1990). A closed population meets the following assumptions: that the population is closed to any additions (birth, immigration) and deletions (death, emigration), animals are equally likely to be captured in each sample, and marks are not lost or become unobservable over time (Seber, 1982). Closed population models, therefore, are only practical when assessing a population over a very short time-span where the researcher can be sure there are no additions or deletions. For longer time series, open capture-recapture models are more appropriate and can be used to estimate not only population size, but also survival and recruitment rates (Lebreton et al., 1992). One such model is the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965). Open and closed models can also be combined, for example in Robust design models. This type of modelling consists of secondary sampling periods within primary sampling periods (Pollock, 1982). The population is assumed to be closed within secondary periods, but open between primary periods (Pollock, 1982). This allows for an estimate of abundance to be generated for each primary period, and estimates of survival and temporary emigration between primary periods (Pollock, 1982).

1.1 The sperm whale

1.1.1 Life History and behaviour

Sperm whales (*Physeter macrocephalus*) are the largest of all toothed whales, and show the greatest sexual dimorphism; mature males grow up to 18m in length, while females rarely reach 11m (Best, 1979). Males weigh up to 57t and females up to 15t (Whitehead, 2003). The global distribution of females and males is also highly differentiated. Generally, males are found at higher latitudes, while females and juveniles inhabit tropical and subtropical waters (Best, 1979). Females, calves and juveniles form “nursery” groups, membership of which can be stable over periods of decades (Gero et al., 2015). During puberty, between 6 and 15 years old, they leave the nursery groups and travel to higher latitudes (Best, 1979; Whitehead, 2003). Once they reach their late-twenties, they return to female groups during breeding seasons (Whitehead, 2003). When not breeding, the largest males are often solitary at higher latitudes, even reaching polar regions (Best, 1979). Smaller males are generally found in loose aggregations, often referred to as bachelor groups (Whitehead & Arnborn, 1987). To date there is no evidence of long-term preferred associations between individuals within these loose bachelor groups (Lettevall et al., 2002), although note that defining an “association” between males is challenging as they do not stay within cohesive “schools” that consist of permanent members (Best, 1979). On occasion, however, males seem to seek each other out, forming tighter clusters (Lettevall et al., 2002) and sometimes even mass strand together (Kompanje & Ruemer, 1995).

Sperm whales are deep diving predators regularly reaching depths of 400 m to 1200 m to feed on fish and squid (Jaquet et al., 2000; Watwood et al., 2006). Dive duration typically ranges from 33 to 53 minutes but there are records of dives up to 138 minutes (Papastavrou et al., 1989). During a dive, sperm whales emit loud broadband clicks, at an average rate of 1 to 2 clicks per second (Douglas et al., 2005), for about 85% of the time they are submerged (Jaquet et al., 2001). Clicks are highly directional (Møhl, 2001) and are used to echolocate on prey (Fais et al., 2016). The highly vocal behaviour of sperm whales allows relatively straightforward tracking of individuals or groups underwater by using a directional hydrophone (Dawson, 2000, 2014). Acoustic information can also be used to estimate length, growth rates and dive behaviour (Rhinelanders & Dawson, 2004; Miller et al., 2013a, 2013b).

1.1.2 Commercial whaling

During the 20th century, most populations of large whales were heavily exploited through whaling. In 1946, the International Convention for the Regulation of Whaling was signed,

forming the basis of the International Whaling Commission. The moratorium on commercial whaling, however, did not come into effect until 1986 (Whitehead et al., 1997). From the 1700s to the 1970s the sperm whale was a primary target for whalers, and especially during the 1960s in response to the depletion of stocks of baleen whales (Whitehead et al., 1997; Whitehead, 2002). Currently, sperm whales are listed as ‘vulnerable’ by the IUCN, because population size has decreased by $\geq 50\%$ in three generations (Taylor et al., 2008). They are classed as ‘vulnerable’ and not ‘endangered’ because the cause of their decline (commercial whaling) is understood and not currently in operation (Taylor et al., 2008). Despite this, there is evidence of lingering impacts on population distribution and fecundity, as whaling concentrated primarily on males of larger size because of their greater value (Whitehead et al., 1997).

1.1.3 Population analyses and photo-ID

During the 1970s and early 1980s, the Scientific Committee of the International Whaling Commission attempted to assess sperm whale populations using catch-per-unit-effort methods. Estimates for male sperm whales in the North Pacific showed a decrease in abundance from 183,630 in 1910 to 46,430 individuals by 1976 (Tillman & Breiwick, 1977). As with attempts to estimate the abundance of other whale populations, these methods included considerable bias (Horwood, 1980; Cooke, 1986; Zemsky et al., 1995). Photo-ID methodology was first applied to sperm whales in the late 1980s, following the first non-invasive research on the species around the Galápagos Islands and Sri Lanka (Whitehead & Gordon, 1986; Gordon, 1987). Sperm whales can be individually identified because the trailing edge of their flukes accumulates natural marks over their lifetime (Arnbom, 1987; Figure 1.1). These marks can be photographed when whales lift their flukes in the air, prior to a long foraging dive (Childerhouse et al., 1995). Photo-ID has now been used to look at an array of sperm whale population characteristics, covering variations in abundance, residency, distribution and social organisation (Richard et al., 1996; Weilgart & Whitehead, 1997; Matthews et al., 2001; Jaquet et al., 2003; Gero et al., 2008; Rødland & Bjørge, 2015).



Figure 1.1: A photo-ID shot of a sperm whale (individual LNL160) from the University of Otago Marine Mammal Research Group's photographic catalogue.

1.2 Male sperm whales at Kaikōura

Aggregations of male sperm whales have received less research attention compared with female and juvenile groups, partly because there are only a few places worldwide where accessible populations of males are found close to shore (Jaquet et al., 2000). Kaikōura is one of these places (Jaquet et al., 2000). The bathymetry is characterised by the Conway Trench which has depths of over 500 m, and the Kaikōura Canyon which drops to over 1,000 m within 2.2 nautical miles (n.mi.)¹ from shore (Jaquet et al., 2000; Richter et al., 2003; Figure 1.2).

¹ N.B. 1 n.mi. = 1.852 km

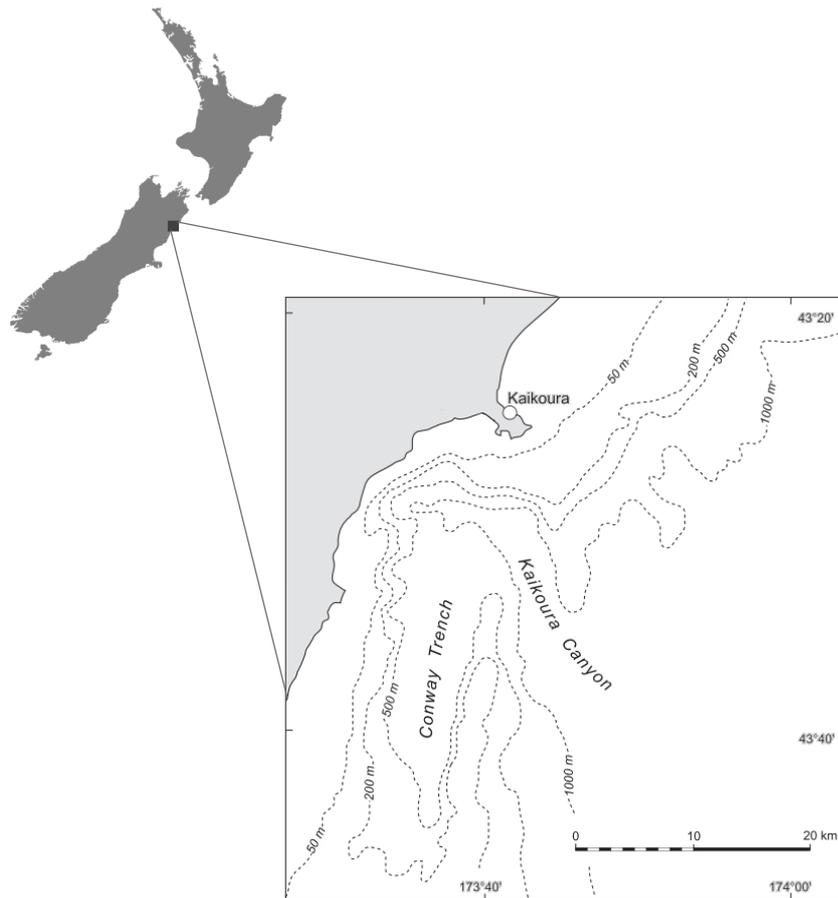


Figure 1.2: The bathymetry of the Conway Trench and Kaikōura Canyon off the coast of Kaikōura. Adapted from Richter et al. (2003).

The Kaikōura Canyon is one of the most productive deep-sea habitats in the world (De Leo et al., 2010) and provides a foraging hotspot for the visiting male sperm whales (Jaquet et al., 2000). Although sperm whales can be sighted year-round, there is no evidence that any individuals are truly resident there (Childerhouse et al., 1995; Jaquet et al., 2000). When in Kaikōura, sperm whales spend most of their time foraging in the canyon (Jaquet et al., 2000). Sperm whales feed at high trophic levels and have large energy requirements, meaning the density of these large mobile predators in an area reflects its productivity (Lockyer, 1981; Moore, 2008). Sperm whales, therefore, can be used as indicators of the health of the deep-sea ecosystem at Kaikōura.

1.2.1 *Whale watching at Kaikōura*

Intense whaling pressure during New Zealand's last phase of whaling resulted in 248 sperm whales taken from the Kaikōura area in 1963 and 1964 (Grady, 1982). Now, the population forms the basis of an important whale watching industry and is one of only two places

worldwide where sperm whales are the main focus of year-round ecotourism (Richter et al., 2003; Markowitz et al., 2011). Tours operate from boats, helicopters and planes throughout the year. Whale Watch Kaikōura (WWK) was formed in the late 1980s, with the motivation to be an economic base for the local Māori people (Te Korowai, 2007). They began operating with one 6.7 m inflatable boat that could carry eight passengers (WWK, 2017). Over the last three decades the industry has expanded considerably and now operates four 17 m catamarans (Markowitz et al., 2011). An estimated 1 million people now visit Kaikōura annually, with up to 100,000 visitors booking with WWK (Spiller & Bhowick, 2014; WWK, 2017). The new boats are powered by on-board diesels with water jet propulsion systems and produce substantially less underwater sound than previous boats (Markowitz et al., 2011).

As whale and dolphin watching industries continue to grow worldwide, it is important to assess the potential negative effects on populations. The impact of vessels (including helicopters and planes) on sperm whales at Kaikōura has been assessed periodically from 1992-2011 (Gordon et al., 1992; Richter et al., 2003, 2006; Markowitz et al., 2011). Previous impacts detected include reduced time at the surface, reduced time to first click following fluke-up, and increased changes in swimming direction at the surface (Richter et al., 2006). Recent shore-based studies detected significant changes in ventilation patterns but observations of known individuals from a research vessel did not (Markowitz et al., 2011). It is probable the individual based dataset from the boat lacked adequate statistical power. It is also possible that a change to much quieter water-jet drives on the WWK tourist vessels may have reduced impacts.

The start of whale watching in Kaikōura addressed high unemployment rates and poverty in the Māori community and wider area (Te Korowai, 2007). As the tourism industry expanded, it continued to be an increasingly important economic asset for the region. For example, an estimated one third of jobs in Kaikōura are related to the tourism industry. Any negative impacts on sperm whales in the area would be a threat to this thriving industry, and the Kaikōura economy as a whole.

1.2.2 Cultural significance

As well as being a crucial component of New Zealand's whale watching industry, sperm whales are also a very important aspect of Māori culture. They have spiritual significance in mythology as taniwha, as well as a distinct role as taonga (treasures) for Māori people (Poharama et al., 1998).

1.2.3 Past research at Kaikōura

The accessibility of this population has also been utilised for research, with data collected by the University of Otago Marine Mammal Research group since 1990. This research has covered a wide range of topics including population structure and dynamics (Childerhouse et al., 1995; Jaquet et al., 2000), acoustics (Douglas et al., 2005; Miller et al., 2013b; Rhinelander & Dawson, 2004), individual identification (Childerhouse et al., 1995; Dawson et al., 1995), photogrammetry (Rhinelander & Dawson, 2004; Growcott et al., 2011), foraging ecology (Miller et al., 2013a; Guerra et al., 2017), impacts of tourism (Richter et al., 2003; Markowitz et al., 2011), and social organisation (Lettevall et al., 2002). The most recent MSc research investigated long-term abundance trends using CJS modelling (van der Linde, 2009). From 1991 to 2007, a significant decline in abundance was detected (van der Linde, 2009; Figure 1.3). Since 2007, photo-ID data collection has continued but without further assessment of abundance. This raises the obvious question of whether the decline has continued and, if so, what could be causing it. Declining trends in abundance can be driven by an actual decrease in population size (eg. Caswell et al., 1999), a change in distribution patterns whereby fewer individuals are using the study area (eg. Bejder et al., 2006), or both (eg. Bart et al., 2007). The potential importance of sperm whales as both an indicator of ecosystem health, and a crucial resource for tourism revenue, means that determining whether a decline is continuing is essential.

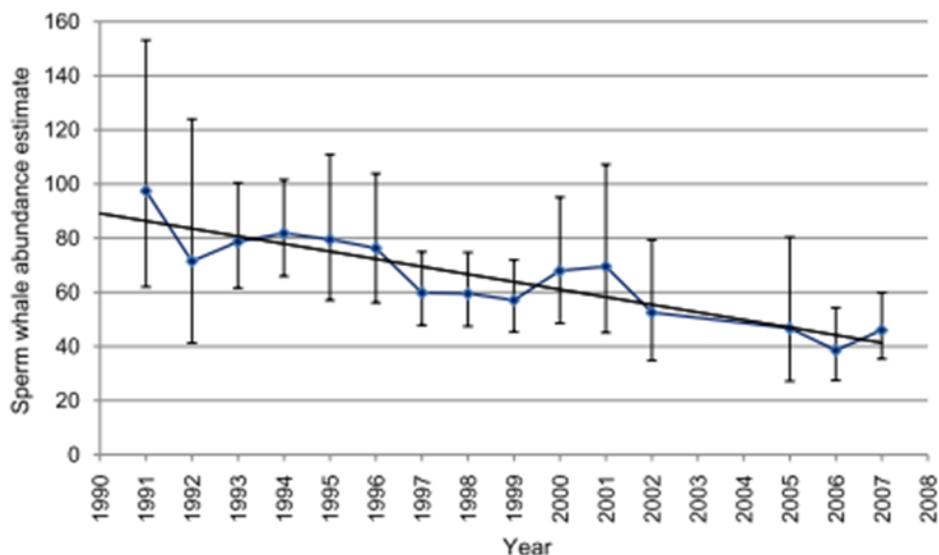


Figure 1.3: Estimates of the annual abundance of sperm whales at Kaikōura calculated by van der Linde (2009), showing a linear regression line through the estimates. Error bars are 95% log-normal confidence intervals.

As with other groups of “bachelor” males, the sperm whales at Kaikōura are generally defined as solitary (Lettevall et al., 2002). However, some individuals seem to forage in the same areas as one another over multiple field seasons, and there are instances of individuals making coordinated surfacings and dives together (Lettevall et al., 2002). There are even records during the 1990s of up to five individuals swimming in coordination and diving together (University of Otago Marine Mammal Group unpublished data). A study in 2002, however, found no preferred associations between individuals (Lettevall et al., 2002).

1.2.4 The 2016 Kaikōura earthquake

A 7.8 magnitude earthquake on the 14th of November (Clark et al., 2017). This included a rupture in the offshore continuation of the Kekerengu Fault, and subsequent underwater mudslides into the Kaikōura Canyon (NIWA, 2017a). Data collection soon after the earthquake meant any immediate responses of the sperm whales to the event could be assessed. The earthquake significantly altered the benthic environment in the Kaikōura Canyon, with no sign of any organisms living on or in the seabed for a stretch of six kilometres, three months after the quake (NIWA, 2017a). Signs of early recovery were reported 10 months after the quake, however, with juvenile benthic organisms beginning to recolonise the canyon (NIWA, 2017b). If the high productivity of the Kaikōura area is supported by the productivity of the benthos, the earthquake’s effects on the ecosystem could be important. The near-constant foraging behaviour of sperm whales at Kaikōura indicates that they are there to feed. It is highly likely that the productivity of the canyon is important for supporting these top predators (Jaquet et al., 2000; De Leo et al., 2010). Results in this thesis will be discussed in light of the earthquake, where appropriate.

1.2.5 Study objectives

The foraging habitat at Kaikōura is almost certainly only a portion of the total range used by the male sperm whales that visit. This means individuals are regularly moving in and out of the study area (Childerhouse et al., 1995; Jaquet et al., 2000). The previous research on abundance used a Cormack-Jolly-Seber capture-recapture modelling approach (van der Linde, 2009), which allows for immigration and emigration from the study population, but only on a permanent basis (Cormack, 1964). Alternative capture-recapture methods such as the Robust design, in contrast, allow for temporary emigration to occur (Pollock, 1982). If including temporary emigration represents the ecology of the study population more faithfully, the resulting demographic estimates should be more reliable (Pollock, 1982). The long-term photo-ID dataset also provides a unique opportunity to investigate social organisation among

male sperm whales using the study area. Since the last study of sociality (Letteval et al., 2002) nine additional years of photo-ID data, spanning 13 years, have been collected. It is possible that associations among males occur on much larger time scales than those among females and juveniles, and could now be detected using a 27 year dataset.

Therefore, my study had the following aims:

1. To investigate trends in abundance of sperm whales at Kaikōura with Cormack-Jolly-Seber modelling, including the new data collected since 2007, to determine if the previously detected decline has continued.
2. To contrast these analyses with an alternative, and potentially more appropriate, approach to modelling abundance (the Robust design), which allows for temporary emigration of whales from the study area.
3. To explore the social structure of male sperm whales visiting Kaikōura by investigating ways to define associations and testing for preferred associations between individuals.

In this study I used data from the long-term study which has been ongoing since 1990 and has involved the work of many researchers. From 2014-2016, I contributed to the collection and processing of photo-ID data during three field seasons. Analysis of the population parameters and sociality will advance our understanding of the status of the sperm whale population at Kaikōura and the implications for the wider ecosystem. Furthermore, it will provide critical information to contribute to the sustainable management of whale watching tourism in the area.

Chapter 2

Estimating the long-term trend in sperm whale abundance at Kaikōura using Cormack-Jolly-Seber modelling

2.1 Introduction

Estimating time-series of abundance is crucial for understanding how populations have changed over time (Hammond et al., 1990). Long-term studies are invaluable for studying trends because the ecological processes affecting population numbers commonly occur over multiple years, rather than weeks or months (Clutton-Brock & Sheldon, 2010). Interest in the abundance of cetaceans was first stimulated by commercial whaling (Evans & Raga, 2001). Whalers and scientists wanted to manage marine mammal populations in order to continue hunting them (Evans & Raga, 2001). Assessments began with catch per unit effort data but it was quickly realised these were unreliable (Cooke, 1986; de la Mare, 2014). From 1980, studies incorporated age and size structure models in an attempt to achieve global population estimates (Whitehead, 2002). However, due to falsified catch data and the wide ranging movements of individuals it was acknowledged that these techniques were also biased (Cooke, 1986).

The current practice for estimating abundance of cetacean populations generally involves capture-recapture or line-transect survey methods (Dawson et al., 2008). Capture-recapture methods are based on resighting individuals and can be used in a variety of ecological studies including estimation of abundance, survival and individual movement (Stevick et al., 2003; Silva et al., 2009; Verborgh, 2009; Fearnbach et al., 2012). While physical tagging is common in studies of many bird and mammal populations, many cetaceans can be recognised using unique, natural marks (e.g. Katona et al., 1979; Bigg, 1982; Arnbohm, 1987; Hammond, 1990). Individuals can therefore be sampled using photo-ID methods, reducing the risks of behavioural change or physical harm to animals caused by capture or handling (Hammond et al., 1990).

2.1.1 *Capture-recapture methods and Cormack-Jolly-Seber modelling*

Abundance estimation typically involves extrapolation of data samples to generate an estimate for a whole population or area (Hammond, 2002). This involves making assumptions about the type of population being studied and the behaviour of the individuals in the population (Hammond, 2002). Estimating abundance using capture-recapture data is based on the concept that if a proportion of the population is marked in an initial sample, then an estimate

based on this proportion can be achieved by observing the number of marked animals in a second sample (Seber, 1982). The number of individuals you marked, together with the proportion of marked individuals in a sample of the population, are used to estimate total population size. This forms the basis of the Lincoln-Peterson method, the most basic capture-recapture model (Seber, 1982). It assumes that the population is demographically closed, i.e. there are no births, deaths, immigration or emigration (Seber, 1982). If the two sampling periods occur close together in time, and the survey area is large enough, this assumption is likely to be valid (Seber, 1982). However, in many studies of mobile animals, it is not reasonable to assume the population is closed to additions and deletions (Pollock et al., 1990). The basic “open” population model is the Jolly-Seber model (Jolly, 1965; Seber, 1965), which provides abundance estimates for each sampling period, as well as estimating apparent survival rates and recruitment parameters (Pollock et al., 1990). A further modification, the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), focuses on estimating survival and capture probabilities (Pledger et al., 2003), from which abundance can be derived (Seber, 1982).

2.1.2 Current abundance trends for sperm whale populations

Modern whaling for sperm whales was most intense during the 1960s (Whitehead, 2009a). In the late 1970s and early 1980s, the Scientific Committee of the International Whaling Commission (IWC) was involved in assessing sperm whale populations in an attempt to better manage exploitation (e.g. Ohsumi, 1983). However, the lack of reliable abundance estimates during this time, and the decline of the whaling industry, meant these assessments became less of a focus (Whitehead, 2002). In 2002, the first estimate of the global population size of sperm whales (360,000) was produced using scaled up data from visual surveys (Whitehead, 2002). This estimate was compromised by the fact that only 24% of global sperm whale habitat had been visually surveyed (Whitehead, 2002). Post-whaling research has, however, begun to generate long-term abundance trends for some sperm whale populations (Whitehead et al., 1997; van der Linde, 2009; Moore & Barlow, 2014; Gero & Whitehead, 2016). Because sperm whale populations are demographically open over the long study periods required to estimate trends in abundance, Jolly-Seber modelling and variations of this method are usually used.

Most long-term studies of sperm whales show a significant decline in population abundance and low recruitment rates (e.g. Whitehead et al., 1997, van der Linde 2009; Gero & Whitehead, 2016). For example, the numbers of female and juvenile sperm whales around the Galápagos Islands have been declining at a rate of 20% per year (Whitehead et al., 1997),

while around the Lesser Antilles, sperm whale numbers have declined by 4.5% per year since 2010 (Gero & Whitehead, 2016).

2.1.3 Abundance of sperm whales at Kaikōura

The only published abundance estimate for sperm whales off the coast of Kaikōura showed that from 1989 to 1992, 60 to 108 individuals were present during any one season (Childerhouse et al., 1995). There was no significant difference between abundance during summer and winter seasons (Childerhouse et al., 1995). Since then, estimates of abundance have been generated via CJS modelling for two MSc projects. Abundance was estimated from 1991 to 2000 (Gormley, 2002) and then reassessed from 1991 to 2007 (van der Linde, 2009). From summer 1990/91 to winter 2000 there was no significant difference in yearly abundance, with estimates ranging from 62 to 122 individuals (Gormley, 2002). The most recent analysis revealed a declining trend, from 97 individuals in 1991 to 46 individuals in 2007 (van der Linde, 2009; Figure 1.3).

2.1.4 Aims

Sperm whales may be an important indicator of the health of their marine ecosystem, as well as being a resource for tourism revenue. Previous research suggested that a decline in the sperm whale population at Kaikōura occurred from 1991 to 2007 (van der Linde, 2009). Since how abundance has changed over time is one of the most important inputs into conservation management (Shea, 1998), it is essential to update the abundance estimate at Kaikōura to investigate whether the decline has continued. I used data gathered since 2007, as well as adding new data I have participated in collecting, to update the time-series of abundance estimates. For comparison with previous work, I also replicated the analysis methods of van der Linde (2009), with some appropriate adjustments.

2.2 Methods

The study site was an 821 km² (221.5 n.mi²) area, south of the Kaikōura Peninsula (Childerhouse et al., 1995; Figure 2.1). For safety and practicality, the study area extends from the Kaikōura Peninsula offshore to 12 n.mi., and to 16 n.mi. south. Data were collected from small (≤ 6 m) research boats, powered by outboard motors. Research was conducted in daylight hours, in sea states of Beaufort 3 or less, with no rain and a swell height of less than 2 m.

Research protocol has remained consistent since 1990, albeit with some slight variations. Between 1990 and 1994 a 10 n.mi. transect was conducted each day, from a randomised start point within the study area (Childerhouse et al., 1995). At 2 n.mi. intervals along the transect, bearings to whales were obtained during a 5 minute listen with a custom-built directional hydrophone (Childerhouse et al., 1995; Dawson, 2000). Once this transect was completed, the closest whale was tracked (Childerhouse et al., 1995). After this whale had been tracked and photographed, the next closest whale was tracked, and so on. From 1994 to 2014, surveying began by tracking the closest whale from a start point at the edge of the Kaikōura Canyon (Childerhouse et al., 1995; Jaquet et al., 2000; van der Linde 2009). For the present study (i.e. from 2014 onwards), the search pattern was modified slightly to facilitate addressing the joint research questions of abundance estimation and distribution analysis (the latter is part of a concurrent PhD project by Marta Guerra). The study area was divided into 4 n.mi. x 4 n.mi. blocks with rows labelled alphabetically and columns labelled numerically (Figure 2.1). Some blocks were smaller than this, however, because of proximity to the shoreline and the study area boundaries. A block was chosen at the beginning of each field day based on weather conditions and previous effort, with the aim to survey the study area uniformly within a field season. Within each block, a randomly chosen coordinate was used as a starting point. Whales were tracked using a custom-built directional hydrophone which had a range of 3-5 n.mi. Surveying began with a 15 minute listen at the randomised starting point. The closest whale was then tracked. If there were no whales vocalising within hydrophone range, a new block was selected, and the process repeated. Blocks adjacent to blocks where whales had been previously encountered that day were avoided in order to distribute search effort throughout the study area. Despite these subtle differences in methodology since 1990, each method achieved the aim of surveying the study area as uniformly as possible over the course of a field season, given the restrictions imposed by weather conditions.

Once a whale was tracked and located at the surface, the vessel was carefully maneuvered behind the whale to no closer than 50 m (measured by laser rangefinder). At the start and end of each encounter, information was stored via a custom-written program running on a Hewlett Packard 200LX palmtop computer, interfaced with an on-board GPS. The date, time of surfacing, time of diving and the vessel position were recorded. On diving, multiple photos were taken of the flukes (Childerhouse et al., 1995). While camera equipment has changed over the 25 years of the study, photographic methods have remained consistent.

Recent photos were taken with Nikon digital SLR cameras and Nikon zoom (80-200 mm f2.8) or telephoto (300 mm f2.8 or f4) lenses.

Photo-ID data were collected during summer and winter field seasons ranging from two weeks to two months in duration, in most years from 1990 to 2017. Lapses in fieldwork effort occurred from 2003 to 2004 and from 2010 to 2012. Data were collected during 2013 but were not appropriate for this analysis because of differing field methodology.

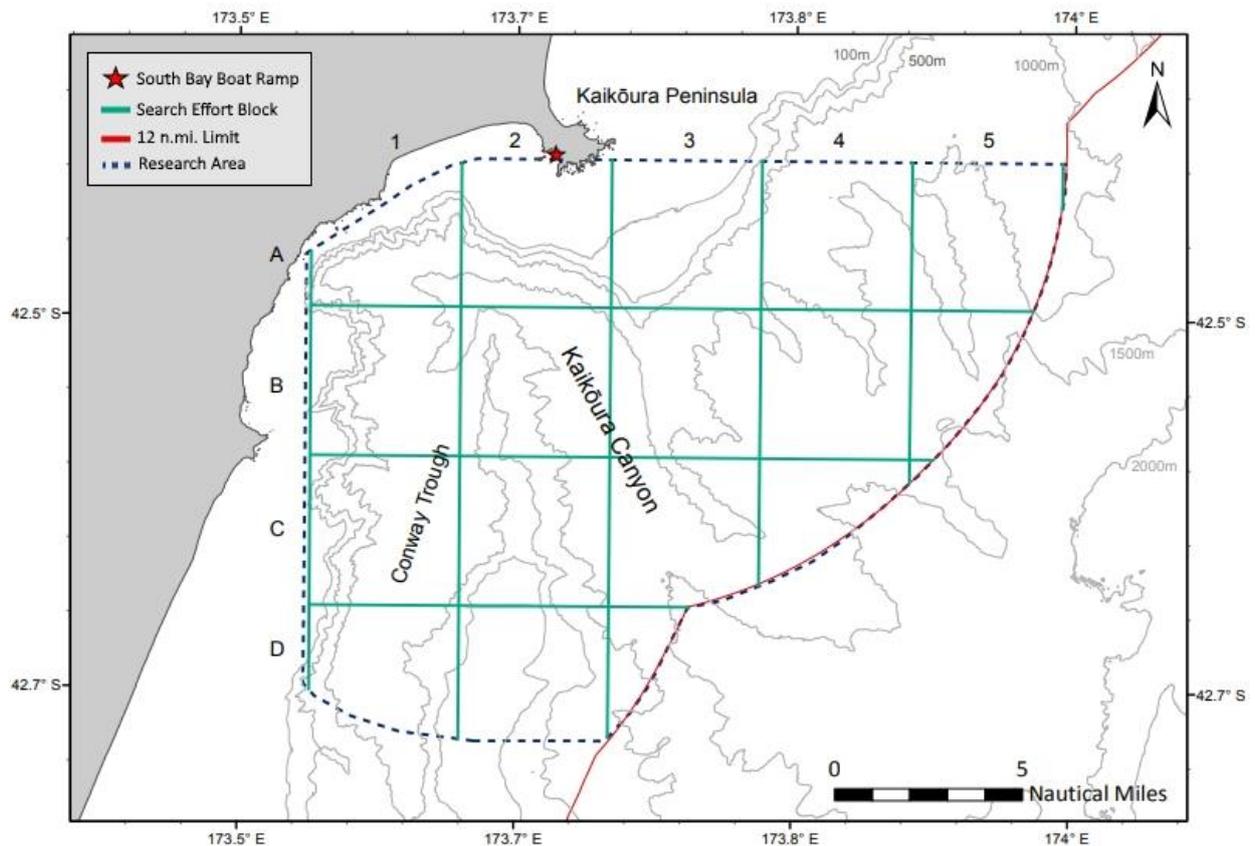


Figure 2.1: A map of the Kaikōura study site also showing the launch site at South Bay. Each study block is 4 n.mi. x 4 n.mi., indicated with blue lines. The red line indicates the 12 n.mi. boundary.

2.2.1 Photo-identification

Each photo used in the capture-recapture analysis had to meet strict quality criteria to reduce potential bias caused by individuals having unequal capture probabilities (Arnbom, 1987; Childerhouse et al., 1995; Urian et al., 2015; Table 2.1). For example, an individual with conspicuous marks, such as the entire right side of the fluke missing, could be easily identified from a poor photo, whereas a subtly marked individual could only be identified from a high quality photo (Urian et al., 2015). Hence the use of poor quality photographs

creates a capture bias towards obviously marked individuals, with the subsequent effect of biasing the population estimate downwards (Arnbom, 1987). More generally, poor quality photos also increase the risk of misidentifying individuals (Urian et al., 2015).

Table 2.1: A list of photo quality criteria which had to be met for identification photos of sperm whales at Kaikōura to be accepted for analysis.

Characteristic	Criterion
Fluke proportion	The notch and entire trailing edge of both flukes must be included in the photo.
Focus	The trailing edge of the flukes must be in sharp focus.
Angle	Photograph must be taken from behind the flukes. Flukes must be vertical or near vertical.

The photo quality criteria are visually depicted in Figure 2.2. In photo A, the whole flukes are in the frame and in focus. The notch between the flukes is included in the photo and the flukes have been photographed at an appropriate angle, i.e. while vertical. This photograph therefore meets the criteria for capture-recapture analysis. In comparison, Photo B is poorly focused and the notch is not included in the frame. As a result it would not be included in the analysis. Photo C is in focus but the flukes are not completely vertical, obscuring the marks in the trailing edge, and therefore must be rejected. Photo D is out of focus and the full flukes are not in frame. Photos which passed the photo quality criteria were compared with the existing photo-ID catalogue of sperm whale flukes from Kaikōura. If the individual photographed was already in the catalogue, the encounter information was added to an existing encounter database. If the individual was new to the catalogue, it was given a unique alphanumeric code and added to the encounter database, as well as the photographic catalogue. All photo-ID matches were confirmed by at least two experienced researchers. The catalogue was audited prior to the addition of new photographs in an attempt to eliminate photo-ID matching errors. The encounter database was used to determine the number of

individuals encountered each year, photographic effort and the cumulative number of unique individuals over the study period.



Figure 2.2: Quality criteria for photo-ID analysis of sperm whale flukes. A is an example of a photograph that meets all quality criteria and would be accepted for analysis. Photos B-D do not meet quality criteria. All photos are of individual MLS70.

2.2.2 Abundance estimation

To estimate abundance, an encounter history was created for each individual by giving a 1 to an individual if it was seen during a sampling period, and a 0 if it was not. To be consistent with previous analyses (van der Linde, 2009), data from field seasons within the same calendar year were pooled. This yielded 22 annual sampling periods between 1990 and 2017 (not including 2003, 2004, 2010, 2011, 2012 and 2013, in which no appropriate data were gathered). Encounter histories for individual sperm whales were processed in Program MARK (White & Burnham, 1999). The CJS model was used to estimate apparent annual survival rate (ϕ) and capture probabilities (p ; White & Burnham, 1999). The following assumptions needed to be addressed for CJS modelling to be appropriate (Seber, 1982; Hammond et al., 1990):

- 1) Individuals are uniquely identifiable and must be identified correctly.

- 2) Marks must not be lost, or change so much that individuals cannot be identified correctly.
- 3) Each individual has the same probability of being captured.

Violations to assumptions 1, 2 and 3 were minimised by using the photo quality criteria previously described above. For assumption 1 and 2, the reliability and stability of fluke markings for sperm whale identification at Kaikōura was previously assessed (Childerhouse, et al., 1996). Small mark changes do occur over time but because a combination of marks are used for identification these small changes do not affect identifiability (Childerhouse et al., 1996). Regardless, any mark changes were noted, and identification photographs were updated in the catalogue when necessary. Even with strict photo quality criteria, however, assumption 3 is likely to be violated in most capture-recapture studies either due to temporary emigration, or inherent differences in catchability between individuals (Hammond, 1986).

A bootstrapped goodness-of-fit test (GOF) was performed for the basic CJS model, with time-dependent survival and time-dependent capture probabilities. The GOF test creates an encounter history based on the survival and capture probabilities for each encounter occasion (White et al., 2001). This simulated encounter history was then compared to the fitted model, resulting in estimates of model deviance and fit (\hat{c}). One thousand GOF simulations were run for this study. To determine the \hat{c} value for the fit of the model, the observed \hat{c} was calculated by dividing the model deviance by the mean deviance of the simulated data (White et al., 2001).

After GOF testing, the following parameterisations of the CJS model were trialled:

ϕp_t – time-dependent survival and capture probabilities.

$\phi p.$ – time-dependent survival and constant capture probabilities.

$\phi . p_t$ – constant survival and time-dependent capture probabilities.

$\phi . p.$ – constant survival and constant capture probabilities.

The assumption of equal catchability also will be violated if the method of capture alters an individual's behaviour. (Brownie & Robson, 1983). During photo-ID, sperm whales are not physically captured, and hence cannot become “trap shy”, but may become more or less tolerant of boats approaching after the first encounter (van der Linde, 2009). A

behavioural response model can incorporate this by allowing a temporary effect on survival for the initial sampling period (Brownie & Robson, 1983). The following behavioural response models were therefore also tested:

$\phi_{t+b}p_t$ – time-dependent survival with a behavioural response and time-dependent capture probabilities.

$\phi_{t+b}p.$ – time-dependent survival with a behavioural response and constant capture probabilities.

$\phi.+bp_t$ – constant survival with a behavioural response and time-dependent capture probabilities.

$\phi.+bp.$ – constant survival with a behavioural response and constant capture probabilities.

The simplified parameter models and the models including behavioural response were ranked using Akaike's information criterion (AIC; Akaike, 1973; Burnham et al., 2011). Only models where all parameters could be estimated were included in the analysis. Models with $\phi(t)$ generally did not perform properly, due to insufficient data. AIC provides a score which reflects the fit of the model to the data, whilst penalising increasing model complexity (Burnham et al., 2011). The aim is to find the simplest model that fits the data well, resulting in the lowest AIC score (Burnham et al., 2011). MARK uses AICc, which is corrected for small sample sizes (Hurvich & Tsai, 1989). $\Delta AICc$ (the relative difference between AICc scores), model weight and deviance (a measure of model fit) are also calculated through MARK. Unless there is clear support for one model over the rest, for example if model weight is ≥ 0.9 , model averaging is recommended (Burnham & Anderson, 2002).

Annual abundance was estimated using the capture probabilities generated by MARK for the best fitting model, and the number of individuals sighted during each sampling period, according to the following equation (Loery et al., 1997):

$$N_j = \frac{n_j}{p_j}$$

Where N_j is the abundance estimate in the j th sampling period (for this study, a specific year), p_j is the estimated capture probability in the j th sampling period, and n_j is the number of individuals sighted in the j th sampling period (Seber, 1982). The precision of each

abundance estimate was expressed as 95% log-normal confidence intervals. This type of confidence interval is typically asymmetric, and generally more appropriate for estimating density or abundance, because there is more uncertainty associated with the upper confidence limit than the lower one. Log-normal confidence intervals also avoid the problem that the lower limit of a standard confidence interval can sometimes extend below zero, which is biologically impossible (Buckland et al., 1993).

Normality of the abundance estimate distribution was assessed using a Shapiro-Wilk test (Shapiro & Wilk, 1965). The abundance estimates from the best fitting model were then analysed to investigate whether there was a trend over time, using a weighted linear regression. The regression was weighted in proportion to the precision of the abundance estimates by using the inverse of the variance of each estimate (Barlow & Taylor, 2005; Kutner et al., 2005). The variance for each estimate was calculated using the following equation:

$$\text{variance} = N_j^2 \times \frac{p_j^2}{se_j^2}$$

Where se_j is the standard error for the j th sampling period (Loery et al., 1997).

An unweighted regression line was also fitted to investigate the sensitivity of the trend to the uncertainty of the abundance estimates. The regression was also fitted on a log-scale. The log-scale can be useful for plotting population abundance trends, since the log-scale prevents abundance trends falling below zero (Limpert et al., 2001). A Davies-test was also performed to assess the appropriateness of a piecewise regression (Davies, 2002; Muggeo, 2017). This type of regression is a model in which two or more lines are joined at “breakpoints”, where the trend changes (Seber & Wild, 1989). The Davies-test checks for a non-zero difference within the slope parameter. If the difference in potential slopes is zero, then there is no support for any breakpoints within the linear regression line (Davies, 2002; Muggeo, 2003, 2017).

Data processing and graphing were performed in R (version 3.2.2; R Core Team, 2015) and Microsoft Excel (2013).

2.3 Results

The data collected from 1990 to 2017 included 4352 encounters that had ID photos which met the quality criteria, representing 239 unique individual sperm whales. New individuals were identified in most seasons, and therefore there was an increase in catalogued individuals over time (Figure 2.3), justifying the use of an open capture-recapture model. This rate of increase has, however, slowed over time. There was variation in the amount of photographic effort and the number of individuals identified each year (Figure 2.4). Generally, with more photographic effort, there was a greater number of unique individuals identified. For example, in 1992 there were 88 encounters from which there were successful ID photos, representing 19 individuals. In 1993, 236 photos of acceptable quality were taken, and the number of unique individuals identified increased to 46. Differences in effort, however, do not result in large changes in the estimate of abundance, because capture probabilities (p) are highly variable.

Careful scrutiny of the existing catalogue found that fourteen whales were misidentified as new individuals between 2007 and 2017. One individual, NN220, was mistakenly catalogued as three separate individuals. These misidentifications contributed to 39 false entries in the long-term database. There were also eleven individuals present in the encounter database that did not have records of fluke photographs in the identification catalogue, and hence they were removed.

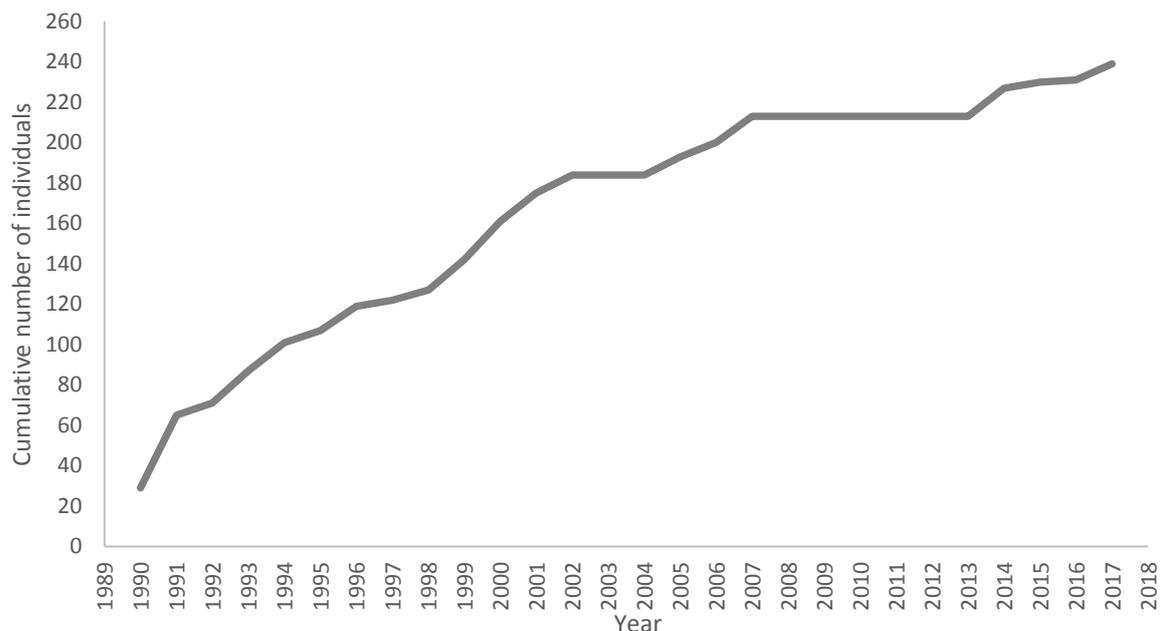


Figure 2.3: A discovery curve of individual sperm whales in the Kaikōura photo-ID catalogue over each year from 1990 to 2017.

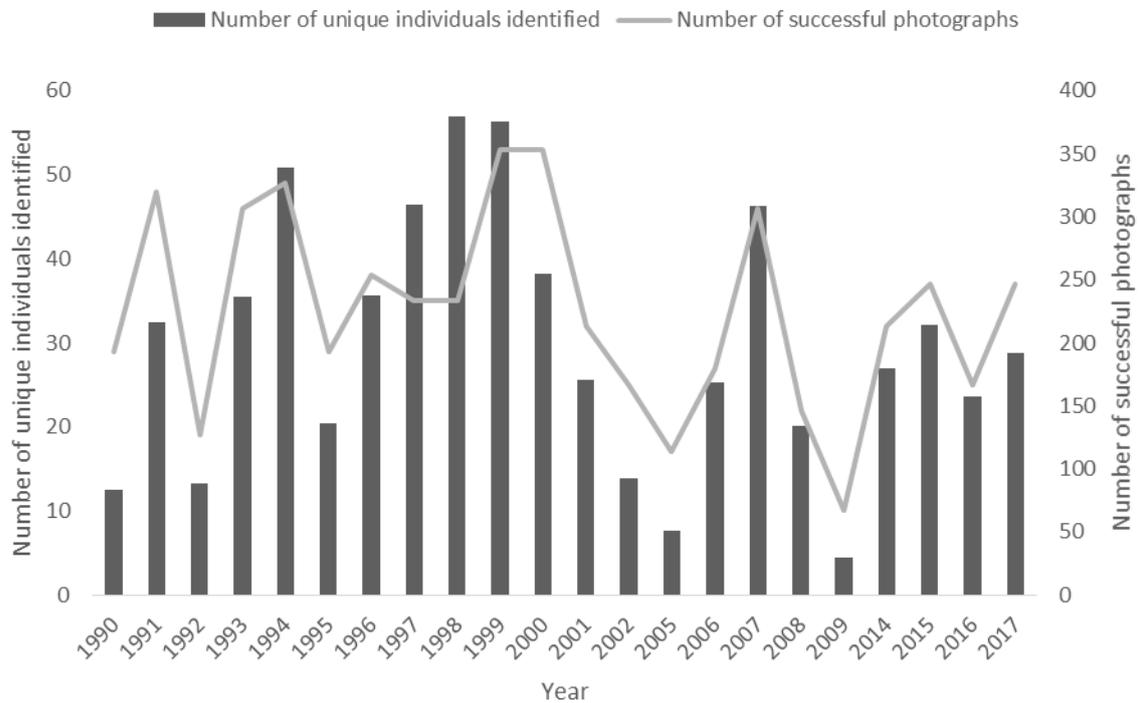


Figure 2.4: The number of identification photographs of acceptable quality taken each year between 1990 to 2017 compared with the number of individual sperm whales identified.

2.3.1 Bootstrap goodness-of-fit

The bootstrap GOF test supported the use of CJS modelling for the sperm whale photo-ID data. The probability of observing a deviance greater than the tested model (ϕp_t ; deviance = 1013.06) was 0.31. A probability lower than 0.05 would indicate that the fit of the CJS model is not appropriate. The \hat{c} value for the tested model was 1.15. A \hat{c} of 1 indicates perfect fit, while a $\hat{c} < 3$ is considered acceptable (Lebreton et al., 1992).

2.3.2 Model selection

According to AICc, the best model out of the candidate models was $\phi_{(.+b)}p_t$ (AICc = 1853.89), the model with constant survival, time-varying capture probabilities and a behavioural response to first capture (Table 2.2). This model was clearly the best supported model since it had a model weight of 1.00, and the second best model had a weight of 0. For this analysis, model averaging was not required because the top model had a weight of >0.9 . The apparent annual survival rate was estimated as 0.89. The estimated annual capture probabilities generated by $\phi_{(.+b)}p_t$ are displayed in Table 2.3.

Table 2.2: The candidate CJS models and model selection metrics for estimating survival (ϕ) and capture (p) probabilities. ‘b’ is a behavioural response, ‘.’ indicates a constant parameter and ‘t’ indicates a time-varying parameter. Models are ranked by AICc scores.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	# Parameters	Deviance
$\phi(.+b)p(t)$	1853.89	0.00	1.00	1.00	23	1025.57
$\phi(.)p(t)$	1876.00	22.12	0.00	0.00	22	1049.83
$\phi(.+b)p(.)$	1936.39	82.50	0.00	0.00	3	1149.65
$\phi(.)p(.)$	1973.90	120.01	0.00	0.00	2	1189.17

2.3.3 Abundance estimation

Annual abundance (N_j) was estimated using the capture probabilities (p_j) of the best model ($\phi_{(c+b)p_i}$) and the number of individuals sighted during each sampling period (n_j) (Table 2.3).

Table 2.3: Values for the number of encounters, ID photos and individuals identified each year (n_j), corresponding estimates of capture probability (p_j) from the best model, and the resulting estimates of abundance (N_j) and 95% log-normal confidence intervals (CI).

Year	Number of Encounters	Number of ID photos	n_j	p_j	N_j	95% log-normal CI
1991	261	216	48	0.54	89	60-131
1992	182	88	19	0.27	70	44-112
1993	262	236	46	0.60	76	60-96
1994	395	339	49	0.61	80	64-99
1995	167	136	29	0.39	74	53-103
1996	279	237	38	0.49	78	58-104
1997	388	309	35	0.59	59	46-74
1998	578	379	35	0.57	61	48-77
1999	580	375	53	0.73	72	61-86
2000	491	255	53	0.63	83	66-104
2001	223	171	32	0.33	95	62-147
2002	97	93	25	0.31	80	50-129
2005	67	51	17	0.20	84	47-150
2006	258	169	27	0.46	58	42-82
2007	478	308	46	0.70	65	53-79
2008	355	134	22	0.42	51	37-72
2009	49	30	10	0.21	46	25-87
2014	223	180	32	0.62	51	38-69
2015	262	214	37	0.86	42	37-49
2016	185	157	28	0.76	36	29-45
2017	223	192	37	0.90	40	33-49

2.3.4 Abundance trend

The Shapiro-Wilk test showed that there was no evidence to reject the null hypothesis of normally distributed data points ($w = 0.96$, $p=0.53$). Estimated abundance declined from 89 (95% CI: 60-131) individuals in 1991 to 40 (95% CI: 33-49) individuals in 2017. The majority of the decline occurred after 2001. From the peak of abundance in 2001, to the abundance in 2017, the population decreased by an estimated 55 individuals. On average, two individuals ($CV=0.16$) were lost from the population per year. The weighted linear regression showed a significant decline in the estimated number of whales using the study area from 1991 to 2017 ($F=89.42$, $p\leq 0.001$; Figure 2.5). The decline was still significant when abundance estimates were unweighted ($F=26.72$, $p\leq 0.001$; Figure 2.5), and when the trend was analysed on the log-scale ($F=32.93$, $p\leq 0.001$). The Davies-test did not support a piecewise regression; the best breakpoint was estimated to be the year 2002, but with a p -value of 0.3.

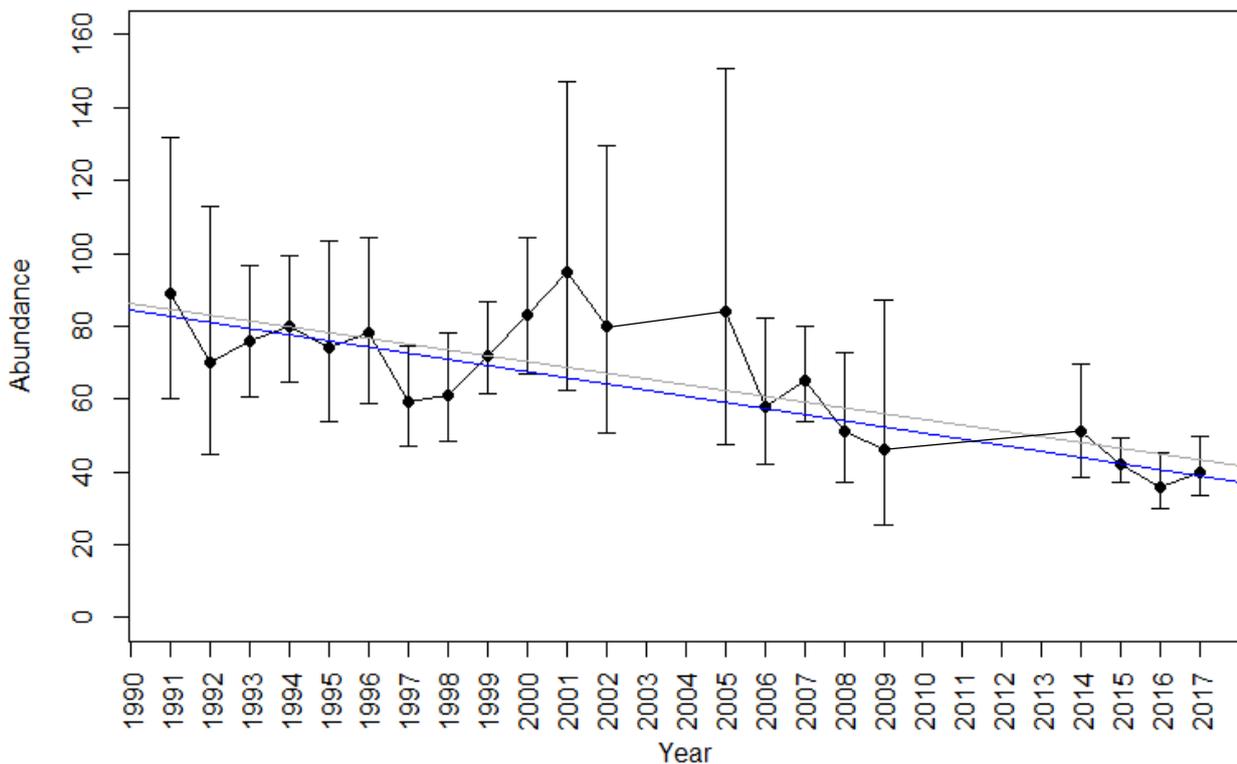


Figure 2.5: Annual abundance estimates for sperm whales at Kaikōura between 1991 and 2017. The 95% log-normal confidence intervals and the linear regression trendline (weighted by the inverse of the variance; in blue) are plotted. The unweighted regression trendline is presented for comparison (in grey).

2.4 Discussion

Capture probabilities were generated by CJS methods and used with the number of individuals sighted each year to generate abundance estimates of sperm whales at Kaikōura from 1991 to 2017. The bootstrapped GOF test suggested the model fit was appropriate. Violations to the assumption of equal catchability were minimised using strict photo quality criteria. When using CJS methods for this population, however, some heterogeneity in capture probabilities is unavoidable, since individuals do temporarily emigrate from the study area (Jaquet et al., 2000). The discovery curve supported the use of an open population model because new individuals were discovered in the population each year. The best fitting model had constant survival and time-varying capture probability with a behavioural effect included at first capture ($\phi_{(\cdot + b)p_i}$). This was also found to be one of the best models in previous research (van der Linde, 2009). Model averaging was not employed in this study because the best fitting model had excellent support.

This study indicates that the declining trend in abundance of sperm whales at Kaikōura first proposed by van der Linde (2009) is continuing. Several methods for presenting the abundance trend were investigated which all resulted in a significant result. These provide confidence in the conclusion that the observed decline is accurate. It is important to note that this trend could be driven by an actual decline in the population, a change in distribution patterns whereby fewer individuals are using the study area, or both.

There were some differences in abundance estimates between this study and estimates from the previous analysis by van der Linde (2009). The current estimate for 2001, for example, was 95 and for the study by van der Linde (2009) it was 70. The top model was the same for both these studies, but these differences may have arisen due to the filtering of errors out of the catalogue.

At Kaikōura, the apparent survival rates represent the annual probability of survival in the study area. Apparent survival rates are biased low because the survival rate is lower than expected for sperm whales (they live for at least 70 years, Rice, 1989). We can conclude, therefore, that permanent emigration is occurring from the study area, and that the apparent annual survival rate does not represent true survival. The apparent annual survival parameter for the top model in the current study was 0.89 and in the study by van der Linde (2009) it was 0.83. The survival rate estimated by van der Linde, however, was estimated using a Pradel model (Pradel, 1996), which is a re-parameterisation of the CJS model. Regardless,

these estimates are similar and indicate that there has not been a notable change in apparent survival rate since the previous analysis.

2.4.1 Possible decline due to food availability

The distribution of cetaceans is determined largely by the distribution of their prey species (Ballance et al., 2006; Friedlaender et al., 2006). Research has shown that sperm whale populations change their distribution in relation to changes in prey abundance (Jaquet & Gendron, 2002). In the Gulf of California, sperm whales aggregated into three sub-populations in response to a decline in abundance of jumbo squid. These aggregations were correlated with areas of highest squid density (Jaquet & Gendron, 2002).

Food availability is likely an important ecological factor driving distribution and abundance of sperm whales at Kaikōura, since they mainly exhibit foraging behaviour in this habitat (Jaquet et al., 2000). Social activity is rarely seen (Childerhouse et al. 1995), and groups of females and calves very seldom venture so far south (Dawson et al., 2008). The diet of sperm whales at Kaikōura is dominated by squid (*Nototodarus sloanei*, *Histioteuthis cookiana* [now renamed *atlantica*], *Architeuthis* sp and *Moroteuthis* sp [now renamed *Onykia*]), but fish such as groper (*Polyprion oxygeneios*) and ling (*Genypterus blacodes*) are also important (Gaskin & Cawthorn, 1967). Squid biomass is known to be highly variable within and between years (O'Dor & Webber, 1986). It is possible, therefore, that the observed decline in abundance of sperm whales at Kaikōura is related to changes in the abundance or distribution of their prey species, particularly squid. Such changes could be related to climate change, but also potential fisheries pressure on groper and ling.

Shifts in the abundance and distribution of fish and squid are occurring in response to climate change (Perry et al., 2005; Field et al., 2006; Zeidberg & Robison, 2007). These shifts have results in changes in growth, survival and reproduction of individuals within these populations (Perry et al., 2005). Squid are known for their flexible life histories, and because of their rapid rates of turnover at the population level, squid can respond quickly to environmental and ecosystem change (Pecl & Jackson, 2008). However, the broad range of life history strategies among species means responses to climate change are likely to be highly variable (Pecl & Jackson, 2008). In general, it is likely that climate change will result in squid that are smaller, require more food and more oxygen (Pecl et al., 2004; Pecl & Jackson, 2008). An increase in ocean temperature means oxygen minimum zones will expand and pH will decrease (Pecl & Jackson, 2008). Increased oxygen minimum zones may reduce activity, growth and reproduction (Seibel, 2015). Lowered pH levels have been shown to decrease the

active metabolism of squid, for example a CO₂ concentration of 1000 ppm decreased the active metabolism for jumbo squid (*Dosidicus gigas*) by 30% (Seibel, 2015). It is therefore hard to predict how different squid species will be affected by climate change. It is possible that individual squid may be smaller and there may be a change in the distribution of populations. As a result, the prey availability for sperm whales may be affected.

Climate change is expected to have a range of effects on both commercially exploited and non-exploited fish species (Perry et al., 2005). Increased ocean temperatures have been correlated with the latitudinal shift of some fish species (Perry et al., 2005; Jung et al., 2013). Some demersal fish species in the North Sea have shown shifts in centres of distribution (measured by mean latitudes) in response to warming (Perry et al., 2005). This trend was shown by 15 of the 36 species investigated, including commercially targeted species such as Atlantic cod (*Gadus morhua*), and non-target species such as scaldfish (*Arnoglossus laterna*) and blenny (*Lumpenus lamprataeformis*) (Perry et al., 2005). Almost all species that showed a significant range shift moved northwards.

Fish growth may also be affected by climate change, with a predicted decrease in size of fish due to the lower oxygen carrying capacity of warmer water (Cheung et al., 2012). The decrease in size is predicted to be largest for fishes in the Pacific and Southern Oceans. Hence fish around New Zealand may be particularly vulnerable, compared to those in the Atlantic, Indian and Arctic Oceans (Cheung et al., 2012). Autumn-winter temperatures at Portobello, Otago have already increased by 1.3°C since 1967 (Shears & Bowen, 2017). A temperature increase of 0.6°C has been linked to shifts in fish distribution in the North Sea (Perry et al., 2005). Therefore, it is expected that fish populations may already be responding to climate change around New Zealand.

The productivity of the Kaikōura peninsula is influenced by alongshore advection, downwelling and upwelling (Chiswell & Schiel, 2001). Because of south-westerly winds, the east coast of the South Island is predominantly a downwelling coast, but strong northerly winds create periods of upwelling (Heath, 1976; Chiswell & Schiel, 2001). Climate-induced changes to areas of upwelling have already been observed in the California current, with surface intensified warming increasing the vertical stratification of the thermocline (Roemmich & McGowan, 1995). This resulted in a suppression of nutrient supply to the ecosystem (Roemmich & McGowan, 1995). If similar changes were also developing around Kaikōura, there could be bottom-up effects decreasing the feeding success of sperm whales.

A strong relationship has been found between ocean temperature and sperm whale feeding success in waters around the Galápagos Islands (Smith & Whitehead, 1993). This has been linked to upwelling of cooler, nutrient-rich water causing increased productivity and as a consequence, increased cephalopod biomass (Smith & Whitehead, 1993). It is thought that the more passive cephalopod species, such as the Histioteuthids, are also transported by currents (Smith & Whitehead, 1993). *Histioteuthis atlantica (cookiana)* is one of the cephalopod species that the sperm whales at Kaikōura feed on (Gaskin & Cawthorn, 1967), and therefore may be reaching the Kaikōura population via important current systems.

Commercial catch of fish around Kaikōura may be indicative of declining fish populations. Groper and ling are both commercially targeted in the Kaikōura area, but catches of both species have been declining since 1991 (MPI, 2015). This decline may have direct effects on sperm whales, as groper have been shown to be an important prey item for sperm whales in the region, especially during winter (Gaskin & Cawthorn, 1967). It could also indicate declining productivity of the Kaikōura marine ecosystem. Between 1991 and 2015 there has been a decrease in the number of high catches of groper and ling in the fisheries area that includes Kaikōura (area 018). The commercial catch for groper in the 1990/1991 fishing season was 11.7 tonnes and 403.6 tonnes for ling (MPI, 2015). A peak groper catch of 33.8 tonnes occurred in 1993/1994, but after the 2004/2005 season there were no catches over 15 tonnes (MPI, 2015). After the 2000/2001 season there were no catches of ling over 200 tonnes (MPI, 2015). Decreases in catch may reflect the status of the targeted fish stocks. These changes may be a reflection of fishing pressure, and/or a result of distribution shifts in response to climate change.

2.4.2 *Impacts of human-caused mortality*

Declines in some marine mammal populations can be attributed to human-caused mortality resulting from fishing and shipping (Schipper et al., 2008). Fisheries provide opportunities for increased feeding efficiency, which attracts marine mammals (Read, 2008). Bycatch of large whales is rare, but increased interactions with fisheries increases the risk of entanglement in fishing gear (Johnson et al., 2005; Kraus et al., 2005; Knowlton et al., 2012). Entanglement hinders locomotion and the ability to feed, therefore decreasing survival rate (Kraus et al., 2005). For right whales (*Eubalaena glacialis*) in the North Atlantic, collision with ships and entanglement in fishing gear are the main sources of mortality (Kraus et al., 2005).

Boat strike and interaction with longline fisheries have previously been linked to sperm whale mortalities (Kock et al., 2006; Laist et al., 2001). For example, entanglement in

fishing gear has been observed where sperm whales take Patagonian toothfish (*Dissostichus eleginoides*) from longlines (Kock et al., 2006). There are anecdotal reports suggesting entanglement of sperm whales in gillnets at Kaikōura is a possibility. Fishers report that nets occasionally go missing in very calm sea conditions, and have suggested that being carried away by an entangled sperm whale is a likely explanation (Melville, pers. comm. to Dawson). As in other large whales, entanglement may not cause immediate mortality but the subsequent decrease in fitness could contribute to future mortality (Kock et al., 2006). Furthermore, evidence of boat strike was observed in one of 11 sperm whale carcasses washed up at Kaikōura between 1990 and 2007, although it is unknown whether this interaction led to the death of the individual (van der Linde, 2009). While direct impacts of fishing and shipping may be resulting in some mortality, it is unlikely this would be on a scale sufficient to fully explain the observed decline.

In marine mammals, high concentrations of pollutants have been linked to increased rate of disease and impaired growth, reproduction and immunity (Béland et al., 1993; Reijnders et al., 2018). However, it is difficult to discern the exact effects of these contaminants since multiple pollutants are present (Reijnders et al., 2018).

Sperm whales, like many marine mammals, are particularly vulnerable to the accumulation of persistent organic pollutants (POPs), such as organochlorine compounds (OCPs), as they are long-lived and at the top of pelagic food webs (Aguilar, 1983; Pinzone et al., 2015). OCPs are highly lipophilic and therefore tend to accumulate in tissues with high fat content (Aguilar, 1983). Information on global levels of pollutants in marine mammals is limited, but available data from baleen whales and bottlenose dolphins indicate that levels of pollutants are generally higher in the Northern Hemisphere compared with the Southern Hemisphere (Reijnders et al., 2018). The large scale movements of sperm whales means individuals from Kaikōura likely come into contact with a range of pollutants and pollutant loads.

Marine debris such as ingestible plastics can also impact sperm whales. Direct mortalities from large plastics have been recorded, arising from ruptures of intestines (de Stephanis et al., 2013), and from blockages leading to starvation (Jacobson et al., 2010). Sperm whales may also accumulate microplastics through their prey; microplastics have been found in the gut of fish (Lusher et al., 2013; Neves et al., 2015). Ingestion of microplastics may increase exposure to chemical pollution directly due to their chemical compositions, and

also since pollutants from seawater accumulate on the surface of the plastics (Rochman , 2015).

2.4.3 Impacts of previous exploitation

The observed decline could also be related to previous exploitation. Whale populations heavily impacted by hunting show lingering effects long after whaling has ceased (Clarke et al., 1980; Whitehead et al., 1997). The most intense period of commercial whaling of sperm whales occurred relatively recently, during the 1960s (Whitehead, 2002). Whaling at Kaikōura during this time resulted in 248 individuals being taken between 1963 and 1964; a large number compared to the population estimates from 1991 onwards (Grady, 1982; Childerhouse et al., 1995). Large reductions in some populations have caused shifts in population distributions (Whitehead et al., 1997).

In the eastern Pacific Ocean near the Galápagos Islands, the decline in sperm whale numbers has partly been attributed to sperm whales repopulating areas around Peru where there had been intense whaling pressure (Whitehead et al., 1997). Furthermore, the social structure of sperm whale populations may still be recovering following whaling, which was primarily directed at large males (Whitehead et al., 1997; Whitehead, 2003). Research in the Galápagos between 1985 and 1995 reported a low number of young calves in the population (Whitehead et al., 1997). There was no evidence for high rates of predation causing mortality of calves, or of poor nutrition or high levels of pollution (Whitehead et al., 1997). The conclusion reached was that the low reproductive rate may have been a consequence of the low number of males visiting breeding grounds (Whitehead et al., 1997). For example, during the breeding season mature males (>12 m) constituted 4% of the Galápagos population (Whitehead et al., 1997). This was lower than the 15% which made up catches in the area between 1830 and 1850, a time when whalers attempted to take whole pods, and also lower than the 16% predicted by the Scientific Committee of the International Whaling Commission (Whitehead et al., 1997). Peruvian whalers targeted large males (generally those >13.5m in length), resulting in a decreased pregnancy rate in females (Clarke et al., 1980). In 1981, only one male larger than 13.5m was recorded being caught (Ramirez, 1989), which indicates the pressure that sperm whale populations were under due to whaling. With males so heavily hunted, a biased sex ratio could explain a continued decline in some areas. A lower reproductive rate at breeding grounds may mean there are fewer new recruits entering the Kaikōura study area.

2.4.4 Tourism pressure

It is possible that an increase in whale watch tourism could also contribute to the observed decline of individuals in the study area off Kaikōura. Whale watching ecotourism is continuing to increase globally, meaning human interaction and disturbance is increasing for easily accessible whale populations. From 1994 to 2000, global whale watching numbers increased from 4 million people annually, to 11 million (Hoyt, 2007). In Kaikōura whale watching numbers have increased from around 3000 people annually in 1990 to 100,000 annually today (WWK, 2017). Coastal cetacean populations are exposed to continually increasing levels of vessel traffic and noise, causing disturbed daily patterns of behaviour (Markowitz et al., 2011). The potential long-term consequences of disturbance include impaired population viability, distribution shifts to cope with stress, and eventually habitat abandonment (Lusseau & Bejder, 2007). Some populations, however, may not be able to move because of dependence on local resources and this may negatively affect survival and reproduction (Lusseau & Bejder, 2007).

Assessing the effect of whale watching usually involves looking at immediate behavioural responses to tourism activity (Janik & Thompson, 1996; Bejder et al., 1999; Bejder et al., 2006). Avoidance behaviour, or changes in time at the surface and mean blow intervals, can indicate disturbance (Richter et al., 2006; Tseng et al., 2011). It is difficult, however, to infer the biological significance of these short term changes since it is rarely known how they translate to effects on fitness and survival (Gill et al., 2001; Bejder et al., 2006). In waters west of Maui, humpback whales (*Megaptera novaeangliae*) have shown a range of short term responses to vessel presence including avoidance, approach and even charging of vessels (Au & Green, 2000). Sperm whales in the Azores have also shown behavioural responses to boat presence. When faced with inappropriate boat manoeuvres, sperm whales showed higher changes in speed and in the frequency of aerial displays (Magalhães et al., 2002). Inappropriate boat manoeuvres were classed as those which did not meet Azorean legislation for whale watching (Magalhães et al., 2002). The requirements include approaching whales from behind within a 60° angle and keeping a minimum distance of 100 m. During the duration of the study, tourist boat observers reported that 40% of boat approaches did not adhere to established regulations (Magalhães et al., 2002)

Behavioural responses to tourism have been monitored for sperm whales at Kaikōura using both shore-based and boat-based techniques (Richter et al., 2003, 2006; Markowitz et al., 2011). Shore-based studies have the advantage of observing behaviour without the added effect of a research vessel (Markowitz et al., 2011), but are restricted to documenting very

obvious responses of whales close to shore. There has been evidence of some behavioural change in response to the approach of planes and boats at Kaikōura (Richter et al., 2006). In the presence of whale watch boats, mean blow intervals and time at the surface decreased, an indication of a stress response (Richter et al., 2006). In a more recent study, however, there was no significant change in mean blow intervals or surface time (Markowitz et al., 2011). Previously, whales did start to click sooner after fluke-up in the presence of boats implying that boat noise may decrease foraging efficiency (Richter et al., 2006). Individuals may begin to click earlier to maximise the number of received echoes, to better understand a noisier environment (Richter et al., 2006).

Even though there is a long-term dataset for Kaikōura sperm whales, there are no long-term data of whale watch effort on specific individuals (Richter et al., 2006). This makes determining the biological significance of these behavioural responses difficult (Richter et al., 2006). The presence of some behavioural responses to tourism vessels means continued research is necessary. The lack of data on distribution and demographic responses to tourism vessels means it is unknown whether individuals may leave the area due to tourism pressure. Whales that are less frequently seen, however, have been shown to be less tolerant of boat approach, both from tourist and research vessels (Richter et al., 2006). This was indicated by increases in shallow diving and more frequent changes in swimming direction (Richter et al., 2006). This may mean sperm whales that visit less frequently are more likely to avoid tourist vessels, resulting in a distribution shift away from the coast.

2.5 Conclusion

Annual abundance estimates of sperm whales at Kaikōura were derived from capture probabilities generated by CJS modelling of photo-ID capture-recapture data. There was a significant decline in the number of sperm whales using the study area from 89 to 40 individuals between 1991 and 2017. The cause of the decline is currently unknown but potential influences include food availability, climate change, tourism and lingering impacts from commercial whaling. Understanding the abundance trend of a population is crucially important for deciding whether management is necessary, and if so, what form it should take. The next step is to prioritise research on the possible causes of sperm whale population decline so that effective management can be developed.

Chapter 3

Estimating trends in seasonal abundance of sperm whales at Kaikōura using Robust design models

3.1 Introduction

All populations experience birth, death, immigration and emigration (Lebreton et al., 1992). In whale and dolphin populations, changes typically occur over large spatial and long temporal scales (Whitehead, 2001). “Open” population models, such as Cormack-Jolly-Seber (CJS), account for these changes, but they assume that emigration from the study population is permanent (Kendall et al., 1997). Often, this is not the case. A population’s home range may be larger than the study area, meaning individuals move in and out over short-term temporal scales (Kendall et al., 1997). Furthermore, individuals undergoing larger-scale movements such as annual migrations may only be present in a study area during one season a year (Kendall et al., 1997). When individuals move into and out of a study area, and are therefore not always available to be sampled, temporary emigration is occurring. For example, North Atlantic humpback whales, *Megaptera novaeangliae*, group together on the banks that surround the Antillean Island chain each winter, to mate and calve (Kennedy et al., 2013). They then migrate to geographically distinct waters off the Gulf of Maine, West Greenland, Iceland and the Barents Sea to forage from spring through to autumn (Kennedy et al., 2013). In this example, temporary emigration occurs from both feeding and breeding areas, and covers large distances (Kennedy et al., 2013).

Temporary emigration violates a basic assumption of many capture-recapture models: that all individuals have equal probability of capture at any one sampling occasion (Pollock, 1982). It is important, therefore, to consider its effect on estimates of population size, recruitment and survival rate (Kendall et al., 1997). Analyses which fail to take temporary emigration into account may result in biased estimates of abundance and survival (Peñaloza et al., 2014). Accurate abundance and survival estimates are vital for properly assessing the status and management needs of a population. One way to allow for temporary emigration in the analysis of capture-recapture data is to use a Robust design model (Pollock, 1982; Kendall et al., 1997).

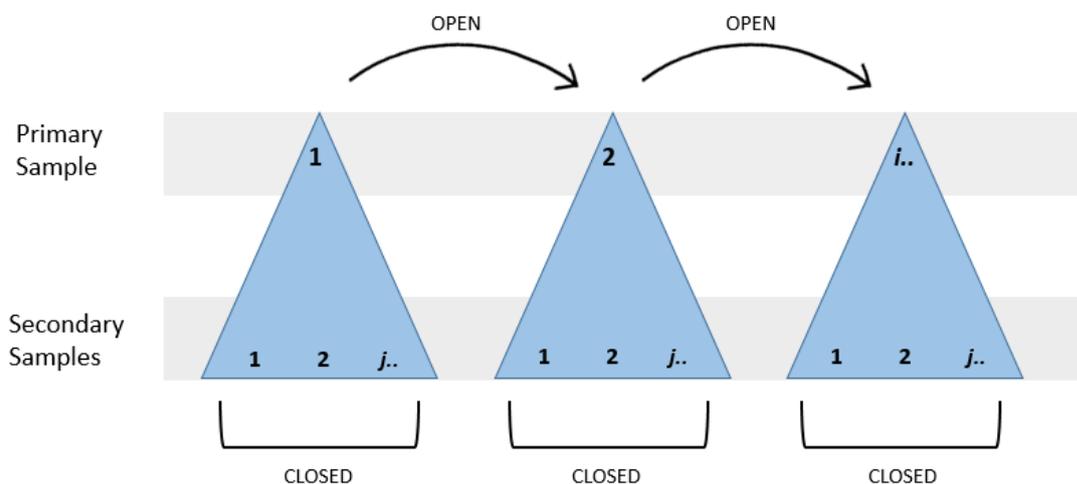


Figure 3.1: Schematic showing the structure of secondary periods within primary periods. The population is closed between secondary periods and open between primary periods. Adapted from Pollock (1982).

3.1.1 Robust design theory and methodology

Robust design methodology consists of secondary sampling periods within primary sampling periods (Pollock, 1982). It is based on a combination of CJS open model and closed model theory (Pollock, 1982). The population is therefore assumed to be closed *within* each primary period, but open *between* primary periods (Pollock, 1982; Figure 3.1). This allows for an estimate of abundance to be generated for each primary period, and estimates of survival rate and temporary emigration between primary periods (Pollock, 1982). The Robust design can be a more robust and appropriate modelling method compared with the CJS methods used in Chapter 2. In a closed population, abundance estimates are reasonably robust to heterogeneity of capture probability (Kendall, 1990). In contrast, open population models are designed to provide robust estimates of survival rate in the presence of emigration and immigration (Kendall, 1990). By using closed population estimators for abundance and open population estimators for survival, the overall analysis is more robust to heterogeneity in capture probability caused by temporary emigration from the study site (Kendall, 1990).

Temporary emigration can be defined as random or Markovian (Kendall et al., 1997). In random temporary emigration, the probability of being available for detection in primary period i is not conditional on the state of the individual at time $i-1$ (Kendall et al., 1997). In Markovian temporary emigration, the probability of being available for detection in primary period i is conditional on the availability of the individual at time $i-1$. Temporary emigration consists of two parameters, γ' (gamma-prime) and γ'' (gamma double-prime). For Markovian

emigration, the parameter γ' is the probability of being unavailable for capture during the current sampling period (i), if the individual was also unavailable during the previous sampling period ($i-1$). The parameter γ'' is the probability of being unavailable for capture during the current sampling period (i), if the individual was available for capture during the previous sampling period ($i-1$). As a result, capture probabilities vary depending on the availability of an individual in the previous capture period. This is not the case with random emigration; the probability of being in the study area during the current primary period is the same regardless of whether or not the individual was in the study area during the previous primary period. An underlying assumption for these temporary emigration parameters is that the probability of an animal alive in period (i) surviving to period ($i+1$) is the same for all animals regardless of availability (Kendall et al., 1997).

Robust design modelling has been used to estimate demographic parameters of several cetacean populations, including coastal populations of bottlenose dolphins (*Tursiops* spp) and large cetaceans such as grey (*Eschrichtius robustus*) and right whales (*Eubalaena* spp; Bradford et al., 2006, 2008; Silva et al., 2009; Conn et al., 2011). For grey whales inhabiting waters of the western North Pacific, including temporary emigration in the population analysis provided better fitting models (Bradford et al., 2006). Survival and abundance of bottlenose dolphins in the Azores were modelled using both CJS methods and the Robust design (Silva et al., 2009).

3.1.2 Robust design and sperm whales at Kaikōura

Male sperm whales migrate through a variety of habitats in search of mating opportunities and food (Steiner et al., 2012). They migrate from tropical breeding areas to mid to high latitudes for feeding. Female sperm whales seldom venture as far south as Kaikōura, and hence the majority of sperm whales at Kaikōura are males. Although there are whales present at Kaikōura all year round, individuals come and go from the study area, and none are truly resident (Childerhouse et al., 1995; Jaquet et al., 2000). A capture-recapture model which allows for temporary emigration is therefore likely to better represent the population at Kaikōura.

At Kaikōura, previous research indicates the distribution of sperm whales within the study area changes depending on the season (Childerhouse et al., 1995; Jaquet et al., 2000). During the summer, sperm whales were generally within the canyon in waters deeper than 1000m, while in winter they were more evenly distributed throughout the study area (Jaquet et al., 2000). Sperm whales have also had a stronger tendency to return regularly in winters

compared with summers (Childerhouse et al., 1995). Consequently, it is important to consider how seasonal differences may be influencing the decline in abundance from 1990-2017.

3.1.3 Aims

Previous estimates of sperm whale abundance at Kaikōura have been derived from CJS models, which assume that all individuals are available to be captured at each sampling opportunity. This assumption is likely to be violated as individuals enter and leave the study area (Childerhouse et al., 1995; Jaquet et al., 2000). The aim of this chapter is to apply a more realistic capture-recapture model, the Robust design, to allow for temporary emigration from the study area. As well as generating estimates of seasonal abundance, the Robust design models will provide apparent annual survival rates for sperm whales at Kaikōura.

3.2 Methods

Data collection and photo-ID methods are described in Chapter 2. Data were further filtered to meet specific requirements of Robust design analyses. In order to account for seasonal differences in distribution and abundance of sperm whales at Kaikōura, analyses were carried out on two separate datasets; summer and winter. Before the analysis, the following assumptions for Robust design modelling were addressed (Pollock, 1982; Urian et al., 2015):

- 1) Individuals are uniquely identifiable and identified correctly.
- 2) Marks must not be lost, or change so much that individuals cannot be identified correctly.
- 3) Each individual has the same probability of being captured.
- 4) The population is closed within primary periods.

Violations to assumptions 1, 2, and 3 were minimised using the strict photo quality criteria in Chapter 2 for the CJS assumptions. Assumption 3 was further addressed by Robust design modelling incorporating temporary emigration (Pollock, 1982). This assumption, however is still likely to be somewhat violated due to inherent differences in catchability between individuals (Hammond, 1986). Violations to assumption 4 were minimised by having primary periods as short as possible, while still having sufficient data for the Robust design analysis.

3.2.1 *Data structuring*

Each field season was considered to be a primary period, and these needed to be of similar length to make meaningful comparisons of abundance among seasons. However, in reality there was a large variation in the length of seasons; the duration of the shortest field season was four days in winter 1990, while the longest season lasted >10 weeks, in winter 2008. Primary periods also needed to be short enough so that violations to the closure assumption were minimised. In summary, it was necessary to include as many seasons as possible while addressing the closure assumption and ensuring that field seasons were both comparable and long enough for Robust estimation. To do this, I imposed the following rules:

- Seasons must occur over 3-5 weeks.
- There must be no breaks of more than two weeks during this time.
- There must be at least 12 survey days.

After filtering the data according to these rules, winter field seasons were defined as June-July and summer field seasons from November-February. This means that winter was represented by 3-5 continuous weeks from the beginning of June to the end of July, and summer was represented by 3-5 continuous weeks between the start of November to the end of February. Each primary period was then divided into two secondary periods (Bejder & Dawson, 2001), consisting of an approximately equal number of survey days (± 1). Models were also built with three and four secondary periods to test the sensitivity of abundance estimation to a larger number of shorter secondary periods. I then tested whether the filtered season duration was correlated with the number of individuals identified in that season.

3.2.2 *Robust design analysis*

Sighting data were summarised as an encounter matrix, with a '1' representing an individual that was encountered during a secondary period, and a '0' indicating an individual that was not. A "Huggins p and c " Robust design model was used to estimate apparent annual survival, capture probability and temporary emigration parameters (Bradford et al., 2006; Huggins, 1991). p is the probability of first capture, whereas c is the probability of recapture (conditional on having been captured before; Kendall, 1990). Generally, c is used to model behavioural effects following the initial capture (p). Compared with physically tagging individuals, photo-ID encounters are unlikely to influence behaviour due to its non-invasive

nature (Urian et al., 2015). Therefore, I assumed that there were no behavioural effects following first capture, and so p and c were specified as equal.

Encounter histories were analysed in Program MARK to test a variety of models. Survival (ϕ), captures (p) and gammas (γ) were allowed to vary with time or stay constant. Capture rates (p) can be specified as constant over the whole study period (\cdot), varying between primary periods only (so equal for the two secondary periods within a primary period; T), or fully time-varying (t) (where each secondary period has a separate capture probability). All possible parameter combinations were tested. Temporary emigration was allowed to be random ($\gamma' = \gamma''$). Markovian emigration was not tested because, as introduced earlier, the probability of being available for detection in primary period i is conditional on the availability of the individual at time $i-1$. Primary periods, however, were not always truly consecutive which makes interpretation of Markovian emigration parameters difficult. I also trialled a “no movement” model ($\gamma' = 1, \gamma'' = 0$), in which survival was specified as constant and capture rates were varying between primary periods (T). This model assumes that individuals cannot emigrate temporarily from the study area and are therefore always available for capture while they are alive. The performance of the “no movement” model is useful for assessing the validity of the Robust design approach. Only models where all parameters could be estimated were included in the analysis. Models with $p(t)$, $\phi(T)$ and $\gamma(T)$ generally did not perform properly, due to insufficient data.

In the CJS analysis in Chapter 2, abundance was estimated to be relatively constant from 1990-2001. The majority of the population decline occurred from 2002-2017. Therefore, a change in emigration and survival rate after 2001 was tested for both summer and winter datasets. This was to investigate if a change in movement patterns or survival rates could explain the step change in abundance. This involved specifying one value for the gamma parameters between 1990 and 2001, and a different value for the gamma parameters from 2002 onwards. Apparent survival was investigated by having one value for the survival up to 2001 and then a different survival value from 2002 onwards.

3.2.3 *Model fit and averaging*

To find the simplest model which fitted the data well (Burnham et al., 2011), I used AICc (as in Chapter 2). Models were ranked according to their AICc score, with the lowest score indicating the best model. To include model uncertainty, abundance estimates were computed via averaging of models with non-zero weights (Burnham et al., 2011), in Program MARK using the “model averaging” function. Apparent survival, emigration and capture

probabilities, however, were not averaged to allow for a change in apparent survival after 2001 to be modelled separately from a change in emigration.

3.2.4 *Linear regression*

The normality of the summer and winter abundance datasets were tested using a Shapiro-Wilk test (Shapiro & Wilk, 1965). Model averaged abundance estimates were then analysed to investigate whether there was a trend over time, using a weighted linear regression as in Chapter 2. Each abundance estimate was weighted in proportion to that estimate's precision using the inverse of variance (Barlow & Taylor, 2005; Kutner et al., 2005). An unweighted regression line was also fitted, and a linear regression was fitted on the log-scale to investigate the sensitivity of the trend to different methods. In addition, a Davies-test was performed to test for the appropriateness of a piecewise regression (Davies, 2002; Muggeo, 2017). Data analyses were performed in R (version 3.2.2; R Core Team, 2015).

3.3 Results

After filtering the data to satisfy the requirements for inclusion in a primary period, there were 1499 successful photo-ID encounters with sperm whales. Of these encounters, 846 were in the summer dataset and 653 in the winter dataset. The filtered winter data consisted of 11 seasons from 1994-2017, while the summer data consisted of 16 seasons from 1990-2017. One hundred unique individuals were seen during winter, and 130 in summer. Thirty-nine individuals seen in winter were not seen in the summer, while 69 individuals identified in the summer dataset were not seen during winter.

The number of unique individuals identified within each primary period varied, despite the standardised durations (Figures 3.2, 3.3). The number of unique individuals per primary period was not significantly correlated with duration for either summer (Pearson's correlation coefficient $r=0.48$; $p=0.07$) or winter ($r=-0.27$; $p=0.42$).

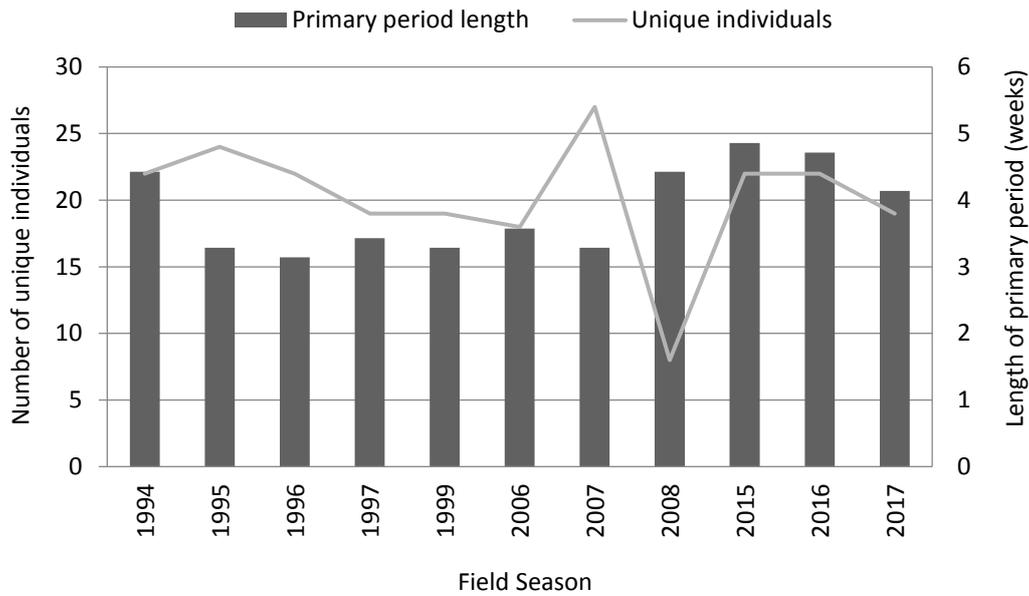


Figure 3.2: Durations of the winter primary periods, compared with the number of unique individuals identified in that season.

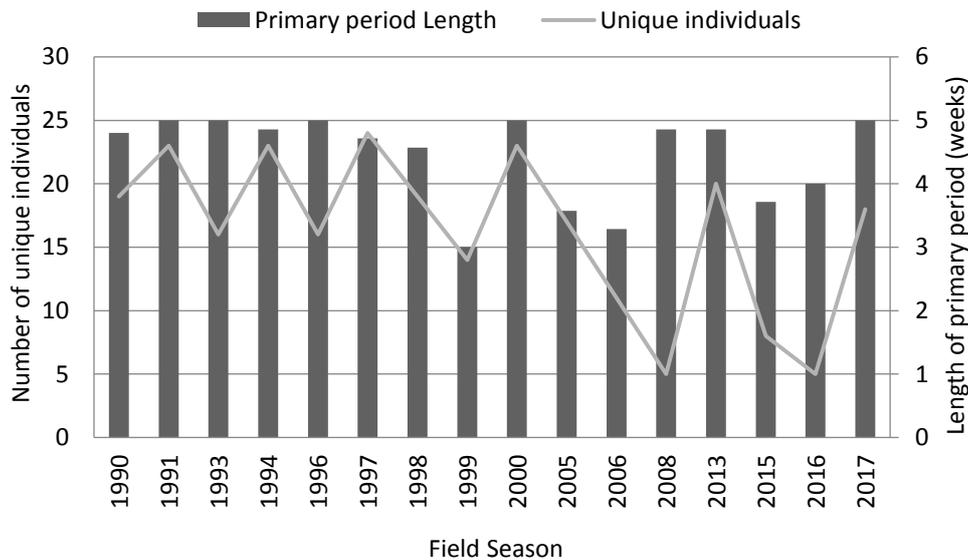


Figure 3.3: Durations of the summer primary periods, compared with the number of unique individuals identified in that season.

3.3.1 Model selection and abundance estimation

The results of the models constructed using two, three and four secondary periods per primary period were very similar, except for one unrealistically high abundance estimate generated using four secondary periods. Therefore, I have chosen to only present the results of the

simplest models here, using two secondary periods. For comparison, the results of the models with three and four secondary periods are presented in Appendix A.

The best model for the summer dataset, as indicated by the lowest AICc score, was the model $\phi(.)p(T)\gamma(R.)$ (AICc=1237.91; Table 3.1). This model specified constant survival, time-varying capture probability between primary periods, and constant random temporary emigration parameters. The top model was clearly favoured having nearly twice the AICc weight of the second ranked model, which was similar except for constant capture probability. The large Δ AICc score for the no movement model (99.34) indicated that having all individuals available for capture in every primary period had no support.

Table 3.1: Candidate models for the Robust design analysis using the summer data for estimating survival (ϕ), probability of not being in the study area in a given primary period (γ), and capture (p) probabilities. ‘.’ specifies a constant parameter, ‘T’ specifies a parameter that is time-varying between primary but not secondary periods, and ‘t’ specifies a parameter that is time-varying for both secondary and primary periods. ‘01’ indicates a change in a parameter after 2001 and ‘R’ indicates random temporary emigration. Models are ranked by AICc scores.

Model	AICc	Δ AICc	AICc Weights	Model Likelihood	# Parameters	Deviance
$\phi(.)p(T)\gamma(R.)$	1237.91	0	0.37	1	18	1190.12
$\phi(.)p(.)\gamma(R.)$	1239.07	1.16	0.21	0.56	3	1223.16
$\phi(01)p(T)\gamma(R.)$	1239.90	1.99	0.14	0.37	19	1189.88
$\phi(.)p(T)\gamma(R01)$	1240.11	2.20	0.12	0.33	19	1191.00
$\phi(01)p(.)\gamma(R.)$	1240.76	2.85	0.09	0.24	4	1222.80
$\phi(.)p(.)\gamma(R01)$	1241.01	3.07	0.08	0.21	4	1223.05
$\phi(.)p(.)\gamma(RT)$	1247.58	9.67	0.00	0.01	17	1202.00
$\phi(.)p(T)\gamma(\text{no movement})$	1337.25	99.34	0.00	0.00	17	1291.67

The apparent annual survival rate (ϕ) from the best model for summer was 0.86 (Table 3.2). The probability that an individual was not in the study area in a given primary period (γ) was 0.57 (Table 3.2).

Table 3.2: The parameter estimates for survival (ϕ), probability of being absent from the study area (γ) and capture (p) probabilities for the top summer model, $\phi(\cdot)$ $p(T)$ γ (R.). Standard errors (SE) and 95% log-normal confidence intervals (LCI, UCI) are also presented.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.86	0.02	0.83	0.89
γ	0.57	0.04	0.49	0.64
p 1990	0.19	0.12	0.05	0.50
p 1991	0.71	0.09	0.51	0.85
p 1993	0.71	0.12	0.43	0.89
p 1994	0.64	0.09	0.45	0.80
p 1996	0.50	0.12	0.28	0.72
p 1997	0.56	0.09	0.39	0.72
p 1998	0.81	0.07	0.63	0.92
p 1999	0.58	0.11	0.36	0.77
p 2000	0.45	0.09	0.29	0.62
p 2005	0.67	0.10	0.45	0.83
p 2006	0.66	0.12	0.41	0.85
p 2008	1.00	0.00	1.00	1.00
p 2013	0.53	0.11	0.32	0.72
p 2015	0.40	0.13	0.18	0.67
p 2016	0.87	0.15	0.35	0.99
p 2017	0.50	0.10	0.32	0.69

Abundance in 1990 was estimated at 43 individuals (95% CI: 12-148), and for 2017 it was estimated at 23 (95% CI: 16–32; Table 3.3).

Table 3.3: Model averaged abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for each summer season.

Parameter	Estimate	SE	LCI	UCI
1990	43	29.64	12	148
1991	26	2.63	21	31
1993	18	2.15	14	22
1994	26	2.83	21	33
1996	21	3.92	15	31
1997	29	3.45	23	37
1998	20	2.27	16	26
1999	16	2.45	12	22
2000	31	5.46	22	43
2005	19	2.24	15	24
2006	12	1.76	9	16
2008	5	0.85	3	7
2013	25	3.92	18	34
2015	13	4.13	7	23
2016	5	0.88	3	7
2017	23	3.87	16	32

As for the summer dataset, according to the AICc scores, the best model for the winter dataset was $\phi(\cdot) p(T) \gamma(R.)$ (AICc=905.86; Table 3.4). There was some support for models with a change in temporary emigration and survival after 2001, and some support for the "no movement" model (AICc=906.33).

Table 3.4: Candidate models for the Robust design analysis using the winter data for estimating survival (ϕ), probability of not being in the study area in a given primary period (γ), and capture (p) probabilities. ‘.’ specifies a constant parameter, ‘T’ specifies a parameter that is time-varying between primary but not secondary periods, and ‘t’ specifies a parameter that is time-varying for both secondary and primary periods. ‘01’ indicates a change in a parameter after 2001 and ‘R’ indicates random temporary emigration. Models are ranked by AICc scores.

Model	AICc	Δ AICc	AICc weights	Likelihood	No. Parameters	Deviance
$\phi(.) p(T) \gamma(R.)$	905.86	0.00	0.27	1.00	13	1038.28
$\phi(.) p(T) \gamma(R01)$	905.88	0.03	0.26	0.99	14	1036.12
$\phi(01) p(T) \gamma(R.)$	905.93	0.07	0.26	0.96	14	1036.16
$\phi(.) p(T) \gamma(\text{no movement})$	906.33	0.47	0.21	0.79	21	1020.83
$\phi(01) p(.) \gamma(R.)$	915.95	10.09	0.00	0.01	4	1067.44
$\phi(.) p(.) \gamma(R.)$	916.50	10.64	0.00	0.00	3	1070.04
$\phi(.) p(.) \gamma(R01)$	918.03	12.18	0.00	0.00	4	1069.53

The best winter model estimated an apparent survival rate (ϕ) of 0.85 (Table 3.5). The probability of an individual being absent from the study area in a primary period (γ) was 0.16 (Table 3.5).

Table 3.5: The parameter estimates for survival (ϕ), probability of being absent from the study area (γ) and capture (p) probabilities for the top winter model, $\phi(.) p(T) \gamma(R.)$. Standard errors (SE) and 95% log-normal confidence intervals (LCI, UCI) are also presented.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.85	0.02	0.81	0.88
γ	0.16	0.07	0.07	0.33
p 1994	0.78	0.08	0.59	0.89
p 1995	0.42	0.09	0.26	0.59
p 1996	0.65	0.09	0.46	0.80
p 1997	0.71	0.10	0.48	0.87
p 1999	0.42	0.09	0.26	0.60
p 2006	0.38	0.10	0.21	0.59
p 2007	0.56	0.08	0.40	0.71
p 2008	0.24	0.07	0.13	0.41
p 2015	0.71	0.08	0.52	0.84
p 2016	0.68	0.08	0.51	0.81
p 2017	0.67	0.09	0.48	0.82

Abundance in 1994 was estimated at 23 individuals (95% CI: 20-26), and for 2017 it was estimated at 21 (95% CI: 17-26; Table 3.6).

Table 3.6: Model averaged abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for each winter season.

Season	Estimate	SE	LCI	UCI
1994	23	1.39	20	26
1995	37	8.18	25	54
1996	24	2.51	20	30
1997	20	2.07	17	24
1999	28	6.11	20	40
2006	29	7.32	17	48
2007	34	4.76	26	43
2008	18	7.36	8	39
2015	24	2.21	20	29
2016	24	2.27	20	29
2017	21	2.33	17	26

3.3.2 Abundance trend

The Shapiro-Wilk test showed that there was no evidence to reject the null hypothesis of a normal distribution of abundance estimates for both summer ($w=0.97$ $p=0.79$) and winter ($w=0.91$, $p=0.2$) datasets. Weighted linear regression showed a significant decline in the estimated number of whales using the study area from summer 1990 to summer 2017 ($F=16.23$, $p<0.01$; Figure 3.4). The number of whales using the study area declined from 43 individuals in 1990 to 23 individuals in 2017. On average, the number of whales using the Kaikōura study area in summer declined by 0.74 individuals per year over the course of the study. The trend was also significant when an unweighted regression line was fitted ($F=6.73$, $p=0.02$; Figure 3.4), and when a weighted regression was fitted using the abundance estimates from 1994-2017 (i.e. the same time-span as the winter data; $F=9.27$, $p=0.01$). The regression trend was also significant with the abundance estimates on the log-scale ($F=7.54$, $p=0.01$). The Davies-test showed that piecewise regression was not a suitable method for modelling the trend. The ‘best’ breakpoint for a shift in trend was found to be at 1991, but the p -value ($p=0.21$) suggested that a linear regression was most appropriate for modelling the summer abundance data.

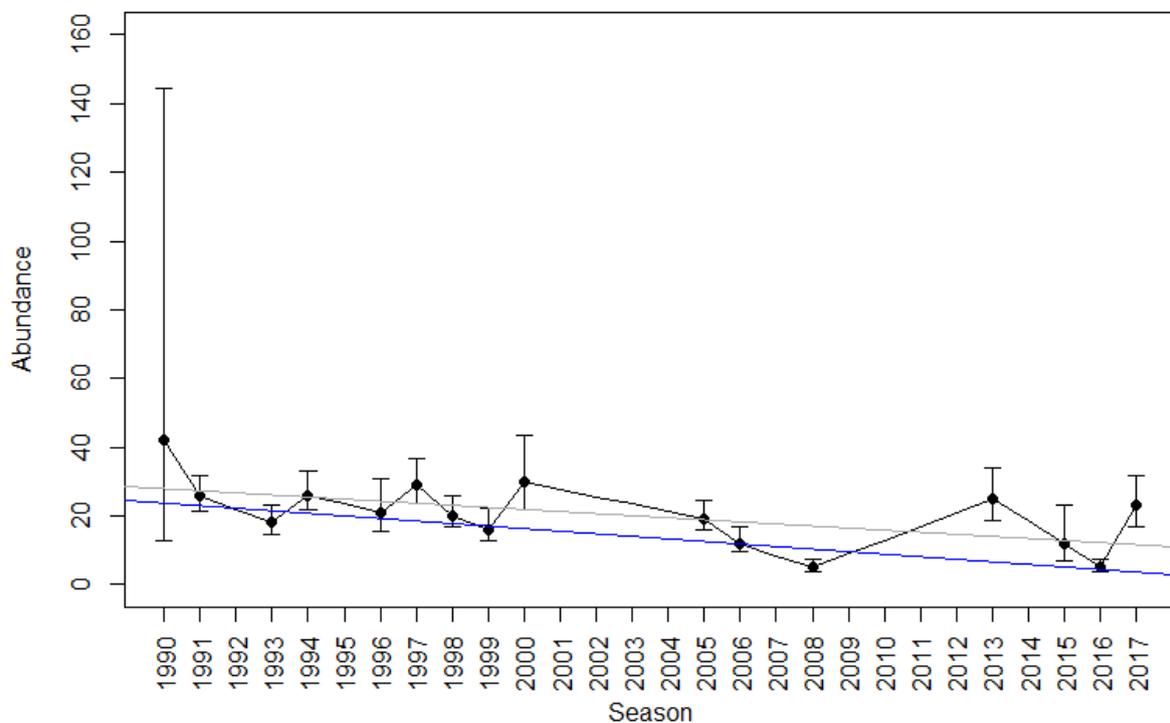


Figure 3.4: Summer abundance estimates for sperm whales at Kaikōura between 1990 and 2017. The 95% log-normal confidence intervals and the linear regression trendline (weighted by the inverse of the variance; in blue) are plotted. The unweighted regression line is also presented for comparison (in grey).

Weighted linear regression showed no significant trend in abundance over the winter seasons from 1994 to 2017 ($F=0.04$, $p=0.84$; Figure 3.5). There was also no support for a piecewise regression model. Regression on the log-scale also showed no significant trend ($F=0.55$, $p=0.36$).

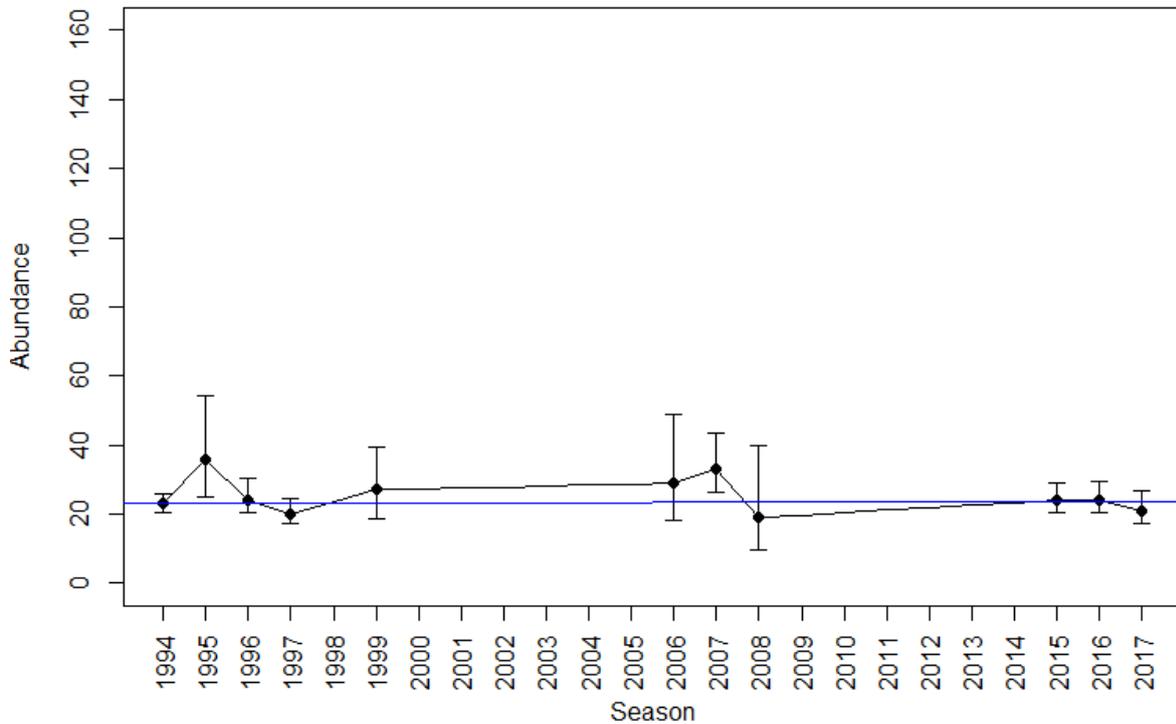


Figure 3.5: Winter abundance estimates for sperm whales at Kaikōura between 1994 and 2017. The 95% log-normal confidence intervals and the linear regression trendline (weighted by the inverse of the variance) are plotted. Note that the slope of the trendline is not significantly different to zero.

3.4 Discussion

Robust design models were used to estimate the seasonal abundance of sperm whales using the study area at Kaikōura. For summer and winter, the best models were those which incorporated temporary emigration. This indicates that sperm whales are not truly resident at Kaikōura, but immigrate and emigrate from the study area over time, and justifies the use of Robust design models, over alternatives which assume that individuals are always available to be sampled.

The abundance estimates from the Robust design models suggested that the number of sperm whales using the study area at Kaikōura in summer had significantly declined between 1990 and 2017. This significant decline was still evident when tested from 1994 to 2017 (the

time frame of the winter analysis), and when an unweighted regression line was fitted from 1990-2017. The log-scale regression also showed a significant decline. These results suggest that the conclusion is not sensitive to different options for regression lines, and provides confidence that the observed decline is real. In contrast, the abundance estimates generated from the winter dataset were relatively consistent and showed no evidence of a trend over time

There were two particularly low abundance estimates for the summer dataset. Five individuals were estimated for both 2008 and 2016. No known abrupt changes to the environment occurred in 2008 that may have impacted this abundance estimate. The abundance estimate for summer in 2016, however, was from data collected directly after the Kaikōura earthquake. There is a lack of information on the response of marine mammals to earthquakes (Gallo-Reynoso et al., 2011). It is possible that the initial seismic activity and noise of earthquakes may displace individuals from that area. For example, observations of fin whales after a 5.5 magnitude earthquake in the Gulf of California showed an individual breached 3 minutes after the quake and proceeded to travel 13 km in 26 minutes, more than three times faster than normal travel speed (Gallo-Reynoso et al., 2011). The loss of benthic productivity at Kaikōura may have resulted in a decrease in prey availability for sperm whales foraging at Kaikōura. As a result, individuals may have had to redistribute further from the canyon to increase foraging efficiency. The abundance estimate for the following summer (23), however, was comparable to estimates prior to the earthquake. This indicates that even if the low 2016 summer estimate was in response to the earthquake, it was a short term response.

The best winter and summer models resulted in very similar apparent annual survival rates: 0.85 and 0.86 respectively. This indicates that whales were using the study area for a similar span of years in both winter and summer. There was no support for a change in apparent annual survival rate after 2001, indicating a change in apparent survival did not drive the decline. These values are close to the previous annual survival rate of 0.83 estimated by van der Linde (2009), and also to the survival rate from the CJS analysis in Chapter 2 (0.89). Although these recent survival estimates are slightly higher than the previous estimate, the 95% confidence estimates do overlap. This indicates that there is no strong evidence for a change in apparent survival since the previous analysis.

The temporary emigration parameter for summer was 0.57, and for winter it was 0.16. This means that individuals are more likely to stay at Kaikōura for multiple winters compared

with summer. The lower temporary emigration parameter in winter also explains the higher support for the “no movement” model in winter, since there was less movement occurring between winters compared with summers. There was no evidence that the significant summer decline was driven by a change in temporary emigration after 2001.

Overall, the parameter estimates suggest that consistent numbers of sperm whales visit the study area at Kaikōura during winter, and a much more variable, slowly declining number of whales use the habitat over summer. Furthermore, individual sperm whales are much more likely to visit Kaikōura during successive winters, than during successive summers. The whales visiting Kaikōura during winter, therefore, come from a smaller pool of unique individuals (100), compared with summer (130), with only 61 individuals seen in both seasons.

In Chapter 2, the significant annual decline was explored in terms of response to prey redistributions, climate change and tourism pressure. Below I will investigate these factors on a seasonal level, in order to understand what environmental influences are occurring in summer, which are not present, or as strong, in winter.

It is evident that the distribution of cetaceans is determined largely by the distribution of their prey species (Tynan et al., 2005; Ballance et al., 2006; Friedlaender et al., 2006; Munger et al., 2009). Sperm whales have demanding food requirements (Lockyer, 1981) and so it is understandable that their distribution would largely reflect ocean productivity; more productive waters should have better feeding opportunities (Bradford et al., 1991; Jaquet et al., 1996).

3.4.1 Possible decline due to seasonal food availability

Squid have flexible life histories which respond quickly to changes in temperature and productivity (Forsythe et al., 2001; Pecl & Jackson, 2008; Kaplan et al., 2013). In warmer temperatures the growth rates of squid are often accelerated, meaning they hatch earlier, are smaller, but grow faster over shorter life spans (Pecl & Jackson, 2008). For many species, this could alter the timing and location of peak abundance (Pecl & Jackson, 2008). The summertime reliance on squid by sperm whales at Kaikōura, means a shift in sperm whale distribution in response to prey could be expected. There is evidence of significant warming of New Zealand’s southern coastal waters over the last 50 years, based on sea-surface temperature (SST) data from Portobello; autumn-winter temperatures have increased by 1.3°C since 1967 (Shears & Bowen, 2017). At Kaikōura specifically, coastal SST has increased by

0.54° C on average over 30 years, and the 5% lowest temperatures have increased by 1.02°C (Schiel et al., 2016). As seen at Portobello, these increases seem to also be driven by autumn and winter temperatures (Schiel et al., 2016). Two squid species likely relied on by sperm whales around Kaikōura, *Nototodarus sloanii* and *Onykia ingens* (Gaskin & Cawthorn, 1967), have hatching periods in winter (Jackson, 2001; Uozumi, 1998). Since changes in ocean temperatures are already occurring, sensitive, flexible species such as squid may already be showing signs of change. Shifts in squid distribution in response to oceanographic changes have been noted elsewhere. For example, over the last 16 years the Humboldt squid, *Dosidicus gigas*, has expanded its geographical range into the waters of central California (Zeidberg & Robison, 2007). There was some evidence of increased abundance of sperm whales around the Gulf of California, during the 1990s, in response to an increase in *D. gigas* abundance (Jaquet et al., 2003).

At Kaikōura, fish, especially groper, appear to be more important in the diet of sperm whales in winter compared with summer (Gaskin & Cawthorn, 1967). The commercial fishing season for groper in Kaikōura occurs over winter in conjunction with consistently high densities of sperm whales (Jaquet et al., 2000; Paul, 2002). There has been a decline in both groper and ling commercial catches since 1991 (MPI, 2015), but since there is no evident decline in sperm whale numbers in winter over the course of the study, it may be that this decline is not significant enough to impact foraging during these months, or that sperm whales do not rely on these species sufficiently for it to have an effect.

New Zealand's ocean productivity is influenced by various water masses and oceanic fronts (Chiswell, 1996; Shaw & Vennell, 2000; Sutton, 2003). The Southland Current flows northward up the east coast of the South Island, diverging over the Chatham Rise (Chiswell & Schiel, 2001). Some water from the Southland Current flows through the Mernoo Gap into the Kaikōura area and interacts with subtropical water flowing from the north, creating fine-scale mixing and eddy structures (Shaw & Vennell, 2000). The Southland Current is made up mainly of subantarctic water mixed with some subtropical water (Sutton, 2003). It is associated with the Southland Front, which separates the warm, high saline subtropical water on the continental shelf, with cold, fresher subantarctic water offshore (Sutton, 2003). The increased productivity at this front has been attributed to the mixing of macronutrient poor but micronutrient rich subtropical water, with macronutrient rich and micronutrient poor subantarctic water (Murphy et al., 2010). The extension of the Southland Current through the Mernoo Gap has been recorded moving further inshore to Kaikōura in summer (Shaw & Vennell, 2000). If it is associated with productivity, annual variability in this oceanographic

feature or a change over time could be a further cause of variability in the number of sperm whales at Kaikōura over the summer months. Climate change is having a demonstrated effect on circulation in the Southern Ocean (e.g. Oke & England, 2004; Böning et al., 2008), but whether there is any influence on the Southland Current system is not yet known.

The Kaikōura peninsula is also influenced by alongshore advection, downwelling and upwelling (Chiswell & Schiel, 2001). The east coast of the South Island is predominantly a downwelling coast, but strong northerly winds create periods of upwelling (Heath, 1976; Chiswell & Schiel, 2001). These upwelling events have been shown to be important for the availability of the zooplankton *Nyctiphanes australis* for red billed gulls, *Larus novaehollandiae scopulinus*, at Kaikōura (Mills et al., 2008). There is also evidence of changes in zooplankton abundance at Kaikōura in relation to monthly SST (Bradford, 1972; Mills et al., 2008). For example, zooplankton abundance at Kaikōura can be negatively impacted by inflows of warm, subtropical water from offshore (Bradford, 1972; Mills et al., 2008). There is already evidence of SST increase with climate change around Kaikōura (Schiel et al., 2016) and westerly wind events are expected to increase (Mullan et al., 2001), potentially reducing localised upwelling (Mills et al., 2008).

Upwelling can be a driver of cooler SSTs, whilst bringing nutrients through the water column to the surface (Chiswell & Schiel, 2001). Low SSTs have been correlated with the feeding success of sperm whales in waters around the Galápagos Islands (Whitehead et al., 1989). Feeding success, as measured by defecation rates, was significantly higher when mean SSTs were particularly cool (25.4°C) compared with a warm El Niño year with a high mean SST (27.5°C). Reduced upwelling and increased SSTs could, therefore, result in a decline in food availability for sperm whales at Kaikōura, due to an overall decrease in ecosystem productivity.

3.4.2 Seasonal whale watching activity

Whale watching activity by boat is highest in summer and autumn, and lowest in winter (Markowitz et al., 2011). Whale watch flights occur for most of the year with twice as many flights occurring in summer compared with winter (Markowitz et al., 2011). Increased boat activity in the Abrolhos Marine National Park in Brazil has been shown to reduce singing by humpback whales (Sousa-Lima & Clark, 2008). This is thought to be due either to displacement of individuals so singing cannot be detected, reduced singing in the study area, or both (Sousa-Lima & Clark, 2008). Humpback whales in the Southern Lagoon of New Caledonia significantly increased their dive time and decreased the linearity of their swim

path in the presence of whale watching vessels (Schaffer et al., 2009). The effect on the linearity of the swim path increased with increased number of vessels (Schaffer et al., 2009). A study in Milford Sound from 1999 to 2002 showed that bottlenose dolphin residency was related to intensity of tourism (Lusseau, 2005). Dolphins spent less time in the fiord when tourism intensity was highest (Lusseau, 2005). Given that behavioural effects of tourism have been detected in the past, higher intensity whale watching at Kaikōura may be contributing to the decline in number of sperm whales visiting the study area during summer.

3.5 Conclusion

Seasonal abundance estimates of sperm whales at Kaikōura were derived from parameters generated by Robust design models. A significant decline in the number of sperm whales using the study area at Kaikōura in summer was evident, with a decline from 43 to 23 individuals from 1990 to 2017. No significant trend was apparent in the winter. The cause of this seasonal decline is currently unknown, but could be related to changes in food availability, climate change and tourism. Research should be prioritised for investigating possible factors in summer which are driving the decline, so that effective management can be implemented.

Chapter 4

Investigating associations between sperm whales visiting Kaikōura

4.1 Introduction

Social organisation is an important aspect of population dynamics, influencing gene flow and spatial patterns of individuals, as well as being the basis of important ecological relationships such as competition, cooperation and dominance (Whitehead, 1997; Whitehead & Dufault, 1999). Cetacean populations display a wide diversity in group size and social structure, from the small fluid groups of Hector's dolphins (*Cephalorhynchus hectori*; Slooten et al., 1993) and Risso's dolphins (*Grampus griseus*; Hartman et al., 2008), to the larger, highly structured groups of some killer whale (*Orcinus orca*) populations (Bigg et al., 1990; Baird & Whitehead, 2000). Understanding different patterns of social behaviour relies on a conceptual framework of interactions, relationships and social structure (Hinde, 1976). Interactions among individuals are the basic units of social behaviour, while a series of interactions between two individuals over time defines a relationship (Hinde, 1976). Finally, social structure results from the nature, quality and patterning of relationships among individuals across the whole society (Hinde 1976). Interactions are observable (Whitehead, 2008a), but many animal groups live under conditions that render such observations difficult or impossible (Vine et al., 2009). Two obvious examples are species that migrate, or live in burrows (Cunningham & Castro, 2011; Hayes et al., 2015). For cetaceans, many behaviours occur under the surface and at depth, and therefore not all interactions are easily observed (Mann & Würsig, 2014). Most cetacean populations are also very wide-ranging and mobile and, as a result, interactions among individuals may occur beyond the study area sampled (Kendall et al., 1997). Accurate description of the social structure of cetacean populations is therefore challenging.

Social relationships vary depending on sex, age, habitat (Jarman, 1974; Gero et al., 2015), reproductive success (Cameron et al., 2009), predation risk (Banks, 2001), and foraging opportunities (Clark & Mangel, 1986). Relationships can be cooperative, competitive or hierarchical (Whitehead, 1997), and may change depending on behavioural context. Observed variation may arise randomly, stemming from imperfect observation, or from preferred or avoided associations within the population (Whitehead, 1999). It is important, therefore, to be able to distinguish between what is random and what are meaningful associations among individuals (Whitehead, 1999). By first understanding the

significance of associations in a population, the question of how social structure may be adaptive for the individual, and consequently the society, can be addressed (Whitehead, 2008a).

4.1.1 Methodology for social analysis

The ability to quantify social patterns and behaviours is necessary to analyse the social organisation of populations with minimal biases. Until the 1970s, methods for studying animal behaviour relied on “*ad libitum*” sampling, where researchers simply noted down what seemed to be an important behaviour at the time (Altmann, 1974; Martin & Bateson, 2007). This introduced significant biases because some individuals may be more visible than others, and some behaviours may be more conspicuous and recognisable to the observer (Altmann, 1974). Since then, studies have focused on quantitative methods such as recording the frequency and duration of recognised behaviours (Beer, 1961), or by recording an individual’s behaviour at preselected moments in time (Richards, 1966).

Social studies of cetaceans more often use associations, rather than interactions, as signifiers of social affiliation (Whitehead, 2009b). This is because many interactions between individuals are occurring below the water surface (Mann & Würsig, 2014). There are also sometimes subtle interactions that occur, without touching or obvious communication, which can be better discovered using associations (Whitehead, 2008a). Associations are generally recorded based on co-occurrence in the same group, so all individuals in a group are associated at the time of sampling (Bejder et al., 1998; Connor, 2000). A group can be defined based on physical proximity (Gero et al., 2008), temporal methods (Johnston et al., 2017) and behavioural observations (Mobley & Herman, 1985), with the strength of the affiliation indicated by the time individuals spend together (Bigg et al., 1990).

Association relationships are measured using association indices, which measure the proportion of time that a pair of individuals (dyad) spend associated over the study period (Whitehead, 2008a). These indices can then be used to explore a variety of social metrics including the patterning of associations in a population, preferred or avoided companionship (Bejder et al., 1998) and the temporal patterning of relationships (Whitehead, 1995). The change in associations over time can be explored by calculating the lagged association rate (Whitehead, 1995). This provides an estimate of the probability that if two individuals are associating now, they will still be associated in the future (Whitehead 1995; Whitehead, 2008a).

Associations can also be defined as being within the range of communication between individuals because both active and passive transmission of information has the potential to result in behavioural changes (Bradbury and Vehrencamp, 1998; Whitehead, 2008a). Individuals with large communication ranges, therefore, may still be considered associated even if they are several kilometres from an individual in the group. Time can be used as a proxy for distance. For example, in species with large communication ranges, two individuals may be considered associated if they are seen within 2 hours of one another (e.g. Lettevall et al., 2002). For bottlenose dolphins in Florida, low frequency calls (7-13 kHz) in shallow water could reach other dolphins up to 487 m away (Quintana-Rizzo et al., 2005). High frequency calls (13-19 kHz) could have a potential detection range of >20 km (Quintana-Rizzo et al., 2005). The communication range for harbour porpoises in comparison, however, is estimated to be within 1 km (Clausen et al., 2010). The communication range between species is, therefore, variable.

4.1.2 Social structure and communication in sperm whale populations

Sperm whales are a long-lived, slow-growing species (Rice, 1989), which means they can form long-term bonds (Coakes & Whitehead, 2004). Female sperm whales are known to have complex social networks (Christal et al., 1998), but social associations among mature males remain among the least well understood aspects of sperm whale biology (Christal & Whitehead, 1997). Mature female sperm whales live in cohesive social groups of 10-30 individuals, including immature animals of both sexes (Richard et al., 1996). The duration of bonds in these groups are highly variable with some associations persisting for at least several years (Richard et al., 1996). Males leave natal groups between 6 and 15 years old to form ‘bachelor schools’ (Best, 1979). Larger males are found in increasingly smaller groups and distributed at higher latitudes (Caldwell et al., 1966). Once males are both sexually and socially mature, around their mid-twenties, they travel back to the tropics for breeding (Best, 1979). Mature males on average spend only 3-6 hours with a nursery pod because they employ a “searching strategy”, visiting multiple females during a season (Whitehead et al., 1991). When not with female groups during breeding, males can be found in loose aggregations spanning a few kilometres or more (Lettevall et al., 2002).

Sperm whales communicate acoustically using patterns of clicks called “codas” (Watkins and Scheville, 1977; Whitehead and Weilgart, 1991). Codas are thought to serve a communication function, because they have primarily been heard to be used by socialising

sperm whales (Watkins and Scheville, 1977; Weilgart and Whitehead, 1993; Rendell and Whitehead, 2003). However, male only groups in Kaikōura and in the Hellinic Trench near Greece do exchange codas (Frantzis and Alexiadou, 2008). Even if codas are not being produced, and individuals are not communicating directly with one another, individuals can “eavesdrop” gaining foraging information from the clicks of others (Madsen et al., 2002). Gaining information from the sounds of conspecifics has been demonstrated in bats (Barclay, 1982; Übernickle et al., 2012) and dolphins (Dawson, 1991; Xitco and Roitblat, 1996). It is thought that the usual clicks of sperm whales have the potential to be heard up to 16 km away and creaks (foraging buzzes, citation) up to 6 km away if both the clicking and listening individuals are at depth (Madsen et al., 2002). Slow clicks in comparison may be able to be detected as far as 60 km away. This indicates that, if males in foraging areas are not communicating directly with codas, they may be still gaining information from the sounds of conspecifics (Madsen et al., 2002).

Currently there is no statistical evidence for preferred associations or long-term bonds between males in any areas where such aggregations have been studied (Lettevall et al., 2002). Males may be aggregating in response to external conditions, such as the presence of prey (Childerhouse et al., 1995; Jaquet et al., 2003), where the location of an individual is therefore not directly related to the presence of others. However, there are many reports of mass strandings of mature and sub-adult males which suggest the presence of social bonds (Rice, 1989). Coordinated travelling has also been noted in some aggregations of males (Whitehead et al., 1997). Therefore, there may be some level of sociality within these aggregations which has yet to be detected.

4.1.3 Sociality of male sperm whales at Kaikōura

Kaikōura is a habitat used primarily for foraging by sub-adult and adult male sperm whales (Dawson et al., 1995). Generally, when individuals are seen at the surface they are solitary, but there are instances throughout the long-term dataset of close associations between whales (Lettevall et al., 2002; personal observation). Clusters of up to five individuals have been observed, but more commonly pairs of whales are seen surfacing and resting together before diving again. Social structure within this population was previously analysed using data from 1990 to 2001, but no preferred associations were found (Lettevall et al., 2002). A pair of whales were considered associated if they were identified within two hours of each other (used as a proxy for a distance of 15 km), or identified on the same day (a proxy for a distance

of 30 km between pairs of individuals; Lettevall et al., 2002). The sampling period for this study was defined as five days, based on calculated residency times (Lettevall et al., 2002).

4.1.4 Aims

As the study area does not encompass the home range of individuals visiting Kaikōura, interactions may easily occur over large spatial scales that might not be revealed by the existing survey data. Due to the range over which individuals may be communicating, they may be interacting even when they are not in close physical proximity. Furthermore, all individuals present in the study area on a given day are not necessarily always identified. It is, therefore, important to consider time windows for defining associations longer than the one day used previously by Lettevall et al. (2002). This chapter, therefore addresses the following questions:

1. Are there preferred associations among sperm whales at Kaikōura? The dataset now has nine years of new data collected over 13 years since the last analysis by Lettevall et al. (2002). This larger dataset should have more power to resolve associations.
2. What is the effect of modifying the criterion for association by increasing the allowed time between sightings? An association will be defined as two individuals being seen on the same day, seen within two consecutive days, or seen over a four-day time-span. I explore how these extended association periods affect association indices and the presence of preferred associations.

4.2 Methods

Data collection and photo-ID methodology was the same as described in Chapter 2. To analyse association data, the social analysis software SOCPROG (v2.8) was used (Whitehead, 2009b).

4.2.1 Data filtering

Three group definitions were tested. Individuals were defined as within the same group, if they were seen on the same survey day, during two consecutive survey days, or over the time-span of four survey days. The four-day definition could not be defined as consecutive days, as there were not enough consecutive four-day periods to use for analysis. SOCPROG requires a sampling period to be defined within the dataset. This is to allow for associations to be

investigated over a temporal scale (Whitehead, 2008a). Associations can then be explored on a short-term scale, within a sampling period, but also among sampling periods to test for long-term associations (Whitehead, 2009b). Individuals were considered associated if they were seen in the same group within a sampling period. The sampling period was defined as a field season and each season trimmed to 3-5 weeks in length, as in Chapter 3.

Individuals that are seldom seen may bias the apparent network within the society, and it is known that using indices based on four or fewer samples will always be inaccurate (Whitehead, 2008a). To address this, if individuals were seen in fewer than five sampling periods they were excluded from the analysis. Sightings should also be spaced at least a day apart, as independent evidence of association (Bejder et al., 1998). Repeat sightings of an individual on the same day were therefore excluded from the dataset.

4.2.2 *Measuring associations*

Association indices were calculated in SOCPROG. These were calculated for each possible dyad using the half weight index (HWI; Cairns & Schwager, 1987; Whitehead, 2008a). This is most appropriate when associations are defined as “present in the same group” but when it is not certain that all individuals in the group have been sighted (Ginsberg & Young, 1992). The HWI index for each possible dyad was calculated with the following equation:

$$\text{HWI} = \frac{x}{x+yab+0.5(ya+yb)}$$

Where x is the number of times that individual A and B were defined as being in the same group, ya is the number of sampling periods where only individual A was identified, yb is the number of sampling periods where only individual B was identified, and yab is the number of sampling periods where both A and B were identified but not associated.

An association index may vary between 0 and 1; 0 means no association (i.e. two individuals are never seen together) and 1 means perfectly associated (i.e. always seen together; Whitehead, 2008).

An estimate of social differentiation (SD) was also calculated to show the variability of association indices within the population. This is calculated by SOCPROG using the following equation:

$$SD = \frac{\sqrt{\text{var}(x_{AB}) - \text{Mean}(x_{AB})}}{\text{Mean}(x_{AB})}$$

Where x_{AB} is the number of observations where individuals A and B were associated. This is a Poisson estimate of SD and relies on the assumption that the probability of an individual being identified in a sampling period is the same for all individuals (Whitehead, 2008). If social differentiation is close to 0, then the relationships in the population are homogenous, whereas a social differentiation close to 1 means relationships are varied. A poorly differentiated population is one with an SD value of <0.2 . A measure of the accuracy of the social representation, r , can be gained from the following equation in Whitehead (2008a):

$$r = \frac{SD}{CV(\alpha_{AB})}$$

Where SD is the social differentiation, and $CV(\alpha_{AB})$ is the coefficient of variation of the estimated association indices. An r value close to 1.0 indicates a very good representation, ~ 0.8 is a good representation, and ~ 0.4 is an acceptable representation (Whitehead, 2008).

4.2.3 Testing for preferred and avoided associations

The null hypothesis of random associations, and therefore no preferred or avoided companions, was conducted via Monte Carlo permutations in SOCPROG (Bejder et al., 1998; Whitehead, 2009b). In this approach, testing is conducted using simulated datasets (Bejder et al., 1998). Alternative datasets are randomly generated, but the number of times each individual is sighted and the number of individuals in each group is constrained (Whitehead et al., 1982; Slooten et al., 1993; Bejder et al., 1998). The random data, therefore, retains important features from the original data (Bejder et al., 1998). The null hypothesis states that there is equal probability of each individual associating with every other individual in the population (Whitehead, 2008a). To reject the null hypothesis, the distribution of association indices from the real data should be significantly different from the distribution of indices from the permuted datasets (Whitehead, 2008a).

The basis of the analysis is the calculation of the S statistic (Manly, 1995), which tests the randomness of co-occurrences within a population. It is calculated for the original dataset and then for each randomly generated dataset (Bejder et al., 1998). The proportion of all randomly generated S values that are larger than or equal to the population S statistic is the p-

value. If this p -value is less than a desired threshold (0.05 in this case), the null hypothesis of random association can be rejected (Bejder et al., 1998; Whitehead, 2009b). Dyads which have significantly high or low association indices are also outputted (Bejder et al., 1998). A significance of 0.05 was specified. This meant that an association index greater than 97.5% of the randomly generated associations indicates a preferred association. In comparison, an association index less than 2.5% of the randomly generated associations indicates an avoided association (Whitehead, 2008). Generally, more permutations are needed, compared with other Monte Carlo methods, to ensure an accurate p -value as the randomly generated datasets have constraints derived from the original dataset (Whitehead, 2009b). For this study 10,000 permutations were used, as recommended by Whitehead (2008a). The permutation chosen for these data was to permute associations within samples. This method assesses long-term companionships or avoidances by looking at associations between sampling periods, rather than within (Whitehead, 2008). This test accounts for differences in gregariousness and migration in and out of the study, and is generally the most robust option (Whitehead, 2008a).

4.2.4 Temporal analysis

An analysis of lagged association rates was performed to investigate the change in associations over time. SOCPROG calculates the lagged association rate based on theory by Whitehead (1995). The lagged association function estimates the changes in association between two individuals, after the sampling period in which they were first associated. So, given that two individuals are associated now, the lagged association rate shows the probability they will be associated so many time units in the future (Whitehead, 1995; 2009). The standardised lagged association was calculated, which is the appropriate parameter when it is not certain that all potential associates of an individual have been recorded (Whitehead, 1995). The lagged association rate is calculated in SOCPROG by using a moving average of the number of potential associations (Whitehead, 2008a). A high enough moving average needs to be set so that the data is somewhat smoothed, but not so high that information is lost (Whitehead, 2008a). For each scenario in this study a moving average between 3800 and 4000 potential associations was specified. This achieved a lagged association rate that was smoothed but did not lose information. The null association rate was also calculated as this is the expected value if there is no preferred association. Estimates of precision for the lagged association rates were obtained by using the jack-knife procedure in SOCPROG (Efron & Gong, 1983).

4.2.5 Multidimensional scaling

Association indices were graphically represented using non-metric multidimensional scaling (MDS) in program UCINET (v6.6.40; Borgatti et al., 2002). MDS consists of a set of points in n -dimensional space arranged so that the more associated dyads are plotted closer together (Whitehead, 2008a). A distance is calculated between each dyad which is inversely proportional to their association index (Whitehead, 2008a). These distances are then plotted to find the best representation of all dyad combinations for the number of dimensions specified beforehand (Whitehead, 2008a). In this analysis, scaling was performed in 2 dimensions. The “non-metric stress” represents the degree of failure in representing associations between individuals, with a stress <0.2 indicating an adequate representation, and a stress <0.05 indicating a good representation (Kruskal, 1964). MDS was more appropriate than a principal coordinate analysis (PCA), as indicated by the large negative eigenvalues produced when PCA was trialled (Manly, 1994; Whitehead, 2008a). This was further supported by less than 40% of the variation in the PCA being explained by the data.

4.3 Results

After the data were filtered in accordance with the rules devised for this study, there were 39 individuals available for the social analysis, represented in 1006 encounters. There were 26 sampling periods with a mean of 10 individuals per sampling period. Social differentiation ranged from 0.851 (SE = 0.140) in the one-day scenario to 0.708 (SE = 0.101) in the four-day scenario, which indicates a well differentiated population in all scenarios (Whitehead, 2008a; Table 4.1). The accuracy of the social representation ranged from 0.612 (SE = 0.046) in the one-day scenario to 0.552 (SE = 0.053) in the four-day scenario (Table 4.1).

Table 4.1: The social differentiation value (SD) and accuracy of social representation (r) for each of the group definition scenarios. ‘SE’ is the standard error.

Group definition (days)	SD	SE	r	SE
1	0.730	0.138	0.612	0.046
2	0.685	0.123	0.578	0.056
4	0.581	0.118	0.552	0.053

4.3.1 Distribution of half-weight association indices

There was a total of 1482 association indices calculated and most association indices ranged from 0 to 0.2 (Figure 4.1). The maximum association index for each individual was ≥ 0.4 in all scenarios (Figure 4.2). The overall mean for the one-day scenario was 0.15, and the mean of the maximum HWI per individual was 0.62. For the two-day scenario the overall mean was 0.17, and the mean of the maximum HWI was 0.65. The overall mean for the four-day scenario was 0.2, and 0.68 was the calculated mean of the maximum HWI per individual. The proportion of zero indices decreased as the time-span for association increased.

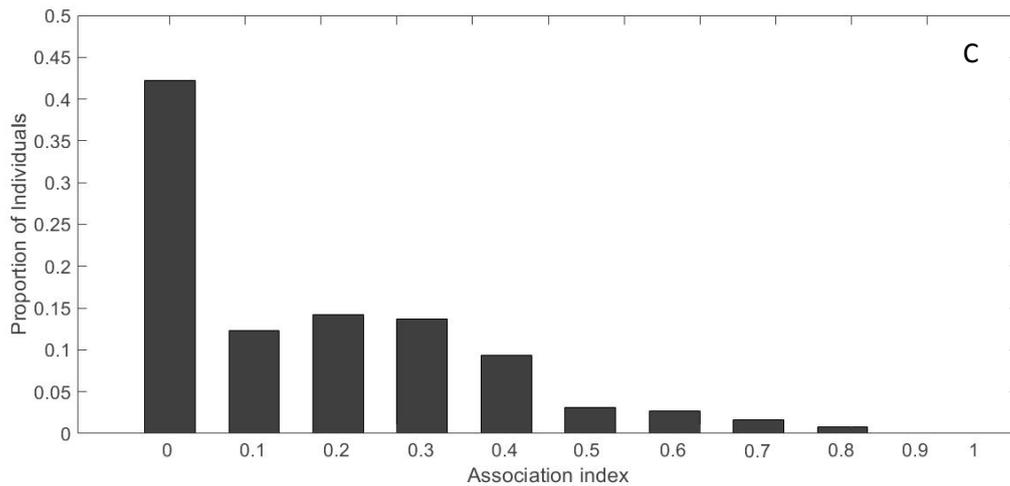
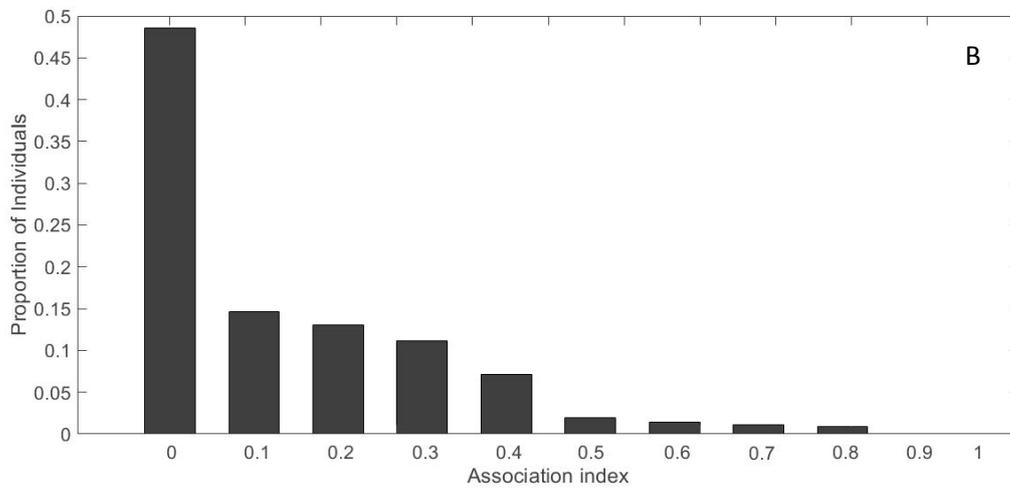
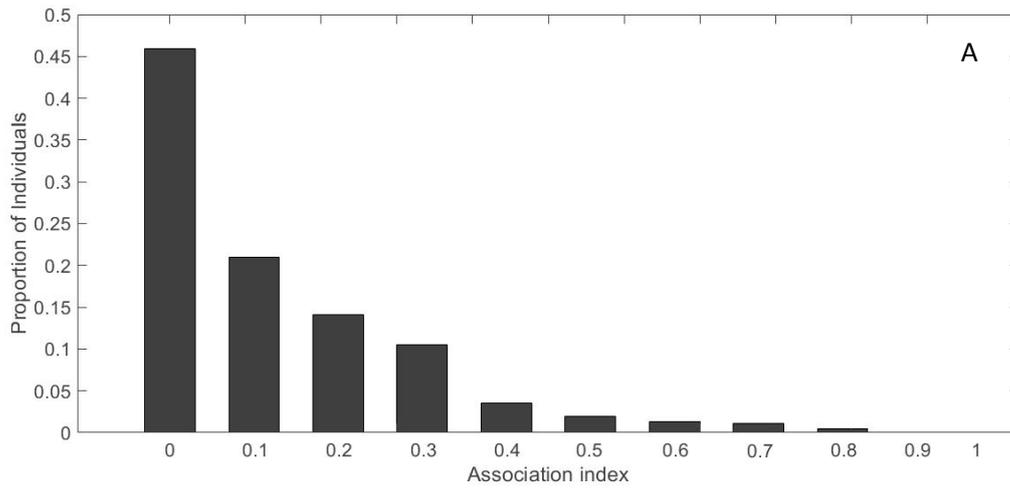


Figure 4.1: The proportional distribution of all association indices ($n=1482$) for each individual, for each of the group definition scenarios. A = one-day scenario, B = two-day scenario, C = four-day scenario.

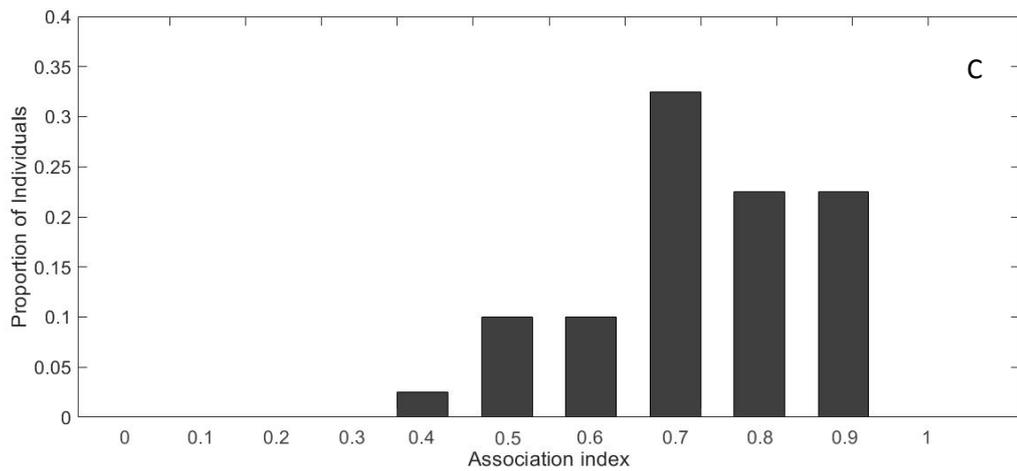
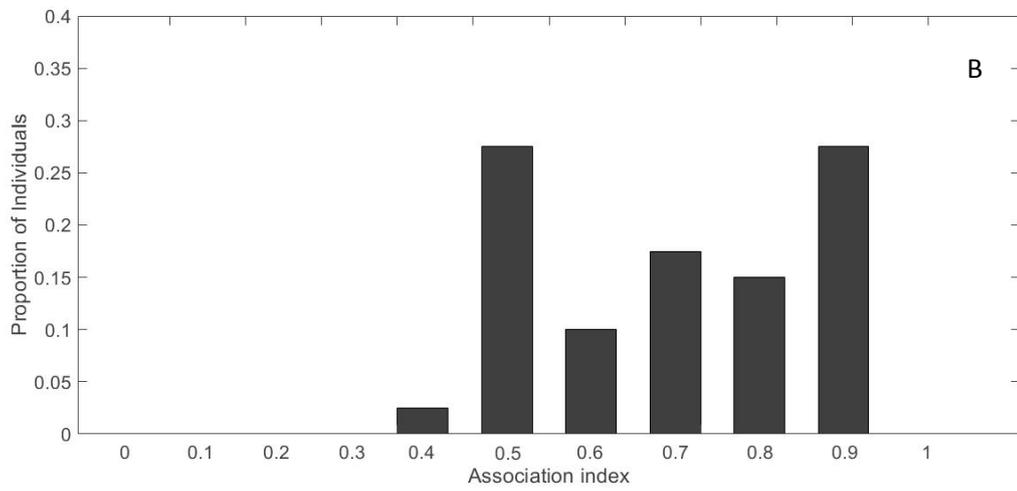
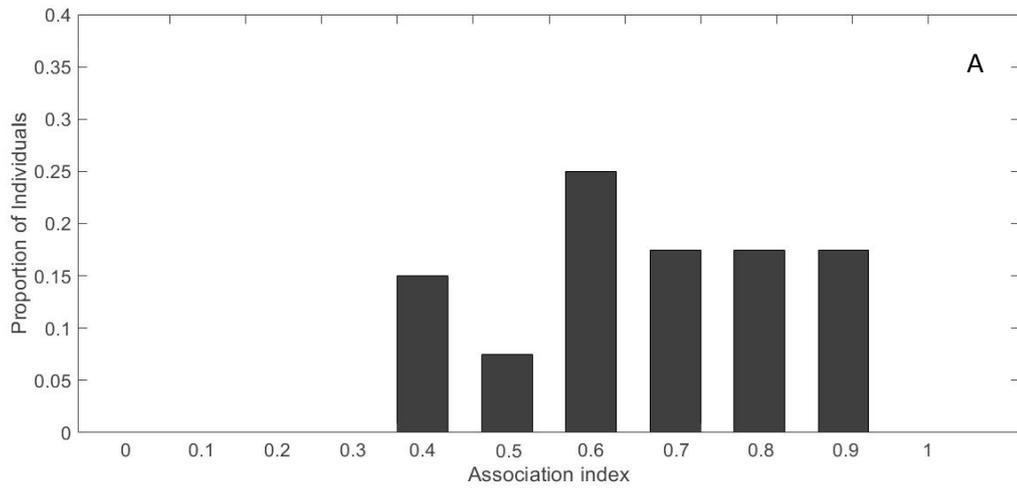


Figure 4.2: The proportional distribution of the maximum association index for each individual, for each of the association definitions ($n = 38$). A = one-day scenario, B = two-day scenario, C = four-day scenario.

4.3.2 Preferred and avoided associations

Based on the p -values derived from the comparison of S with randomly permuted dated sets, there is evidence for preferred or avoided social associations between individuals in each association definition scenario (one-day: $p < 0.001$, two-day: $p < 0.01$, four-day: $p < 0.01$). The one-day association scenario had both preferred and avoided relationships (Table 4.2), while the other two scenarios only had preferred associations (Tables 4.3, 4.4). In the one-day scenario there were eight preferred associations and two avoidance associations. In the two-day scenario there were also eight preferred associations, and in the four-day scenario there were six preferred associations. The preferred association of MTB160 and HL250 was shared between all three scenarios. The two-day and four-day scenarios also shared three more dyads, NN70 and MTR140, MTR100 and LNL160, and LNL240 and HR100.

Table 4.2: The significant long-term preferred and avoided relationships between individuals in the one-day association scenario. ‘HWI’ is the half weight index and ‘times seen at the surface together’ is the number of times a dyad were seen together at the surface as part of an encounter. p -values indicate avoided or preferred relationships.

Individual A	Individual B	p -value	HWI	Times seen at the surface together	Relationship Type
MTL40	HR80	0.018	0.00	0	Avoided
NN80	LNL120	0.023	0.00	0	Avoided
MLS100	LNR100	0.985	0.15	0	Preferred
MTB160	HL250	0.999	0.33	0	Preferred
MTR80	MTL80	0.989	0.33	0	Preferred
LNL160	HR110	0.986	0.48	0	Preferred
MLS140	HL120	0.998	0.57	3	Preferred
MLN200	LNL120	0.989	0.60	0	Preferred
MTB80	LNL100	0.981	0.67	0	Preferred
NN70	MLN190	0.990	0.83	2	Preferred

Table 4.3: The significant long-term preferred relationships between individuals in the two-day scenario. ‘HWI’ is the half weight index and ‘times seen at the surface together’ is the number of times a dyad were seen at the surface together as part of the same encounter. *p*-values indicate preferred relationships.

Individual A	Individual B	<i>p</i> -value	HWI	Times seen at the surface together	Relationship Type
MTB170	MLS100	0.987	0.20	0	Preferred
NN70	MTR140	0.997	0.46	0	Preferred
MTR100	HL160	0.981	0.48	2	Preferred
MTB160	HL250	0.985	0.50	0	Preferred
MTR80	MLS100	0.983	0.55	0	Preferred
MTR100	LNL160	0.987	0.59	4	Preferred
MLS140	HL120	0.996	0.62	3	Preferred
LNL240	HR100	0.996	0.73	1	Preferred

Table 4.4: The significant long-term preferred relationships between individuals in the four-day scenario. ‘HWI’ is the half weight index and ‘times seen together at the surface’ is the number of times a dyad were seen at the surface as part of the same encounter. *p*-values indicate preferred relationships.

Individual A	Individual B	<i>p</i> -value	HWI	Times seen at the surface together	Relationship Type
NN70	MTR140	0.987	0.17	0	Preferred
LSR60	LNL120	0.979	0.2	0	Preferred
MTB160	HL250	0.995	0.5	0	Preferred
MTR100	LNL160	0.993	0.50	0	Preferred
MTR80	LNL120	0.978	0.55	1	Preferred
LNL240	HR100	0.998	0.73	1	Preferred

4.3.3 *Temporal analysis*

The lagged association rate showed that preferred associations occur over a time lag of eight field seasons, or approximately four years (two field seasons were conducted per year on average; Figure 4.3). After this time, the lagged association rate overlapped with the null association rate in all scenarios, indicating that preferred associations end after this time lag. Overall, the three different scenarios showed similar time lag patterning.

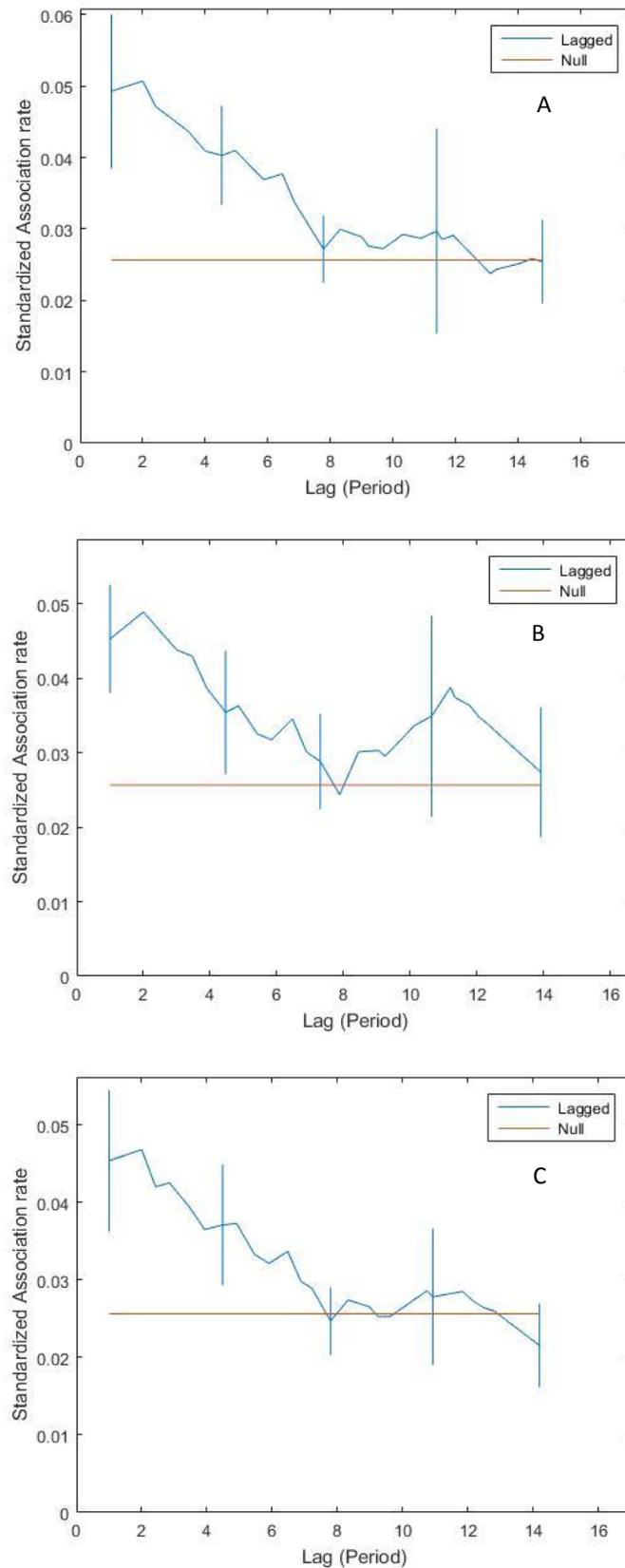


Figure 4.3: The lagged association rate for each group definition scenario, where the association rate is standardised and the lag is the sampling period. The null association rate is presented for comparison. Estimates of precision are shown via the jackknife procedure. A = one-day scenario, B = two-day scenario, C = four-day scenario.

4.3.4 Multidimensional scaling

For each scenario the MDS plots showed some clustering of individuals. Clusters were tighter in the one-day and two-day scenarios (Figures 4.4, 4.5), and both these scenarios had a lower stress value compared with the four-day scenario (Figure 4.6). In the one-day scenario avoided associates did not appear to be spaced further apart than preferred associates. Preferred associates were generally not placed the closest together. The exception to this was the dyad NN70 and MLN190 (indicated by the black arrows) which were preferred associated and close to one another in the MDS diagram. In the two-day scenario LNL240 and HR100 were the only preferred associates placed closest together. In the four-day scenario there were no preferred associates placed closest to their corresponding preferred associate. Groupings varied between the three scenarios but MTB160 was consistently at the outer edge of the MDS and MTL80 was also on the outer edge for the one-day and two-day scenarios.

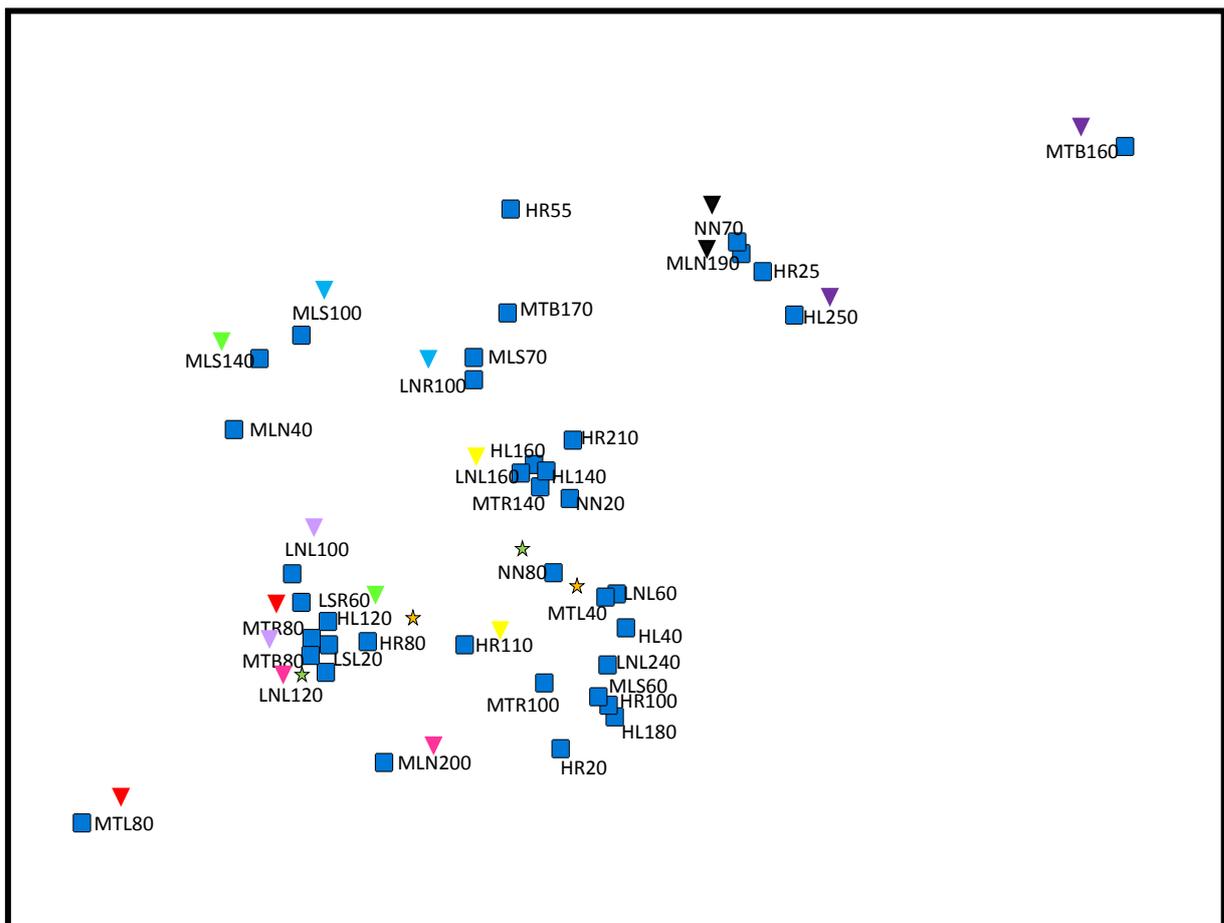


Figure 4.4: The MDS diagram for the one-day association scenario. Preferred associates are indicated with the same coloured arrows. Avoided associates are indicated by the same coloured star. Non-metric stress = 0.12.

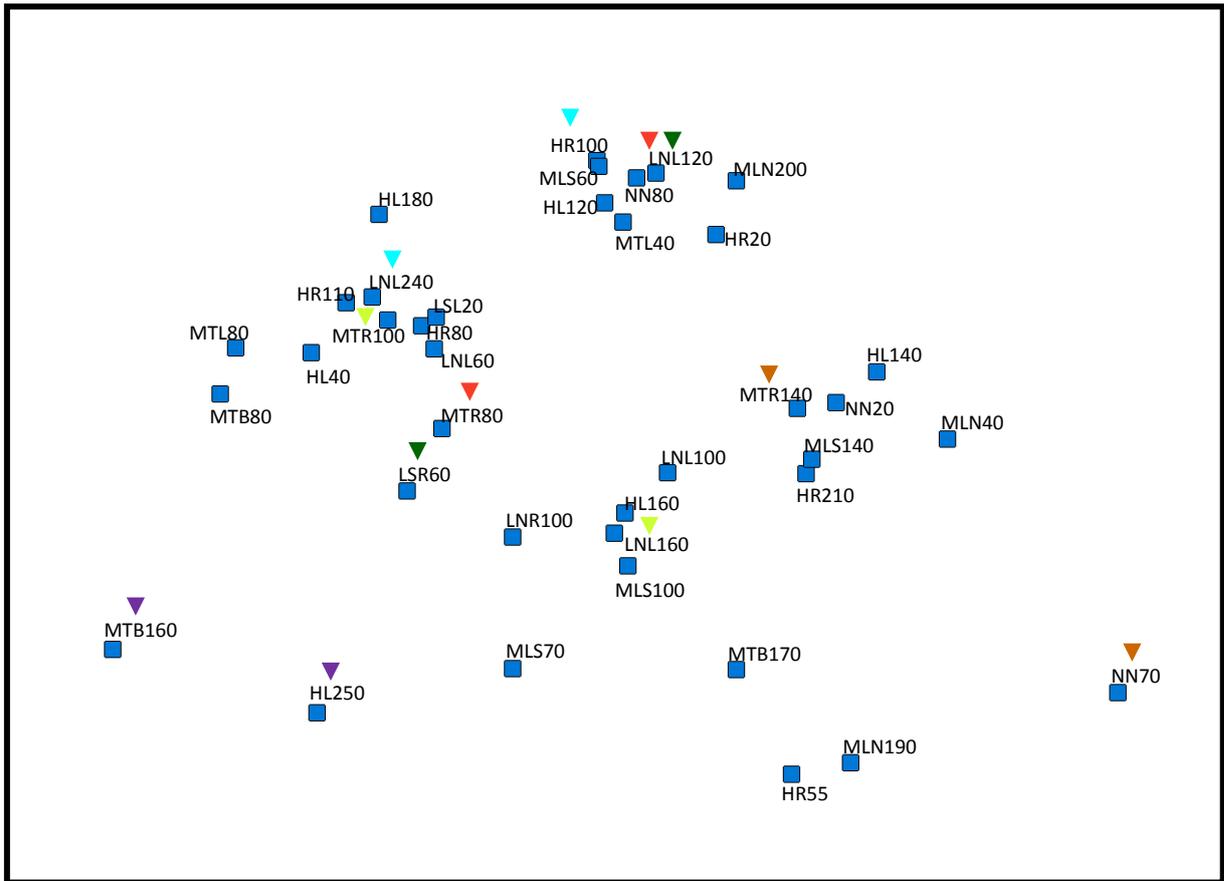


Figure 4.6: The MDS diagram for the four-day association scenario. Preferred associates are indicated with the same coloured arrows. Non-metric stress = 0.18.

4.4 Discussion

The social structure of male sperm whales at Kaikōura was explored via preferred association permutation tests, temporal analyses and multi-dimensional scaling. Significant preferred and avoided associations were present in this population, the first time this has been detected in any male population of sperm whales and contrasts with the previous findings at Kaikōura (Lettevall et al., 2002). This may be due to the longer time series available, meaning there were more data with which to examine social structure. The temporal analyses showed that preferred associations occurred over a time-span of approximately four years. There was some clustering evident in the MDS plots but these generally did not reflect the preferred associations which were found.

The use of novel ways for defining associations has the potential to reveal new insights into social structure of wild populations (e.g. Johnston et al., 2017). In this chapter, varying the “group definition” scenario was important for showing how social structure and

preferred associations may change when all potential associating individuals are not sampled over a small time frame, such as one day. As the group definition scenario increased in time-span, the number of non-zero association indices increased, meaning more individuals were associating with each other in the four-day scenario compared with the one-day scenario. The distribution of mean association indices was also more skewed towards one, with an increase in the group definition time-span. This was expected as an increase in the time-span over which associations can occur, potentially allowed for more association opportunities between individuals that would otherwise be missed due to not being sighted on a particular day. Social differentiation decreased as the time-span of the “group definition” increased, so the population was less socially differentiated in the four-day scenario compared with the two-day and one-day scenarios. The number of preferred associates also decreased and there seemed to be less of a clustering tendency in the four-day MDS diagram compared with the shorter time-span scenarios. Regardless of the group definition scenario chosen, however, there was still evidence of some social structure in the population and preferred associations were present in each one.

Overall, most associations were weak (mean HWI for all scenarios ≤ 0.2). There were some strong associations, and a small number of preferred associations. Indices >0.5 indicate a relatively strong association between a dyad (Slooten et al., 1993; Würsig & Pearson, 2014). For the sperm whale population at Kaikōura, 65-75% of individuals had non-zero association indices (depending on the group membership scenario used), but only 5% had indices of 0.6 or higher. This means only a small proportion of sperm whales at Kaikōura were associating in a potentially significant way. The mean association index for each individual reflects this, as most individuals have a mean index less than 0.5. Most individuals, therefore, are associating, but only with a few other individuals. This is not unexpected as the calculated social differentiation was relatively high (>1).

The social differentiation within the population can be also seen via the multidimensional scaling diagrams, which plot pairs of individuals relative to each other according to their HWIs. There is some indication of groupings, with certain individuals placed closer together over all three association day scenarios. These closer grouped individuals may represent “acquaintances” rather than preferred associates, as there were only at most 10 preferred associate dyads over the study period. There are many more individuals clustered in different groups in the MDS diagrams. The MDS diagrams, however, had stress values between 0.1 and 0.2, indicating that they only represented the population to an adequate level (Kruskal, 1964). It also may be that not all preferred associations were detected

using the permutation test. For one, this study only looked for evidence of long-term preferred associations over seasons, but not short-term associations within seasons. This was primarily due to lack of statistical power within each sampling period (Whitehead, 2008b). Finer scale associations may also be occurring that are not detectable by the association definitions due to the relatively small sample sizes.

This study was based on individuals being associated if they were seen during a certain time-span (one, two or four days). However, sometimes individuals are also physically seen together in the field. For example, individuals will sometimes approach each other, swim side by side, and dive together (Lettevall et al., 2002; personal observation). These pairs of individuals will sometimes resurface together after their next dive cycle (Lettevall et al., 2002; personal observation). Some of the “significant” dyads found in the analysis were of individuals previously seen together in the field. Preferred associates LNL160 and MTR100 have been seen at the surface together four times between 1997 and 2002. HL120 and MLS140, also preferred associates, were seen at the surface together three times between 1997 and 2000. Maybe these co-occurrences are also indicative of preferential associations. There were an additional 74 instances of individuals sighted at the surface together but which did not include preferred associates.

The preferred associations observed in this analysis may be beneficial to individuals and therefore adaptive for the population as a whole. By associating with conspecifics in the area, individuals may be sharing foraging information actively and/or passively. It is likely that individual feeding is improved by foraging in a group, as information can be rapidly shared, such as where prey are concentrated (Würsig, 1986). This can be advantageous even when the actual securing of the prey is done individually (Würsig, 1986). There is evidence that group foraging in spinner dolphins (*Stenella longirostris*), for example, is thought to increase the efficiency of prey capture, as dolphins in groups are able to herd together larger prey aggregations compared with solitary foraging (Bernoit-Bird and Au, 2009). The use of “eavesdropping” on conspecifics rather than actively communicating and coordinating foraging has been theorised for Hector’s dolphins (Dawson, 1991). Codas are occasionally heard at Kaikōura and, therefore, sperm whales may be actively communicating foraging information. These codas are uncommon, however, so if individuals are gaining foraging information from one another it is more likely occurring through eavesdropping.

Even with the presence of preferred long-term associations, it seems that long-lasting units of consistently associated individuals are not a numerically important component of the

population structure in Kaikōura. In general, loose social groupings have been linked to the use of areas primarily for feeding by sub-adult and adult whales (Lettevall et al., 2002). Being social, however can be adaptive for a population (Whitehead, 2008). The social structure of female and juvenile groups, for example, is thought to have evolved, at least partly, for helping in the care of young. Alloparental care, in which other individuals in a group “babysit” calves, has been observed in sperm whales (Whitehead, 1996). Young males are fully involved in the cooperative behaviour within their mother’s social unit for years (Connor et al., 1998) but this behaviour seems to be lost once they disperse from their natal group (Connor et al., 1998; Christal et al., 1998). This pattern of male behaviour, from juvenile to adult, is also seen in elephants (Elephantidae) (Moss & Poole, 1983; Moss, 2001). The social system of sperm whales and elephants, in general, have converged, with female groups displaying similar levels of social organisation (Weilgart et al., 1996; Whitehead, 2003).

Previously it was believed that adult male elephants, like sperm whales, did not form associations with one another (Croze, 1974). Male African elephants (*Loxodonta africana*) do in fact have short term, but strong associations between some individuals. Some pairs are repeatedly seen together, at times despite long periods of separation (Chiyo et al., 2011). Often, it seems that most associations are weak between individuals, with a few very strong associations (Croze, 1974; Moss & Poole, 1983), similar to what is seen in this study. Male African elephants which are genetically related or are of similar age, are also more likely to have strong associations with one another (Chiyo et al., 2011). In addition, when male elephants are in a sexually inactive state they seek out other males of a similar age (Goldenberg et al., 2014). At Kaikōura, male sperm whales are all between 13 m and 15 m long (Dawson et al., 1995; Rhinelander & Dawson, 2004; Growcott et al., 2011; Miller et al., 2013b). These total lengths suggest that most males at Kaikōura are sexually mature, but not yet socially mature (Rhinelander & Dawson, 2004). In turn this suggests that some individuals may be associating in the area partly based on the needs of a particular life-history state. Since only the largest males travel to the tropical breeding grounds to find receptive females (Best, 1979), there is a premium on growing large quickly, and hence associating with a very productive foraging area.

It is also possible that the few very strong associations in the population could be between individuals that are more genetically similar than those with weaker associations, as seen between male elephants in Africa (Chiyo et al., 2011). Preferred associations observed between male sperm whales in high latitude feeding habitats, therefore, may be a remnant of

strong associations which occurred in low latitude breeding areas before these individuals dispersed.

4.5 Conclusion

This chapter explores the temporal social structure and preferred associations of male sperm whales at Kaikōura. A small number of preferred associations were found within a primarily loosely structured population. There was also evidence for some clustering within the study area. The tendency to form stable bonds in natal groups may not be entirely lost once males leave and become sexually mature, as previously thought. Further information may be gained by undertaking genetic analyses to see if preferred associates are related, and to analyse the size of individuals in relation to the level of association.

Chapter 5

General Discussion

This thesis used a long-term photo-ID dataset to investigate the demographic parameters and social organisation of sperm whales visiting Kaikōura between 1990 and 2017. Long-term datasets are invaluable for investigating population trends, as many ecological processes occur over multiple years, rather than days or weeks (Clutton-Brock and Sheldon, 2010). Research protocol at Kaikōura has remained fairly consistent since 1990, providing the opportunity to assess population trends over a long temporal scale. Previously, a decline in number of whales using the study area each year had been detected from 1991 to 2007 (van der Linde, 2009). My research (Chapter 2) has updated the database and Cormack-Jolly-Seber analyses to determine whether the decline had continued. A significant decline in the number of sperm whales visiting Kaikōura from 1991-2017 was found. I also wanted to apply a different modelling framework, the Robust design (Pollock, 1982), so that temporary emigration could be included. Sperm whales are temporary visitors to Kaikōura: many return over multiple years but none are truly resident (Childerhouse et al., 1995; Jaquet et al., 2000). The Robust design model, therefore, is a more realistic capture-recapture model for sperm whales at Kaikōura. Due to the structure of Robust design models it was appropriate to model summer and winter seasons separately. The Robust design models revealed a significant decline in the number of individuals using the study area during summer, but not in winter (Chapter 3). Furthermore, there was no evidence that the decline is being driven by a step change in survival rate or temporary emigration probability. Modelling the data using two different techniques adds weight to the conclusion that the trend in abundance at Kaikōura is real, and enables us to focus our attention on what might be causing the decline.

The dataset also provided a unique opportunity to investigate the social organisation of sperm whales using the Kaikōura study area. Previous studies had not detected evidence of associations among males outside nursery groups (Lettevall et al., 2002). Nursery groups are highly social and young males contribute fully to the social organisation of these groups (Gordon, 1987). It would not be surprising, therefore, that some form of sociality persists after leaving these mixed groups. In Chapter 4, associations were investigated over time windows of one, two and four days to reflect that, even though male sperm whales do not typically spend time in groups, they may still be associating over larger scales. Significant preferred associations were detected in all three scenarios, and the timelag analysis showed that these

relationships typically occur over a four year period. Groups of male sperm whales have previously been thought to congregate in specific areas primarily due to food availability (Connor, 2000). While this may be the main reason that brings male sperm whales to the same area, there is now evidence for a level of sociality which could be partly responsible for males grouping together in particular areas.

5.1 Potential causes of a decline

A decline in the number of sperm whales visiting Kaikōura may reflect an actual decline in the local sperm whale population, a redistribution of individuals away from the coast, or a change in foraging area. Sperm whales use the habitat at Kaikōura primarily for feeding; they display foraging behaviour most of the time (Childerhouse et al., 1995; Jaquet et al., 2000). A decline in the use of the area may mean that this habitat is changing, and foraging there is not as efficient as before. Alternatively, it may mean that the greater amount of tourism in summer is deterring whales from the area. It is still unknown where whales that visit Kaikōura go when they are not in the study area, as no sightings in other parts of New Zealand, or matches to international catalogues, have been found. The analyses of Chapter 2 and 3 indicate that the main decline in whales using the study area at Kaikōura is during summer. This may be related to changes in food availability or tourism pressure.

Squid are likely the primary food source for sperm whales at Kaikōura (Gaskin & Cawthorn, 1967), so a decline in sperm whales visiting Kaikōura in summer may be a response to changes in the abundance and distribution of squid. Sperm whale populations in other areas have been shown to respond to variability in squid populations (Jaquet et al., 2003). Squid growth, distribution and abundance is variable and responds quickly to environmental changes such as temperature (Vidal et al., 2010; Moreno et al., 2012). Evidence of warming ocean temperatures have already been noted in Kaikōura (Schiel et al., 2016), meaning squid populations in the region may already be impacted.

Squid abundance and distribution may also be impacted by oceanographic productivity. Sperm whale distribution has been correlated with areas of upwelling (Smith and Whitehead, 1993) and increased chlorophyll concentration (Jaquet et al., 1996). These areas are thought to be supporting productive feeding grounds for sperm whales. Periods of increased primary productivity have been shown to coincide with peaks in pelagic squid abundance (Costa and Fernandes, 1993; Vidal et al., 2010), thereby supporting top predators such as sperm whales (Smith and Whitehead, 1993). The productivity of Kaikōura may be influenced by upwelling

(Chiswell & Schiel), so changes to circulation and upwelling in summer may affect food availability for higher trophic levels, and ultimately sperm whales.

The decline in summer may also be the result of increasing tourism pressure. There is evidence that tourism may result in behavioural effects at Kaikōura (Richter et al., 2006). Sperm whales which visit Kaikōura less frequently, for example, display behaviours which indicate they are less tolerant of boat presence (Richter et al., 2006). Since tourism activity is highest during summer and autumn, it may be that less tolerant individuals are displaced further from the coast during these busier months.

5.2 Recommendations for management

A set of protected areas, matāitai reserves and taiāpures have been established with the aim to recognize and maintain the biodiversity of the Kaikōura area (Figure 5.1; MPI & DoC, 2013). The Hikurangi marine reserve and whale sanctuary were established in 2014 to protect the wide range of habitats represented at Kaikōura and to protect whales and other marine mammals from negative impacts from seismic surveying (MPI & DoC, 2013). The Hikurangi marine reserve covers 104km² including 1.9km of rocky shore coastline, and extends to the head of the Kaikōura canyon (Fig. 5.1). The latter is important sperm whale foraging habitat and fishing in this area is prohibited (MPI & DoC, 2013). The reserve's design was, however, strongly influenced by a wish to minimise effects on commercial fishing (MPI & DoC, 2013), compromising its benefits to fish stocks and their predators.

Due to the mobility of many species within marine reserves, the effective size of a protected area is often less than its actual size (Kellner et al., 2007; Freeman et al., 2009; NZMSS, 2014). This is due to “edge effects”, such as fishing pressure removing catch at or near the boundary (Kellner et al., 2007; NZMSS, 2014). Although the Hikurangi reserve covers 104km², its complex shape offers considerable scope for edge effects (NZMSS, 2014). Analyses of sperm whale habitat use at Kaikōura show that the reserve encompasses a very small portion of the area used by sperm whales (Jaquet et al., 2000). Any benefit to sperm whales from the Hikurangi Marine Reserve is likely to be marginal at best.

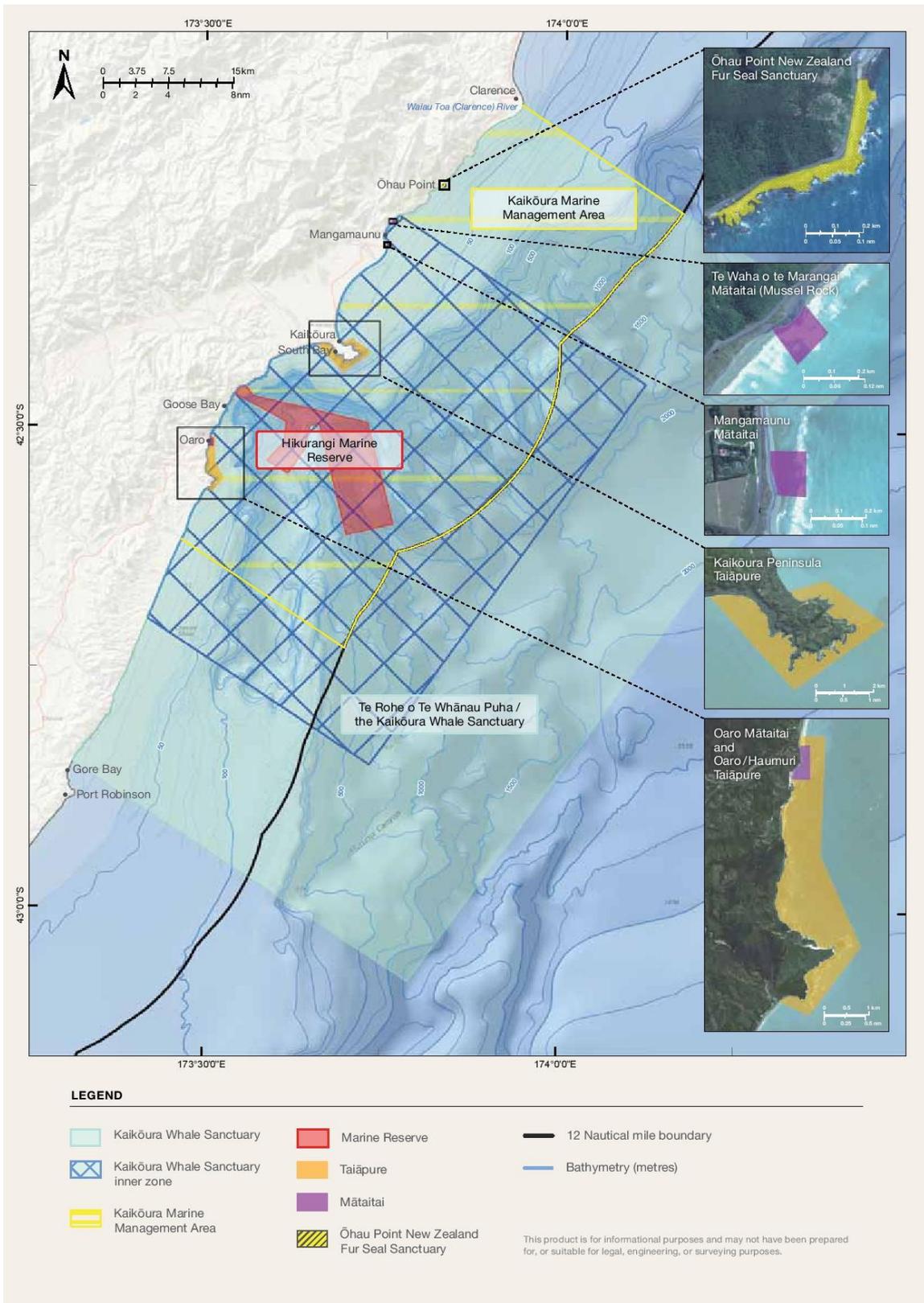


Figure 5.1: Map of the Hikurangi Marine Reserve, Marine Mammal/Whale Sanctuary, taiāpures and mātaitis established in Kaikōura. Figure from the Department of Conservation (2014).

The marine mammal sanctuary protects inshore marine mammals from being exposed to high levels of seismic surveying noise (DoC, 2013; MPI & DoC, 2013). Level 1 surveys, which are generally geophysical surveys for oil and gas, are banned from the sanctuary (MPI & DoC, 2013). There is a moratorium on future permits for oil and gas exploration in New Zealand, but current permits may allow surveying to continue for at least a decade (Young, 2018). The sanctuary extends past the 12 n.mi. (22.23 km) boundary to 56 km and covers a total of 4686 km², however, because sperm whales are likely ranging outside the sanctuary boundary, they may still come into contact with high levels of anthropogenic noise. Even when current oil and gas permits end, sperm whales may still be impacted by anthropogenic noise from other sources, such as shipping (Richardson et al., 1995).

In order to maximize the protection of sperm whales at Kaikōura, a better understanding of their habitat use is necessary. At this stage, however, we know that sperm whales are utilising areas which are under fisheries pressure since they range outside of the marine reserve. Understanding the causes for the observed decline would also allow the most influential threats to be addressed and protected areas to be established with these in mind. Because the causes for the observed decline in the number of sperm whales visiting Kaikōura are unclear, a precautionary management approach is recommended.

5.3 Implications of preferred and avoided associations

The social analyses for the sperm whales visiting Kaikōura showed that there are a small number of preferred associations in all three association scenarios tested. The sociality of mature male sperm whales, however, is still not well understood. Immature males live in highly social networks at mid latitudes, but leave their natal groups around the age of six to spend time in ‘bachelor schools’ of young males (Best, 1979). As they get older, they are found in increasingly smaller groups at higher latitudes (Caldwell et al., 1966). They visit the mixed nursery groups around their mid-twenties, when they are ready to breed (Best, 1979). In mixed schools, the duration of bonds is highly variable, from associations persisting for at least several years, to casual associations spanning a couple of weeks at most (Whitehead et al., 1991). Previous to this study, there was no statistical evidence of associations between mature males in loose aggregations. It is not unexpected, however, that mature males would be social since they are fully involved in complex social organization as immatures (Gordon, 1987). Previous observations suggested some sociality; mature males sometimes travel together (Whitehead et al., 1997) and, at Kaikōura, sometimes surface side by side after

foraging dives (Letteval et al., 2002). Being social can be adaptive for individuals and consequently the society as a whole (Whitehead, 2008a). For example the high sociality of female and immature sperm whales is advantageous for foraging success (Arnbom and Whitehead, 1989), and the protection of young (Whitehead, 1996).

Scarring on the nose and heads of larger males (Best, 1979; Kato, 1984), and broken teeth (Clarke and Paliza, 1988), indicate that some interactions between males are aggressive, however there are very few accounts of this behaviour being observed (Caldwell et al., 1966; Clarke & Paliza, 1988). It may occur at breeding grounds when males of similar sizes arrive at the same group of females (Whitehead, 1993). The male sperm whales sighted at Kaikōura are between 9-16 m in length (Dawson et al 1995; Miller et al., 2013b). In general males larger than 13 m are likely to have large scars caused by the teeth of other large males (Best, 1979). By associating with males of a similar size at feeding grounds, male sperm whales could benefit by physically interacting with each other before being in serious aggressive encounters at breeding areas, as is hypothesized for all-male foraging groups of elephants (Chiyo et al., 2011). This aggressive behaviour, however, has never been witnessed at Kaikōura.

5.4 Study Limitations

Sampling across field seasons was not consistent over the 27 years of this study. A few years had no sampling, and the timing of field seasons varied due to changes to the University calendar and weather. Some seasons were much shorter than others and therefore could not be used in the seasonal analysis. Furthermore, filtering of the data prior to the Robust design analysis meant that the summer and winter analyses also did not include all the same years, and the summer dataset started several years earlier than the winter set. As most of the decline occurred in the latter half of the time series, testing the summer data with the same starting point as winter showed that the decline was still significant. There may be a decline occurring in winter which was not detected due to the shorter and sparser data available. The missing data also meant that Markovian emigration Robust design models could not be comprehensively investigated as this model structure is based on primary periods being consecutive in time.

Studying social relationships between male sperm whales, in general, is limited because it is not fully understood how sociality occurs between individuals. The very large

scale of movement in sperm whales means that our studies at Kaikōura cover a very small part of their distribution. If sperm whales chose to socialise far offshore, we would never know. Additionally, the fact that sperm whale clicks can be heard over ranges of up to at least 8 km means that individuals may be in acoustic contact over large ranges. However, these factors were accounted for as much as possible by testing for associations over the longer time-spans of two and four days. As a result, there is evidence from this study that preferred associations occur over greater physical distances than previously examined, using time as a proxy. This suggests that there may be some social structure but it may depend strongly on the time frame used for defining an association. Further investigation into more precisely defining associations is recommended.

This study was also limited to only investigating long-term preferred/avoided associations. This is because the test for long-term associations accounts for differences in gregariousness and temporary emigration (Whitehead, 2008a), which is more representative for the sperm whale population at Kaikōura. Investigations into how short-term associations could be tested would be useful for further understanding sociality among male sperm whales.

5.5 Future research

5.5.1 Continued data collection

The photo-ID dataset from Kaikōura allows us to assess trends over a 27 year time scale. However there were gaps in data collection between 2002 and 2005, and between 2009 and 2014. Because of the length of the dataset and the amount of data collected before and after these gaps, useful trends could still be estimated. A more complete data series would be more useful for detecting accurate trends. Therefore, it should be a priority that photographic data continues to be collected each year. The continuation of regular data collection will also be important for further social analyses.

5.5.2 Investigating causes for the decline

Now that it has been established that the decline in the number of sperm whales using the area first revealed by van der Linde (2009) has continued, the next step is to investigate why. An improved understanding of the seasonal distribution and diet of sperm whales visiting Kaikōura is important for investigating whether individuals may be responding to a change in food availability. Currently our knowledge of the diet of sperm whales in the region is based on stomach content analysis from whales caught in the Kaikōura and Cook Strait region in

1963 and 1964 (Gaskin and Cawthorn, 1967). Information on diet, however, can also be gained from stable isotope analyses of sloughed skin (Ruiz-Cooley et al., 2004). Cetaceans constantly slough skin to minimise fouling, and small pieces of sperm whale skin can be observed floating in the slick after an individual has just dived. Sloughed skin from sperm whales has been collected at Kaikōura opportunistically since 1994. Since 2014, collecting available skin after each sperm whale encounter has been a focus in the field and there are now skin samples from 37 whales. Stable isotope analysis of sloughed skin may reveal differences in prey targeted in summer and winter.

Investigating the primary productivity and oceanographic features of Kaikōura could aid in better determining what makes an ideal foraging habitat for sperm whales. By comparing areas where whales forage often to areas with less foraging activity, we could gain more information on the environmental factors which could be contributing to the decline.

The demographic cause of the decline should also be investigated. The Robust design analyses showed that there was no evidence that the decline was driven by a change in survival or temporary emigration over the study period. It may be that recruitment has changed over time, whereby less individuals are being recruited into the Kaikōura study area. Recruitment into the study area could be impacted by a decline in food availability, but also by increased tourism pressure. There is a lack of data on the demographic responses of sperm whales to boat presence, however, and further research in this area would be beneficial. Future research should investigate changes in recruitment and if there has been a change, what might be causing this.

5.5.3 Movements of individuals outside of Kaikōura

There are no individual sperm whales at Kaikōura which are considered permanent residents. Individuals move in and out of the study area throughout the year, and many are not present for consecutive field seasons (Jaquet et al., 2000). It is still unknown where sperm whales travel to and what they do when they are not at Kaikōura. There are multiple ways in which this can be investigated. One method is to compare the sperm whale photo-ID catalogue from Kaikōura to other existing catalogues around the world. This has been done for the photo-ID catalogue from the Dalhousie Lab in Canada, which has individuals from the eastern Pacific (mainly Ecuador, the Galápagos, Chile and the Sea of Cortez), but no matches have been found. When possible, sperm whale fluke photos from sighted or stranded individuals elsewhere in NZ, should be compared with the Kaikōura catalogue.

Movements of individuals could be tracked by physically tagging them (Block et al., 2011). Tagging has been used in sperm whale populations to explore movement patterns (Block et al., 2011), and diving and acoustic behaviour (Fais et al., 2016; Watwood et al., 2006). There is a risk, however, that the behaviour is altered due to the stress of the tagging process, thereby creating bias in the results (Hammond et al., 1990). While suction cups can be used to hold tags in place for short periods (hours to a few days; Guerra et al., 2017), retaining tags in place for extended periods is technically difficult and highly invasive. Significant injury can occur due to water movement over the animal and water pressure when diving (Mate et al., 2007) and shear stress between the muscle (into which the tag attachment must penetrate) and overlying blubber (Moore & Zerbini, 2017). Tags therefore provide the opportunity to collect important information on the movements of individuals but the methods and impact to the individual need to be taken into consideration.

5.5.4 Further investigations into social structure

Having a “skin bank” also provides the opportunity to look at the genetic relationships of sperm whales at Kaikōura, which may provide more insight into the social structure of the population. In groups of male elephants in Africa, individuals which were more closely related, also had the strongest social associations (Chiyo et al., 2011). Male elephants also have stronger associations with individuals of similar size (Chiyo et al., 2011). Given the similarities known between sperm whale and elephant societies, exploring genetics and size to assess the similarities between preferred associates is a sensible next step.

5.6 Conclusion

The number of sperm whales visiting the Kaikōura study area in summer is declining. In light of their importance economically, ecologically and culturally, it is crucial that drivers of this decline are now investigated. This study also includes the first evidence of preferred associations between mature male sperm whales. Continued research on this population and influences on social structure will aid in furthering the overall knowledge of this species.

Appendix A

A.1 The summer parameter estimates for the top model $\phi(\cdot)p(T)\gamma(R.)$, when three secondary periods were used.

Table A.1: The parameter estimates for survival (ϕ), probability of being absent from the study area (γ), and capture (p) probabilities for the top summer model, $\phi(\cdot)p(T)\gamma(R.)$.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.86	0.02	0.83	0.89
γ	0.59	0.04	0.52	0.66
p 1990	0.23	0.08	0.10	0.42
p 1991	0.69	0.06	0.55	0.79
p 1993	0.61	0.09	0.43	0.76
p 1994	0.51	0.07	0.37	0.65
p 1996	0.52	0.09	0.35	0.69
p 1997	0.41	0.07	0.29	0.55
p 1998	0.76	0.06	0.63	0.86
p 1999	0.52	0.09	0.35	0.68
p 2000	0.34	0.07	0.23	0.48
p 2005	0.49	0.08	0.33	0.64
p 2006	0.60	0.09	0.41	0.77
p 2008	0.86	0.09	0.57	0.97
p 2013	0.42	0.08	0.27	0.58
p 2015	0.40	0.11	0.21	0.63
p 2016	0.70	0.14	0.38	0.90
p 2017	0.49	0.08	0.33	0.65

Table A.2: Abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for the top summer model $\phi(\cdot)p(T)\gamma(R)$.

Season	Estimate	SE	LCI	UCI
1990	35	11.30	23	74
1991	23	0.99	23	28
1993	17	1.29	16	22
1994	26	2.39	23	34
1996	19	2.03	17	27
1997	28	3.78	24	41
1998	19	0.55	19	22
1999	15	1.78	14	23
2000	32	5.25	26	49
2005	19	2.27	17	28
2006	11	1.04	11	16
2008	5	0.12	5	5
2013	24	3.57	21	37
2015	11	2.50	9	21
2016	5	0.44	5	7
2017	17	2.11	15	25

A.2 The summer parameter estimates for the top model $\phi(\cdot)p(T)\gamma(R.)$, when four secondary periods were used.

Table A.3: The parameter estimates for survival (ϕ), probability of being absent from the study area (γ) capture (p) probabilities for the top summer model, $\phi(\cdot) p(T) \gamma (R.)$.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.85	0.02	0.82	0.88
γ	0.42	0.04	0.35	0.50
p 1990	0.09	0.03	0.05	0.17
p 1991	0.41	0.05	0.32	0.51
p 1993	0.34	0.06	0.24	0.46
p 1994	0.32	0.05	0.23	0.42
p 1996	0.23	0.05	0.15	0.35
p 1997	0.49	0.06	0.38	0.60
p 1998	0.55	0.06	0.43	0.66
p 1999	0.43	0.07	0.30	0.58
p 2000	0.32	0.07	0.20	0.46
p 2005	0.42	0.07	0.30	0.56
p 2006	0.57	0.08	0.40	0.72
p 2008	0.74	0.11	0.49	0.89
p 2013	0.36	0.07	0.24	0.49
p 2015	0.29	0.09	0.15	0.49
p 2016	0.61	0.14	0.34	0.83
p 2017	0.45	0.07	0.32	0.59

Table A.4: Abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for the top summer model $\phi(\cdot)p(T)\gamma(R)$.

Season	Estimate	SE	LCI	UCI
1990	92	28.71	57	179
1991	35	2.71	32	44
1993	27	3.39	23	38
1994	37	4.37	31	50
1996	32	6.16	25	51
1997	24	1.58	23	31
1998	20	1.07	20	25
1999	16	1.71	15	23
2000	30	5.65	24	48
2005	19	1.89	17	26
2006	11	0.72	11	15
2008	5	0.16	5	6
2013	24	2.97	21	34
2015	12	2.85	9	23
2016	5	0.39	5	7
2017	16	1.52	15	22

A.3 The winter parameter estimates for the top model $\phi(\cdot)p(T)\gamma(R.)$, when three secondary periods were used.

Table A.5: The estimates for apparent survival (ϕ), probability of being absent from the study area (γ), and capture (p) probabilities for the top winter model, $\phi(\cdot)p(T)\gamma(R.)$.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.85	0.02	0.81	0.88
γ	0.20	0.06	0.11	0.34
p 1994	0.65	0.07	0.52	0.77
p 1995	0.36	0.07	0.24	0.50
p 1996	0.61	0.07	0.47	0.73
p 1997	0.61	0.08	0.45	0.75
p 1999	0.31	0.07	0.19	0.45
p 2006	0.42	0.08	0.27	0.58
p 2007	0.44	0.06	0.32	0.56
p 2008	0.19	0.06	0.10	0.32
p 2015	0.58	0.07	0.44	0.71
p 2016	0.63	0.06	0.50	0.74
p 2017	0.60	0.07	0.45	0.73

Table A.6: Abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for the top winter model $\phi(\cdot)p(T)\gamma(R.)$.

Season	Estimate	SE	LCI	UCI
1994	22	1.15	22	28
1995	32	5.12	27	49
1996	23	1.47	22	29
1997	20	1.36	19	26
1999	28	5.54	22	46
2006	22	3.28	19	34
2007	32	3.60	28	44
2008	17	6.11	10	38
2015	23	1.68	22	30
2016	23	1.28	22	28
2017	20	1.40	19	26

A.4 The winter parameter estimates for the top model $\phi(\cdot)p(T)\gamma(R.)$, when four secondary periods were used.

Table A.7: The estimates for apparent survival (ϕ), probability of being absent from the study area (γ), and capture (p) probabilities for the top winter model, $\phi(\cdot)p(T)\gamma(R.)$.

Parameter	Estimate	SE	LCI	UCI
ϕ	0.85	0.02	0.81	0.88
γ	0.21	0.06	0.12	0.35
p 1994	0.52	0.06	0.40	0.63
p 1995	0.31	0.06	0.21	0.43
p 1996	0.51	0.06	0.39	0.63
p 1997	0.51	0.07	0.38	0.63
p 1999	0.24	0.05	0.15	0.36
p 2006	0.32	0.07	0.21	0.46
p 2007	0.39	0.05	0.29	0.49
p 2008	0.14	0.04	0.08	0.25
p 2015	0.48	0.06	0.36	0.59
p 2016	0.59	0.05	0.48	0.69
p 2017	0.49	0.06	0.37	0.61

Table A.8: Abundance estimates, standard error (SE) and 95% log-normal confidence intervals (LCI, UCI) derived from the Huggins Robust design parameter estimates, for the top winter model $\phi(\cdot)p(T)\gamma(R.)$.

Season	Estimate	SE	LCI	UCI
1994	23	1.34	22	28
1995	30	4.18	26	44
1996	23	1.38	22	29
1997	20	1.32	19	25
1999	28	5.47	22	46
2006	22	3.45	19	34
2007	31	2.89	28	41
2008	17	6.21	10	38
2015	23	1.64	22	30
2016	22	0.88	22	26
2017	20	1.45	19	26

References

- Aguilar, A. (1983). Organochlorine pollution in sperm whales, *Physeter macrocephalus*, from the temperate waters of the eastern North Atlantic. *Marine Pollution Bulletin* **14**, 349-352.
- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. *2nd International Symposium on Information Theory*. Petrov, B.N & Csaki, F. (eds). Budapest: Akademiai Kiado, pp 267–281.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour* **49**, 227–267.
- Arnobom, T. (1987). Individual identification of sperm whales. *Report of the International Whaling Commission*. **37**, 201–204.
- Arnobom, T. & Whitehead, H. (1989). Observations on the composition and behaviour of groups of female sperm whales near the Galápagos Islands. *Canadian Journal of Zoology* **67**, 1–7.
- Au, W.W.L. & Green, M. (2000). Acoustic interaction of humpback whales and whale-watching boats. *Marine Environmental Research* **49**, 469–481.
- Baird, R. & Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology* **78**, 2096–2105.
- Ballance, L.T., Pitman, R.L. & Fiedler, P.C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography* **69**, 360–390.
- Banks, P.B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: A field experiment. *Animal Behaviour*. **61**, 1013–1021.
- Barclay, R.M. (1982) Interindividual use of echolocation calls: Eavesdropping by bats. *Behavioural Ecology and Sociobiology* **10**, 271-275.
- Barker, S. & Williamson, J.. (2010). Collaborative photo-identification and monitoring of grey nurse sharks (*Carcharias taurus*) at key aggregation sites along the eastern coast of Australia. *Marine and Freshwater Research* **61**, 971–979.

- Barlow, J. & Taylor, B.L. (2005). Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science* **21**, 429–445.
- Bart, J., Brown, S., Harrington, B. & Morrison, R.I. (2007). Survey trends of North American shore birds: Population declines or shifting distributions? *Journal of Avian Biology* **38**, 73–82.
- Beer, C. (1961). Incubation and nest building behaviour of black-headed gulls. I: Incubation behaviour in the incubation period. *Behaviour* **18**, 62–105.
- Bejder, L., Fletcher, D. & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour* **56**, 719–725.
- Bejder, L., Dawson, S.M. & Harraway, J.A. (1999). Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* **15**, 738–750.
- Bejder, L. & Dawson, S. (2001). Abundance, residency and habitat utilisation of Hector's dolphins (*Cephalorhynchus hectori*) in Porpoise Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **35**, 277–287.
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C. & Krützen, M. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* **20**, 1791–1798.
- Bèland, P., DeGuise, S., Girard, C., Lagacè, A., Martineau, D., Michaud, R., Muir, D.C.G., Norstrom, R.J., Pelletier, E., Ray, S. & Shugart, L.R. (1993). Toxic compounds and health and reproductive effects in St. Lawrence beluga whales. *Journal of Great Lakes Research* **19**, 766-775.
- Benoit-Bird, K.J. & Au, W.W.L. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *The Journal of the Acoustical Society America* **125**, 125–137.
- Best, P.B. (1979). Social organization in sperm whales, *Physeter macrocephalus*. In *Behaviour of Marine Mammals*. New York: Plenum Press, pp 227–289
- Bigg, M. (1982). An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island,

- British Columbia. *Report of the International Whaling Commission* **32**, 655–666.
- Bigg M. A., Olesiuk P. F., Ellis G. M., Ford J. K. B. & Balcomb K. C. (1990) Social organisation and geology 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**, 383–405.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., ... Costa, D.P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90.
- Böning, C. W., Dispert, A., Visbeck, M., Rintoul, S. & Schwarzkopf, F. U. (2008). The response of the Antarctic Circumpolar Current to recent climate change. *Nature Geoscience* **1**, 864–869.
- Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002). Ucinet for Windows: Software for social network analysis. Harvard: Analytical Technologies.
- Bradbury, J.W. & Vehrencamp, S.L. (1998). *Principles of Animal Communication*, 2nd edition. Sunderland: Sinauer Associates.
- Bradfield, K. (2004). Photographic identification of individual Archey's frogs, *Leiopelma archeyi*, from natural markings. Wellington: Department of Conservation.
- Bradford, A.L., Wade, P.R., Weller, D.W., Burdin, A.M., Ivashchenko, Y. V., Tsidulko, G. A. & Vanblaricom, G.R. (2006). Survival estimates of western gray whales. *Marine Ecology Progress Series* **315**, 293–307.
- Bradford, A.L., Weller, D.W., Wade, P.R., Burdin, A.M. & Brownell, R.L. (2008). Population abundance and growth rate of western gray whales *Eschrichtius robustus*. *Endangered Species Research* **6**, 1–14.
- Bradford, J.M. (1972). Systematics and ecology of New Zealand central east coast plankton sampled at Kaikōura. Bulletin: *New Zealand Department of Scientific and industrial Research* **207**, 1–8.
- Bradford, J.M., Cranfield, H.J. & Michael, K.P. (1991). Phytoplankton biomass in relation to the surface hydrography of southern New Zealand and possible effects on the food chain.

- Brownie, C. & Robson, D.S. (1983). Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly-Seber model. *Biometrics* **39**, 437–453.
- Buckland, S., Anderson, D.R., Burnham, K.P., Laake, J.L. (1993). *Distance sampling: estimating abundance of biological populations*. London: Chapman and Hall.
- Burnham, K.P. & Anderson, D.R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. In *Model Selection and Multimodel Inference*. Burnham, K.P. & Anderson, D.R. (eds). New York: Springer, pp 149–205
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**, 23–35.
- Caci, G., Biscaccianti, A.B., Cistrone, L., Bosso, L., Garonna, A. P. & Russo, D. (2013). Spotting the right spot: Computer-aided individual identification of the threatened
- Cairns, S.J. & Schwager, S.J. (1987). A comparison of association indices. *Animal Behaviour* **35**, 1454–1469.
- Caldwell, K.D., Caldwell, M.C. & Rice, D.W. (1966). Behaviour of sperm whales, *Physeter catodon*. In *Whales, dolphins and porpoises*. Norris, K.S. (ed). Berkley: University of California Press, pp 677–717.
- Cameron, E.Z., Setsaas, T.H. & Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences* **106**, 13850–13853.
- Cantor, M., Wedekin, L.L., Daura-Jorge, F.G., Rossi-Santos, M.R. & Simões-Lopes, P.C. (2012). Assessing population parameters and trends of Guiana dolphins (*Sotalia guianensis*): An eight-year mark-recapture study. *Marine Mammal Science* **28**, 63–83.
- Caswell, H., Fujiwara, M. & Brault, S. (1999). Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Science* **96**, 3308–3313.
- Cerchio, S. (1998). Estimates of humpback whale abundance off Kauai, 1989 to 1993:

- Evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. *Marine Ecology Progress Series* **175**, 23–34.
- Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., Watson, R. & Pauly, D. (2012). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **3**, 254–258.
- Childerhouse, S.J., Dawson, S.M. & Slooten, E. (1995). Abundance and seasonal residence of sperm whales at Kaikōura, New Zealand. *Canadian Journal of Zoology* **73**: 723–731.
- Childerhouse, S.J., Dawson, S.M. & Slooten, E. (1996). Stability of fluke marks used in individual photoidentification of male sperm whales at Kaikōura, New Zealand. *Marine Mammal Science* **12**, 447–451.
- Chiswell, S.M. (1996). Variability in the Southland Current, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **30**, 1–17.
- Chiswell, S.M. & Schiel, D.R. (2001). Influence of along-shore advection and upwelling on coastal temperature at Kaikōura Peninsula, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **35**, 307–317.
- Chiyo, P.I., Archie, E.A., Hollister-Smith, J.A., Lee, P.C., Poole, J.H., Moss, C.J. & Alberts, S.C. (2011). Association patterns of African elephants in all-male groups : the role of age and genetic relatedness. *Animal Behaviour* **81**, 1093–1099.
- Christal, J. & Whitehead, H. (1997). Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. *Marine Mammal Science* **13**, 59–69.
- Christal, J., Whitehead, H. & Lettevall, E. (1998). Sperm whale social units: variation and change. *Canadian Journal of Zoology* **76**, 1431–1440.
- Clark, K.J., Nissen, E.K., Howarth, J.D., Hamling, I.J., Mountjoy, J.J., Ries, W.F., Jones, K., Goldstien, S., Cochran, U.A., Villamor, P., Hreinsdóttir, S., Litchfield, N.J., Mueller, C., Berryman, K.R. & Strong, D.T. (2017). Highly variable coastal deformation in the 2016 $M_w7.8$ Kaikōura earthquake reflects rupture complexity along a transpressional plate boundary. *Earth and Planetary Science Letters* **474**, 334–344.
- Clark, W. & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical*

Population Biology **75**, 45–75.

Clarke, R., Aguayo, A. & Paliza, O. (1980). Pregnancy rates of sperm whales in the southeast Pacific between 1959 and 1962 and in comparison with those from Paita, Peru between 1975 and 1977. *Report of the International Whaling Commission (Special Issue)* **2**, 151–158.

Clarke, R. & Paliza, O. (1988). Intraspecific fighting in Sperm Whales. *Report of the International Whaling Commission* **38**, 235–241.

Clutton-Brock, T. & Sheldon, B.C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution* **25**, 562–573.

Coakes, A.K. & Whitehead, H. (2004). Social structure and mating system of sperm whales off northern Chile. *Canadian Journal of Zoology* **82**, 1360–1369.

Conn, P.B., Gorgone, A.M., Jugovich, A.R., Byrd, B.L. & Hansen, L.J. (2011). Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *The Journal of Wildlife Management* **75**, 569–579.

Connor, R.C. (2000). Group living in whales and dolphins. In: *Cetacean Societies: Field Studies of Dolphins and Whales*. Mann, J., Connor, R.C., Tyack, P.T. & Whitehead, H. (eds). Chicago and London: the University of Chicago Press, pp 199–218.

Connor, R.C., Mann, J., Tyack, P.L. & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology and Evolution* **13**, 228–232.

Cooke, J. (1986). A review of some problems relating to the assessment of sperm whale stocks, with reference to the western North Pacific. *Report of the International Whaling Commission* **36**, 187–190.

Cormack, R.M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**, 429–438.

Costa, P.A.S. & Fernandes, F.C. (1993). Seasonal and spatial changes of cephalopods caught in the Cabo Frio (Brazil) upwelling ecosystem. *Bulletin of Marine Science* **52**, 751–759.

Crawshaw, P.G. & Quigley, H.B. (1991). Jaguar spacing, activity and habitat use in a

- seasonally flooded environment in Brazil. *Journal of Zoology* **223**, 357–370.
- Croze, H. (1974). The Seronera bull problem: The elephants. *African Journal of Ecology* **12**, 1–27.
- Cunningham, S.J. & Castro, I. (2011). The secret life of wild brown kiwi: studying behaviour of a cryptic species by direct observation. *New Zealand Journal of Ecology* **35**, 209–219.
- Davies, R.. (2002). Hypothesis testing when a nuisance parameter is present only under the alternative: Linear model case. *Biometrika* **89**, 484–489.
- Dawson, S.M. (1991). Clicks and communication: The behavioural and social contexts of Hector's dolphin vocalizations. *Ethology* **88**: 265–276.
- Dawson, S.M. (2000). Building the “CETOS” directional hydrophone.
<http://whaledolphintrust.org.nz/wp-content/uploads/Building-Directional-HPs.pdf>
- Dawson, S.M, Chessum, C., Hunt, P. & Slooten, E. (1995). An inexpensive, stereophotographic technique to measure sperm whales from small boats. *Report of the International Whaling Commission* **45**, 431–436.
- Dawson, S.M., Wade, P., Slooten, E. & Barlow, J. (2008). Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. *Mammal Review* **38**, 19–49.
- De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A. & Clark, M.R. (2010). Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2783–2792. Department of Conservation. (2013). 2013 Code of conduct for minimising acoustic disturbance to marine mammals for seismic survey operations. Wellington: Department of Conservation.
- Department of Conservation. (2014). Te Korowai o te tai ō marokura: Kaikōura marine management area. Wellington: Department of Conservation.
- Douglas, L.A., Dawson, S.M. & Jaquet, N. (2005). Click rates and silences of sperm whales at Kaikōura, New Zealand. *The Journal of the Acoustical Society America* **118**, 523–529.
- Dufault, S., Whitehead, H. & Dillon, M. (1999). An examination of the current knowledge of the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. *Journal of*

- Efron, B. & Gong, G. (1983). A leisurely look at the bootstrap, the jackknife, and cross-Validation. *The American Statistician*. **37**, 36–48.
- Evans, P.G. & Raga, J. (eds). (2001). *Marine Mammals: Biology and Conservation*, 1st edition. New York: Springer US.
- Fais, A., Lewis, T.P., Zitterbart, D.P., Álvarez, O., Tejedor, A. & Aguilar Soto, N. (2016). Abundance and distribution of sperm whales in the canary islands: Can sperm whales in the archipelago sustain the current level of ship-strike mortalities? *PLoS One* **11**, 1–16.
- Fearnbach, H., Durban, J., Parsons, K. & Claridge, D.E. (2012). Photographic mark–recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications* **22**, 1689–1700.
- Field, J.C., Francis, R.C. & Aydin, K. (2006). Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography* **68**, 238–270.
- Forsythe, J.W., Walsh, L.S., Turk, P.E. & Lee, P.G. (2001). Impact of temperature on juvenile growth age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. *Marine Biology* **138**, 103–112.
- Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., Ginneken, A. Van & Croft, D.P. (2012). Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. *Animal Behaviour* **83**, 731–736.
- Fox, S., Foisy, I., De La Parra Venegas, R., Galván Pastoriza, B.E., Graham, R.T., Hoffmayer, E.R., Holmberg, J. & Pierce, S.J. (2013). Population structure and residency of whale sharks *Rhincodon typus* at Utila, Bay Islands, Honduras. *Journal of Fish Biology* **83**, 574–587.
- Frantzis, A. & Alexiadou, P. (2008). Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. *Canadian Journal of Zoology* **86**, 62–75.
- Freeman, D.J., MacDiarmid, A.B. & Taylor, R.B. (2009). Habitat patches that cross marine

- reserve boundaries: Consequences for the lobster *Jasus edwardsii*. *Marine Ecology Progress Series* **388**, 159–167.
- Friedlaender, A., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D. & Read, A.J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series*. **317**, 297–310.
- Gallo-Reynoso, J.P., Egado-Villarreal, J. & Martined-Villalba, G.L. (2011). Reaction of fin whales *Balaenoptera physalus* to an earthquake. *Bioacoustics*. **20**, 317–330.
- Gaskin, D.E. (1973). Sperm whales in the western south pacific. *New Zealand Journal of Marine and Freshwater Research* **7**, 1–20.
- Gaskin, D.E. & Cawthorn, M.W. (1967). Diet and feeding habits of the sperm whale (*Physeter Catodon L.*) in the Cook Strait region of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **1**, 156–179.
- Gero, S., Engelhaupt, D. & Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioural Ecology and Sociobiology* **63**, 143–151.
- Gero, S., Gordon, J. & Whitehead, H. (2015). Individualized social preferences and long-term social fidelity between social units of sperm whales. *Animal Behaviour* **102**, 15–23.
- Gero, S. & Whitehead, H. (2016). Critical decline of the eastern Caribbean sperm whale population. *PLoS One* **11**, 1–11.
- Gill, J.A., Norris, K. & Sutherland, W.J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* **97**, 265–268.
- Ginsberg, J.R. & Young, T.P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour* **44**, 377–379.
- Goldenberg, S.Z., de Silva, S., Rasmussen, H.B., Douglas-Hamilton, I. & Wittemyer, G. (2014). Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*. *Animal Behaviour* **95**, 111–119.

- Gordon, J. (1987). Sperm whale groups and social behavior observed off Sri Lanka. *Report of the International Whaling Commission* **37**, 205–217.
- Gordon, J., Leaper, R., Hartley, F. & Chappell, O. (1992). Effects of whale-watching vessels on the surface and underwater acoustic behaviour of sperm whales off Kaikōura, New Zealand. *Science and Research Series* **52**, 1–64.
- Gormley, A. (2002). Use of mark-recapture for estimating the abundance of four marine mammal species in New Zealand: A thesis submitted in partial fulfilment for the degree of Master of Science in Marine Science at the University of Otago, Dunedin, New Zealand.
- Gormley, A.M., Dawson, S.M., Slooten, E. & Bräger, S. (2005). Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* **21**, 204–216.
- Gowans, S., Whitehead, H., Arch, J.K. & Hooker, S.K. (2000). Population size and residency patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia. *Journal of Cetacean Research and Management* **2**, 201–210.
- Grady, D. (1982). *The Perano whalers of Cook Strait: 1911 – 1964*. Wellington: A.H. and A.W. Reed Ltd.
- Growcott, A., Miller, B., Sirguy, P., Slooten, E. & Dawson, S. (2011). Measuring body length of male sperm whales from their clicks: The relationship between inter-pulse intervals and photogrammetrically measured lengths. *The Journal of the Acoustical Society America* **130**, 568.
- Guerra, M., Hickmott, L., van der Hoop, J., Rayment, W., Leunissen, E., Slooten, E. & Moore, M. (2017). Diverse foraging strategies by a marine top predator: Sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon. *Deep-Sea Research Part I* **128**, 98–108.
- Hammond, P.S. (1986). Estimating the size of naturally marked whale populations using capture-recapture techniques. *Report of the International Whaling Commission (Special Issue)* **8**, 253–282.
- Hammond, P.S. (1990). Capturing whales on film - Estimating cetacean population

- parameters from individual recognition data. *Mammal Review* **20**, 17–22.
- Hammond, P.S. (2002). Assessment of marine mammal population size and status. In *Marine Mammals: Biology and Conservation*, 1st edition. Evans, P.G. & Raga, J. (eds.). New York: Springer US, pp 269–291.
- Hammond, P.S., Mizroch, S. a. & Donovan, G. (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**, 113–118.
- Hartman, K.L., Visser, F. & Hendriks, A.J.E. (2008). Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units. *Canadian Journal of Zoology* **306**, 294–306.
- Hayes, M.A., Cryan, P.M. & Wunder, M.B. (2015). Seasonally-dynamic presence-only species distribution models for a cryptic migratory bat impacted by wind energy development. *PLoS One* **10**, 1–20.
- Heath, R.A. (1976). Oceanic circulation in the head of the Hikurangi trench, East Coast, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **10**, 651–674.
- Hinde, R.A. (1976). Interactions, relationships and social structure. *Man* **11**, 1–17.
- Horwood, J.W. (1980). Comparative efficiency of catcher boats with and without Asdic in Japanese pelagic whaling fleets. *Report of the International Whaling Commission (Special Issue)* **22**, 45–249.
- Hoyt, E. (2007). *A Blueprint for Dolphin and Whale Watching Development*. Washington, DC: Humane Society International.
- Huffard, C.L., Caldwell, R.L., Deloach, N., Gentry, D.W., Humann, P., Moore, B., Ross, R., Uno, T. & Wong, S. (2008). Individually unique body color patterns in octopus (*Wunderpus photogenicus*) allow for photoidentification. *PLoS One* **3**, 1–5.
- Huggins, R.M. (1991). Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* **47**, 725–732.
- Hurvich, C.M. & Tsai, C.L. (1989). Regression and time series model selection in small samples. *Biometrika* **76**, 297–307.

- Jackson, G.D. (2001). Confirmation of winter spawning of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Chatham Rise region of New Zealand. *Polar Biology* **24**, 97–100.
- Jacobson, J.K., Massey, L. & Gulland, F. (2010). Fatal ingestion of floating net debris by two sperm whales (*Physeter macrocephalus*). *Marine Pollution Bulletin* **60**, 765–767.
- Janik, V.M. & Thompson, P.M. (1996). Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science* **12**, 597–602.
- Jaquet, N., Dawson, S. & Douglas, L. (2001). Vocal behavior of male sperm whales: Why do they click? *The Journal of the Acoustical Society America* **109**, 2254–2259.
- Jaquet, N., Dawson, S. & Slooten, E. (2000). Seasonal distribution and diving behaviour of male sperm whales off Kaikōura: foraging implications. *Canadian Journal of Zoology* **78**, 407–419.
- Jaquet, N. & Gendron, D. (2002). Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. *Marine Biology* **141**, 591–601.
- Jaquet, N., Gendron, D. & Coakes, A. (2003). Sperm whales in the Gulf of California: Residency, movements, behavior and the possible influence of variation in food supply. *Marine Mammal Science* **19**, 545–562.
- Jaquet, N., Whitehead, H. & Lewis, M. (1996). Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. *Marine Ecology Progress Series* **145**, 1–10.
- Jarman, P.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* **48**, 215–267.
- Johnson, A., Salvador, G., Kenney, J., Robbins, J., Kraus, S., Landry, S. & Clapham, P. (2005). Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science* **21**, 635–645.
- Johnston, D.R., Rayment, W., Slooten, E. & Dawson, S.M. (2017). A time-based method for defining associations using photo-identification. *Behaviour* **154**, 1029–1050.

- Jolly, G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration- stochastic model. *Biometrika* **52**, 225–247.
- Jung, S., Pang, I., Lee, J., Choi, H. & Cha, H. (2013). Latitudinal shifts in the distribution of exploited fishes in Korean waters during the last 30 years: A consequence of climate change. *Reviews in Fish Biology and Fisheries* **24**, 443–462.
- Kaplan, M.B., Mooney, T.A., McCorkle, D.C. & Cohen, A.L. (2013). Adverse effects of ocean acidification on early development of squid (*Doryteuthis pealeii*). *PLoS One* **8**, 1–10.
- Karczmarski, L., Würsig, B., Gailey, G., Larson, K.W. & Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: Social grouping and population structure. *Behavioural Ecology* **16**, 675–685.
- Kato, H. (1984). Observations on tooth scars on the head of male sperm whale, as an indication of intra-sexual fightings. *Scientific Reports of the Whales Research Institute* **35**, 39–46.
- Katona, S., Baxter, B., Brazier, O., Kraus, S.D., Perkins, J. & Whitehead, H. (1979). Identification of humpback whales by fluke photographs. In *Behavior of Marine Animals*. Winn, H. & Olla, B. (eds) . Boston: Springer, pp 33-44.
- Kellner, J.B., Tetreault, I., Gaines, S.D. & Nisbet, R.M. (2007). Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications* **17**, 1039–1054.
- Kelly, M.J. (2001). Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. *Journal of Mammology* **82**, 440–449.
- Kendall, W.L. (1990). The Robust design for capture-recapture studies: Analysis using Program MARK. *International Wildlife Management Congress*, 357–360.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997). Estimating temporary emigration using capture-recapture data with Pollock’s Robust Design. *Ecology* **78**, 563–578.
- Kennedy, A.S., Zerbini, A.N., Vasquez, O.V., Gandilhon, N., Clapham, P.J. & Adam, O. (2013). Local and migratory movements of humpback whales Atlantic Ocean. *NRC Research Press* **18**, 9–18.

- Kluijver, H. (1951). The population ecology of the great tit *Parus m. major* L. *Ardea* **39**, 1–135.
- Knowlton, A.R., Hamilton, P.K., Marx, M.K., Pettis, H.M. & Kraus, S.D. (2012). Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: A 30 yr retrospective. *Marine Ecology Progress Series* **466**, 293–302.
- Kock, K.H., Purves, M.G. & Duhamel, G. (2006). Interactions between cetacean and fisheries in the Southern Ocean. *Polar Biology* **29**, 379–388.
- Kompanje, E. & Reumer, J. (1995). Strandings of male sperm whales *Physeter macrocephalus* Linnaeus, 1758 in Western Europe between October 1994 and January 1995. *Deinsea* **2**, 89–94.
- Kraus, S.D., Brown, M.W., Caswell, H., Clark, C.W., Fujiwara, M., Hamilton, P.K., ... Rolland, R.M. (2005). North Atlantic Right Whales in Crisis. *Science* **309**, 561–562.
- Kruskal, J.B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* **29**, 1–27.
- Kuningas, S., Similä, T. & Hammond, P.S. (2014). 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**, 1277–1291.
- Kutner, M., Nachtsheim, C., Neter, J. & Li, W. (2005). Building the regression model III: Remedial measures. In *Applied Linear Statistical Models*. New York: McGraw-Hill/Irwin Series, pp 421–480.
- Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S. & Podestà, M. (2001). Collisions between ships and whales. *Marine Mammal Science* **17**, 35–75.
- Lebreton, J., Burnham, K., Clobert, J. & Anderson, D. (1992). Modeling survival and testing biological hypotheses using marked animals : A unified approach with case studies. *Ecological Monographs* **62**, 67–118.
- Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J. & Howard, P.M. (2002). Social structure and residency in aggregations of male sperm whales. *Canadian Journal of Zoology* **80**, 1189–1196.

- Limpert, E., Stahel, W.A. & Abbt, M. (2001). Log-normal distributions across the sciences: Keys and clues. *Bioscience* **51**, 341–352.
- van der Linde, M. (2009). Long-term monitoring of sperm whales in Kaikōura , New Zealand: Data management, abundance, and population Dynamics: A thesis submitted for the degree of Master of Science at the University of Otago, Dunedin, New Zealand.
- Lockyer, C. (1981). Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. *Food and Agricultural Organisation of the United Nations Fisheries Series No. 53*, 489–504.
- Loery, G., Nichols, J.D. & Hines, J.E. (1997). Capture-recapture analysis of a wintering black-capped chickadee population in Connecticut, 1958-1993. *The Auk* **114**, 431–442.
- Lusher, A.L., McHugh, M. & Thompson, R.C. (2013). Occurrence of microplastics in the gastrointestinal tract of pelagic and demersal fish from the English Channel. *Marine Pollution Bulletin* **67**, 94-99.
- Lusseau, D. (2005). Residency pattern of bottlenose dolphins *Tursiops* spp. in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series* **295**, 265–272.
- Lusseau, D. & Bejder, L. (2007). The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment. *International Journal of Comparative Psychology* **20**, 228–236.
- Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I. & Møhl, B. (2002). Sperm whale sound production studied with ultrasound time/depth-recording tags. *The Journal of Experimental Biology* **205**, 1899–1906.
- Magalhães, S., Prieto, R., Silva, M.A., Gonçalves, J., Afonso-dias, M. & Santos, R.S. (2002). Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. *Aquatic Mammals* **28**, 267–274.
- Manly, B. (1994). *Multivariate Statistical methods*. New York: Chapman and Hall.
- Manly, B. (1995). A note on the analysis of species co-occurrences. *Ecology* **76**, 1109–1115.
- Mann, J. & Würsig, B. (2014). Observing and quantifying cetacean behavior in the wild: Current problems, limitations, and future directions. In *Primates and Cetaceans: Field*

- Research and Conservation of complex Mammalian Societies*. Yamagiwa, J. & Karczmarski, L. (eds). Japan: Springer, pp 335–344.
- de la Mare, W.K. (2014). Estimating relative abundance of whales from historical Antarctic whaling records. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 106–119.
- Markowitz, T., Richter, C., Gordon, J., Sagnol, O., Markowitz, W., Macaulay, J., Isojunno, S. & Fernandes, M. (2011). Effects of Tourism on the Behaviour of Sperm Whales Inhabiting the Kaikōura Canyon. Report submitted to Department of Conservation.
- Martin, P. & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*, 3rd edition. Cambridge: Cambridge University Press.
- Mate, B., Mesecar, R. & Lagerquist, B. (2007). The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. *Deep-Sea Research II* **54**, 224–247.
- Matthews, J.N., Steiner, L. & Gordon, J. (2001). Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-ID data from the Azores (1987-1995). *Journal of Cetacean Research and Management* **3**, 219–226.
- McConkey, S.D., Heinrich, S., Lallas, C., Mcconnell, H. & McNally, N. (2002). Pattern of immigration of New Zealand sea lions *Phocarctos hookeri* to Otago, New Zealand: Implications for management. *Australian Mammalogy* **24**, 107–116.
- Miller, B.S, Dawson, S. & Vennell, R. (2013a). Underwater behavior of sperm whales off Kaikōura, New Zealand, as revealed by a three-dimensional hydrophone array. *The Journal of the Acoustical Society America* **134**, 2690.
- Miller, B.S., Growcott, A., Slooten, E. & Dawson, S.M. (2013b). Acoustically derived growth rates of sperm whales (*Physeter macrocephalus*) in Kaikōura, New Zealand. *The Journal of the Acoustical Society America* **134**, 2438.
- Mills, J.A., Yarrall, J.W., Bradford-Grieve, J.M., Uddstrom, M.J., Renwick, J.A. & Merilä, J. (2008). The impact of climate fluctuation on food availability and reproductive performance of the planktivorous red-billed gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology* **77**, 1129–1142.
- Ministry for Primary Industries. (2015). NABIS. <http://www.nabis.govt.nz/>

- Ministry for Primary Industries & Department of Conservation. (2013). *Implementing key components of the Kaikōura Marine Strategy*.
- Mobley, J. & Herman, L. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology* **63**, 762-772.
- Møhl, B. (2001). Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study. *Journal of Comparative Physiology A* **187**, 335–340.
- Moore, S.E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy* **89**, 534–540.
- Moore, J.E. & Barlow, J.P. (2014). Improved abundance and trend estimates for sperm whales in the eastern North Pacific from Bayesian hierarchical modeling. *Endangered Species Research* **25**, 141–150.
- Moore, M.J. & Zerbini, A.N. (2017). Dolphin blubber/axial muscle shear: implications for rigid trans-dermal intra muscular tracking tag trauma in whales. *Journal of Experimental Biology* **220**, 3717–3723.
- Moreno, A., Pierce, G.J., Azevedo, M., Pereira, J. & Santos, A.M.P. (2012). The effect of temperature on growth of early life stages of the common squid *Loligo vulgaris*. *Journal of the Marine Biological Association of the United Kingdom* **92**, 1619–1628.
- Morrison, T.A. & Bolger, D.T. (2014). Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. *Oryx* **48**, 613–621.
- Moss, C.J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* **255**, 145–156.
- Moss, C. & Poole, J. (1983). Relationships and social structure of African elephants. In *Primate Social Relationships: an Intergrated Approach*. Hinde, R. (ed). Oxford: Blackwell Scientific, pp 315–325.
- Muggeo, V.M.R. (2003). Estimating regression models with unknown break-points. *Statistics in Medicine* **22**, 3055–3071.
- Muggeo, V.M.R. (2017). Package “segmented”. *Biometrika* **58**, 525–534.

- Mullan, A.B., Wratt, D.S. & Renwick, J.A. (2001). Transient Model Scenarios of Climate Changes for New Zealand. *Weather and Climate* **21**: 3–33.
- Munger, L.M., Camacho, D., Havron, A., Campbell, G., Calambokidis, J., Douglas, A. & Hildebrand, J. (2009). Baleen whale distribution relative to surface temperature and zooplankton abundance off Southern California. *California Cooperative Oceanic Fisheries Investigations Report* **50**, 115–168.
- Murphy, R.J., Pinkerton, M.H., Richardson, K.M., Grieve, J.M.B., Boyd, W., Pinkerton, M.H., Richardson, K.M. & Grieve, J.M.B. (2010). Phytoplankton distributions around New Zealand derived from SeaWiFS remotely - sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research* **35**, 343–362.
- Neves, D., Sobral, P., Ferreira, J.L. & Pereira, T. (2015). Ingestion of microplastics by commercial fish off the Portuguese coast. *Marine Pollution Bulletin* **101**, 119-126.
- New Zealand Marine Sciences Society. (2014). Submission on the Kaikōura (Te Tai-o-Marokura) Marine Management Bill. <http://nzms.org/assets/Documents/statement-release/NZMSS-submissionKaikōura-MM-Bill07042014-FINAL.pdf>
- NIWA. (2017a). Massive mudslides in Kaikōura Canyon destroy seabed life. News release: www.niwa.co.nz/news/massive-mudslides-in-Kaikōura-canyon-destroy-seabed-life
- NIWA. (2017b). Kaikōura Canyon shows early signs of ecosystem recovery. News release: www.niwa.co.nz/news/Kaikōura-canyon-shows-early-signs-of-ecosystem-recovery
- O’Dor, R.K. & Webber, D.M. (1986). The constraints on cephalopods: why squid aren’t fish. *Canadian Journal of Zoology*. **64**, 1591–1605.
- Ohsumi, S. (1983). Population assessment of Baird’s beaked whales in the waters adjacent to Japan. *Report of the International Whaling Commission* **33**, 633–641.
- Oke, P.R. & England, M.H. (2004). Oceanic response to changes in the latitude of the Southern Hemisphere subpolar westerly winds. *Journal of Climate* **17**, 1040–1054.
- Papastavrou, V., Smith, S. & Whitehead, H. (1989). Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galápagos Islands. *Canadian Journal of Zoology* **67**,

199–206.

- Paul, L.J. (2002). A description of the New Zealand fisheries for the two groper species, hapuku. *New Zealand Fisheries Assessment Report 2002/13*. Wellington: Ministry of Fisheries.
- Pecl, G.T. & Jackson, G.D. (2008). The potential impacts of climate change on inshore squid: Biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries* **18**, 373–385.
- Pecl, G.T., Steer, M.A. & Hodgson, K.E. (2004). The role of hatchling size in generating the intrinsic size-at-age variability of cephalopods: Extending the Forsythe Hypothesis. *Marine and Freshwater Research* **55**, 387–394.
- Peñaloza, C.L., Kendall, W.L. & Langtimm, C. (2014). Reducing bias in survival under nonrandom temporary emigration. *Ecological Applications* **24**, 1155–1166.
- Perry, A., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005). Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915.
- Pinzone, M., Budzinski, H., Tasciotti, A., Ody, D., Lepoint, G., Schnitzler, J., Scholl, G., Thomé, J.P., Tapie, N., Eppe, G. & Das, K. (2015). POPs in free-ranging pilot whales, sperm whales and fin whales from the Mediterranean Sea: Influence of biological and ecological factors. *Environmental Research* **142**, 185–196.
- Pledger, S., Pollock, K.H. & Norris, J.L. (2003). Open capture-recapture models with heterogeneity: I: Cormack-Jolly-Seber model. *Biometrics* **59**, 786–794.
- Poharama, A., Henley, M., Smith, A., Fairweather, J.R. & Simmons, D.G. (1998). The impact of tourism on the Māori community in Kaikōura. Report No. 7, Tourism Recreation Research and Education Centre, Lincoln University, New Zealand.
- Pollock, K. (1982). A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management* **46**, 752–757.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**, 3–97.
- Pradel, R. (1996). Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.

- Quintana-Rizzo, E., Mann, D. & Wells, R. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America* **120**: 1671–1683.
- Ramirez, P. (1989). Captura de cachalots en Paita: 1976-1981. *Boletín de Lima* **63**, 80–88.
- Rayment, W., Dawson, S., Slooten, E., Bräger, S., Fresne, S. Du & Webster, T. (2009). Kernel density estimates of alongshore home range of Hector's dolphins at Banks Peninsula, New Zealand. *Marine Mammal Science* **25**, 537–556.
- Read, A.J. (2008). The looming crisis: interactions between marine mammals and fisheries. *Journal of Mammalogy* **89**, 541–548.
- Reijnders, P.J.H., Borrell, A., Van Franeker, J.A. & Aguilar, A. (2018). Pollution. In: *Encyclopedia of Marine Mammals*, 3rd edition. Würsig, B., Thewissen, J.G.M. and Kovacs, K.M. (eds). London: Elsevier, pp 746-753.
- Rendell, L.E. & Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society London* **270**, 225–231.
- Rhineland, M.Q. & Dawson, S.M. (2004). Measuring sperm whales from their clicks: Stability of interpulse intervals and validation that they indicate whale length. *The Journal of the Acoustical Society America* **115**, 1826.
- Rice, D. (1989). Sperm Whale *Physeter macrocephalus* Linnaeus, 1758. In *Handbook of Marine Mammals Vol 4: River Dolphins and the Large Toothed Whales*. Ridgway, S. & Harrison, R. (eds). London: Academic Press, pp 177–233.
- Richard, K.R., Dillon, M.C., Whitehead, H. & Wright, J.M. (1996). Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. *Proceedings of the National Academy of Sciences U. S. A.* **93**, 8792–8795.
- Richards, M. (1966). Activity measured by running wheels and observation during the oestrous cycle, pregnancy and pseudopregnancy in the golden hamster. *Animal Behaviour* **14**, 450–458.
- Richardson, W. J., Greene, C. R. Jr., Malme, C. I. & Thomson, D. H. (1995). *Marine*

mammals and noise. San Diego: Academic Press.

- Richter, C.F., Dawson, S.M. & Slooten, E. (2003). Sperm whale watching off Kaikōura, New Zealand: Effects of current activities on surfacing and vocalisation patterns. *Science for Conservation* 219. Wellington: Department of Conservation.
- Richter, C., Dawson, S.M. & Slooten, E. (2006). Impacts of commercial whale watching on male sperm whales at Kaikōura, New Zealand. *Marine Mammal Science* 22, 46–63.
- Rochman, C. (2015). The complex mixture, fate and toxicity of chemicals associated with plastic debris in the marine environment. In *Marine Anthropogenic Litter*. Bergmann, M., Gutow, L. & Klages, M. (eds). Berlin: Springer, pp 117-140.
- Rødland, E.S. & Bjørge, A. (2015). Residency and abundance of sperm whales (*Physeter macrocephalus*) in the Bleik Canyon, Norway. *Marine Biology Research* 11, 974–982.
- Roemmich, D. & McGowan, J. (1995). Climatic warming and the decline of zooplankton in the California current. *Science* 267, 1324–1326.
- Ruiz-Cooley, R.I., Gendron, D., Aguíñiga, S., Mesnick, S. & Carriquiry, J.D. (2004). Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Marine Ecology Progress Series* 277, 275–283.
- Schaffar, A., Madon, B., Garrigue, C. & Constantine, R. (2009). Avoidance of whale watching boats by humpback whales in their main breeding ground in New Caledonia, *SC/61/WW6*, International Whaling Commission, pp 9.
- Schiel, D., Lilley, S., South, P. & Coggins, J. (2016). Decadal changes in sea surface temperature, wave forces and intertidal structure in New Zealand. *Marine Ecology Progress Series* 548, 77–95.
- Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffman, M., Katariya, V., ... Young, B.E. (2008). The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* 322, 225–230.
- Schwartz, O.A., Armitage, K.B. & Vuren, D. Van. (1998). A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology London* 246, 337–346.
- Seber, G.A.F. (1965). A note on the multiple-recapture census. *Biometrika* 52, 249–259.

- Seber, G.A.F. (1982). *The Estimation of Animal Abundance and Related Parameters*, 2nd edition. UK: Charles and Griffin and Company Limited.
- Seber, G.A.F. & Wild, C.J. (1989). Multiphase and spline regressions. In *Nonlinear Regression*. Hoboken: John Wiley & Sons Inc, pp 433–490.
- Seibel, B.A. (2015). Environmental physiology of the jumbo squid, *Dosidicus gigas* (d’Orbigny, 1835) (Cephalopoda: Ommastrephidae): Implications for changing climate. *American Malacological Bulletin* **33**, 1–13.
- Shapiro, S.S. & Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika* **52**, 591–611.
- Shaw, A.G.P. & Vennell, R. (2000). Variability of water masses through the Mernoo Saddle , South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **34**, 103–116.
- Shea, K. (1998). Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* **13**, 371–375.
- Shears, N.T. & Bowen, M.M. (2017). Half a century of coastal temperature records reveal complex warming trends in western boundary currents. *Scientific Reports* **7**, 1–9.
- Silva, M.A., Magalhães, S., Prieto, R., Santos, R.S. & Hammond, P.S. (2009). Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series* **392**, 263–276.
- Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gómez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**, 148–154.
- Slooten, E., Dawson, S.M. & Whitehead, H. (1993). Associations among photographically identified Hector’s dolphins. *Canadian Journal of Zoology* **71**, 2311–2318.
- Smith, S.C. & Whitehead, H. (1993). Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. *Canadian Journal of Zoology* **71**, 1991–1996.
- Sousa-Lima, R.S & Clark, C.W. (2008). Modeling the effect of boat traffic on the fluctuation

- of humpback whale singing activity in the Arbrothos National Marine Park, Brazil. *Canadian Acoustics* **36**, 174-181.
- Spiller, C. & Bhowmick, S. (2014). Whale Watch Kaikōura - New Zealand. In *Global Entrepreneurship: Case Studies of Entrepreneurial Firms Operating around the World*. New York: Taylor and Francis, pp 137–151 .
- Steiner, L., Lamoni, L., Acosta Plata, M., Jensen, S., Lettevall, E. & Gordon, J. (2012). A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. *Journal of the Marine Biological Association of the United Kingdom* **92**, 1751–1756.
- de Stephanis, R., Giménez, J., Carpinelli, E., Gutierrez-Exposito, C. & Canadas, A. (2013) As a main meal for sperm whales: Plastics debris. *Marine Pollution Bulletin* **69**, 206-214.
- Stevick, P.T., Allen, J., Clapham, P.J., Friday, N., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsbøll, P.J., Sigurjónsson, J., Smith, T.D., Øien, N. & Hammond, P.S. (2003). North Atlantic humpback whale abundance and rate of increase four decades after protection from whaling. *Marine Ecology Progress Series* **258**, 263–273.
- Stevick, P.T., Palsbøll, P.J., Smith, T.D., Bravington, M. V & Hammond, P.S. (2001). Errors in identification using natural markings: rates, sources, and effects on capture – recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1861–1870.
- Sutton, P.J.. (2003). Variability in the Southland Current, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **37**, 645–652.
- Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G., Notarbartolo di Sciara, G., Wade, P. & Pitman, R.L. (2008). *Physeter macrocephalus*. *IUCN Red List Threat. Species*. <http://www.iucnredlist.org/details/41755/0>.
- Taylor, B.L. & Gerrodette, T. (1993). The uses of statistical power in conservation biology : the vaquita and northern spotted owl. *Conservation Biology* **7**, 489–500.
- Te Korowai. (2007). Kaikōura coastal marine values and uses: A characterisation report. http://www.teamkorowai.org.nz/docs/Kaikōura_Coastal_Marine_Values_and_Uses_Second_edition_Low_Res.pdf

- Thompson, P.M. & Wheeler, H. (2008). Photo-ID-based estimates of reproductive patterns in female harbor seals. *Marine Mammal Science* **24**, 138–146.
- Tillman, M.F. & Breiwick, J.M. (1977). Estimates of stock size for exploitable North Pacific male sperm whales. *Report of the International Whaling Commission*. **27**, 180–185.
- Treilibs, C.E., Pavey, C.R., Hutchinson, M.N. & Bull, C.M. (2016). Photographic identification of individuals of a free-ranging, small terrestrial vertebrate. *Ecology and Evolution* **6**, 800–809.
- Tseng, Y.P., Huang, Y.C., Kyle, G.T. & Yang, M.C. (2011). Modeling the impacts of cetacean-focused tourism in Taiwan: Observations from cetacean watching boats: 2002–2005. *Environmental Management* **47**, 56–66.
- Tynan, C.T. (1998). Redistributions of cetaceans in the southeast Bering Sea relative to anomalous oceanographic conditions during the 1997 El Niño. *Marine Ecology Progress Series* **173**, 5–7.
- Tynan, C.T., Ainley, D.G., Barth, J.A., Cowles, T.J., Pierce, S.D. & Spear, L.B. (2005). Cetacean distributions relative to ocean processes in the northern California Current System. *Deep Sea Research Part II* **52**, 145–167.
- Übernickle, K., Tschapka, M. & Kalko, E.K.V. (2012). Selective eavesdropping behaviour in three neotropical bat species. *Ethology* **119**
- Uozumi, Y. (1998). Fishery biology of arrow squids, *Nototodarus gouldi* and *N. sloanii*, in New Zealand waters. *Bulletin of the National Research Institute of Far Seas Fisheries* **35**, 1–111.
- Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R.S., Berggren, P., Durban, J., Eguchi, T., Rayment, W. & Hammond, P.S. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science* **31**, 298–321.
- Verborgh, P. (2009). Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* **25**, 523–536.
- Vidal, E. A. G., DiMarco, F., Wormuth, J. & Lee, P. (1996). Influence of temperature and

- food availability on survival, growth and yolk utilization in hatchling squid. *Bulletin of Marine Science* **71**, 915–931.
- Vidal, E. A. G., Haimovici, M. & Hackbart, V.C.S. (2010). Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. *ICES Journal of Marine Science* **67**, 1346–1352.
- Vine, S.J., Crowther, M., Lapidge, S., Dickman, C.R., Mooney, N., Piggott, M.P. & English, A. (2009). Comparison of methods to detect rare and cryptic species: A case study using the red fox (*Vulpes vulpes*). *Wildlife Research* **36**, 436–446.
- Watkins, W.A. & Schevill, W.E. (1977). Sperm whale codas. *The Journal of the Acoustical Society of America* **62**, 1485–1490.
- Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T. & Tyack, P.L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology* **75**, 814–825.
- Weilgart, L. & Whitehead, H. (1993). Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Canadian Journal of Zoology* **71**, 744–752.
- Weilgart, L. & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology* **40**, 277–285.
- Weilgart, L., Whitehead, H., Payne, K., Weilgart, L., Whitehead, H. & Payne, K. (1996). A Colossal Convergence. *American Scientist* **84**, 278–287.
- Whale Watch Kaikōura. (2017). Who we are. <https://www.whalewatch.co.nz/our-people/who-we-are/>.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–139.
- White, G.C., Burnham, K.P. & Anderson, D.R. (2001). Advanced feature of Program Mark. In *Integrating People and Wildlife for a Sustainable Future*: 368–377. Fields, R. (ed.). Bethesda: The Wildlife Society.
- Whitehead, H. (1993). The behaviour of mature male sperm whales on the Galápagos Islands

- breeding grounds. *Canadian Journal of Zoology* **71**, 689–699.
- Whitehead, H. (1995). Investigating structure and temporal scale in social organisations using identified individuals. *Behavioural Ecology* **6**, 199–208.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioural Ecology and Sociobiology* **38**, 237–244.
- Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour* **53**, 1053–1067.
- Whitehead, H. (1999). Testing association patterns of social animals. *Animal Behaviour* **57**, 26–29.
- Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications : Application to sperm whales. *Ecology* **82**, 1417–1432.
- Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series* **242**, 295–304.
- Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean*. London: The University of Chicago Press.
- Whitehead, H. (2008a). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago: The University of Chicago Press.
- Whitehead, H. (2008b). Precision and power in the analysis of social structure using associations. *Animal Behaviour* **75**, 1093–1099.
- Whitehead, H. (2009a). Sperm whale: *Physeter macrocephalus*. In: *Encyclopedia of Marine Mammals*, 2nd edition. Würsig, B., Thewissen, J.G.M & Kovacs, K.M. (eds). Oxford: Elsevier Science and Technology Books, pp 1091–1097.
- Whitehead, H. (2009b). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology* **63**, 765–778.
- Whitehead, H. & Arnbohm, T. (1987). Social organization of sperm whales off the Galápagos Islands, February–April 1985. *Canadian Journal of Zoology*. **65**, 913–919.
- Whitehead, H., Christal, J. & Dufault, S. (1997). Past and distant whaling and the rapid

- decline of sperm whales off the Galápagos Islands. *Conservation Biology* **11**, 1387–1396.
- Whitehead, H & Dufault, S. (1999) Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. *Advances in the Study of Behaviour* **28**, 33–74.
- Whitehead, H. & Gordon, J.C.D. (1986). Methods of obtaining data for assessing and modeling sperm whale populations which do not depend on catches. *Report of the International Whaling Commission (Special Issue)* **8**, 149–165.
- Whitehead, H., Papastavrou, V. & Smith, S.C. (1989). Feeding success of sperm whales and sea-surface temperature off the Galápagos Islands. *Marine Ecology Progress Series* **53**, 201–203.
- Whitehead, H., Silver, R. & Harcourt, P. (1982). The migration of humpback whales along the northeast coast of Newfoundland. *Canadian Journal of Zoology*. **60**, 2173–2179.
- Whitehead, H., Waters, S. & Lyrholm, T. (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology* **29**, 385–389.
- Whitehead, H. & Weilgart, L.S. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**, 275–296.
- Würsig B. (1986) Delphinid foraging strategies. In: *Dolphin cognition and behaviour: a comparative approach*. Schusterman R. J., Thomas J. A. & Wood F. G. (eds). New Jersey: Lawrence Erlbaum Associates, pp 347–359.
- Würsig, B. & Jefferson, T. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission (Special Issue)* **12**, 43–52.
- Würsig, B. & Pearson, H.C. (2014). Dusky dolphins: Flexibility in foraging and social strategies. In: *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies*. Yamagiwa, J. & Karczmarski, L. (eds). Japan: Springer, pp 25–42.
- Xitco, M.J., & Roitblat, H.L. (1996). Object recognition through eavesdropping, Passive

echolocation in bottlenose dolphins. *Animal Learning and Behaviour* **24**, 355–365.

Young, A. (2018). Prime Minister Jacinda Ardern bans new offshore oil and gas exploration in New Zealand. News release:

https://www.nzherald.co.nz/news/article.cfm?c_id=1&objectid=12030723.

Zeidberg, L.D. & Robison, B.H. (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences U. S. A.* **104**, 12948–12950.

Zemsky, V.A., Berzin, A.A., Mikhalev, Y.A. & Tormosov, D.D. (1995). Soviet Antarctic pelagic whaling after WWII: Review of actual catch data. *Report of the International Whaling Commission* **46**, 131–135.