The role of long-term diet change in the decline of the New Zealand sea lion population

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ABSTRACT

The New Zealand sea lion (*Phocarctos hookeri*) is an endangered pinniped endemic to New Zealand (Wilkinson, Burges et al. 2003). Declared “nationally critical” under the NZ threat classification system and “vulnerable in decline” by IUCN, they have shown a 49% decline in pup production since 1995 (Chilvers, Wilkinson et al. 2010). I investigated the role of long-term changes in diet on the population ecology of NZ sea lions. I was interested in the role played by long-term changes in diet into the observed decline of the sea lion population. My study is set apart from others in that it spans 13 years of routine sampling, and represents one of the longest timelines of diet data for any pinniped species. I used scat and regurgitate samples from New Zealand sea lions that were collected at the Auckland Islands between the summer of 1995/1996 and 2012/2013. I identified 11 main prey types from hard parts including otoliths, beaks and other diagnostic bones. In scats these main prey types were opalfish (*Hemerocoetes spp.*), rattail (Macrouridae), red cod (*Pseudophycis bachus*), octopus (*Octopus sp.*) and arrow squid (Ommastrephidae), Ling (*Genypterus blacodes*), smallscaled cod (*Paranotothenia sp.*), hoki (*Macruronus novaezelandiae*), triplefin (*Tripterygiidae*), fur seal (*Arctocephalus forsteri*) and giant octopus (*Enteroctopus zealandicus*). Main prey types found in regurgitates were similar but there was a higher proportion of cephalopods than in scat samples. When assessing long-term trends in occurrence of main prey species I found that smaller prey types such as opalfish and *Octopus* sp. have been increasing in the diet over time, while larger species hoki and giant octopus have been decreasing. The ratio of fish:cephalopods in NZ sea lion diet has also been decreasing with time, possibly indicating an overall reduction in diet quality. I used catch per unit effort as a proxy for prey availability in the environment and compared this to frequency of occurrence (%FO) of main prey types over time. The best models for functional response by sea lions to increased prey availability were those that incorporated random variation among years, suggesting that abundance of prey species is not the only variable affecting intake of prey by NZ sea lions. Resource competition or habitat destruction imposed by fisheries could restrict intake by sea lions, or force prey shifts to species not commercially harvested. Lastly, I investigated age-related survival and breeding probability of NZ sea lions with reference to the amount of main prey species in the diet over time. Models were run to test the relationship between each prey type, and breeding and survival probabilities over time. Survival probability is best explained by the null model, indicating that survival is not significantly affected by the amount of any one prey type in the diet. Smallscaled cod and hoki have the best predictive capacity after the null; hoki was correlated with an increase in survival for all age groups, while smallscaled cod predicted an increase in survival for all age classes except individuals over 15 years. In contrast, breeding probability is better explained by the amount of hoki and ling in the diet than by the null model. Consequently, the estimated finite rate of increase (λ) of the sea lion population rises with increased hoki in the diet. λ

was estimated to be < 1 (population decline) under observed conditions (hoki found in 0-15% of scats depending on year), but λ was extrapolated to become >1 (population increase) if hoki were sufficiently abundant to be found in 35% of scats, a level that may have been reached historically (pre 1988). Similarly, λ was extrapolated to become > 1 if ling was found in > 30% of scats. The greater effect of prey types on breeding over survival makes biological sense when resources may be limiting population growth. Adult female NZ sea lions limited by prey availability may have enough food to survive but may choose not to invest in energetically expensive breeding. This would buffer the observed effect on survival since we would re-sight individuals that are alive but perhaps not in body condition to breed. If valuable prey stocks like ling and hoki continue to decline in the diet we could also see a significant impact on survival. Hoki has begun to recover but stock levels are still low in the Auckland Islands' region (MPI 2013).

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1. CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

New Zealand sea lion pup showing ear tags on Enderby Island.

1.1 GENERAL INTRODUCTION

Conservation biology is broadly the study of biodiversity, with the aim to protect species, habitats and ecosystems from the rate of extinction and collapse of ecosystems; that we as humans are oft times responsible for. Threats to species are often multi-pronged but we can see common themes throughout the literature. Jared Diamond describes an "Evil Quartet" of habitat destruction, overkill, introduced species, and secondary extinctions (Caughley 1994), whereas Edward O. Wilson prefers the acronym "HIPPO", standing for habitat destruction, invasive species, pollution, human overpopulation, and over-harvesting (Wilson 2003). In this thesis I indirectly investigate human-induced competition as a driver of population decline via the study of diet, which could fall under the banner of habitat destruction.

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) is an endangered pinniped endemic to New Zealand (Wilkinson, Burges et al. 2003). Declared "nationally critical" under the NZ threat classification system and "vulnerable in decline" by IUCN, they have the smallest population estimate of any otariid with only about 12,000 individuals (Baker, Chilvers et al. 2010; IUCN 2012; MPI 2012). The current distribution of NZ sea lions is at the margin of their historical range, with 71-87% of pup production occurring on the Auckland islands (Chilvers, Wilkinson et al. 2007; MPI 2012). Despite being protected under the NZ Marine Mammal Protection Act 1978, the NZ sea lion has shown a 49% decline in pup production since 1995 (Chilvers, Wilkinson et al. 2010). One hypothesis for this decline is that the population is being limited by prey availability, as a result of competition with commercial fisheries (Meynier 2009). The main objective of this thesis was to investigate the role of long term changes in diet in the population ecology of NZ sea lions.

The aim of this chapter is to introduce the thesis in a wider context by 1) reviewing current methods used to study the diet of marine mammals, and 2) compiling dietary data on NZ sea lions at Enderby Island, and subsequently Otago Peninsula from research prior to this work. An outline of this thesis is presented at the end of this chapter.

1.2 BACKGROUND NZ SEA LIONS

The New Zealand (NZ) sea lion is one of the two species of otariids breeding in NZ. The species was once widely distributed around NZ main islands, as suggested by remains found in archaeological sites (Childerhouse and Gales 1998). Subsistence hunting and commercial harvest of seal skin and oil resulted in a drastic reduction of the population and its range. The breeding range of the NZ sea lion is now limited to the Sub-Antarctics, except for a small number of breeding females in the south of NZ (Stewart Island and Otago Peninsula) (Chilvers 2008). Despite some effort to protect the species since the 1890s, it failed to recolonize its former range (Childerhouse and Gales 1998). The Auckland

Islands (50° 30’ S, 166° E) represent ~70% of the total pup production of the species (1500 pups in 2009) (Robertson and Chilvers 2011) and host a population of ~12000 individuals (estimated from a Bayesian population model in 2009) (Breen, Fu et al. 2010). Since 1995, pup production diminished by 49% at the Auckland Islands (Chilvers, Wilkinson et al. 2010). Population monitoring identified several epizootics that significantly impacted pup numbers (Castinel, Duignan et al. 2007; Castinel, Grinberg et al. 2007), and a decline in the number of breeding adults (Robertson and Chilvers 2011). The possible causes affecting the number of adults at the Auckland Islands are reviewed in Robertson and Chilvers (2011). This endemic species has been updated “vulnerable in decline” in 2008 by the International Union for the Conservation of Nature (IUCN 2012) and “nationally critical” in 2010 under the NZ Threat Classification System(Baker, Chilvers et al. 2010).

Like any other otariid, sea lions depend on land to rest, breed, give birth, raise their young, and moult. They rely on the marine environment for their food by making regular foraging trips from their colony. Information on diet and foraging behaviour allows to understand the functional role of these top predators in the marine environment, and to determine the boundaries of their ecological niche to implement optimal management measures (Bowen 1997). In the case of the endangered NZ sea lion, it is a conservation priority to assess their foraging range and diet to determine the direct (e.g. bycatch) and indirect (e.g. trophic) overlap with the commercial fisheries (DoC 2009). Since 1995, the Department of Conservation has organised summer trips to the Auckland Islands every year to collect valuable information on demographic parameters, pathogens affecting individuals, and diet (scat collection and sampling of adipose tissues such as milk and blubber) (Wilkinson, Burges et al. 2003; Chilvers 2008). Foraging studies have predominantly focused on lactating females (Chilvers, Robertson et al. 2005; Chilvers and Wilkinson 2008; Chilvers 2009). Information on diet and foraging are sparse for other segments of the population and outside summer time. Dietary methods used to assess the diet of NZ sea lions are diverse, from the identification of gut hard remains to the determination of stable isotopes and fatty acids from sea lion tissues (Lalas 1997; Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010; Augé, Lalas et al. 2011). The dietary time frame represented by these different methods also varies from several days (e.g. hard part analysis) to the whole life of the animal (e.g. stable isotopes from whiskers or teeth). Additionally, NZ sea lions are opportunistic feeders and seem to prey on what is available in their foraging environment, inducing variation in their diet through time following changes in prey availability (Meynier, Morel et al. 2010). With different reproductive constraints, energetic needs, and diving abilities, dietary variation between males and females is also to be expected. Consequently, with all these factors influencing dietary data (methods, season, segment of the population), one may find it difficult to identify the main dietary characteristics of the NZ sea lion. This review attempts to clarify the information available on the diet of NZ sea lions by summing up dietary data by season and by segment of the population (lactating females, non-lactating females, males, and juveniles) and compare the dietary methods used.

Approximately 70% of the total pup production occurs at the Auckland Islands, distributed at three breeding colonies: Enderby Island (15% of total pup production), Dundas Island (52%), and Figure of Eight (3%) (Chilvers, Wilkinson et al. 2007). Most of the diet samples collected in the past two decades were from Enderby Island. Campbell Island hosts 29% of total pup production, but no dietary sample is available due to challenges of sample collection (Meynier 2012). Outside the sub Antarctics, Otago Peninsula (south east South Island) is the only colony that has been regularly studied (Lalas 1997; McConkey, McConnell et al. 2002; Augé, Chilvers et al. 2011; Augé, Lalas et al. 2011).

1.3 DIETARY METHODS: A BRIEF REVIEW

Studying the diet of otariids is challenging as most of the feeding events occur below the sea surface. Therefore, researchers rely on indirect methods such as the analyses of hard parts in stomach contents, faeces and regurgitates. These methods are named “traditional”, in contrast to “new” methods such as DNA extraction from faeces, FA signatures of body lipids, or stable isotopes in various tissues, which have been increasingly used in the last two decades. None of these methods are perfect, and each has advantages and disadvantages which are summarised in Table 1-1. There are recent reviews in the literature that present these methods in more details (Tollit, Pierce et al. 2010; Bowen and Iverson 2013). I do not mention DNA extraction from faeces here as it has not been tested for NZ sea lions.

1.3.1 Hard prey analysis

Analysis of prey hard parts from faecal samples is a common technique for estimating the diet of pinnipeds (Prime and Hammond 1990; Thompson, Pierce et al. 1991; Cherel, Guinet et al. 1997; Pierce and Santos 2003; Littnan, Arnould et al. 2007; Trites and Calkins 2008; Casaux, Carlini et al. 2009) since faeces are easy to collect on haul out sites, can be collected without disturbance on animals, and their analysis is inexpensive (Tollit, Pierce et al. 2010). However, estimating the proportion and the size of prey from hard part remains is not straightforward, and includes well recognised biases such as differential rates of food passage and digestion (Pierce and Boyle 1991; Bowen 2000). Sagittal otoliths of fish and lower beaks of cephalopods are the most commonly used structures to identify such prey (Pierce and Boyle 1991). However, otoliths are subject to erosion by digestive juices and can be completely digested (Jobling and Breiby 1986; Murie and Lavigne 1986; Jobling 1987; Dellinger and Trillmich 1988). Thus fish consumed would not necessarily be recovered in faeces, especially if it is a species with small otoliths which digest faster than large ones (Pierce and Boyle 1991; Christiansen, Gamst Moen et al. 2005). In contrast, beaks are not affected by digestion (Harvey 1989; Gales and Cheal 1992; Tollit, Steward et al. 1997), but large beaks tend to accumulate in stomachs, as they do not pass through the pylorus (Bigg and Fawcett 1985; Yonezaki, Kiyota et al. 2003). Therefore, the proportion of fish with fragile otoliths and the proportion of cephalopods with large beaks are underestimated in scat analysis.

Table 1-1: Pros and cons from Meynier (2009) of the main methods used to examine the diet of marine mammals. The term "regression" means the relationship between hard part measurement and length or mass of individual prey. HP refers to hard parts; IS to isotopic signatures; TL to trophic levels; FA to fatty acids; and QFASA to quantitative fatty acid signature analysis (Meynier 2009).

Methods	**Impact on individual**	**Dietary time period**	**Identification of prey**	**Prey size estimate**	**Mass percentage (needed in food consumption models)**	**Requirements**	**Expected limitations**
Faeces, hard remains	No	Few days	Yes (reference collection needed)	Yes (length regressions needed)	Yes (mass regressions needed)	- Reference collection - regressions - correction factors for loss and size reduction of HP	- individual characteristics generally unknown - differential prey digestion and retention (prey without HP not represented, prey with fragile HP underestimated, large beaks underestimated)
Regurgitates, hard remains	No	Few days	Yes (reference collection needed)	Yes (length regressions needed)	Yes (mass regressions needed)	- Reference collection - regressions	- individual characteristics generally unknown - differential prey digestion and retention (overestimation of large HP)
Stomachs, hard remains	Extreme (from dead animals)	Few days	Yes (reference collection needed)	Yes (length regressions needed)	Yes (mass regressions needed)	- Reference collection - regressions	- differential prey digestion and retention (prey with fragile HP underestimated, opposite with large HP or beaks) - information from dead animals only, so representation of whole population uncertain
Stable isotopes	Moderate (capture or dart projector)	Days to years depending on tissue	No but possible estimation if IS of prey	No	No	- IS from lower TL	- limited in estimation of prey species - interpretation of comparison between different environments and time-scales difficult without IS from lower TL
FA signatures	Moderate (capture or dart projector)	Weeks to months	Possible if QFASA (prey FA library needed)	No	Possible if QFASA (prey FA library needed)	- prey FA library and calibration coefficients for QFASA	- time frame not known precisely - FA metabolism not known precisely and can be underestimated - species not in prey FA library are not identified

Stomach analysis is hampered by biases similar to scat analysis (Pierce and Boyle 1991; Pierce, Santos et al. 2004). The majority of the studies on stomach contents rely on opportunistic sampling of dead animals from stranding or by-catch events (Meynier, Stockin et al. 2008; Mintzer, Gannon et al. 2008; Meynier, Mackenzie et al. 2009). However, the diet of dead animals is not necessarily representative of the feeding of the population (Pierce and Boyle 1991; Pierce, Santos et al. 2004). The recent diet of animals incidentally captured in commercial fisheries can be biased towards the targeted species of that fishery. If an animal ingested food just before death, fresh material (named the fresh fraction) will be found in the stomachs among digested prey from previous feeding events (named digested fraction) (Pusineri, Magnin et al. 2007). If the fresh fraction is analysed alone, it can provide an unbiased estimate of actual intake because all items are ingested over a restricted period and are not subject to digestion. However, as mentioned earlier, the fresh fraction from by-caught animals tends to be biased towards the targeted species of the fishery. In the digested fraction, beaks tend to accumulate (Bigg and Fawcett 1985; Yonezaki, Kiyota et al. 2003), although some are regurgitated (Fea and Harcourt 1997; Childerhouse, Dix et al. 2001; Hume, Hindell et al. 2004).

1.3.2 Stable isotope analysis

Diet information provided from faeces and stomach contents is limited to what the animal ate in the days preceding sampling. Biochemical methods such as stable isotopes and fatty acid (FA) analyses allow the inference of a broader diet picture by analysing tissues which retain assimilated nutrients for up to years (*e.g.,* stable isotopes in bones) and overcome the biases related to hard part recovery and digestion. Stable isotope analysis can give an insight into the trophic relations and sources of feeding of consumers since there is a predictable relationship between the isotopic composition of a predator and its prey. The isotopes generally used are those of nitrogen (^{14}N and ^{15}N) and carbon (^{12}C and ^{13}C). $\delta^{15}N$ of a consumer is typically enriched by 3-4‰ relative to its diet (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Hobson, Schell et al. 1996), hence $\delta^{15}N$ serves as an indicator of the trophic level. In contrast, $\delta^{13}C$ varies little along the food chain, and is mainly used to determine the sources of primary productivity at the base of the trophic web (Fry and Sherr 1984; Peterson and Fry 1987). $\delta^{13}C$ varies between benthic and pelagic ecosystems - more enriched in benthic prey (Hobson, Schell et al. 1996; Hobson, Sease et al. 1997), and with latitude - more depleted towards higher latitude (Rau, Sweeney et al. 1982). Therefore, $\delta^{15}N$ and $\delta^{13}C$ provide a two-dimensional estimate of the dietary niche occupied by a consumer relative to other consumers in an ecosystem. They cannot however provide quantitative estimates of the species composition of diets.

1.3.3 Fatty acid analysis

Although FA analysis is categorised a “new method” to infer the diet, the first attempt at comparing FAs from the blubber of a marine mammal and its prey occurred in the 1960s (Ackman, Burgher et al. 1963). Ackman *et al.* (1963) compared FAs in seal blubber oil with FAs in menhaden and herring oils, and found some similarities between FA compositions. Since, several experimental studies showed that the FA composition of depot fat is influenced by dietary FA composition (Xu, Hung et al. 1993; Cha and Jones 1996; Kirsch, Iverson et al. 1998; Kirsch, Iverson et al. 2000). Consequently, FA analysis has been increasingly popular in dietary studies on marine mammals in the last twenty years, as it can overcome biases related to hard part analysis (Iverson, Frost et al. 1997; Dahl, Lydersen et al. 2000; Walton, Henderson et al. 2000; Lea, Hindell et al. 2002; Olsen and Grahl-Nielsen 2003; Staniland and Pond 2005; Budge, Springer et al. 2008; Tucker, Bowen et al. 2008). The underlying principle of this method is the assumption that long-chain FAs in prey species are conservatively deposited into the adipose tissue of a monogastric predator, thus providing an integrated record of dietary intake over time. However fatty acid composition is affected by deposition from dietary lipids, differing metabolism, and de novo biosynthesis. Fatty acid metabolism may vary with nutritional and reproductive states of the animal making it difficult to infer differences in diet between animals of different states or gender (Meynier, Morel et al. 2008).

The most ambitious way to use FA analysis is to estimate proportions of prey by the comparison of prey and predator FAs *via* a mathematical model. This method is named quantitative FA signature analysis (QFASA), and was initiated by Iverson et al. (2004). QFASA is an optimisation model that requires information on the FA profiles of potential prey species and predator adipose tissues (e.g. blubber) and calibration coefficients that take into account the predator metabolism of ingested FAs. Sampling all potential prey for a given predator means a preliminary understanding of key species in an ecosystem, and of the predator’s foraging habit. Therefore, the potential prey library is generally built from diet information provided by traditional methods. Calibration coefficients are certainly the most challenging parameter to obtain for QFASA, as they are calculated from captive animals fed on a controlled diet for several months. Even if the pattern of deposition is similar among marine species for which long-term diet studies were carried out (Iverson, Field et al. 2004; Iverson, Springer et al. 2007; Nordstrom, Wilson et al. 2008; Rosen and Tollit 2012), the calibration coefficient for a particular FA seems to depend on the predator considered, or even on the meals eaten by the same predator (Rosen and Tollit 2012). This is an important drawback limiting the use of QFASA to species or gender for which calibration coefficients are available.

1.4 THE DIET OF NZ SEA LIONS

1.4.1 Auckland Islands - Summer

Females and males gather at breeding colonies at the end of November. Pupping peak occurs around Christmas and females make their first postpartum foraging trip (2 to 3 days) ~ 9 days after parturition (Chilvers, Robertson et al. 2007). This is the most critical time for lactating females as they have to produce a rich energy milk to sustain their pup growth (150g per day) (Chilvers, Robertson et al. 2007). The Department of Conservation conducts research on sea lions at Enderby Island over summer (beginning of December to end of February), and scat samples and regurgitates are collected weekly during this period. Although individual characteristics cannot be identified, most of the scats and regurgitates are likely to come from males, as most of the material is collected on the grassy sward where males rest. Females tend to stay on the beach with their pup where scat collection is difficult due to bird scavenging and high densities of animals (L. Chilvers, pers. comm.).

Childerhouse et al. (2001) analysed 142 scat and 64 regurgitate samples from the Auckland Islands, mostly Enderby Island between 1994 and 1997. The four most common prey species (>10% occurrence O) contributed to 73% of total abundance (%N): octopus (*Enteroctopus zelandicus*, 19%N), opalfish (*Hemerocoetes* species, 37%N), oblique-banded rattail (*Coelorhynchus aspercephalus,* 6%N), and hoki (*Macruronus novaezelandiae,* 11%N) (Childerhouse, Dix et al. 2001). The authors highlighted the underestimation of cephalopods in scats, and the reverse in regurgitates. The arrow squid (*Nototodarus sloanii*), which is commercially important in the region, totals 1%N only with a 9%O. Its contribution is likely underestimated in a sampling dominated by scat material such as in this study. Scat samples collected in austral summer between 1999 and 2013 (~1800 samples) have been analysed for my MSc project at Massey University.

Samples of blubber of 26 lactating females captured at Enderby Island in late January 2000 was analysed for fatty acids (FA). QFASA was applied by using a prey library of eight species (arrow squid, hoki, javelin fish (*Lepidorhynchus denticulatus)* representing the rattails, red cod (*Pseudophycis bachus)*, opalfish, Octopus, scampi (*Metanephrops challengeri)* representing the benthic crustaceans, and dogfish (*Squalus acanthias*). Calibration coefficients were calculated from captive juvenile Steller sea lions fed on herring (Rosen and Tollit 2012). Blubber FAs would represent the diet over the foraging trips made by females since parturition (end of December), ie ~ a month period. Hoki and rattails were the most important species by mass (25%M and 34%M respectively) (Meynier, Mackenzie et al. 2009). These results are not directly comparable with the scat samples (Childerhouse, Dix et al. 2001) considering the biases related to each method used and the fact that the diet was described in %N by one and in %M by the other. Also, the FA results from lactating females came from one year of sampling (year 2000). Young NZ sea lions have a restricted foraging range in summer compared to adults (Leung, Chilvers et al. 2013), a pattern consistent with the Australian sea lions (*Neophoca cinerea)* (Fowler, Costa et al. 2007). They also have a lesser capability of diving than the adults because of their lower mass. We would expect them to forage on prey other than deep-living species such as hoki and rattails. There are presently no diet samples available for juveniles or non-lactating females over summer. Some dietary information is however available in autumn for these two segments of the population, and could be extrapolated to summer time knowing the strong foraging site fidelity displayed by NZ sea lions (Chilvers 2008; Chilvers and Wilkinson 2008). Summer is the most critical season for NZ sea lions as it represents the first months of lactation when the pups are most dependent on their mothers. The diet information gathered so far in summer is limited to samples before 2000 (Childerhouse, Dix et al. 2001). The analysis of scat samples collected from 2000 to 2013 is of great value because it will give the only insight into the summer diet up until present time.

1.4.2 Auckland Islands - autumn

In austral autumn lactating NZ sea lion females alternate between nursing their pup and foraging at sea. Pups are believed to be completely weaned by the end of winter (Gales and Fletcher 1999). Males that stay at the breeding colonies during this period are non-territorial individuals. The southern arrow squid trawl fishery operates around the Auckland Islands shelf from February to June. By-catch of sea lions is reported on-board vessels with government observers (Chilvers 2008), and until 2010, carcasses were sent to Massey University for full necropsies. Diet studies over autumn are from these by-caught animals only, as no capture of sea lions was conducted to collect tissue samples during this season. Meynier and colleagues (2009) analysed the stomach contents and blubber FA of by-caught NZ sea lions of different gender and reproductive status from the years 1997 to 2006. The authors clearly differentiated a fresh and a digested fraction in the stomach contents. The fresh fraction, representing the food ingested before drowning, was obviously biased towards the commercial target species, arrow squid (79%M in the fresh fraction *vs* 18%M in the digested fraction). Thus, the digested fraction was believed to be the best representation of the diet of NZ sea lions from stomach contents. The common prey species found in the digested contents of both by-caught males and females were rattails (Macrouridae), opalfish, red cod, arrow squid and octopus (Meynier, Mackenzie et al. 2009). The contribution of opalfish in the diet was the only significant difference between genders (60%N in females *vs.* 15%N for non-territorial males). Hoki, the important commercial species with arrow squid, had a low occurrence (less than 10%) and low

%N but a significant contribution by mass due to large sizes ingested (1 ± 0.46 kg). The long-term diet of by-caught sea lions was estimated by QFASA from blubber FA, and consisted mostly of hoki (17% to 29%M depending on simulations), rattail (16% to 29%M), and arrow squid (23% to 30%M) (Meynier, Morel et al. 2010). Although stomach and blubber FA analyses are not directly comparable because they are associated with different time frames (several days *vs.* weeks to months), several points can be highlighted: The contribution by mass of octopus in the stomach contents is high (28%M), whereas it was estimated at only 2-3% with QFASA. This result is consistent with cephalopod beaks accumulating in the stomach, and then being overestimated with stomach analysis. Benthic crustaceans could be a significant part of NZ sea lions' diet, especially males (up to 38%M) according to QFASA. Traditional hard part analyses are not efficient to detect crustaceans because this taxon has no hard part resistant to digestion. QFASA estimated different diets between males and females based on different blubber FA profiles. However, because the role played by different rates of FA metabolism on the variation of the blubber FA is not known, it is currently difficult to make conclusions on the dietary differences between males and females (Meynier, Morel et al. 2010). Non-lactating and lactating females seem to have similar diets when estimated from stomach or FA analyses. Because female NZ sea lions are creatures of habits and tend to utilize the same foraging locations between and within seasons while lactating (Chilvers 2008; Chilvers and Wilkinson 2008), one would expect they behave similarly in years with no pup. The only available information on the diet of juveniles in autumn comes from stomach contents. By-caught juveniles of 3-4 years old fed on deep-sea fish such as the adults, therefore they must be able to forage deeper than 200 m, or dive only at night when most of the deep-sea fish such as rattails and hoki migrate vertically to the surface. Only diving records from juveniles could clarify these assumptions. Diving data from lactating NZ sea lions showed that they dive continually throughout the day (Chilvers, Wilkinson et al. 2006).

The diet of female sea lions showed year variation in their FA profiles, especially between the year 2000 and the pooled years 2005-06 (Meynier et al., 2010). These changes in the diet estimated by QFASA (hoki lower in 05 2006, and vice versa for squid) were in agreement with changes in prey availability through time (MPI 2013). QFASA has been used on captured females' blubber in January 2000, thus representing a dietary picture over early summer (Meynier et al., in prep), and on bycaught females' blubber from 2000 to 2006 representing a dietary picture over the end of summer-autumn (Meynier, Morel et al. 2010). Hoki and rattails, fish species living at depth >200 m, are key prey species throughout summer and autumn. There are no foraging data for autumn but the dietary results confirm that NZ sea lions are foraging at the edges of the Auckland Islands' shelf from the beginning of the lactation period to the end of autumn. Arrow squid had low %M (8%M) in the diet of females captured at Enderby in January 2000, but made a significant contribution for individual's by-caught the same year (30%M). Despite a possible overestimation of arrow squid from animals caught in the squid fishery, there are plausible ecological explanations for this seasonal difference in diet. The arrow squid stock at the Auckland Islands spawns around June-July on the shelf (MPI 2013). Juvenile squid migrate to offshore waters until they attain maturity (7 to 9 months of age) (Uozumi 1998), while mature squid migrate back to the shelf around February. Diet estimates are consistent with lactating females taking advantage of a greater abundance of arrow squid on the slope and shelf of the Auckland Islands in autumn.

1.4.3 Auckland Islands - Winter

In winter, lactating females continue to provide milk to their pups. However, feeding events are expected to be less frequent as the pups get more independent. This is confirmed by foraging data in the winters 1996 and 1997 from lactating females captured at Enderby Island, showing longer foraging trips in winter than in summer (5.5 days *vs.* 3 days) (Chilvers, Childerhouse et al. 2013). They had similar diving characteristics and utilised similar foraging areas compared to summer, although the winter foraging grounds were larger. Scat and regurgitates were collected at Enderby Island over the winters 2010 to 2012, and analysis of samples is on-going (Lalas & McConnel, unpublished data). This study would allow a comparison with scats and regurgitates collected in summer time for similar years. However, it is noteworthy that a scat sample collected in winter will not represent a whole foraging trip but only the last part of the trip, as this method represents a dietary window of a couple of days before collection, and winter foraging trips are more than 5 days long (Chilvers, Childerhouse et al. 2013).

1.4.4 Otago Peninsula

Although most breeding occurs in the sub Antarctic, NZ sea lions have begun to recolonize the Otago peninsula on mainland New Zealand over the past 50 years (McConkey, Lalas et al. 2002). A small breeding colony was established by a single female that gave birth to a pup at Otago peninsula in the summer 1993. Up to 2010, 45 pups had been born at the peninsula (Augé, Chilvers et al. 2011). From June 1991 to May 1992, 490 scats and 29 regurgitates coming from male NZ sea lions were collected on Papanui Beach, Otago peninsula (45°52'S, 170°44'E) (Lalas 1997). Barracouta (*Thyrsites atun)*, Jack mackerel (*Trachurus* sp.), and *Octopus maorum* had significant contributions both by number (5%N, 9%N and 5%N respectively) and by mass (25%M, 13%M, and 14% respectively). Ahuru (*Auchenoceros punctatus)* was the most numerous prey (23%N), but contributed little to the diet by mass (0.5%M). Jack mackerel was a seasonal prey caught only in summer and autumn, which correlates with the seasonal distribution of this fish species (Lalas 1997; Augé, Lalas et al. 2011). No deep-sea species was found in the remains, suggesting that males limited their foraging to the shelf.

Eighteen years after the study by Lalas (1997), sea lion research in the region focused on the foraging and feeding behaviour of female NZ sea lions at Otago Peninsula (Augé, Chilvers et al. 2011; Augé, Chilvers et al. 2011; Augé, Lalas et al. 2011). In this context, 571 scats and 110 regurgitates coming from females were collected from March to May 2008 and 2009. The autumn diet showed strong similarities with the male diet identified more than a decade before: barracouta and jack mackerel were the most consumed prey (30%M and 28%M), and no prey species living predominantly at depths >200 m was found (Lalas 1997; Augé, Lalas et al. 2011). This corroborates the results of satellite tracking of females that stayed on the continental shelf during autumn (Augé, Chilvers et al. 2011). The female NZ sea lions at the Otago peninsula are all benthic foragers, with larger deviation between individuals than the Auckland Islands (Augé, Chilvers et al. 2011). Otago females showed less specialisation, reflecting an environment with more abundant and higher quality food resources (Augé, Chilvers et al. 2011).

1.5 CONCLUSIONS

Studying the diet of otariids is difficult as most foraging behaviour occurs below the sea surface. None of the dietary methods reviewed here is perfect, and each has advantages and disadvantages (Table 1-1**)**. Dietary methods used to assess the diet of NZ sea lions are many and varied, from identification of hard remains in the digestive system to the determination of stable isotopes and fatty acids from sea lion tissues (Lalas 1997; Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010; Augé, Lalas et al. 2011). The dietary time-frame represented by these different techniques varies from days (e.g. hard part analysis) to the whole lifetime of the individual (e.g. stable isotopes from whiskers or teeth). Ontogenic, seasonal and location effects of diet were reviewed here in order to gain an overall view of the diet of NZ sea lions thus far. The analysis of scat samples collected from 2000 to 2013 is of great value because it will give the only insight into the summer diet up until present time. For the endangered NZ sea lion, it is a conservation priority to assess their foraging range and diet to determine the direct (e.g. bycatch) and indirect (e.g. trophic) overlap with the commercial fisheries (DoC 2009).

1.6 OUTLINE OF THE THESIS

This thesis is composed of five chapters: chapter 1 is the general introduction and literature review, chapters 2 to 4 are research chapters, and chapter 5 is the general discussion. Each chapter is mostly independent and written in a publication format. I was assisted by my co-authors (supervisors) but I designed the research, analysed the data and wrote the chapters. Since chapters 2 to 4 use hard part analysis of scats and regurgitates, there is some repetition which I have tried to keep to a minimum.

In **Chapter 2**: DIET OF NEW ZEALAND SEA LION OVER 13 YEARS AT THE AUCKLAND ISLANDS, NEW ZEALAND - I describe the overall dietary composition, investigate long-term annual changes in diet composition, and identify main prey types.

In **Chapter 3**: LONG-TERM TRENDS IN THE DIET OF NZ SEA LION AND FUNCTIONAL RESPONSE TO CHANGE IN PREY AVAILABILITY IN THE AUCKLAND ISLANDS -
I investigated the following 1) long-term trends in occurrence of main prey species in both scat and regurgitate samples, 2) long-term shifts in diet quality using contribution of fish and cephalopods to diet as a proxy, 3) patterns of occurrence of main prey species of NZ sea lion in relation to abundance in the environment, and 4) Type I or Type II functional response to changes in prey availability.

In **Chapter 4**: EFFECTS OF OCCURRENCE OF MAIN PREY TYPES IN THE DIET OF NEW ZEALAND SEA LIONS ON SURVIVAL AND BREEDING IN THE AUCKLAND ISLANDS - I investigate the relationship between the occurrence of main prey types in the diet, and age-related probability of survival and breeding in female NZ sea lions over time.

In **Chapter 5**: GENERAL DISCUSSION - I summarise the results of the research chapters and the main interpretations in terms of the long term feeding ecology and run on effects for conservation management. I also discuss future research that should be considered for the NZ sea lion.

2. CHAPTER 2

DIET OF NEW ZEALAND SEA LION OVER 13 YEARS AT THE AUCKLAND ISLANDS, NEW ZEALAND

Colony of New Zealand sea lions at Sandy Bay on Enderby Island.

2.1 INTRODUCTION

Studying the diet of animals allows us to better understand their habitat needs and possible impacts of human activities (McKenzie and Wynne 2008). Understanding sea lion diet and habitat use can help us to manage interactions with fisheries and mitigate impacts upon population viability (Augé, Lalas et al. 2011). The New Zealand sea lion (*Phocarctos hookeri*) is an endangered pinniped endemic to New Zealand (Wilkinson, Burges et al. 2003). Declared "nationally critical" under the NZ threat classification system and "vulnerable in decline" by IUCN, they have the smallest population estimate of any otariid with only about 12,000 individuals (Baker, Chilvers et al. 2010; IUCN 2012; MPI 2012). The current distribution of NZ sea lions is at the margin of their historical range, with 71-87% of pup production occurring on the Auckland islands (Chilvers, Wilkinson et al. 2007; MPI 2012). Despite being protected under the NZ Marine Mammal Protection Act 1978, the NZ sea lion has shown a 49% decline in pup production since 1995 (Chilvers, Wilkinson et al. 2010). One hypothesis of the cause of decline is that the population growth of the species is limited by the availability of suitable prey on the Auckland islands shelf (50°30'S, 166°E) and by direct and indirect impacts of the arrow squid fishery (Meynier 2009). The Arrow squid (*Nototodarus sloanii*) trawl fishery operates on the Auckland Island's shelf February through June each year (Gales 1995). Fisheries directly impact on sea lion population via incidental by-catch of foraging sea lions. Indirectly, competitive effects may also be important in the decline of this species since the commercial species arrow squid and hoki comprise part of the sea lions diet (Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009). Management efforts to date address direct interactions with fisheries in the form of by-catch, but not possible resource competition (Wilkinson, Burges et al. 2003; Meynier 2009). Other possible causes for the decline include disease epizootics, permanent dispersal and environmental change (Robertson and Chilvers 2011).

Previous studies have assessed diet of NZ sea lions by examining stomach contents of by-caught animals and fatty acids from blubber (Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010). Analysis of diet based on scat remains have also been conducted on the Otago peninsula (Lalas 1997; Augé, Lalas et al. 2011), Macquarie Island (McMahon, Holley et al. 1999), and in the Auckland islands between 1994 and 1997 (Childerhouse, Dix et al. 2001). Each method has its own biases, and gives information on diet over different time frames, from several days (e.g. hard part analysis) to whole lifespans (e.g. stable isotope analysis on bones) (Meynier 2009). Identification of prey hard parts in scats and regurgitations is non-invasive, low-cost and samples are easily collected. Identification of prey is usually based on otoliths for fish and beaks for cephalopods (Tollit, Heaslip et al. 2007), but identification of other unique structures for fish increases accuracy by detecting more prey items. Digestion of otoliths results in the proportion of large fish in the diet being overestimated since smaller otoliths are digested more readily (Browne, Laake et al. 2002). Using a combination of scats and regurgitates reduces bias when compared to analysis of scat samples alone (Lalas 1997).

Given the endangered status of the NZ sea lion, it is a conservation priority to assess their diet and possible overlap with commercial fisheries (DoC 2009). The diet of sea lions by-caught by fisheries from 2000-2006 were analysed by examining stomach contents (Meynier, Mackenzie et al. 2009). Here I examine scat samples, which helps to overcome bias inherent in samples from animals only by-caught in fishing nets. This dataset spans 13 years of routine sampling, and represents the longest timeline of diet data for any pinniped species. In this study. I determine the diet of sea lions based on the Auckland islands, during the summer of 1999/2000 through to 2012/2013, using undigested prey remains in scats and regurgitations. My aims were to; 1) describe diet composition and identify important prey types and 2) investigate long-term annual changes in diet.

2.2 METHODS

2.2.1 Study site and Sample collection

Scat and regurgitate samples were collected from different sites at the Auckland Islands. Most sites were located on Enderby Island, but also Dundas and some smaller islands (Figure 2-1). The main collection sites were Sandy Bay (SB) and South East Point (SEP), both located on Enderby Island. Only fresh, intact scat and regurgitate samples were collected. Samples were collected opportunistically and were not linked to individuals. In this study, I have scat and regurgitate samples from the summer of 1999/2000 to 2012/2013, with the exception of 2004/2005 which was lost. Collection was carried out through summer, usually from December to the end of February. The aim was to collect 10 scat samples per week at the main sites (SB and SEP) plus any regurgitate samples, but the numbers collected varied. In some years, no regurgitate samples were collected.

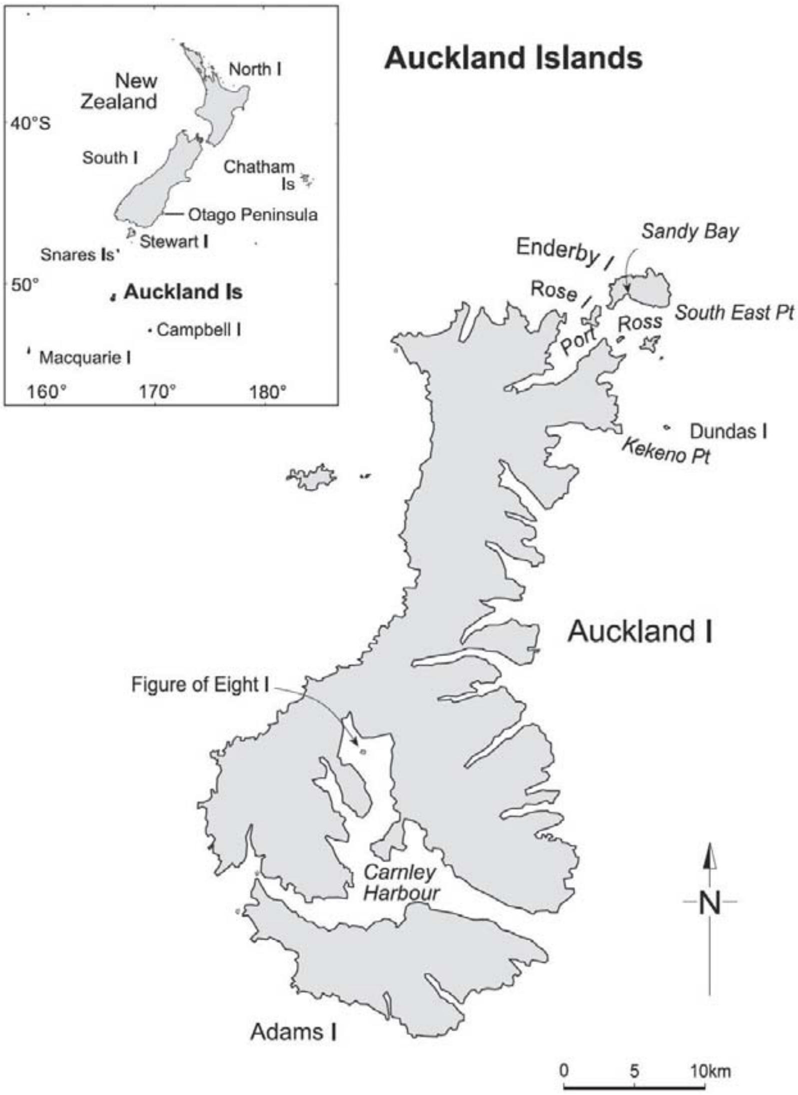

Figure 2-1: Auckland Islands' main breeding areas for NZ sea lions are in Sandy Bay on Enderby Island, Dundas Island and Figure of Eight Island in Carnley Harbour. Most scat and regurgitate sample collection was conducted at Sandy Bay. Inset is New Zealand mainland and sub-Antarctic showing Otago Peninsula, Stewart Island, Snares Islands, Auckland Islands and Campbell Island (Robertson and Chilvers 2011).

2.2.2 Sample processing

Samples were collected, stored and labelled in individual self-sealing bag or plastic bottles. Samples were soaked in a weak detergent solution for 12-36 h, then washed in running water and processed through a series of sieves of decreasing mesh size (smallest 0.5 mm). All hard parts remaining after sieving were removed and stored in water (Childerhouse, Dix et al. 2001). Samples were sorted and diagnostic hard parts removed in the laboratory at *Institute of Veterinary, Animal and Biomedical Sciences (*IVABS) at Massey University in Palmerston North, New Zealand. Whole and partial otoliths and fish bones were removed with tweezers and stored dried. Beaks were collected and stored in 70% ethanol. Crustacean, shark/ray and bird remains were noted but not stored.

2.2.3 Sample identification

Prey remains were identified using all diagnostic hard parts including fish otoliths, diagnostic bones (dentaries, premaxillaries, maxillaries, post-temporals, and hyomandibulars) and cephalopod beaks using a reference collection held at Massey University and published guides (Clarke 1986; Smale, Watson et al. 1995; McKenzie and Wynne 2008; Meynier, Mackenzie et al. 2009). Taxa with very similar beaks or otoliths were identified to the highest taxonomic level possible; however some otoliths and beaks show no or little specific difference. In such cases, the hard parts were attributed to the most abundant species occurring in the area where the sample was taken (Meynier, Mackenzie et al. 2009). For example, remains identified as belonging to Ommastrephidae are most likely arrow squid (*Nototodarus sloanii*) but could also be *Todarodes fillippovae*. Here I assume remains identified as Ommastrephidae are arrow squid. If more than one species belonging to the same genus was present in the area then they were grouped together for analysis. Opalfish (*Hemerocoetes* spp.), redbait (*Scopelosaurus* spp.), conger eel (*Bassanago* sp.), lanternfish (*Myctophid* sp.), smallscaled cod (*Paranotothenia* sp.), octopus (*Octopus* sp.) and *Teuthowenia* sp. were identified to genus level. Rattail (Macrouridae), Ommastrephidae, triplefin blennies (Tripterygiidae), hooked squid (Onychoteuthidae) and bobtail squid (Sepiolidae) were identified to family. Birds, crustaceans and sharks/rays were only identified as being in one of these taxa.

The occurrence of crustaceans was noted by recovery of exoskeletal remains which were considered to belong to one individual when found in a sample, although this is likely to be an underestimation (Childerhouse, Dix et al. 2001). Pinniped remains (i.e. fur, bones, skin) and seabird (i.e. bones, feathers, feet) found in samples were used for identification. Presence of pinniped or seabird remains in a sample was recorded as a single individual. Sea bird remains were noted but no attempt was made to identify to species level since they were seen only very rarely in this study. Pinniped remains are likely to be New Zealand fur seal (*Arctocephalus forsteri),* which is the only other type of pinniped inhabiting this area and are known prey species of New Zealand sea lion in this region (Childerhouse, Dix et al. 2001). Giant octopus were separated from smaller Octopus sp. for analysis.

In the laboratory, the minimum number of individuals (MNI) of each taxon in each sample was determined. For fish, the MNI was based on the number of otoliths, or jaw bones depending on the species. If less than 30 otoliths per taxon were found, left and right otoliths were sorted and the highest number was used for MNI. The same method applied for species with diagnostic jawbones (e.g. *Hemerocoetes* spp.). If more than 30, the total number was divided by 2. Otoliths that could not be identified to taxonomic group, usually due to extreme erosion, were recorded as unidentified (Kirkwood, Hume et al. 2008). The MNI of cephalopods was found by counting upper and lower beaks, whichever was higher (Pierce and Boyle 1991). Samples with only unidentifiable hard parts (e.g. non-unique vertebra, teeth, and scales) were recorded as containing a single individual (Browne, Laake et al. 2002). This is likely to be an underestimation but these kinds of structures do not allow me to count the number of individuals. For samples with unidentifiable remains but which contained unique structures, an overall MNI was recorded (all species combined based on maximum paired numbers of eye lenses or other unique identifiable structures) (Trites and Calkins 2008). Empty scats or scats containing only unidentifiable remains were excluded from analysis (McKenzie and Wynne 2008). Size of prey species of New Zealand sea lions have been investigated elsewhere, but this requires measurement of diagnostic hard parts (otoliths, and beaks) to which species-specific digestion correction factors are applied, unavailable in this study (McKenzie and Wynne 2008). Mass of species is useful for quantifying energetic requirements, however in this study I focus on long term diet trends therefore I do not require mass estimates.

2.2.4 Data Analysis

Scat and regurgitate samples were separated for all statistical analysis due to inherent differences in bias between sample types (Fea, Harcourt et al. 1999). To determine diet composition and to identify important prey species, I calculated three standard indices which are expressed as a percentage (McKenzie and Wynne 2008; Hofmeyr, Bester et al. 2010). Frequency of occurrence (FO) is the proportion of scats containing a given prey type. FO is defined as:

$$\%FO_i = \frac{\sum_{j=1}^{s} O_{ij}}{s} \times 100$$

where O_{ij} = presence of taxon i in scat j, and s = the total number of scats that contained identifiable prey remains (Zeppelin and Orr 2010). Relative occurrence (RO) is the proportion of total occurrences (sum of FO for all prey types), made up of a given prey type. Relative occurrence produces the same relative values as FO but instead sums to 100% and so allows easier comparison between collections, giving a clearer picture of diet composition. Relative abundance (RA) is the proportion of the total number of prey items made up of individuals from a given prey type. The total number of prey items includes unidentified individuals from scats with identifiable prey types. Scats with no identifiable remains are excluded from analysis. To combine information on both abundance and occurrence, I calculated an index of importance (IIMP). This index buffers effects of schooling prey items that are present in large numbers but in few samples, or commonly occurring species that are found singly. The percentage IIMP was calculated as follows:

$$IIMP_i = 100 \times [\frac{1}{U}\sum_{j=1}^{U}\frac{X_{ij}}{X_j}]$$

where X_{ij} is the number of individuals (MNI) of prey type *i* in scat *j*, X_j is the total number of individuals from all prey found in scat *j*, and *U* is the total number of scats in the sample with identifiable prey (García-Rodríguez and Aurioles-Gamboa 2004).

To compare diet composition between years I used the Bray-Curtis coefficient of Similarity (BC_{ij}) using total number of individuals found in each year for each species (Bray and Curtis 1957). The equation is:

$$BC_{ij} = \sum_{x=1}^{x}\frac{n_{xi} - n_{xj}}{S_i + S_j}$$

, where x is the number of species, $n_{xi} – n_{xj}$ is the number of prey types in common between year i and year j. S_i and S_j is the total number of prey types counted in both years. Each collection was made up of scat of regurgitate samples collected in a given week. All samples not collected on Enderby Island (such as those collected on Dundas and Stewart Islands) were excluded to reduce location effects. Rare species were not excluded since the similarity measure already down-weights rare species (McKenzie and Wynne 2008). Diet composition was then compared between years.

Species accumulation curves were constructed in R for both scats and regurgitates to assess whether sample sizes in collections were sufficient to accurately describe diet composition (Ihaka and Gentleman 1996; McKenzie and Wynne 2008; Zeppelin and Orr 2010). A curve was constructed for each year using randomization procedures (x100) based on the occurrence of main prey types. To remove influence of rare species, prey types that occurred in less than 5% of samples in any one year were excluded from analysis (McKenzie and Wynne 2008). Unidentified fish and squid were removed from scats with identifiable remains. All samples were pooled for all locations in a given year. Sampling adequacy was assessed by visually identifying the asymptote of the curve.

2.2.5 Statistical Analyses

I tested overall differences in diet between years by using a non-parametric analysis of similarities (ANOSIM) on the Bray-Curtis similarities matrices and 999 randomisations of collections (Clarke 1993; McKenzie and Wynne 2008). Only collections where more than 1 week of samples contains identifiable remains were included in analysis of similarity. ANOSIM tests the null hypothesis that within-group similarities do not exceed between-group similarities. ANOSIM does not assume the variability of within-group replications is similar for all groups. All analyses were considered significant if $p < 0.05$. If significant differences between groups were found, pairwise tests were used to identify important differences. Some years had few replicates (weeks of collections); in these cases the value of the test statistic R, was used to assess differences between groups. Values of R close to zero indicate little or no difference between groups, whereas higher values indicate completely different groups (Clarke and Warwick 2001). Similarity of percentage (SIMPER) analysis was used to determine main prey types contributing to observed differences between groups (Clarke 1993). The value of S ranges from 0 to 1; $S = 0$ indicates no overlap in diet composition and $S = 1$ indicates complete overlap. Two collections were considered relatively similar for $S \geq 60\%$, based on examination of multi-dimensional scaling (MDS) plots and dendograms of collections (PRIMER v. 5). I assumed an MDS stress factor of <0.2 indicates that the MDS plot was an accurate representation of the relationships between collections (McKenzie and Wynne 2008). Only species contributing >10% to the observed dissimilarity between groups are reported. Analysis was conducted using all 3 indices (FO, RO and RA), but only analyses based on RO are presented (McKenzie and Wynne 2008). Relative occurrence (RO) sums to 100% so is easier to compare with other indices than frequency of occurrence (FO). Relative occurrence also is less biased than relative abundance (RA), which tends to put higher weight on rare species found in high numbers.

2.3 RESULTS

2.3.1 Sample distribution

Out of 1681 scats collected from the summer (December – February) of 1999/2000 to 2012/2013, 1009 contained identifiable prey, 633 contained only unidentifiable prey and 39 were empty of remains. From these scats, a total of 14,087 prey items were found. A total of 114 regurgitate samples were collected, of which 109 contained identifiable prey, and 5 contained only unidentifiable remains. From the regurgitate samples a total of 1189 prey items were counted.

Collection was dependant on access to sites and changes in New Zealand sea lion distribution. As a result, the number and type of samples collected varied across sites and years. Most scats were collected from Sandy Bay and South East Point (95.3%), the remaining 4.7% collected at other sites on Enderby Island (Table 2-1). The total number of scats collected varied between years (mean = 78.3, range = 20 – 121), the collection made in summer 2012/2013 is much smaller than other years, with only 20 samples containing identifiable remains. In this year, scats were only collected for 3 weeks in January. Most regurgitates were collected at Sandy Bay (54.1%). The total number of regurgitates containing identifiable remains varies widely between years (mean = 18.2, range = 1 – 51). From 2005 through 2010 and 2012/2013 no regurgitate samples were collected.

Table 2-1: Number of New Zealand sea lion scat and regurgitate samples with identifiable prey collected from Sandy Bay (SB) and South East Point (SEP) and other sites on Enderby Island from the summer of 1999/2000 to 2012/2013, excluding 2004/2005. For analysis, annual collections began in December (summer) through to February/March.

Scats					**Regurgitates**			
Year	**SB**	**SEP**	**Other**	**total**	**SB**	**SEP**	**Other**	**total**
1999/2000	37	21	4	62	32	7	12	51
2000/2001	29	10	13	52	6	5	5	16
2001/2002	58	47	7	112	4	4	0	8
2002/2003	61	39	12	112	14	1	16	31
2003/2004	52	50	0	102	1	0	0	1
2005/2006	44	23	0	67	-	-	-	-
2006/2007	64	38	0	102	-	-	-	-
2007/2008	43	23	0	66	-	-	-	-
2008/2009	52	34	0	86	-	-	-	-
2009/2010	64	33	0	97	-	-	-	-
2010/2011	64	0	0	64	-	-	-	-
2011/2012	63	1	3	67	2	0	0	2
2012/2013	20	0	0	20	-	-	-	-
total	**651**	**319**	**39**	**1009**	**59**	**17**	**33**	**109**

2.3.2 Scat sample analysis

In total 35 prey types were identified in scat samples across all years, of which 24 were fish, 8 were cephalopods, and 3 other (NZ fur seal, crustaceans, birds). Identification was to lowest possible taxonomic level with 20 identified to species level, 6 to genus, 6 to family and 2 to group. Of the total number of prey items found in scats with identifiable remains, 91.6% were fish, 7.8% cephalopods, and 0.6% other.

When samples were pooled across years and sites, 11 main prey types were identified with FO >10% in at least one year (Table 2-12). Common prey types accounted for more than 30% by occurrence and were opalfish, rattail and red cod (*Pseudophycis bachus*). Important prey types occur in 10-30% of samples and were octopus and arrow squid. Ling (*Genypterus blacodes*), smallscaled cod, hoki (*Macruronus novaezelandiae*), triplefin, fur seal and giant octopus (*Enteroctopus zealandicus*) were important prey (10-30% FO) in some years but not overall.

Based on a minimum number of 9549 individual prey identified, the most abundant prey was opalfish which contributed 22.8%, then dwarf cod 14.6%, followed by red cod 6.9%, rattail 6.3%, and lanternfish 3.2%. On average, opalfish were the most abundant prey when present.

Table 2-2: Overall percentage frequency of occurrence (FO), relative occurrence (RO), relative abundance (RA), and index of importance (IIMP) of prey identified in New Zealand sea lion scats collected from sites at Enderby Island (1999/2000 to 2012/2013, excluding 2004/2005). Prey highlighted in bold occurred with ≥10% FO in any single collection. Prey with values of 0.0 indicate actual value was <0.1.

Prey types	Occurrence	FO %	RO %	MNI	RA %	IIMP
Fish						
Opalfish *Hemerocoetes* spp	**360**	**35.4**	**15.8**	**3205**	**22.8**	**17.5**
Rattail Macrouridae	**359**	**35.3**	**15.7**	**893**	**6.3**	**11**
Red cod *Pseudophycis bachus*	**333**	**32.7**	**14.6**	**971**	**6.9**	**11.7**
Ling *Genypterus blacodes*	**96**	**9.4**	**4.2**	**149**	**1.1**	**2.1**
Smallscaled cod *Paranotothenia* sp.	**83**	**8.2**	**3.6**	**155**	**1.1**	**2.9**
Dark toadfish *Neophrynichthys latus*	75	7.4	3.3	130	0.9	1.3
Hoki *Macruronus novaezelandiae*	**72**	**7.1**	**3.2**	**207**	**1.5**	**3.6**
Triplefin Tripterygiidae	**62**	**6.1**	**2.7**	**121**	**0.9**	**1.3**
Lanternfish Myctophidae	42	4.1	1.8	456	3.2	1.4
Dwarf cod *Austrophycis marginata*	34	3.3	1.5	2052	14.6	1.1
Southern blue whiting *Micromesistius australis*	31	3	1.4	54	0.4	0.9
Deepsea pigfish *Congiopodus coriaceus*	28	2.8	1.2	35	0.2	0.5
Conger eel *Bassanago sp*.	27	2.7	1.2	77	0.5	1
Silverside *Argentina elongata*	24	2.4	1.1	34	0.2	0.4
Witch *Arnoglossus scapha*	15	1.5	0.7	18	0.1	0.3
Silver warehou *Seriolella punctata*	15	1.5	0.7	17	0.1	0.6
Ribaldo *Mora moro*	2	0.2	0.1	2	0	0
Slender tuna *Allothunnus fallai*	2	0.2	0.1	2	0	0.1
Flounder *Rhombosolea tapirina*	1	0.1	0	1	0	0
Monkfish *Kathetostoma giganteum*	1	0.1	0	1	0	0
Lighthouse fish *Phosichthys argenteus*	1	0.1	0	1	0	0
Redbait *Scopelosaurus* spp	1	0.1	0	1	0	0
Barracouta *Thyrsites atun*	1	0.1	0	1	0	0
Cephalopods						
Octopus *Octopus* sp.	**259**	**25.4**	**11.3**	**409**	**2.9**	**5.7**
Ommastrephidae (likely arrow squid)	**165**	**16.2**	**7.2**	**293**	**2.1**	**4.3**
Giant octopus *Enteroctopus zealandicus*	**51**	**5**	**2.2**	**88**	**0.6**	**1.4**
Hooked squid Onychoteuthidae	34	3.3	1.5	47	0.3	1.1
Bobtail squid *Sepiolidae*	15	1.5	0.7	18	0.1	0.5
Teuthowenia sp.	4	0.4	0.2	4	0	0.1
Histioteuthis atlantica	1	0.1	0	1	0	0
Greater hooked squid *Moroteuthis ingens*	1	0.1	0	1	0	0
Other						
NZ Fur seal *Arctocephalus forsteri*	**60**	**5.9**	**2.6**	**60**	**0.4**	**4.2**
Bird	15	1.5	0.7	15	0.1	0.6
Crustacean	14	1.4	0.6	14	0.1	0.3
Unidentified prey	-	-	-	4554	32.3	24.1

The relative importance of each prey type based on 3 indices (RO, RA, and IIMP) was similar with only a few principle differences. Namely the 5 most important species are the same for RO and IIMP, but for RA, octopus and arrow squid are not in the top 5. Dwarf cod (Table 2-3) was ranked as the second most important prey based on their relative abundance, and lanternfish as the 5th most important. In terms of IIMP these two species were ranked 14th and 10th respectively. This indicates that although these species occurred less frequently than other main prey, they occurred in high abundance when present in scats. Ling (Table 2-3) were ranked lower in terms of RA and IIMP than RO since, although commonly present in scat samples, most samples (91.7%) contained only 1 or 2 individuals. IIMP showed a stronger relationship with RO which reflects the greater weighting of occurrence in IIMP, and down-weighting of individual scats with high abundance of some prey types like dwarf cod and lanternfish.

Table 2-3: Primary prey (≥10% frequency of occurrence for any year) of NZ sea lions at Enderby Island, ranked by percentage relative occurrence (RO), relative abundance (RA), and index of importance (IIMP). The minimum number of individuals (MNI) per scat when present is given as a mean and range. Values are for all 1018 scats with identifiable remains pooled. Prey highlighted in bold had IIMP values ≥10% in any 1 year.

Prey types	**RO**	(Rank)	**RA**	(Rank)	**IIMP**	(Rank)	**MNI per scat**	
							Mean	**Range**
Hemerocoetes spp	**15.8**	**1**	**22.8**	**1**	**17.5**	**1**	**8.9**	**1 - 437**
Macrouridae	**15.7**	**2**	**6.3**	**4**	**11.0**	**3**	**2.5**	**1 - 36**
Pseudophycis bachus	**14.6**	**3**	**6.9**	**3**	**11.7**	**2**	**2.9**	**1 - 34**
Octopus sp.	**11.3**	**4**	**2.9**	**6**	**5.7**	**4**	**1.6**	**1 - 12**
Ommastrephidae	**7.2**	**5**	**2.1**	**7**	**4.3**	**5**	**1.8**	**1 - 21**
Genypterus blacodes	4.2	6	1.1	9	2.1	9	1.6	1 - 22
Paranotothenia sp.	3.6	7	1.1	9	2.9	8	1.9	1 - 16
Neophrynichthys latus	3.3	8	0.9	11	1.3	12	1.7	1 - 13
Macruronus novaezelandiae	**3.2**	**9**	**1.5**	**8**	**3.6**	**7**	**2.9**	**1 - 18**
Tripterygiidae	2.7	10	0.9	11	1.3	12	2.0	1 - 15
Arctocephalus forsteri	**2.6**	**11**	**0.4**	**15**	**4.2**	**6**	**1.0**	**1**
Enteroctopus zealandicus	2.2	12	0.6	13	1.4	10	1.7	1 - 8

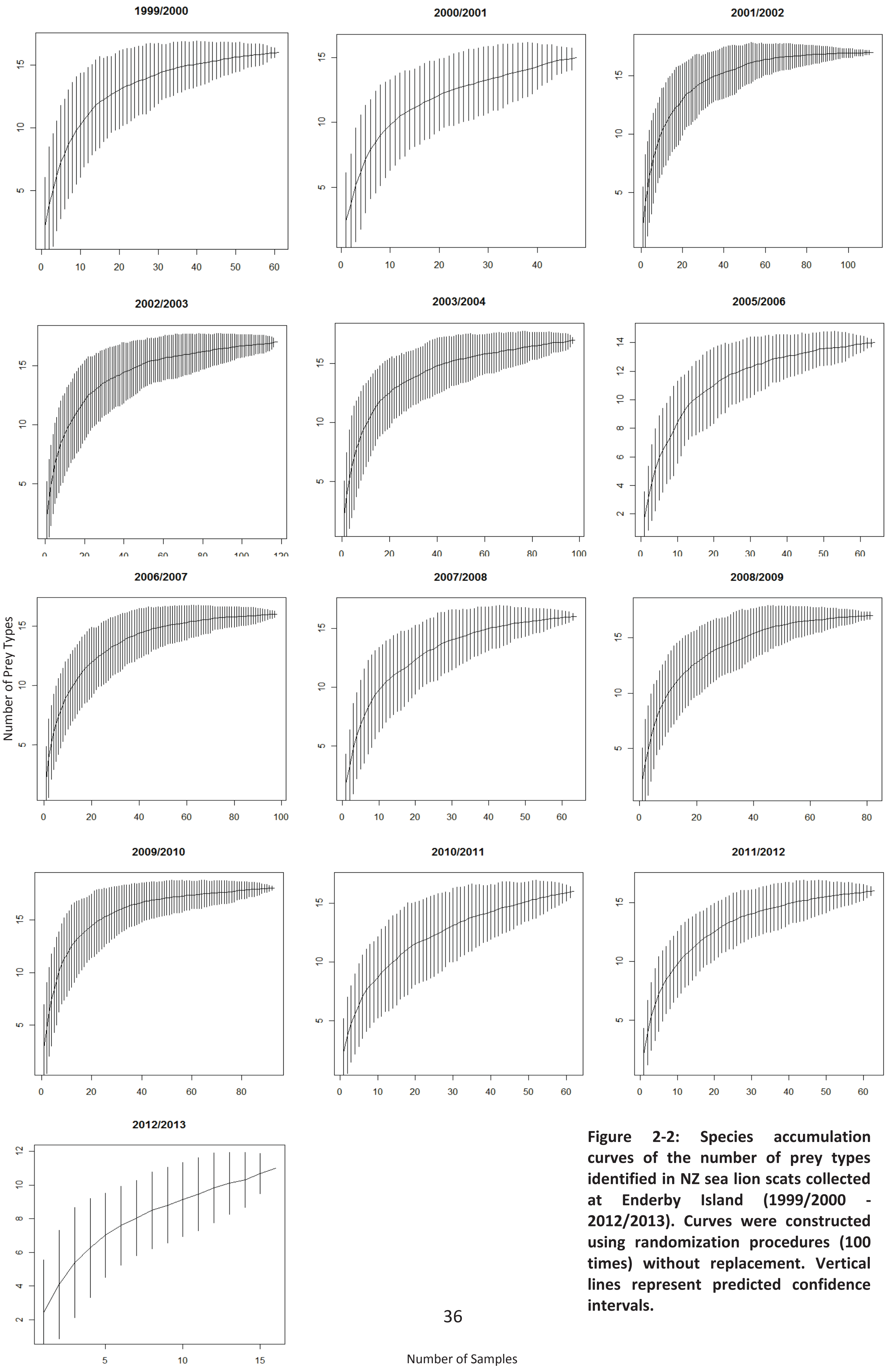

Figure 2-2: Species accumulation curves of the number of prey types identified in NZ sea lion scats collected at Enderby Island (1999/2000 - 2012/2013). Curves were constructed using randomization procedures (100 times) without replacement. Vertical lines represent predicted confidence intervals.

Species accumulation curves indicate that the increase in the number of new prey items identified in scat samples was relatively small following examination of 50 scats (**Error! Reference source not found.**). Fifty samples recovered a mean of 74.9 – 94.1% of prey types in scats and 69.1% in regurgitates. To reduce bias in diet composition due to small sample size, years with less than 50 scat samples containing identifiable remains were removed from further analysis. This excluded scats from the 2012/2013 field season (**Error! Reference source not found.**). Collections with ≥50 samples were considered sufficient to accurately represent the diet composition of NZ sea lions (Trites and Joy 2005).

2.3.2.1 Annual Variation in diet composition

Using the Bray-Curtis similarity matrices based on the relative occurrence of prey, differences in diet composition were significant between some years (Table 2-4). Interannual differences in diet were mainly attributed to variation in occurrence of most dominant prey: Opalfish, Rattail, Red cod, Fur seal, and Octopus (Table 2-5). The most common prey from 1999/2000 to 2003/2004 were Red cod, Rattail and Opalfish. In 2005/2006 Octopus became more common than Red cod. In 2006/2007 there were relatively equal proportions of Red cod, Rattail, Opalfish and Octopus. In 2007/2008 Opalfish and Octopus were the most important prey types. 2008/2009 was similar to 2006/2007 in having similar proportions of Red cod, Rattail, Opalfish and Octopus. The occurrence of Octopus decreased in 2009/2010 to 9%, leaving Opalfish and Rattail as the most important prey species, followed by Red cod. The occurrence of Opalfish was highest in 2010/2011, contributing 24% to diet composition, with rattails also being very important. This is in contrast to 2012/2012 where Opalfish only represent 8% of diet by occurrence, and rattail and red cod are the most important prey items (**Error! Reference source not found.**).

Table 2-4: Analysis of similarity (ANOSIM) for diet composition of New Zealand sea lion scats between years. Mid- to high-range values of R indicate complete distinction between groups, whereas those close to zero imply little difference. Values highlighted in bold have significance level <5%.

Year	**1999/2000**	**2000/2001**	**2001/2002**	**2002/2003**	**2003/2004**	**2005/2006**	**2006/2007**	**2007/2008**	**2008/2009**	**2009/2010**	**2010/2011**
1999/2000											
2000/2001	-0.06										
2001/2002	0.11	0.07									
2002/2003	0.12	0.09	-0.03								
2003/2004	**0.19**	0.13	0.08	0.01							
2005/2006	0.10	0.12	**0.16**	**0.21**	**0.16**						
2006/2007	**0.23**	0.07	0.02	0.03	**0.19**	**0.24**					
2007/2008	0.11	0.02	**0.20**	**0.28**	**0.20**	0.03	**0.25**				
2008/2009	0.03	-0.01	**0.09**	**0.16**	0.09	-0.02	**0.15**	0.05			
2009/2010	**0.24**	0.14	**0.11**	**0.10**	-0.03	**0.20**	**0.22**	**0.19**	0.03		
2010/2011	**0.26**	**0.22**	**0.23**	**0.13**	0.09	0.02	**0.17**	**0.22**	0.03	0.03	
2011/2012	**0.18**	0.12	0.08	0.07	**0.21**	**0.16**	0.11	**0.21**	0.03	**0.17**	**0.29**

Table 2-5: Pairwise tests between years showing significant differences in diet composition of scats from SIMPER analysis, significance is indicated by p < 0.05. A low similarity in diet is indicated by S < 60%. Mid- to high-range values of R reflect strong separation between groups. Only species contributing >10% of the observed dissimilarity between groups are listed.

Comparison		Mean S (%)	R	p	Prey type	Contribution (%)
1999/2000	2003/2004	53.13	0.19	0.02	Macrouridae	18.47
	2006/2007	51.94	0.23	0.022	Macrouridae	19.35
	2009/2010	56.16	0.24	0.008	Macrouridae	17.56
					Hemerocoetes spp	10.02
	2010/2011	54.58	0.26	0.007	Macrouridae	18.85
					Hemerocoetes spp	12.17
	2011/2012	54.95	0.18	0.022	Macrouridae	17.59
2000/2001	2010/2011	49.38	0.22	0.024	Hemerocoetes spp	12.91
2001/2002	2005/2006	54.83	0.16	0.007	Hemerocoetes spp	16.54
	2007/2008	57.43	0.2	0.011	*Arctocephalus forsteri*	12.75
	2008/2009	53.3	0.09	0.025	Hemerocoetes spp	10.47
	2009/2010	46.96	0.11	0.044	-	-
	2010/2011	47.58	0.23	0.004	Hemerocoetes spp	13.05
2002/2003	2005/2006	55.82	0.21	0.003	Hemerocoetes spp	16.3
					Octopus sp.	10.09
	2007/2008	58.79	0.28	0.001	*Arctocephalus forsteri*	11.61
					Pseudophycis bachus	10.48
					Macrouridae	10.12
	2008/2009	54.29	0.16	0.003	Hemerocoetes spp	11.95
					Octopus sp.	10.62
	2009/2010	47.33	0.1	0.05	Hemerocoetes spp	10.3
					Pseudophycis bachus	10.28
	2010/2011	46.44	0.13	0.042	Hemerocoetes spp	11.64
					Octopus sp.	10.79
					Pseudophycis bachus	10.6
2003/2004	2005/2006	54.97	0.16	0.017	Hemerocoetes spp	16.73
	2006/2007	44.43	0.19	0.009	Hemerocoetes spp	10.3
					Pseudophycis bachus	10.11
	2007/2008	57.51	0.2	0.003	*Arctocephalus forsteri*	11.81
	2011/2012	47.68	0.21,	0.002	Hemerocoetes spp	12.39
					Pseudophycis bachus	10.07
2005/2006	2006/2007	53.99	0.24	0.002	Hemerocoetes spp	17.05
	2009/2010	57.09	0.2	0.006	Hemerocoetes spp	16.57
	2011/2012	57.14	0.16	0.018	Hemerocoetes spp	17.32
2006/2007	2007/2008	55.01	0.25	0.005	*Arctocephalus forsteri*	12.23
					Pseudophycis bachus	10.11
	2008/2009	51.53	0.15	0.014	Hemerocoetes spp	13.2
					Pseudophycis bachus	10.37
	2009/2010	46.57	0.22	0.008	Hemerocoetes spp	11.02
	2010/2011	44.39	0.17	0.022	Hemerocoetes spp	12.41
					Pseudophycis bachus	10.55
					Macrouridae	10.55

Table 2-5 cont: Pairwise tests between years showing significant differences in diet composition of scats from SIMPER analysis, significance is indicated by p < 0.05. A low similarity in diet is indicated by S < 60%. Mid- to high-range values of R reflect strong separation between groups. Only species contributing >10% of the observed dissimilarity between groups are listed.

2007/2008	2009/2010	58.67	0.19	0.016	*Arctocephalus forsteri*	11.58
					Hemerocoetes spp	10.34
	2010/2011	57.69	0.22	0.005	Hemerocoetes spp	11.81
					Arctocephalus forsteri	11.59
					Macrouridae	11.22
	2011/2012	60.14	0.21	0.006	*Arctocephalus forsteri*	11.67
					Pseudophycis bachus	10.24
2009/2010	2011/2012	48.94	0.17	0.012	Hemerocoetes spp	12.67
					Pseudophycis bachus	10.08
2010/2011	2011/2012	49.32	0.29	0.003	Hemerocoetes spp	17.04
					Pseudophycis bachus	10.1

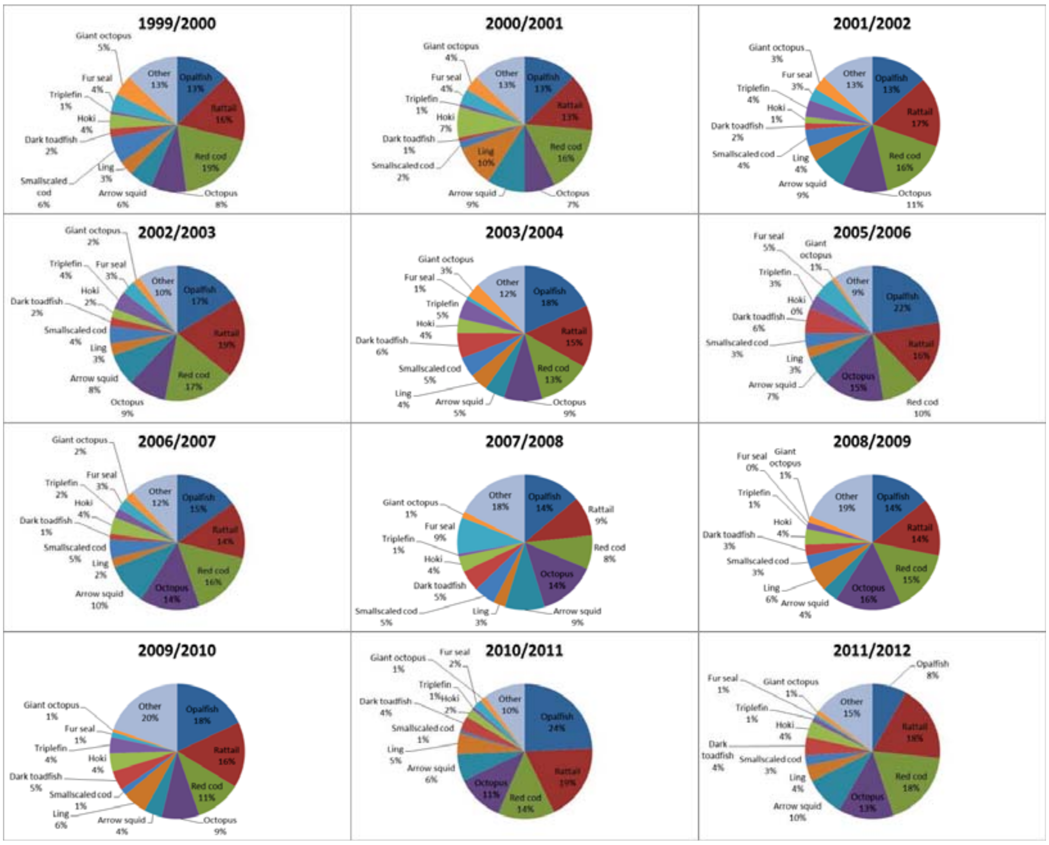

Figure 2-3: Changes in proportions of main prey species in scat samples of NZ sea lions collected on Enderby Island from 1999/2000 to 2011/2012. Main prey types are those present in >10% of samples in any one year. Each slice is the relative occurrence (%) or each prey type.

2.3.3 Regurgitate sample analysis

A total of 16 prey types were identified in regurgitate samples, 4 cephalopods, 8 fish, and 4 other. Seven prey types were identified to species level, 3 to genus, 3 to family and 3 to group. When prey items were pooled across all regurgitate samples, 26.2% were fish, 70.1 cephalopods, and 3.7% other. Other includes Fur seal, birds, shark/rays and crustaceans.

When regurgitate samples were pooled across years and sites, 11 main prey species were identified with FO>10% in any one year (Table 2-6). Giant octopus was the most important prey species, occurring in 67% of regurgitate samples. Arrow squid is also common, occurring in 48.6% of samples. Other important (>10% FO) prey types are Fur seals, Octopus, Red cod, Birds, Hooked squid, Shark/Rays, Opalfish, and Hoki. Based on a minimum number of 1087 individual prey items identified in regurgitate samples, the most abundant prey types were Giant octopus and Arrow squid which accounted for 65.6% of prey. The 11 main prey types accounted for 94.7% of prey by occurrence and 82.2% by abundance.

Table 2-6: Overall percentage frequency of occurrence (FO), relative occurrence (RO), relative abundance (RA), and index of importance (IIMP) of prey identified in New Zealand sea lion regurgitates collected from sites at Enderby Island (1999/2000 to 2011/2012, excluding 2005-2011). Prey highlighted in bold occurred with ≥10% FO in any single collection. Prey with values of 0.0 indicate actual value was <0.1

Prey types	Occurrence	FO %	RO %	MNI	RA %	IIMP %
Fish						
Red cod *Pseudophycis bachus*	**14**	**12.8**	**6.3**	**39**	**3.3**	**3.1**
Rattail Macrouridae	6	5.5	2.7	100	8.4	1.7
Opalfish *Hemerocoetes* spp	**2**	**1.8**	**0.9**	**59**	**5**	**0.5**
Dark toadfish *Neophrynichthys latus*	2	1.8	0.9	2	0.2	0.1
Silverside *Argentina elongata*	1	0.9	0.5	2	0.2	0
Dwarf cod *Austrophycis marginata*	**1**	**0.9**	**0.5**	**1**	**0.1**	**0**
Conger eel *Bassanago* sp.	1	0.9	0.5	1	0.1	0.1
Hoki *Macruronus novaezelandiae*	**1**	**0.9**	**0.5**	**2**	**0.2**	**0.6**
Cephalopods						
Giant octopus *Enteroctopus zealandicus*	**73**	**67**	**33**	**476**	**40**	**43.5**
Arrow squid Ommastrephidae	**53**	**48.6**	**24**	**304**	**25.6**	**18**
Octopus *Octopus* sp.	**19**	**17.4**	**8.6**	**48**	**4**	**4.6**
Hooked squid Onychoteuthidae	**3**	**2.8**	**1.4**	**3**	**0.3**	**0.3**
Other						
Fur seal *Arctocephalus forsteri*	**32**	**29.4**	**14.5**	**32**	**2.7**	**22**
Bird	**9**	**8.3**	**4.1**	**9**	**0.8**	**2.9**
Shark/Ray	**2**	**1.8**	**0.9**	**2**	**0.2**	**0.2**
Crustacean	2	1.8	0.9	2	0.2	0.1
Unidentified prey	-	-	-	105	8.7	2.3

The relative importance of each prey type in regurgitates was similar for all indices (Table2-7). Giant octopus, Arrow squid and fur seals are consistently the 3 most important prey types. The importance of Rattail and Opalfish is overestimated in RA, due to high weight placed on outlying samples with many individuals. These species were the most abundant prey types when present with average MNI of 29.5 and 16.7 respectively.

Table 2-7: Primary prey in regurgitates (≥10% frequency of occurrence for any collection) of NZ sea lions on Enderby Island, ranked by percentage relative occurrence (RO), relative abundance (RA), and index of importance (IIMP). The minimum number of individuals (MNI) per regurgitate when present is given as a mean and range. Values are for all 109 regurgitates with identifiable remains pooled. Prey highlighted in bold had IIMP values of >10% for any one year.

Prey Species	**RO**	(Rank)	**RA**	(Rank)	**IIMP**	(Rank)	**MNI per scat**	
							Mean	**Range**
Enteroctopus zealandicus	**33.0**	**1**	**40.0**	**1**	**43.5**	**1**	**6.5**	**1 - 50**
Ommastrephidae	**24.0**	**2**	**25.6**	**2**	**18.0**	**3**	**5.7**	**1 - 65**
Arctocephalus forsteri	**14.5**	**3**	**2.7**	**7**	**22.0**	**2**	**1.0**	**1**
***Octopus* sp.**	**8.6**	**4**	**4.0**	**5**	**4.6**	**4**	**2.5**	**1 - 7**
Pseudophycis bachus	6.3	5	3.3	6	3.1	5	2.8	1 - 7
Bird	4.1	6	0.8	8	2.9	6	1.0	1
Onychoteuthidae	1.4	8	0.3	9	0.3	10	1.0	1
Hemerocoetes spp	0.9	9	5.0	4	0.5	9	29.5	28 - 31
Shark/Ray	0.9	9	0.2	10	0.2	11	1.0	1
Macruronus novaezelandiae	0.5	13	0.2	10	0.6	8	2.0	2
Austrophycis marginata	0.5	13	0.1	15	0.0	16	1.0	1

2.4 DISCUSSION

Common prey of New Zealand sea lion based on scat samples collected at Enderby Island, from 1999/2000 to 2012/2013, were opalfish, rattail, red cod, octopus, arrow squid, ling, smallscaled cod, hoki, triplefin, fur seals and giant octopus. Most of these are demersal species, and NZ sea lions feed on or near the sea floor at depths more than 200m. Interannual variation is evident between some years, mainly due to fluctuations in dominant species opalfish, rattail, red cod, fur seal and octopus. Differences in important prey species between scat and regurgitate collections show biases these two methods produce and confirm importance of prey that appeared to make up a high proportion of the diet based on both types of samples. Prey taxa found here are in line with recent studies of diet in the Auckland islands, with some notable differences from an earlier study (Childerhouse, Dix et al. 2001). Importance of commercially caught species such as arrow squid and red cod are highlighted here, as well as the importance of the Auckland Islands shelf as foraging grounds. Biases inherent in scat analysis may have overestimated the importance of large prey items (Browne, Laake et al. 2002). This study of 13 years of routine sampling represents the longest time series of diet data available for this or any pinniped species.

2.4.1 Potential biases and limitations

Analysis of pinniped scats and regurgitates has been used to determine diet composition via identification of hard parts remaining after digestion, and to estimate the number and size of prey ingested (Tollit, Steward et al. 1997). This technique has advantages over others; it’s non-invasive, uncomplicated and cost-effective. Scat sampling can also deliver sample sizes much larger than other techniques that require capture or by-caught animals. However scat sampling produces error due to differential erosion and passage rate of prey items in relation to their size, shape and consistency. Larger squid beaks have lower recovery in scats than smaller (Staniland 2002). Smaller fish otoliths are digested faster than larger and so fish with larger otoliths may be overestimated (Browne, Laake et al. 2002; Arim and Naya 2003; Christiansen, Gamst Moen et al. 2005). Recovery rates of prey species in scat and regurgitates vary depending on species, but are increased when all diagnostic structures (such as vertebrae, jaw bones, and teeth) are included in analysis (Orr and Harvey 2001; Cottrell and Trites 2002; Staniland 2002; Tollit, Wong et al. 2003; Phillips and Harvey 2009). These biases can hinder accurate diet quantification, but do not prevent spatial or temporal comparisons (Tollit, Heaslip et al. 2006).

I chose to use the relative occurrence (RO) index to make comparisons between years. This was based on my comparison of indices which showed that indices based on occurrence as opposed to abundance reduced error produced by samples containing minor prey species in large numbers.

Relative occurrence gives the same important prey species as frequency of occurrence (FO) but sums all prey types to 100%, allowing us to more easily compare diet composition with other studies (McKenzie and Wynne 2008).

Scats collected in this study are male-biased since many were collected on the grassy sward on Sandy bay, where there are more male sea lions. Female sea lions are more likely to spend time on the beach, where scats are harder to collect (Augé, Chilvers et al. 2009). The collections of scats made each year were large enough for us to be confident of the conclusions drawn from their analysis, except for 2012/2013, where scats were only collected for 3 weeks. I validated my sample sizes by constructing prey accumulation curves (**Error! Reference source not found.**).

2.4.2 Scat versus regurgitate samples

Fish remains are more common in scats than regurgitates, whereas cephalopods are more common in regurgitates (Pierce and Boyle 1991; Gales and Cheal 1992). Cephalopod beaks tend to accumulate in the stomach over several meals, while otoliths are passed relatively quickly (Tollit, Steward et al. 1997). This was found in my study, where diet composition was different for regurgitates and scats. The most important prey species in regurgitate samples from 1999/2000 to 2002/2003 were giant octopus, followed by arrow squid, fur seals, octopus, red cod, birds, hooked squid, sharks/rays, opalfish, and hoki. Giant octopus and arrow squid accounted for 65.6% of prey items found in regurgitates by abundance (

Table 2-6). In comparison, opalfish were the most important prey species by abundance in scats (Table 2-3). Giant octopus, arrow squid and hooked squid beaks are likely accumulated in the stomach due to their large size, and then regurgitated. I found that fur from fur seal and egg-casings from sharks/rays are also hard to digest and are regurgitated.

2.4.3 Comparison with historical studies

The diet of New Zealand sea lion from 1999/2000 to 2012/2013 were diverse with 35 prey types identified (Table 2-2). However, only 3 of these taxa were common over whole time period (>30% FO) – Opalfish, Rattail, and Red cod – in scats, and only 2 – giant octopus and arrow squid – in regurgitates (Table 2-6). Differences in diet composition of NZ sea lions found in this study compared to other studies may be the result of 1) difference in methods or sources, 2) differences over time, or 3) differences between sexes. Sampling procedures between this study and Childerhouse et al. (2001) are comparable, whereas stomach content analysis by Meynier et al. (2009) has less error associated with digestion. In addition, the animals whose stomach contents were analysed were by caught in squid fisheries and so the contribution of squid to diet is likely to be overestimated in these animals (Meynier, Mackenzie et al. 2009). Stomach content analysis by Meynier et al. (2009) was biased towards female sea lions, whereas scat and regurgitate analysis in this study and in Childerhouse et al. (2001) were biased towards males (Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009).

Compared with this study the diet of NZ sea lions from 1994-1997 had higher occurrence of hoki and crustaceans and lower occurrence of red cod and ling (Childerhouse, Dix et al. 2001). Childerhouse et al. (2001) found higher occurrence of giant octopus (25% FO) than was found in scat samples in this study but lower than regurgitate samples (Table 2-2, 2-6). This is due to an overall decline in giant octopus in the diet over time. Main prey species (>10% FO) identified in this study were the same as those identified by stomach content analysis of by-caught sea lions from 1997-2006 (Meynier, Mackenzie et al. 2009). Meynier *et al.* (2010) identified a shift to lower proportions of hoki in diet of female sea lions from ~30% to <5% from 2004 to 2006. Lower importance of hoki in the present study is likely due to declining hoki population as opposed to a change in prey preference (Chilvers 2012). However, hoki may have been found less in this study due to large otoliths not passing through the digestive system, or females in Meynier *et al.* (2009) may eat more hoki than the male-biased population sampled here.

2.4.4 Feeding ecology

By identifying important prey types in the diet of New Zealand sea lion I can make inferences about foraging behaviour and habitat use. Opalfish and octopus are benthic species found on the Auckland Islands shelf, occupying sandy beds on the sea floor and rock holes respectively (Paul 2000). Arrow squid live in the water column predominantly at depths shallower than 600 m, with large aggregations in waters less than 300 m (Jackson, Shaw et al. 2000). Arrow squid occur on the shelf, offshore, and on the edge of the plateau (Jackson, Shaw et al. 2000). Rattail species also live on the edge of the shelf, at depths greater than 200 m near the bottom (Paul 2000). Red cod are a seasonally abundant, demersal species found in depths of up to 600 m (Paul 2000; McMillan 2011). Ling are a long-lived demersal species that live at depths of 100-900 m. Smallscaled cod are little known, but have been caught offshore by trawling in waters up to 1000 m (McMillan 2011). Hoki are usually found in waters 200 to 600 m deep and feed on midwater fish (McMillan 2011).

The importance of these species in the diet of New Zealand sea lion confirms benthic foraging behaviour. Female NZ sea lions typically dive in waters deeper than 150 m, with a U-shaped dive consistent with diving to the sea floor (Chilvers, Wilkinson et al. 2006). Studies of male NZ sea lions at the Otago peninsula also found their diet to contain a wide range of demersal or benthic species with a few pelagic species (Lalas 1997). Pelagic species are most likely taken opportunistically at the beginning or end of a dive to the sea floor, or during dives in the water column for individuals that exhibit a meso-pelagic dive profile (Chilvers and Wilkinson 2009). In the summer, female NZ sea lions forage in the water column over the shelf, and at the edge, where they consistently dive to depths of more than 150 m (Chilvers, Wilkinson et al. 2005; Chilvers, Wilkinson et al. 2006). Deep diving is more energetically expensive than travelling between foraging grounds (Costa and Gales 2000), so benthic diving must provide sufficient energetic payoff for this to be a successful strategy for NZ sea lions. The edge of the Auckland Islands shelf is where female NZ sea lions concentrate most of their foraging time (Chilvers, Wilkinson et al. 2005), indicating this area is important as a source of predictable and concentrated resources (Meynier, Mackenzie et al. 2009). The edge of the Auckland Islands shelf is >50 km from rookeries, and travelling there represents an energetic risk that may return greater availability of prey that is available closer to shore. By foraging at the edge of the Auckland Islands shelf, NZ sea lions can access concentrated prey in fewer dives, maximising foraging profit per dive. Arrow squid and rattail form dense schools in this area at depths >200 m (Jackson, Shaw et al. 2000; Paul 2000). Opalfish and octopus however, are not schooling species and inhabit the sea floor at the bottom of the shelf (Paul 2000). These species represent a large part of the diet but have higher handling time for less return.

2.4.5 Interannual variation in diet

Annual variation in diet composition was investigated by pooling scat samples for each year. Differences in prey composition between years could mainly be attributed to variation in dominant prey species opalfish, rattail, red cod, fur seal, and octopus (Table 2-4). The ranking of the 5 most dominant prey species (opalfish, rattail, red cod, octopus, and arrow squid) generally varied from year to year. Variation of dominant prey species is likely to reflect availability in foraging habitat since New Zealand sea lions are opportunistic generalist feeders (Lalas 1997). Further work correlating diet composition with other ecological factors such as prey availability in the environment (Chapter 3) and probability of survival (Chapter 4) could help to explain these variations, and effects on population viability (Kirkwood, Hume et al. 2008).

2.5 CONCLUSION

Resource competition between NZ sea lions and commercial fishery operations is a very real possibility and could have flow on effects for the breeding population at the Auckland islands. Red cod, arrow squid, ling and hoki are harvested commercially (MPI 2013), and are main prey species of NZ sea lions from 1999/2000 to 2012/2013. These fish accounted for 29.2% and 30.8% of total prey by occurrence, and 11.6% and 29.1% by abundance in scats and regurgitates respectively. The Auckland Islands has been suggested as marginal habitat for NZ sea lions, which operate at their physiological limit while diving (Chilvers, Wilkinson et al. 2006). New Zealand sea lions are generalist feeders, taking prey opportunistically based on what is available in the environment (Lalas 1997; Meynier, Mackenzie et al. 2009). This leads to direct interactions with fisheries in the form of incidental deaths, and likely indirect resource competition for the aforementioned important prey species. The edges of the Auckland Islands shelf are highlighted in this study as important foraging grounds for NZ sea lions, where prey resources can be found reliably and in high abundance. This key area is outside the protected area and is open to commercial fishery operations (MPI 2013). However the shelf is key for NZ sea lions too, as is evident by their consistent travel to forage there, despite being far from rookeries and females having dependant pups onshore (Chilvers, Wilkinson et al. 2005). This area may contain the only prey resources rich enough in this marginal habitat to provide for the energy requirements of the deepest diving, slowest breeding, and only endemic otariid of NZ (Gales and Mattlin 1997; Chilvers, Wilkinson et al. 2010).

This study documents changes in important prey species in the diet of NZ sea lion over an unparalleled 13 years of sampling. By comparing these data with earlier observations I can examine shifts in prey over an even longer time frame. Furthermore by modelling fluctuations in main prey species against their abundance in the environment, I can understand whether diet changes are the result of availability in the environment or due to behavioural changes. In chapter 3, I will investigate this question, followed in chapter 4 by the impacts of prey fluctuations in the diet on population vital statistics.

3. CHAPTER 3

LONG-TERM TRENDS IN THE DIET OF NZ SEA LION AND FUNCTIONAL RESPONSE TO CHANGE IN PREY AVAILABILITY IN THE AUCKLAND ISLANDS

Female New Zealand sea lions heading out to sea to feed, on Sandy Bay, at Enderby Island.

3.1 INTRODUCTION

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) is an endangered pinniped endemic to New Zealand (Wilkinson, Burges et al. 2003). Declared “nationally critical” under the NZ threat classification system and “vulnerable in decline” by IUCN, they have the smallest population estimate of any otariid with only about 12,000 individuals (Baker, Chilvers et al. 2010; IUCN 2012; MPI 2012). The current distribution of NZ sea lions is at the margin of their historical range, with 71-87% of pup production occurring on the Auckland islands (Chilvers, Wilkinson et al. 2007; MPI 2012). Despite being protected under the NZ Marine Mammal Protection Act 1978, the NZ sea lion has shown a 49% decline in pup production since 1995 (Chilvers, Wilkinson et al. 2010).

Understanding the causes of population decline is vital for wildlife management of species at risk of extinction. However this is difficult to determine when studying marine species because much behaviour occurs under water making it hard to observe. Population decline may be the result of reduced survival, immigration or reproduction. Resource competition as a result of fisheries operating on the Auckland Island’s shelf could result in prey shifts, nutrient stress, and subsequent lowered survival and reproductive output (Robertson and Chilvers 2011).

New Zealand sea lions in the Auckland Islands may be operating at their physiological limit in a marginal habitat. There is a difference in diet composition between the Otago peninsula and the Auckland Islands where more cephalopods are taken. The quality of prey found from 2008-2009 in the diet of the population at the Auckland Islands is lower than at the Otago peninsula (Augé, Lalas et al. 2011). In general fish species have higher energy content than cephalopod species (Lalas 1997). It is important to investigate not just prey quality between populations of sea lions, but also over time. We have seen a difference in diet of NZ sea lions between these two locations in 2008 and 2009 but it is uncertain if this is also true over longer timeframes. Declining prey quality can have significant impact upon population viability, through reduced survival of vulnerable lactating females and nursing pups (Meynier, Mackenzie et al. 2009).

NZ sea lions are, in general, opportunistic feeders and eat a wide range of foods including algae, crustaceans (crabs and krill), molluscs (cephalopods, gastropods and bivalves), fish, seabirds, and seals (Lalas 1997). Fish are the most common prey item, with cephalopods and crustaceans constituting lesser but still significant parts of the diet (Lalas 1997; Childerhouse, Dix et al. 2001; Chilvers 2008; Meynier, Morel et al. 2008; Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010). Generalist feeding has advantages over specialist feeding by increasing a populations’ adaptability to changes in availability of prey species.

Holling (1966) identified types of functional responses that describe the intake rate of a consumer as a function of food density. In a type I response intake rate increases linearly with prey availability up to a maximum, after which it is constant. This assumes that nothing is limiting intake of prey at high densities, such as handling time, or at low densities, such as search time. In this system NZ sea lions could theoretically consume infinite prey in an environment where they are infinitely available (Holling 1966). Functional response curves for single species can be used to infer foraging behaviour; e.g. a type I response shows that prey are taken in proportion to their abundance in the environment, which could suggest generalist feeding behaviour. Conversely, generalist feeding behaviour is not indicated if NZ sea lions show preference for certain prey types, shown by a higher occurrence in the diet at low prey densities, due to sea lions actively searching for this species. A type II response predicts a curved relationship, where foraging is restricted at higher densities in some way. This could indicate distaste for this species or preference for a different species. However, NZ sea lions could be restricted in their prey intake by another limiting factor, such as satiation or competition for resources. Satiation results in the consumption of prey approaching a plateau (Holling 1966), where sea lions would be limited by the time needed for handling/processing prey.

In this study I examine long-term trends in the diet of NZ sea lions based on Enderby Island, from the summer of 1994/1995 through to 2012/2013. This study spans 16 years of routine sampling over 19 years, and represents the longest timeline of diet data for any pinniped. Frequency of occurrence (%FO) in scats was used to represent the contribution of a prey type to the diet for a given year. Temporal changes in density of prey species in the environment were examined using catch per unit effort (CPUE) by fisheries as a proxy for true availability. My aims were to; 1) assess long-term trends in occurrence of main prey species in both scat and regurgitate samples, 2) investigate long-term shifts in diet quality using contribution of fish and cephalopods to diet as a proxy, 3) identify patterns of occurrence of main prey species of NZ sea lion in relation to abundance in the environment, and 4) investigate whether NZ sea lions are displaying a Type I or Type II functional response to changes in prey availability of commercially targeted main prey types.

3.2 METHODS

Dr. Simon Childerhouse gave permission to use raw data from NZ sea lion scats and regurgitates in this study. Samples from Childerhouse *et al.* (2001) were collected in the Auckland Islands from 1994/1995 to 1996/1997 and were used to extend the timeline for my dataset. Scats and regurgitates were collected over the same season from 1999/2000 to 2012/2013 with the exception of winter 1996. Only samples collected at sites on Enderby Island were included in this study. Methods for hard part identification and analysis were consistent with this study.

3.2.1 Study site and Sample collection – as in chapter 2

3.2.2 Sample processing– as in chapter 2

3.2.3 Sample identification – as in chapter 2

3.2.4 Data analysis

Scat and regurgitate samples were separated for all statistical analysis due to inherent differences in bias between sample types (Fea, Harcourt et al. 1999). Long-term trends in the occurrence of main prey species in scats and regurgitates were determined by examining frequency of occurrence (FO) over time. I used FO because I found in chapter 2 that occurrence indices were less sensitive to rare species found in high numbers. I used FO over relative occurrence (RO) since I was not comparing prey species directly to one another.

FO is defined as the proportion of scats containing a given prey type:

$$\%FO_i = \frac{\sum_{j=1}^{s} O_{ij}}{s} \times 100$$

where *Oij* = presence of taxon *i* in scat *j*; and *s* = the total number of scats that contained identifiable prey remains (Zeppelin and Orr 2010). Scats with no identifiable remains are excluded from analysis.

Eleven main prey species (>10% FO) were identified from scat samples in chapter 2; opalfish (*Hemerocoetes spp.*), rattail (Macrouridae) and red cod (*Pseudophycis bachus*), octopus (*Octopus sp.*) and arrow squid (Ommastrephidae), ling (*Genypterus blacodes*), smallscaled cod (*Paranotothenia sp.*), hoki (*Macruronus novaezelandiae*), triplefin (*Tripterygiidae*), fur seal (*Arctocephalus forsteri*) and giant octopus (*Enteroctopus zealandicus*). Main prey species used here are not the main prey species identified in Childerhouse *et al.* (2001) from 1995-1997, but instead those identified in this study from 2000-2013.

To examine changes in prey type and possible prey quality over time all fish species were pooled to determine the frequency of occurrence (FO) of fish in scats/regurgitates. The same was done for all cephalopod species. The ratio of occurrence of fish:cephalopod species was used as a proxy to determine a shift in prey quality over time.

Of the main prey species, those that are taken by commercial fisheries were included in an analysis of occurrence with reference to catch per unit effort (CPUE). These were red cod (*Pseudophycis bachus*), arrow squid (Ommastrephidae), and hoki (*Macruronus novaezelandiae*). Commercial trawl fishery catch and effort data were obtained from the Ministry of Primary industries warehou database and collected from 1978/79 to 2011/12. Annual estimates are referred to here by the year at the end of the fishing season (i.e. 2006/2007 fishing season referred to as 2007), which runs over the new year. Catch and effort data were taken from the Auckland Islands region, approximating the SQU6T management area used in the management of the southern arrow squid trawl fishery. Red cod is not commercially targeted in the sub Antarctic, and so estimates come from records of by-caught red cod. Standardised catch per unit effort (CPUE, as catch kg per tow) was estimated from GAM/GLM modelling, correcting for location (horizontal and vertical), year, month, vessel ID, gear type and tow duration effects (Dr. J. Roberts, personal communication, August 2013).

3.2.5 Statistical Analyses

It was expected that the relationship between CPUE and PO would be positive since NZ sea lions are generalist feeders, but I was unsure whether this relationship would be linear or curved. To confirm a positive relationship between abundance in the environment (CPUE; independent/explanatory variable) and occurrence in the diet (%FO; dependent/response variable) I performed linear regression using least squares method and a pearson correlation coefficient.

Holling (1966) identified three types of functional responses that describe the intake rate of a consumer as a function of food density. Type I and Type II are tested here as alternative hypotheses for foraging response of NZ sea lions in relation to abundance of main prey species in the environment. The type I response is the result of the assumption that the probability of a predator encountering prey in a fixed time interval Tt, within a fixed spatial region, depends linearly on the density of prey (Dawes and Souza 2013). Using the notation from Holling (1966) we express this relationship in the form

$$Y = aT_sX,$$

where Y is the number of prey consumed by one predator, X is prey density, T_s is the time available for searching and a is a constant termed the 'discovery rate' (Holling 1966). The overall type I response is as a linear relationship for small prey densities, but with a hard cut-off at larger prey densities. I adapted this equation to

$$p = a \times CPUE + b,$$

where p is the mean probability of a species occurring in a given sample and CPUE is the catch per unit effort in a single year.

A type II functional response is characterized by a decelerating intake rate, which follows from the assumption that the consumer is limited by its capacity to process food, or other predators exploiting the resource (Holling 1966). I used Holling's equation which assumes that processing food and hunting for food are mutually exclusive. The equation is: $f(R) = \dfrac{a \times R}{1 + a \times h \times R}$

where *f* denotes intake rate and *R* denotes resource density (in this case CPUE). The rate at which the consumer encounters food items per unit of food density is called the attack rate, *a*. The average time spent on processing a food item is called the handling time, *h* (Holling 1966). I assumed that *a* and *h* are both constant which gives,

$$p = \frac{a \times CPUE}{(1 + a \times h \times CPUE)}$$

where p is the mean probability of a species occurring in a given sample, and CPUE is the catch per unit effort in a single year.

To model functional response to changes in prey density, the probability of a prey species occurring in a sample (PO) was generated by bootstrapping the observed number of samples a prey type was seen in, as a proportion of total number of samples for each year. A mean probability of occurrence was calculated for each year, including standard deviation, median, and 2.5 and 97.5 percentiles. Actual catch per unit effort was modelled against mean probability of occurrence in WinBUGS (Lunn, Thomas et al. 2000), by fitting generalised linear models (GLM) to sample data. Catch per unit effort is used as a proxy for true abundance of the species in the environment. This is based on the notion that a qualitative measure of abundance can be measured by ease of capture. This allows us to look at temporal trends in abundance. For the code used to create models in WinBUGS refer to Appendix 3-2. The proportion of each prey species in the diet is assumed to be independent of each other. Data from scat samples in the 2013 season were excluded since CPUE data were unavailable for this year.

Random variation among years was incorporated into both Type I and Type II models with a normal distribution. Thus, four models were constructed; two each for a type I and a type II response with and without random error incorporated. I used deviance information criterion (DIC) to compare the fit of the models to my sample data for each species. The DIC is a hierarchical modelling generalization of the AIC (Akaike information criterion) and BIC (Bayesian information criterion). DIC is useful in Bayesian model selection problems where the posterior distributions of the models are generated by Markov chain Monte Carlo (MCMC) simulation. DIC is similar to Akaike's information criterion (AIC), in that it is a measure of model quality incorporating both goodness of fit and simplicity (Akaike 1974; Burnham and Anderson 2002). The lower the DIC value, the better the fit of the model to the data. The model with the smallest DIC is estimated to be the model that would best predict a replicate dataset which has the same structure as that currently observed. Important differences in DIC roughly follow; >10 can rule out models with higher DIC, 5-10 substantial difference but cannot confidently discard worse model, <5 if models make very different inferences, then it could be misleading just to report the model with the lowest DIC (Lunn, Thomas et al. 2000).

All analyses were repeated for regurgitates as for scats since cephalopod remains are better represented in regurgitates, and likewise fish in scats (Tollit, Steward et al. 1997). Results were consistent for regurgitates and sample sizes were larger in the scat dataset so only scat results are presented here.

3.3 RESULTS

A total of 1132 scats and 175 regurgitates were analysed to examine diet content, including 122 scats and 66 regurgitates from Childerhouse *et al.* (2001).

Table 3-1: Number of NZ sea lion scat and regurgitate samples collected on Enderby Island from 1994/1995 to 2012/2013. Samples collected on islands other than Enderby Island were excluded.

Year	Scats	Regurgitates
1994/1995	31	28
1995/1996	57	33
1996/1997	34	5
1999/2000	62	51
2000/2001	52	16
2001/2002	112	8
2002/2003	112	31
2003/2004	102	1
2005/2006	67	-
2006/2007	102	-
2007/2008	66	-
2008/2009	86	-
2009/2010	97	-
2010/2011	64	-
2011/2012	67	2
2012/2013	20	-

3.3.1 Long-term trends

Octopus sp. have been steadily increasing in diet from 1995 to 2013 as indicated by remains in scats Red cod, rattail and arrow squid show an increase when comparing my data (2000 – 2013) to Childerhouse et al. (2001) diet data (1995 – 1997) (Figure 3-1). Opalfish show a weak increasing trend, but this is not clear. Ling and triplefin are not present (or almost absent) in Childerhouse et al. (2001) time period, and show large annual differences in occurrence (Figure 3-1). Rattail and red cod show a decrease in occurrence from 2004 to 2008 but then increase again in the final years of this study. Giant octopus have been decreasing in diet of NZ sea lions over time, with hoki also decreasing to a lesser degree (Figure 3-1). The decrease of Giant octopus is most evident from 2000 to 2012, with highest occurrence in the diet from 2000 to 2004 (Figure 3-1). The ratio of fish to cephalopods in scats has been decreasing over time, indicating a change in diet to lower proportion of fish and higher proportion of cephalopods (Figure 3-2). However from 2000 onwards, this ratio has been stable, with no noticeable trend.

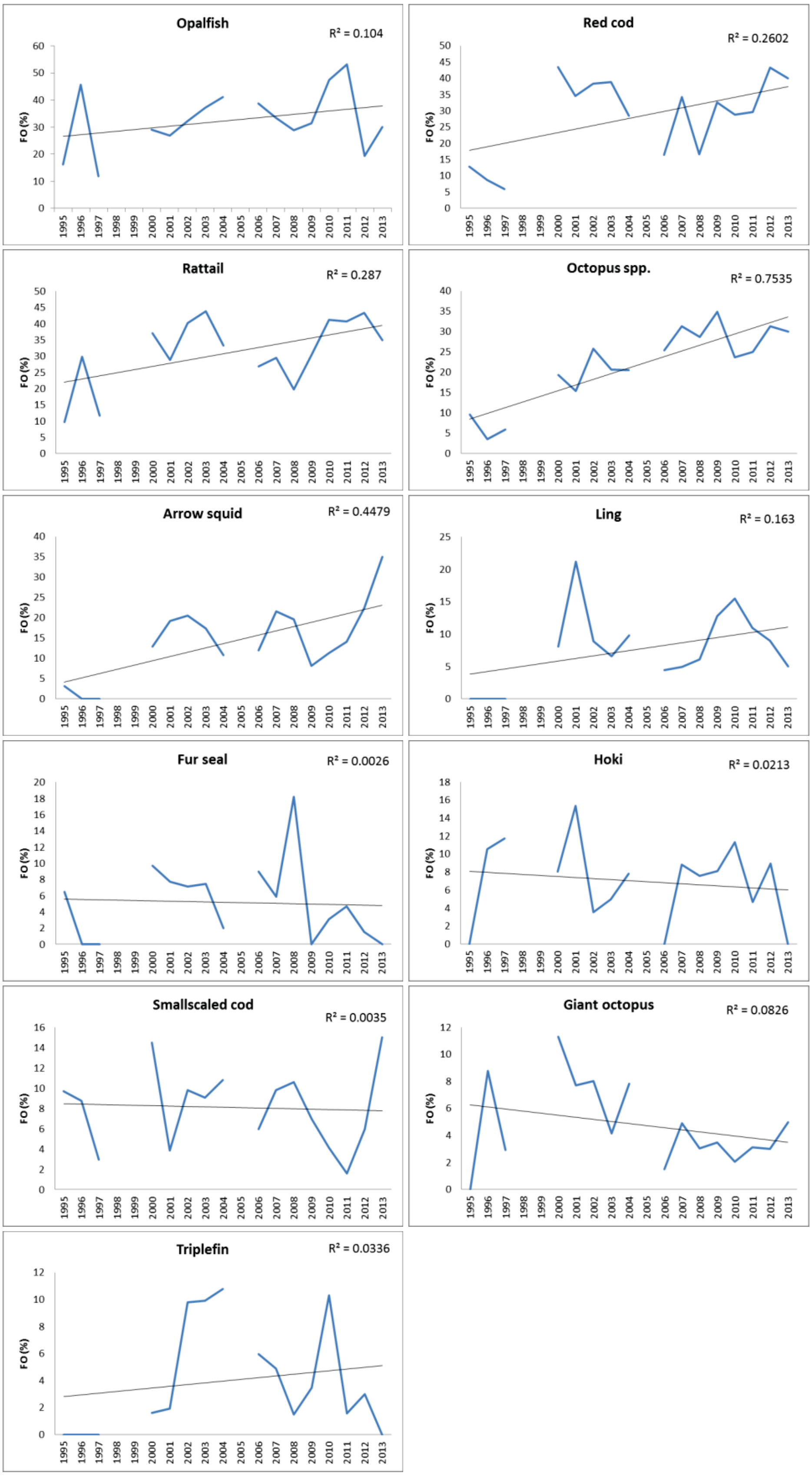

Figure 3-1: Percentage frequency of occurrence of main prey of NZ sea lions found in scats from 1995 to 2013. Main prey types were defined as being present in more than 10% of samples in any one year. Gaps in graph represent years where no samples were collected. The R2 value is the coefficient of determination and quantifies goodness of fit of the trendline to the data.

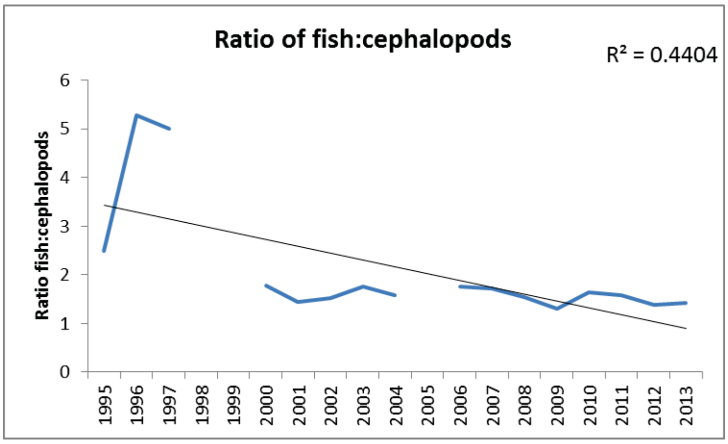

Figure 3-2: Ratio of occurrence (FO) of fish: cephalopods in scats of NZ sea lions over time. Samples were collected at Enderby Island from 1995 to 2013. Blanks on graph show years where samples were not analysed or where there were no samples with identifiable remains. All fish and all cephalopod species were pooled to calculate FO for each prey type within each year.

3.3.2 CPUE vs FO correlations

Prey availability in the environment was compared to occurrence in the diet from 1995 through to 2012. Overall there is a weakly positive relationship between availability in the environment and presence in the diet for these species. Hoki (r = 0.476, p=0.082) showed the strongest relationship between occurrence in scats and availability in the environment when analysed using Pearson correlation coefficient. Hoki occurrence in diet show a similar pattern to CPUE, with most peaks and troughs in the same years (Figure 3-3). Red cod (r = 0.397, p = 0.139) shows a weaker correlation with occurrence (%FO) in scat samples following a roughly similar trend to CPUE for 1995 - 2004 then opposing trends from 2006 – 2010. Arrow squid (r = 0.160, p = 0.568) showed the weakest relationship with occurrence low from 1995-1998 but increasing from 2000 – 2013 with peaks at roughly the same times as CPUE.

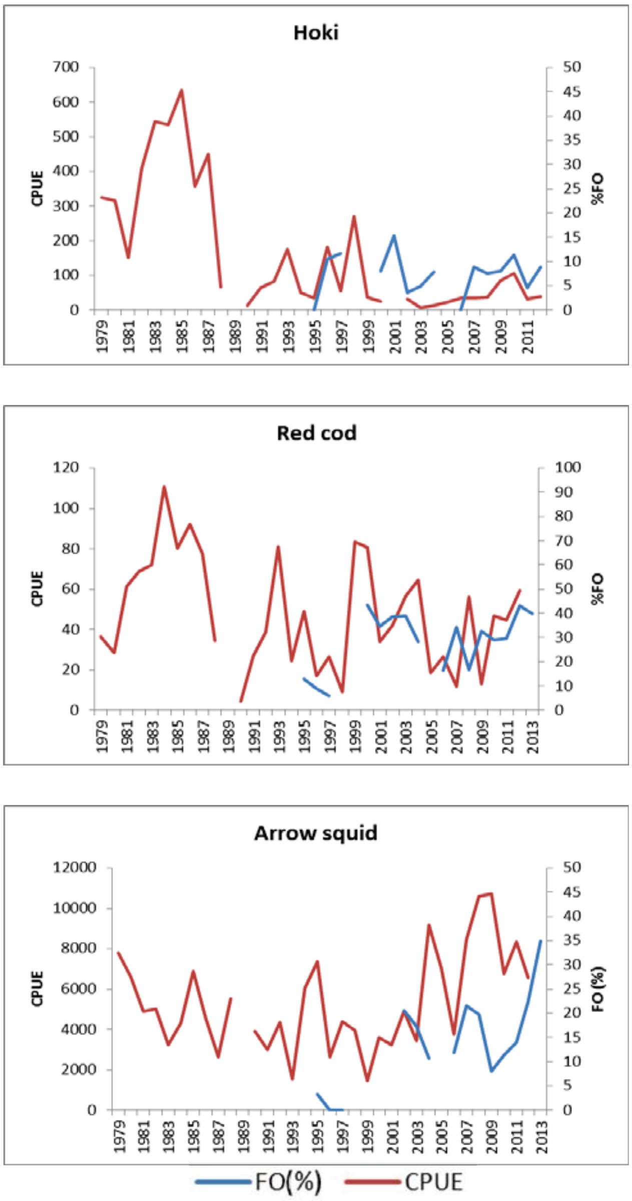

Figure 3-3: Percentage frequency of occurrence of main prey species of NZ sea lions found in scats from 1995 to 2012 and catch per unit effort from 1979 to 2012. Gaps in graph represent years where no samples were analysed. Catch per unit effort (CPUE) is used here as a proxy for true abundance in the environment. Species shown are those that are both commercially harvested in the Auckland Island's region and present occur in >10% of scat samples in any one year.

3.3.3 Functional response

Overall the best models for occurrence of main prey in diet with reference to CPUE were those that incorporated random error (Table 3-2). Incorporating random error allows PO to vary annually, indicating that annual variation has high predictive power for these prey types (Table 3-2). The deviance information criterion (DIC) values failed to resolve whether type I or type II with random error were better models for occurrence of the prey types. If DIC values differ by less than 5 we cannot reasonably discount the poorer models. Here, the difference between Type I and Type II models with random error differed by no more than 1.5 (Table 3-2). Visual inspection of graphs showing the relationship between prey availability (CPUE) and occurrence in diet (%FO) indicate that type II may be a better fit for hoki and arrow squid (Figure 3-4). Due to a large amount of scatter it was unclear graphically which was the better model for red cod, but DIC value indicates type II is a better predictor. Probability of occurrence of arrow squid in diet was relatively constant irrespective of availability (Figure 3-4).

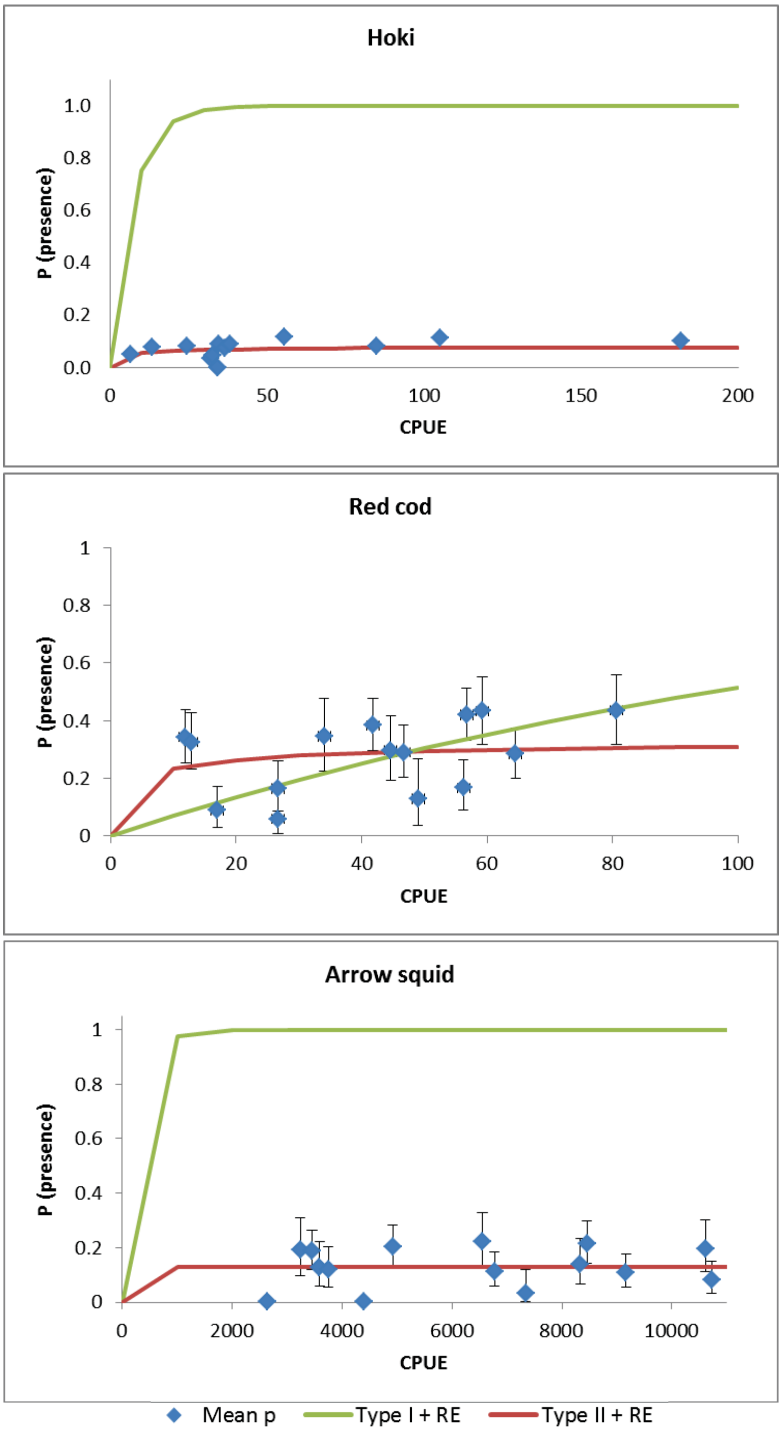

Figure 3-4: Two most parsimonious models of functional response by NZ sea lions to changes in abundance of prey species in scat samples. Catch per unit effort is used here as a proxy for true abundance in the environment. Species shown are main prey species and commercially harvested in the Auckland Islands region. Main prey species are defined as any that occur in >10% of samples in any one year. Mean probability of presence of a species in a scat sample is generated using samples from Enderby Island from 1995 to 2013. Error bars represent 2.5 and 97.5 percentiles of the mean probability. Models without random error were a poor fit to the data and are not shown.

Table 3-2: Model comparison showing four models fitted to probability of observing a prey type in a NZ sea lion scat sample from 1995-2013. Prey species shown are main prey species of NZ sea lion that are taken by commercial fishery operations in the Auckland Islands region. Main prey species are defined by occurring in >10% of samples in any one year. Parameters a and b are constants and sd represents standard deviation. Type I and Type II predict functional response of sea lions to changes in prey availability. Random error (RE) allows for annual variation in data. Models in bold indicate highest quality model with lowest DIC value.

Hoki	**node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**	**DIC**
Type I	a	0.0	0.0	0.0	0.0	0.0	92.3
Type II	a	0.1	0.0	0.1	0.1	0.1	67.5
	b	6.8	5.3	-1.1	5.9	19.3	
Type I + RE	**a**	**0.1**	**0.0**	**0.1**	**0.1**	**0.1**	**65.8**
	sd	**7.6**	**1.2**	**5.4**	**7.6**	**9.8**	
Type II + RE	a	0.1	0.0	0.1	0.1	0.1	66.0
	b	7.7	6.3	-1.4	6.5	22.7	
	sd	0.0	0.0	0.0	0.0	0.1	
Red cod							
Type I	a	0.0	0.0	0.0	0.0	0.0	190.7
Type II	a	0.4	0.0	0.3	0.4	0.5	135.3
	b	5.1	3.9	-1.0	4.6	13.7	
Type I + RE	a	0.2	0.0	0.2	0.2	0.2	94.6
	sd	8.1	1.1	6.0	8.1	9.9	
Type II + RE	**a**	**0.4**	**0.1**	**0.2**	**0.4**	**0.5**	**93.2**
	b	**5.8**	**6.7**	**-4.7**	**5.1**	**20.9**	
	sd	**0.2**	**0.0**	**0.1**	**0.2**	**0.3**	
Arrow squid							
Type I	a	0.0	0.0	0.0	0.0	0.0	129.9
Type II	a	0.2	0.0	0.1	0.2	0.2	106.0
	b	-0.1	9.9	-18.7	-0.2	20.3	
Type I + RE	**a**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**77.4**
	sd	**9.8**	**0.2**	**9.4**	**9.9**	**10.0**	
Type II + RE	a	0.1	0.0	0.1	0.1	0.2	78.9
	b	0.0	9.9	-19.2	-0.3	19.4	
	sd	0.1	0.0	0.1	0.1	0.2	

3.4 DISCUSSION

The population of NZ sea lions has undergone a 49% reduction in the number of pups produced at the Auckland Islands since 1995 (Chilvers, Wilkinson et al. 2010). This magnitude of decline has not been seen in the population since historic commercial sealing (Childerhouse and Gales 1998). In this study I examine long-term trends in the diet of NZ sea lions based on Enderby Island, from the summer of 1994/1995 through to 2012/2013. I aimed to investigate the relationship between foraging of NZ sea lions, and prey availability in the environment by examining long term trends in main prey species.

3.4.1 Limitations/assumptions

3.4.1.1 Limitations of hard-part analysis – as in chap 2

3.4.1.2 Limitations of this study

I chose to use the frequency of occurrence (%FO) index to infer true intake in the diet. This was based on my comparison of indices which showed that indices based on occurrence as opposed to abundance reduced error produced by samples containing minor prey species in large numbers. Scats collected in this study are male-biased since many were collected on the grassy sward on Sandy bay, where there are more male sea lions. Female sea lions are more likely to spend time on the beach, where scats are harder to collect (Augé, Chilvers et al. 2009). I included raw data from 1995 to 1997 and 2013 to extend the timeframe for this study and better examine long term trends (Childerhouse, Dix et al. 2001). However samples sizes in these years were small (n = around 30) and so more biased than years with larger scat collections; some prey types could have been missed. In chapter 2 I excluded 2012/2013 season due to small sample size, however in this study I decided that extending the timeline for data was important enough to disregard this possible bias. I used CPUE as a proxy for true abundance of prey in the environment. Although CPUE is an indirect measure of abundance it is useful in that it does not interfere with harvesting and data is easily collected (Maunder, Sibert et al. 2006). CPUE can sometimes be used to calculate true abundance, but in this study it is used to show trends in abundance over time. When correlating occurrence of a species in diet with abundance in the environment, I assume that occurrence is independent of the occurrence of other prey types.

3.4.2 Long term trends

I investigated long term trends of main prey species in the diet of NZ sea lions. There is a higher occcurence of red cod and rattail when comparing my timeframe (2000 – 2013) to Childerhouse *et al.* (2001) diet data (1995 – 1997) (Figure 3-1). These species show a decrease in occurrence from 2004 to 2008 but then increase again in the final years of this study. None of these are commercially targeted in the Auckland Island's region (MPI 2013). However red cod is caught as by catch and also shows a corresponding increase in environmental availability (CPUE) over these years (2000-2013) (Figure 3-3).

Octopus species are not commercially targeted in the Auckland Islands region. In this study, giant octopus, and smaller octopus spp. were identified as being main prey species of NZ sea lions (Chapter 2). The smaller *Octopus* sp. showed a clear increase in the diet from 1995 to 2013 (Figure 3-1). Giant octopus, however, appear to be slowly decreasing in the diet over time; if we consider the 2000-2013 timeframe, this decline is dramatic (Figure 3-1). The decrease in diet of giant octopus may indicate a shift from preying on large octopus which are energetically valuable, to smaller species that are less worthwhile. It is hard to quantify if this is due to a decline in abundance of giant octopus in the environment, or due to a behavioural shift. Octopus are not commercially harvested and are usually discarded when by-caught (MPI 2013). By-caught species are those that are caught incidentally by operations fishing for other species. The importance of octopus may reflect an increase in foraging effort as octopus are solitary animals that live in rocky areas on the sea floor of the Auckland Island's shelf (Paul 2000; Meynier, Mackenzie et al. 2009).

Arrow squid are almost completely absent in Childerhouse *et al.* (2001) time period, and show large temporal differences in occurrence from 2000-2013 (Figure 3-1). However, arrow squid appears to have shown a steep increase in the diet since 2009 (Figure 3-1). Arrow squid catch varies annually but very rarely meets total allowable commercial catch (TACC) (MPI 2013). The TACC is the total quantity of each fish stock that the commercial fishing industry can catch in a given year. The increase in the importance of Arrow squid in the diet since 2009 is a conservation concern for NZ sea lion since the Arrow squid fishery is the largest commercial fishing operation in this region (MPI 2013). Arrow squid is increasing in availability in the environment since 1999 after a decrease from 1995 to 1999 (Figure 3-3).

Hoki show a slight decrease in the diet over from time but this is highly variable with some years completely devoid of hoki in diet samples and others hoki is an important prey species (Figure 3-1). Hoki are the only fish species that is both one of the main prey of NZ sea lions and commercially targeted in the Auckland Islands region (MPI 2012). The commercial catch (CPUE) of Hoki has also been declining since 1999, which indicates that Hoki are less available in the environment, rather than a shift in prey preference (MPI 2013). Hoki may have been more prevalent in the diet historically when it was more abundant in the environment in the 1980's (Figure 3-3). A similar drop in Hoki and increase in Arrow squid in diet of female NZ sea lions between 2000-2006, was identified by Meynier *et al.* (2010) using fatty acid analysis.

NZ sea lions are generalist feeders that prey on a variety of marine life, allowing them to adapt to changes in prey availability. I investigated whether NZ sea lions fed on main prey species in accordance with their abundance in the environment. Patterns of occurrence in diet of main prey species mainly tracked the abundance in the environment (Figure 3-3), with some differences. Deviation from this trend may be due to competition for resources, where sea lions are not able to take full advantage of abundant resources. Fisheries remove prey from the environment, potentially competitively excluding sea lions from taking prey that may have been initially abundant. Alternately, NZ sea lions may show preference for some prey types over others, meaning prey occurrence in the diet are not independent of one another. On the functional response curves, this would show a plateau at high abundance.

Fish species in general have higher energy content than cephalopod species, however this is not significant (7.1 kJ g-1 compared with 6.3 kJ g-1 for squid; Meynier *et al*. 2008). The increase of cephalopod prey in diet and concurrent decrease in fish species suggests a shift to lower quality diet (Chilvers 2012). My analysis of scat samples from 1995 to 2013 found that the ratio of fish:cephalopods in NZ sea lion diet has been decreasing with time (Figure 3-2). This indicates an overall reduction in diet quality. The arrow squid trawl fishery (SQU6T) operates on the Auckland Islands shelf from February til May (Chilvers 2009). This fishery removes substantial amounts of arrow squid, hoki and red cod from foraging areas of NZ sea lions during the lactation period, when breeding females and pups are at their most reliant on easily accessible and abundant food sources (Chilvers 2009). Reduction in prey availability/quality could impact upon female body condition, and therefore pup growth and survival (Augé, Chilvers et al. 2011). Changes in prey abundance and quality have reduced reproductive output of Steller sea lions (*Eumetopias jubatus*) (Trites and Donnelly 2003) and Southern elephant seals (*Mirounga leonina*) (Atkinson, DeMaster et al. 2008). In addition, smaller prey types such as opalfish and *Octopus* sp. have been increasing while larger species hoki and giant octopus have been decreasing in the diet over time (Figure 3-1). A reduction in these large prey types is likely to put further physiological stress on these animals. NZ sea lions are said to already be operating at their physiological limit, diving beyond their aerobic limits on most dives (Chilvers, Wilkinson et al. 2006). As such it is not possible for NZ sea lions to increase their energetic output to compensate for scarce or hard to catch prey.

3.4.3 Functional response to changes in prey density

Holling (1966) devised models for expressing the relationship between resource availability and consumption rate, which are now widely used and applied to a wide range of ecological systems. I modified these equations to allow for my index (FO) to relate to actual consumption rate. I aimed to compare biologically sensible models to determine if consumption related to availability in the environment. A type I functional response is linear with reference to prey availability with unrestricted predation to a maximum, after which consumption rate is constant. Type II functional response shows restriction of feeding at high prey availability (Holling 1966). I created alternate models to investigate whether NZ sea lions display a Type I (constant) or Type II (decelerating) functional response to changes in prey availability. Models with random error incorporated were best for all prey types indicating that annual variation in take by sea lions is likely to be affected by factors other than availability in the environment (Table 3-2). A plateau in consumption by sea lions (Type II) would indicate satiation, foraging specialisation, or perhaps competitive exclusion. A linear response (Type 1) indicates a generalist feeding regime, where consumption tracks availability in the environment. A linear response to increasing prey density (Type I) is not seen by any models of prey occurrence in diet, indicating that sea lions are not feeding unrestricted on prey. It was unclear what was the best model for take of red cod which show opposing trends in diet to density from 2005/2006 to 2009/2010 (Figure 3-3). Arrow squid and hoki occurrence both fit models with random error incorporated, and graphically seem to be showing a type II response to prey availability (Figure 3-4). A drop in hoki occurrence suggests that satiation is an unlikely explanation for foraging response by sea lions (Figure 3-1). This is backed up by low hoki abundance in the environment (CPUE) during the time period considered here (Figure 3-3). Arrow squid show similar patterns of occurrence in diet to peaks in CPUE, both increasing with time since 1995 (Figure 3-3). Arrow squid occurrence varies annually with respect to availability but overall is increasing in importance in the diet of NZ sea lions over time (Figure 5). Reductions in other important prey stocks by fisheries, such as hoki, make increasing stocks such as arrow squid all the more important for sea lions. It is possible that in years of high abundance of arrow squid and hoki, sea lions are not limited by handling time, but may instead be limited by fisheries - imposed competition.

3.5 CONCLUSION

Results from this research show clear long-term trends in main prey species that may be influencing the decline of the NZ sea lion population (Figure 3-1). There has been a marked decline in the occurrence of giant octopus in the diet over time. Reduction in large prey types such as giant octopus and hoki and may force sea lions to take more readily available prey. This could explain the observed increase in less energetically rewarding prey types, smaller *Octopus* spp and opalfish (Figure 3-1). Increased contribution of cephalopod species such as arrow squid and *Octopus* sp. may lower the overall quality of diet when compared to a diet higher in fish species (Figure 3-2). Arrow squid and hoki are both targeted commercially in the Auckland Islands region during the breeding season of NZ sea lions (MPI 2013). Greater importance in the diet of commercially valuable Arrow squid is a conservation concern due to heavy take by trawl fisheries (MPI 2013).

Arrow squid and hoki were best represented by Type II models indicating that foraging by sea lions is not unrestricted. Occurrence of these species in the diet never reaches a plateau of plenty where sea lions are only limited by how much food they can consume. Resource competition imposed by fisheries could restrict intake by sea lions, or force prey shifts to species not commercially harvested. Uncertainty in resource availability puts pressure on an already stressed population that may be operating at it's physiological limit (Chilvers, Wilkinson et al. 2006). Lactating females and dependent pups are particularly vulnerable to changes in resource availability (Meynier, Morel et al. 2010). A shortage of high quality or abundant food could lead to reduced reproductive output and survival, with no behavioural means to buffer the impacts on the population.

3.5.1 Further studies

Changes in occurrence main prey species in the diet are important to note due to the vulnerability of breeding animals to prey availability. In my next chapter I have investigated the relationship between occurrence of main prey species in the diet, and age-related survival and breeding statistics. The effects of reductions of important prey species are most likely to impact the population via reduced/increased survival and breeding success. To quantify potential resource competition, we need further studies into the relationship between fisheries catch and occurrence in the diet. It is hard to quantify resource competition imposed by fisheries without examining fisheries catch. Fisheries remove a significant quantity of resources from the environment; I recommend future studies where fisheries catch is examined with reference to sea lion diet.

4. CHAPTER 4

EFFECTS OF OCCURRENCE OF MAIN PREY TYPES IN THE DIET OF NEW ZEALAND SEA LIONS ON SURVIVAL AND BREEDING IN THE AUCKLAND ISLANDS

Female New Zealand sea lion feeding a pup that has been flipper tagged, on Enderby Island.

4.1 INTRODUCTION

Studying the causes of decline of long-lived and slow breeding species is difficult in that long time-series of data are required to identify trends and potential threats. Studying marine species is even more challenging due to their aquatic nature. Marine mammal species with restricted distributions are particularly vulnerable to localised threats such as disease outbreaks and anthropogenic pressure (Chilvers 2012). New Zealand (NZ) sea lions (*Phocarctos hookeri)* are at risk of negative anthropogenic impacts via fishery related mortality and potential competition for resources (Robertson and Chilvers 2011). The current distribution of NZ sea lions is at the margin of their historical range, with 71-87% of pup production occurring on the Auckland islands (Chilvers, Wilkinson et al. 2007; MPI 2012). Despite being protected under the NZ Marine Mammal Protection Act 1978, the population has shown a 49% decline in pup production since 1995 (Chilvers, Wilkinson et al. 2010).

Incidental by-catch by trawling operations leads to mortality of foraging sea lions. Fishing-related mortality of sea lions is currently being managed by setting a Fisheries-Related Mortality Limit (FRML) which requires the closure of fisheries activity once this limit has been reached. However indirect effects, such as potential competition for resources and habitat modification caused by trawling, are not currently managed in any way (Robertson and Chilvers 2011). Habitat modification of the ocean floor by trawling operations can negatively impact upon benthic-dwelling prey types not directly targeted by fisheries (e.g. smallscaled cod). In addition, many of the main prey species of NZ sea lions are commercially harvested in the waters surrounding the Auckland Islands during the breeding season. This leads to conflict when sea lions and fisheries both target the same prey species (Gales 1995). Competition with fisheries for the same resources can result in nutrient stress, and in subsequently lowered reproductive output, with females choosing not to breed in hard years. Past studies have suggested potential competition between NZ sea lions and commercial fisheries; particularly arrow squid and hoki fisheries (Cawthorn, Crawley et al. 1985; Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010). A bioenergetic model estimated the amount of prey consumed by NZ sea lions each year (95% CI 17 738–18 000 tonnes) was equivalent to ~30% of arrow squid, and ~15% of hoki harvested annually by the fisheries in the Sub-Antarctic from 2000-2006 (Meynier 2010). In addition, the energy content of prey species was determined to be low-medium energy levels, but did contain all essential amino acids (Meynier 2010).

The NZ sea lion population is sensitive to age-related changes in survival and reproductive output. For marine mammals, changes in prey availability and consumption can negatively impact upon growth, condition, breeding success and survival (Chilvers 2012). Female NZ sea lions give birth to a single pup on land which they feed for 10 months (Gales 1995). During lactation, females are vulnerable to changes in resource availability due to the need to return to shore to suckle their pups. Typically, females will spend 1.5 days onshore with their dependent pup, followed by 2 days foraging at sea (Chilvers, Wilkinson et al. 2006). Females are highly philopatric, and so are unlikely to emigrate from breeding grounds in years of low prey availability (Chilvers and Wilkinson 2008). As a result, both breeding females and pups are impacted by changes in prey availability and food intake during pregnancy and lactation (Chilvers 2012). After a pup is weaned, females are able to forage further afield and gain body condition for the next breeding season (Gales 1995). Survival of pups is dependent on body condition of their mothers, and so is indirectly affected by prey quality/availability (Chilvers 2012). Growth rate of pups of NZ sea lions is lower than other sea lion species, perhaps as a result of low lipid concentration in milk during early lactation (Chilvers 2008). In NZ sea lions, Reduced quantity of prey and low energy content of remaining prey is thought to be responsible for low milk fat content (Chilvers 2008). Of all female NZ sea lions, 27% of all females that live to age three are predicted to never breed and 29% will not rear a pup that survives beyond 8 weeks (Chilvers, Wilkinson et al. 2010). Low reproductive rates, low pup growth and low milk fat composition lead to lower survival and reproductive ability in individuals, and subsequently affect population stability and growth (McMahon and Burton 2005). It was suggested by Chilvers *et al.* (2006) and Chilvers and Wilkinson (2009) that NZ sea lions may be operating at/near their physiological limit; as indicated by long, deep-dives exceeding ADL, and overall poorer condition of sea lions at the Auckland Islands when compared to those at Otago (MPI 2012).

In the Auckland Islands NZ sea lion individuals have been flipper tagged annually since 1997/1998, and subsequently re-sighted since 1998/1999 (Chilvers, Wilkinson et al. 2007). This allows for mark-recapture analysis of the population fluctuations over time. My aim was to investigate the relationship between the occurrence of main prey types in the diet, and age-related probability of survival and breeding in female NZ sea lions from 1997/1998 to 2009/2010. Prey types most important for survival and breeding success can thus be separated from less influential prey types.

4.2 METHODS

4.2.1 Study site and data collection

Scat samples were collected from different sites at the Auckland Islands. Only those collected on Enderby Island were used here. The main collection sites were Sandy Bay (SB) and South East Point (SEP). Only fresh, intact scat samples were collected opportunistically and were not linked to individuals. In this study, I have scat samples from the summer of 1999/2000 to 2012/2013, with the exception of 2004/2005 which was lost. Collection was carried out through summer, usually from December to the end of February.

NZ sea lion pups are tagged annually on Sandy Bay with individual flipper tags at approximately 3 weeks of age (Chilvers, Robertson et al. 2007). The breeding area at Sandy Bay is the second largest for NZ sea lions species with 400-500 pups born each year (Chilvers, Wilkinson, and Childerhouse 2007). Regular annual tagging of pups began in the summer of 1997/1998; prior to this there was only occasional tagging (Chilvers and MacKenzie 2010). Sex was determined at tagging by observation of genitalia. The tag-resight data used here were initially extracted from the Auckland Island sea lion database and was filtered and provided by Darryl MacKenzie (Proteus, personal communication, November 2013). Only survival and breeding data from females resighted between 1997/1998 and 2009/2010 were used due to inconsistent field effort prior to 1997/1998. The data set used for this analysis is the same as those used in MacKenzie (2011) except that I included data on juveniles (individuals younger than five years) as well as adults (MacKenzie 2011). Younger animals were included here because I was interested in the effects of the mothers' diet on the survival of pups and older juveniles. Female sea lions were defined as breeders in a given year by the liberal definition in MacKenzie (2011) where the female was either 1) confirmed to have pupped (seen nursing, or giving birth), or 2) probably pupped - seen on three or more occasions including at least one sighting in the presence of a pup (but not seen giving birth, or nursing a pup). MacKenzie (2011) found no difference in temporal patterns of breeding probabilities between liberal and strict definitions of breeders.

Sandy Bay is 400m long with a grassy sward running inland of the beach. Breeding females and pups spend most time on the beach, while males can be found on both the beach and the grassy sward (Augé, Chilvers et al. 2009). Most scats were collected on the grassy sward, and so are likely to be male biased, whereas mark recapture analysis here follows females only.

4.2.2 Scat sample processing– as in chap 2

4.2.3 Scat sample identification – as in chap 2

4.2.4 Data analysis

4.2.4.1 Prey type occurrence

Eleven main prey species were identified in scat samples in chapter 2; opalfish (*Hemerocoetes spp.*), rattail (Macrouridae) and red cod (*Pseudophycis bachus*), octopus (*Octopus sp.*) and arrow squid (Ommastrephidae), Ling (*Genypterus blacodes*), smallscaled cod (*Paranotothenia sp.*), hoki (*Macruronus novaezelandiae*), triplefin (*Tripterygiidae*), fur seal (*Arctocephalus forsteri*) and giant octopus (*Enteroctopus zealandicus*). These species were modelled separately against probability of survival/breeding. The number of occurrences of a prey type each year was sampled from a binomial distribution to estimate its probability of occurrence (PO) in a scat. This approached allowed me to account for uncertainty in PO due to sampling error, which was especially important in years with small numbers of scat samples. In some years we have no diet information (1997/1998, 1998/1999 and 2004/2005); to infer probability distributions of PO for years with few or no data we assumed the logit of PO to be normally distributed among years. The logit of PO was used as the predictor of survival and breeding because probability of breeding was also modelled using a logit link (i.e. the logit of survival or breeding probability was assumed to have a linear relationship with logit of PO).

4.2.4.2 Survival and breeding modelling

I analysed the tag-resight data using mark-recapture techniques in WinBUGS to model the effects of diet on survival and breeding of female sea lions (Lunn, Thomas et al. 2000). See Appendix 4-2 and Appendix 4-3 for code used to run models. Each model was run for 10,000 iterations, following a burn-in of at least 4000 iterations. I used the CUT function in WinBUGS to ensure a one-way flow of information; i.e. the models were set up so estimation of survival/breeding probability was affected by the predictor (logit PO), but survival/breeding did not affect PO. The probabilities of survival/breeding fall between 0 and 1 so were defined on the logit scale; hence we were essentially using logistic regression to model the effect of diet on survival/breeding of each age group. For survival modelling I constructed a Cormack-Jolly-Seber (CJS) model with likelihood calculations which is done in two parts: 1) the surveys up to the last time the animal was encountered alive; and 2) subsequent surveys (Appendix 4-1). Breeding data were modelled similarly to survival data except re-sighting probability was not incorporated, and variation among individual females was accounted for by including the female's identity as a random effect. First and last sightings for each individual were not included in the model due to years where breeding status is indeterminate for a female (too young, unknown, or emigrated away). For both survival and breeding analyses a null model was built where age related survival and breeding was estimated without the covariate of prey type included. This tested the null hypothesis that survival/breeding probability was not affected by amount of a prey type in the diet.

4.2.4.3 Age effects

Age effects on survival were incorporated into each model by grouping individuals into four age classes based on biological knowledge of NZ sea lions: 1) animals aged <1 year old, 2) animals aged 1-3, 3) animals aged 4-14, and 4) animals aged 15+. I was interested in the survival of pups less than one year old since they are dependent on their mother for nourishment and are indirectly affected by diet of breeding adults. Individuals aged 1-3 are sub-adult and do not breed but at this stage feed independently and are directly affected by food availability. Female sea lions aged 4 – 14 are of breeding age, while animals ages 15+ are expected to show a decline in survival due to old age. I used the same age classes for breeding except that I excluded pups and juveniles aged 0 – 3 from the analysis. Age effects were incorporated into models by setting the youngest age class (<1 year old for survival models; 4-14 years for breeding models) as an intercept term, with subsequent age classes showing cumulative effects of aging on survival/breeding probabilities. Tag loss can lead to underestimation of survival, since mortality can be overestimated (MacKenzie 2011). However tag loss was not incorporated into my models, since unaccounted for it underestimates survival a small amount which we can assume to be consistent over time (MacKenzie 2011).

4.2.4.4 Model comparison

In addition to the null models constructed for both survival and breeding analyses; models representing the 11 main prey species (>10%FO) defined in Chapter 2 were compared within each age group for survival probability (11 x 4 age groups; n=44), and breeding probability (11 x 2 age groups; n=22). Model quality was assessed by using the deviance information criterion (DIC) which is a hierarchical modelling generalization of the AIC (Akaike information criterion). It is useful in Bayesian model selection where the posterior distributions of the models have been estimated by Markov chain Monte Carlo (MCMC) simulation. The model with the smallest DIC is estimated to be the model that would best predict a replicate dataset which has the same structure as that currently observed. DIC is calculated over all age groups so identifies the highest quality models for survival for all age groups. Therefore DIC of important prey types (best models) for survival/breeding are the *same* across age groups; but the relationship between prey types and survival/breeding may be different *within* each age group. Important differences in DIC roughly follow: >10 can rule out models with higher DIC, 5-10 substantial difference but cannot rule out, <5 models are of similar quality (Lunn, Thomas et al. 2000). As such, only models within 10 DIC of the best model are shown graphically.

4.2.4.5 Finite rate of increase (λ)

I used a leslie matrix to calculate the finite rate of increase of the population (λ) at various levels (PO) of a prey type in the diet. I aimed to estimate the growth rate (or decline rate) of the population when the age structure had stabilised. A λ value of 1 indicates a stable population whereas values λ>1 indicates population growth, and λ<1 indicates population decline. I modelled λ by building a deterministic model incorporating age-related survival and breeding estimates for each model (hoki, smallscaled cod and ling). I used prey types represented by models that were better than, or comparable to, the null model for survival or breeding models (Table 4-1).

4.3 RESULTS

Survival estimates varied between models for age classes but overall survival probability was highest for juveniles aged 1-3 years, followed by adults aged 4 – 14 years, and lowest for pups aged less than one year (Appendix 4-4). Breeding estimates showed that adults aged 4 – 14 had a higher breeding probability than those aged older than 15 years (Appendix 4-5).

4.3.1 Overall model comparison

I compared occurrence of main prey types in diet of NZ sea lion to survival and breeding probability from 1998 to 2010. Based on DIC the best models for predicting survival of all age groups were hoki and smallscaled cod (Table 4-1); however none of the models incorporating prey type were better than the null model. Breeding probability was most closely correlated with ling and hoki. These were the only models that were better than the null model (Table 4-1). For survival and breeding probability combined, hoki was the only model that had a predictive capacity comparable to the null model (Table 4-1).

Table 4-1: Model comparison of influence of main prey types on survival and breeding probability of NZ sea lions from 1998 to 2010. DIC is a measure of the quality of the models, with lower DIC values indicating better predictive capacity. Here DIC compares quality of a model (prey type) over all age groups, which are modelled independently against %PO of prey types. DIC values in bold are those within ~10 of best model, and Δ stands for "change in".

Model	**Survival**		**Breeding**		**Total**	
	DIC	**ΔDIC**	**DIC**	**ΔDIC**	**DIC**	**ΔDIC**
Null model	**10521.7**	**0.0**	**3900.4**	**6.8**	**14422.1**	**0.0**
Hoki	10536.4	14.7	**3895.3**	**1.7**	**14431.7**	**9.6**
Smallscaled cod	**10532.3**	**10.6**	**3904.2**	**10.5**	14436.5	14.4
Ling	10547.1	25.4	**3893.6**	**0.0**	14440.7	18.6
Fur seal	10542.7	21.0	3905.2	11.6	14447.9	25.9
Giant octopus	10542.5	20.8	3909.8	16.2	14452.3	30.2
Opalfish	10550.2	28.5	3907.0	13.4	14457.2	35.2
Arrow squid	10566.7	45.0	3905.6	12.0	14472.3	50.2
Octopus sp.	10573.9	52.2	3910.1	16.5	14484.0	61.9
Rattail	10596.6	74.9	3907.2	13.5	14503.8	81.7
Red cod	10649.0	127.3	3909.3	15.7	14558.3	136.3
Triplefin	10686.0	164.3	3904.1	10.5	14590.1	168.0

4.3.2 Finite rate of increase

I used prey types hoki, smallscaled cod and ling to model the finite rate of increase under various levels of these prey types in the diet of NZ sea lions (Figure 4-1). Increased PO of hoki and ling increase λ until the population stabilisies (λ=1) and even begins to grow (λ>1) for hoki (PO >0.35) and ling (PO >0.3). However these values of λ are only obtained at levels of PO twice that observed in the 13 period examined in Chapter 2, where the highest %FO of hoki in any year was ~15%, and ~21% for Ling. Increased smallscaled cod initially decreased population growth (Figure 4-1) but then begins to increase λ, however even at a PO of 0.4 there is still no population growth (λ<1) (Figure 4-1).

4.3.3 Survival probability

I could not reject the null model for survival since it had the best predictive capacity of all modes; however I presented the results for two best prey models (smallscaled cod and hoki) due to their high overall quality (Table 4-1). In pups aged <1 year old, sub-adult sea lions aged 1-3 years old, and adult female's aged 4 – 14 probability of survival was higher with increased smallscaled cod and hoki in the diet (Figure 4-2). In older individuals aged more than 15 years old, we see opposing trends to the other age groups, where survival is decreased by increased smallscaled cod (Figure 4-2).

4.3.4 Breeding probability

Ling and hoki had better predictive capacity than the null model (ΔDIC of >5), indicating that the correlation between these prey types and breeding probability is significant (Table 4-1). Thus, we can reject the null model and conclude that there is a positive relationship between ling, hoki and breeding probability. For females aged 4 – 14, increased ling and hoki in the diet predicts an increase in the probability of breeding (Figure 4-3). The same trends can be seen in females aged over 15 years (Figure 4-3).

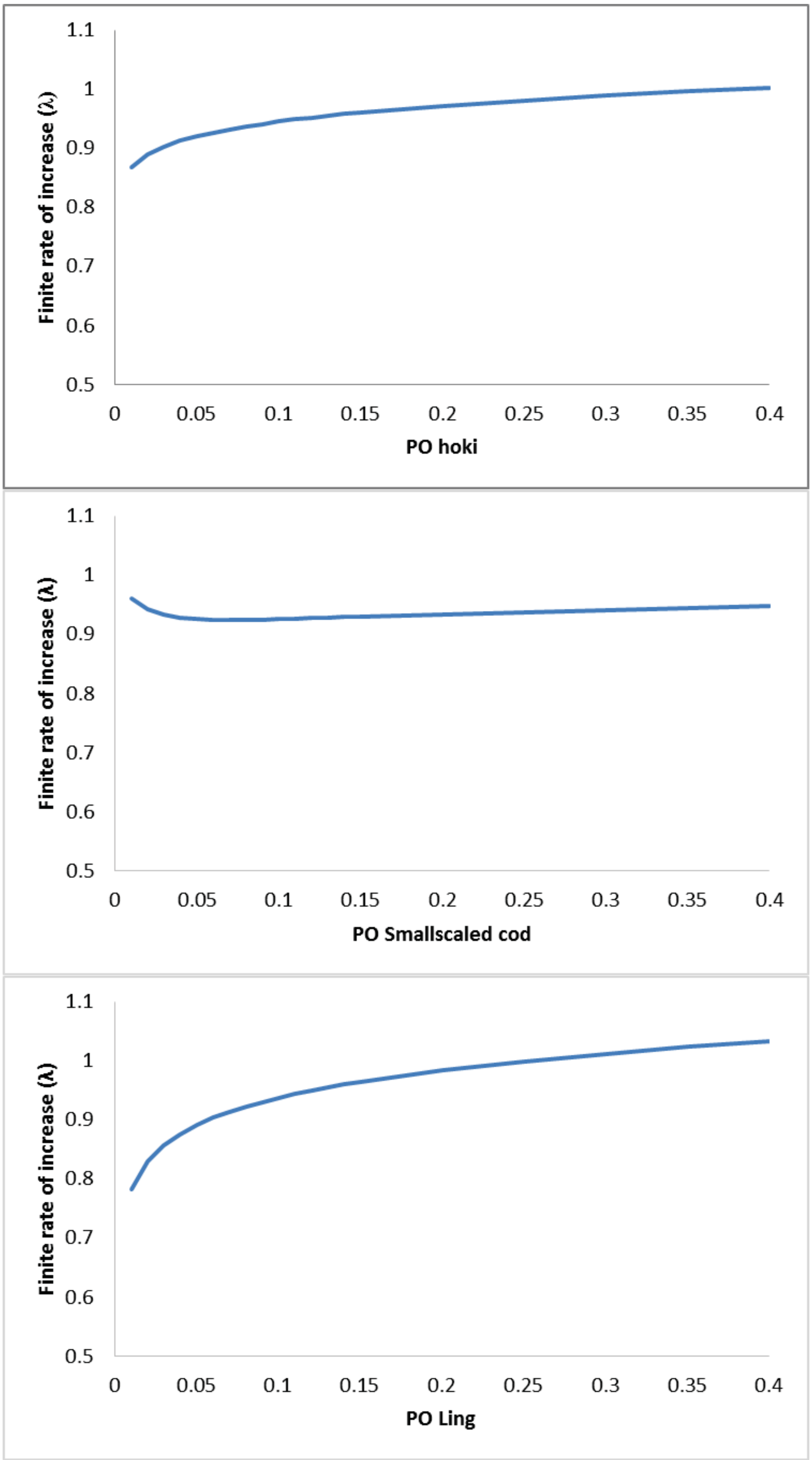

Figure 4-1: Finite rate of increase (λ) of the NZ sea lion population as calculated with reference to significant models hoki, smallscaled cod and ling. A λ value of 1 indicates a stable population whereas values λ>1 indicate population growth, and λ<1 indicates population decline.

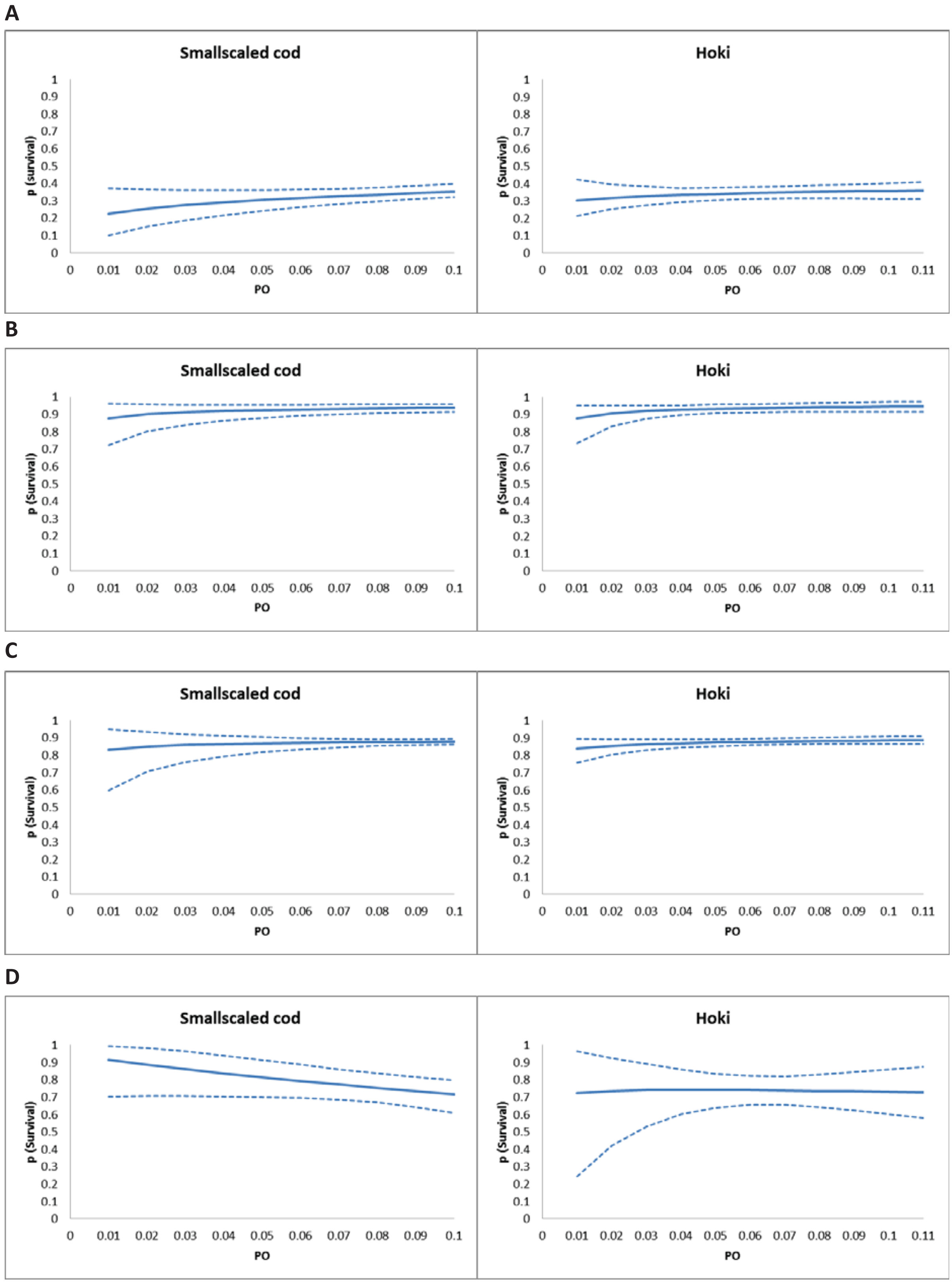

Figure 4-2: Relationship between occurrence of prey types in the diet and annual survival of female NZ sea lions; A) < 1 year old, B) 1-3 years old, C) 4 – 14 years old and D) > 15 years old. The amount of prey in the diet (PO) is the probability of a prey type occurring in a scat. Probability of survival is defined as the probability of surviving one year. Prey types presented here are those with the highest capacity to predict survival, as indicated by model fitting (Table 4-1).

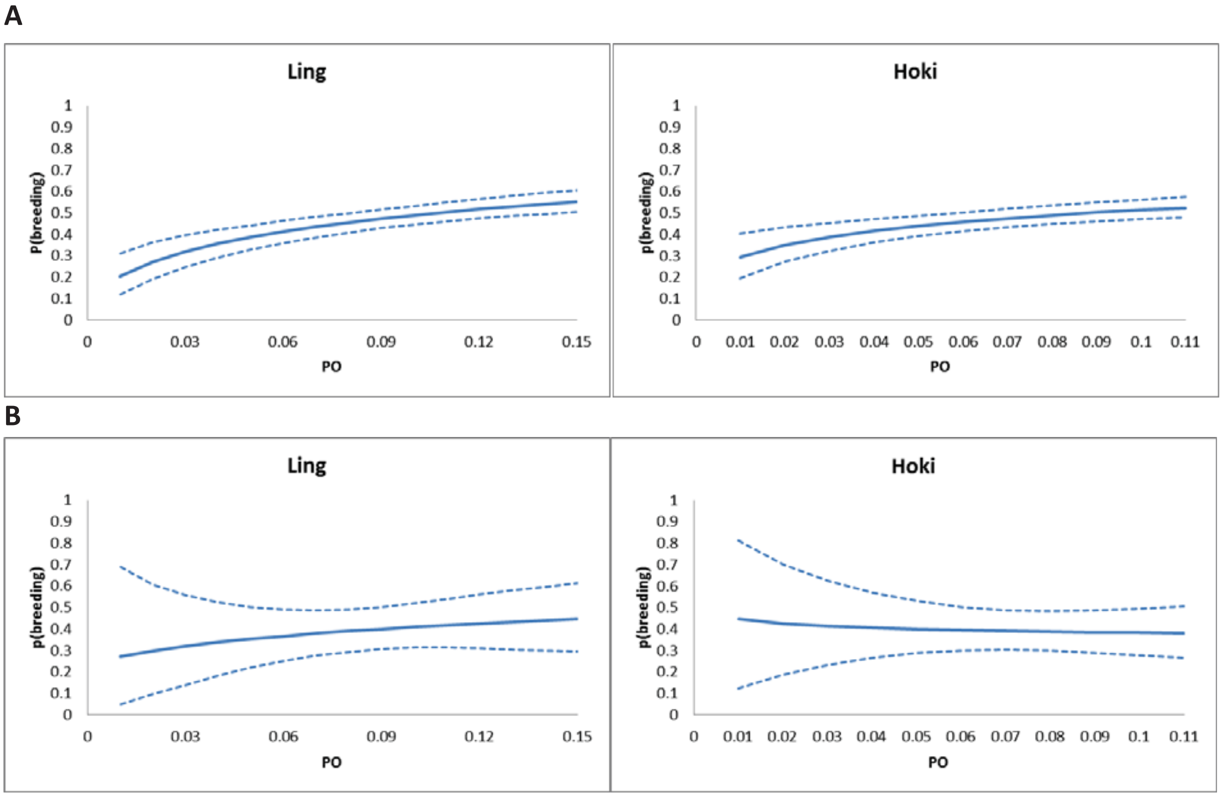

Figure 4-3: Relationship between occurrence of prey types in the diet and breeding probability of female NZ sea lions; A) 4 – 14 years old and B) > 15 years old. The amount of prey in the diet (PO) is the probability of a prey type occurring in a scat. Probability of survival is defined as the probability of surviving one year. Prey types presented here are those with the highest capacity to predict breeding probability, as indicated by model fitting (Table 4-1).

4.4 DISCUSSION

I investigated survival and breeding probability of NZ sea lions with reference to the amount of main prey species in the diet from 1997/1998 to 2009/2010. Survival probability is best explained by the null model (Table 4-1), indicating that survival is not significantly affected by the amount of any one prey type in the diet. Smallscaled cod and hoki have the best predictive capacity after the null model; hoki was correlated with an increase in survival for all age groups, while smallscaled cod predicted an increase in survival for all age classes except individuals over 15 years (Figure 4-2). In contrast, breeding probability is better explained by the amount of hoki and ling in the diet than by the null model (Table 4-1), perhaps helping to explain the decline in pup production in the last 20 years. The greater effect of prey types on breeding over survival makes biological sense when resources may be limiting population growth. Adult female NZ sea lions limited by prey availability may have enough food to survive but may choose not to invest in energetically expensive breeding. This would buffer the observed effect on survival since we would re-sight individuals that are alive but perhaps not in body condition to breed. The declining pup production in the Auckland islands (Chilvers, Wilkinson et al. 2010) is in line with this reasoning. If valuable prey stocks like ling and hoki continue to decline in the diet we may see a significant impact on survival not seen here.

4.4.1 Limitations

NZ sea lions are generalist feeders at a population level, with a varied diet including finfish, cephalopods and crustaceans (MPI 2012). I was interested in determining the main prey types which were most influential in survival and breeding probability of female sea lions in the Auckland Islands. Diet was studied in this project by examining scats of NZ sea lions collected on Enderby Island. Scat and regurgitate samples are biased towards less digestible prey that leave behind identifiable hard parts. Scat samples in particular are likely to contain more finfish and less cephalopods when compared to regurgitates (Pierce and Boyle 1991). Scats collected in this study are male-biased since many were collected on the grassy sward on Sandy bay, where there are more male sea lions. Female sea lions are more likely to spend time on the beach, where scats are harder to collect due to territorial males and sea birds eating scats (Augé, Chilvers et al. 2009). In contrast, all survival and breeding probabilities are estimated using tag-resight data of female sea lions tagged on Enderby Island. The diet of female and male sea lions differ in that females consume a greater amount of opalfish according to stomach contents (Meynier, Mackenzie et al. 2009); and more arrow squid, and less red cod and scampi according to QFASA (Meynier, Morel et al. 2010). However we can still gain valuable information by comparing male biased diet data with survival and breeding of females since fluctuations in prey species over time is still documented. Likewise the impacts on survival and breeding of females is relevant to males, even though they are not constrained in their foraging as females are, they are still susceptible to nutritional stress and would demonstrate lowered survival and breeding probability as females do. Scats collected are also likely to be biased towards adult sea lions, with fewer juvenile scats. Age effects are important to consider since estimation of survival and breeding probabilities is dependent on individual age. The survival of pups aged less than one year is dependent on body condition of adult females. Females return to nurse pups after spending 2 days foraging at sea (Chilvers, Wilkinson et al. 2006). Yearlings and 2 year olds are smaller than adults and likely to forage in shallow areas closer to breeding grounds (Meynier, Mackenzie et al. 2009). Incidentally their diet would contain less deepwater species such as opalfish and octopus. The influence of diet on survival and breeding in adult females can be directly calculated from diet information, given male biases. Adult females consume more deepwater species than juveniles (aged 1-3). Older individuals aged more than 15 years would presumably target similar species to prime-aged females. However, young males not large enough to be competitive during the breeding season will still be represented within the diet data making it applicable to analysis of survival in juvenile female NZ sea lions.

4.4.2 Diet impacts on survival and breeding

Hoki is the most important overall species for positively influencing survival and breeding in female NZ sea lions (Table 4-1). Hoki was the only species overall (for both survival and breeding probability) that was comparable (i.e. within ~10 DIC) of the null model (Table 4-1). The occurrence of hoki in the diet has a positive correlation with estimated survival and breeding probabilities (Figure 4-2; Figure 4-3). For breeding probability, hoki was a significantly (>5 DIC) higher quality than the null model indicating this species is important for breeding in NZ sea lions. In addition, the finite rate of increase (λ) rises with increased hoki in the diet (Figure 4-1) to the point where the population decline has stabilised (PO > 0.35). The PO required to reach λ≥1 is twice that seen in the 13 year study period examined in Chapter 2 (%F0 >15%) but this level may have been reached historically (pre 1988), when CPUE data shows that hoki were much more abundant in the environment (Chapter 3; Figure 3-4). Hoki are large fish reaching at least 142cm and so represent an energetically valuable prey for NZ sea lions (McMillan 2011). They are widely distributed around New Zealand to depths of 1200m, with larger individuals found in deeper waters (McMillan 2011). This is in line with the deep diving behaviour of female NZ sea lions in the Auckland Islands (Chilvers and Wilkinson 2009), where targeting hoki would result in large energetic returns for relatively small output. Hoki fisheries impact on NZ sea lions not only by removing hoki from the environment, but also via by-catch of sealions inducing mortality, and by-catch of other sea lion prey species. Captures of NZ sea lions in fisheries vessels are most common close to the Auckland Islands or nearby on the Stewart-Snares shelf. Substantial changes in biomass of hoki have taken place since fishing began (MPI 2013). Year round fishing for hoki increased fishing effort to a peak between 1997-98 and 2003-04, after which fishing effort has been reduced by TACC reductions (MPI 2013). The main commercial by-caught species of the hoki fishery are hake, ling, silver warehou, jack mackerel and spiny dogfish (MPI 2013). Of these, ling is a main prey species (>10% FO) of NZ sea lions (Chapter 2). Ling models had significantly better predictive capacity for breeding probability than the null model (Table 4-1) indicating these species have a positive impact on breeding. The positive effect of ling and hoki is more clearly pronounced in females aged 4-14 than older individuals (Figure 4-3). Ling increases λ more quickly than hoki and surpasses 1 at PO 0.3 in the diet (Figure 4-1) where the NZ sea lion population would be projected to actually start increasing. They are a valuable prey species, reaching 200cm (McMillan 2011), with an average size of 80-120cm in length and weighing 5-20kg (Paul 2000). They inhabit rough ground and muddy sea floor in depths up to 900m (McMillan 2011). This habitat compares with foraging behaviour of adult female NZ sea lions of breeding age (Chilvers, Amey et al. 2011). They are widespread in New Zealand, particularly south of 40° S (MPI 2013). They are caught by long line and trawl fisheries; however since 2000 there has been declining trend in catches taken by line vessels. To offset this decline, trawl effort has been increased including the waters of the Auckland Islands area (MPI 2013). Long liners in the Auckland Islands LIN 6 fishery have undercaught their TACC by 76% in 2011-2012.

Fishery operations impact on prey availability for NZ sea lions not only by targeting the same species; but also by catching non-target species through the use of non-specific fishing techniques such as trawling. Commercially valuable by-caught species include NZ sea lion main prey species hoki and ling which were found to be important for survival and reproduction in this study. By-caught species that are not commercially valuable are discarded on site and estimated to range from 1 540 to 5 140 t per year (2.5kg of discard for every 1kg of scampi) from 1999–00 to 2005–06. Smallscaled cod are one such commercially worthless species and are likely caught in arrow squid and scampi trawl fisheries (MPI 2013), and then discarded as by-catch (McMillan 2011). Increased occurrence of smallscaled cod in the diet increased survival for all age groups with the exception of individuals over 15 years old (Table 4-1; Figure 4-2). They inhabit rocky shorelines which is perhaps more suited to juvenile sea lions which forage in shallower areas (Meynier, Mackenzie et al. 2009); and the open shelf down to 1000m, which is an important foraging area for lactating female NZ sea lions (Paul 2000; Chilvers 2009; Meynier 2009). Smallscaled cod represent a lesser energetic reward than hoki, growing to about 65cm (McMillan 2011), but with an average length of 25-35cm (Paul 2000). The negative relationship between breeding and abundant smallscaled cod in the diet may be due to sea lions hunting this smaller, less valuable species, when larger species such as hoki or ling are unavailable.

4.4.3 Conclusions

I investigated survival and breeding probability of NZ sea lions with reference to the amount of main prey species in the diet from 1997/1998 to 2009/2010. Breeding probability is better explained by the amount of hoki and ling in the diet, than by the null model (Table 4-1), perhaps helping to explain the decline in pup production in the last 20 years (Chilvers, Wilkinson et al. 2010). The PO of hoki required to reach λ≥1 is twice that seen in the 13 year study period examined in Chapter 2 but this level may have been higher historically, when CPUE data shows that hoki were much more abundant in the environment (Chapter 3; Figure 3-4). Ling is an extremely energetically valuable prey item that increases breeding probability and is predicted to allow λ≥1 and the NZ sea lion population to grow. Survival is not significantly affected by the amount of any one prey type in the diet. Smallscaled cod have the best predictive capacity after the null but are likely by-caught in trawl operations and discarded since they are not commercially viable. The greater effect of prey types on breeding over survival makes biological sense when resources may be limiting population growth. Adult female NZ sea lions limited by prey availability may have enough food to survive but may choose not to invest in energetically expensive breeding. This is further exacerbated by the overall low reproductive ability and output of NZ sea lions (Chilvers and MacKenzie 2010). If females indeed neglect to breed in years of low prey availability this would buffer the observed effect on survival since we would re-sight individuals that are alive but perhaps not in poor body condition. If valuable prey stocks like ling and hoki continue to decline in the diet we may see a significant impact on survival not seen here. Reduction in prey stocks by fishery operations via targeted removal, by-catch or destruction of habitat can lead to nutrient stress in NZ sea lions (Robertson and Chilvers 2011). Population stability may then be affected by reduced survival and reproductive output as a result of nutrient stress; this can lead to population decline.

4.4.4 Recommendations

Monitoring important prey types like hoki and ling in the Auckland islands region is important to reduce the competitive effects of fisheries operations on NZ sea lions. Squid and scampi trawl fisheries are also likely to have an impact on the decline of NZ sea lion population by removing prey biomass via by-catch of main prey types. To reduce the indirect effects of fisheries on the decline of NZ sea lions we need to re-evaluate current methods, and take more extreme action. Changing fishing methods from trawling to jigging would reduce by-catch, habitat modification and mortality of sea lions. Alternatively extending the marine reserve to the edge of the Auckland islands' shelf where sea lions forage would dramatically reduce overlap between fisheries and sea lions. Restrictions on fisheries so that operations are suspended during the breeding season would reduce temporal overlap. The indirect impacts of fishing operations need to be considered along with the more obvious direct impacts. More research is needed as the population continues to decline, and greater measures put in place for their conservation. Continue to monitor diet and perhaps more noticeable effects on the population, such as female body condition (in addition to survival), to validate the theory that females may be unable to breed in hard years.

5 CHAPTER 5

LONG TERM DIET OF THE NEW ZEALAND SEA LION - GENERAL DISCUSSION

Female New Zealand sea lions and pups on the beach at Sandy Bay, on Enderby Island.

The diet of the New Zealand (NZ) sea lion was investigated using hard part analysis of scats and regurgitates. In chapter 2 I examined the long term diet of NZ sea lions at Enderby Island based on scats and regurgitates collected from 2000 to 2013. In chapter 3 I investigated long term trends of main prey species in the diet, and how these related to availability in the environment, indicating functional response. In chapter 4 I explored the relationship between main prey species in the diet, and effects on survival and breeding probability. The purpose of this general discussion is to integrate the main research outcomes of my thesis, and put these into wider context of NZ sea lion conservation.

Past studies have identified potential competition between NZ sea lions and commercial fisheries, particularly arrow squid and hoki fisheries (Cawthorn, Crawley et al. 1985; Childerhouse, Dix et al. 2001; Meynier, Mackenzie et al. 2009; Meynier, Morel et al. 2010). Competition with fisheries for the same resources can result in nutrient stress, and subsequent lowered reproductive output, with females choosing not to breed in hard years. For marine mammals, changes in prey availability and consumption can negatively impact upon growth, condition, breeding success and survival (Chilvers 2012). Survival of pups is dependent on body condition of their mothers, and so is indirectly affected by prey quality/availability (Chilvers 2012). Growth rate of pups of NZ sea lions is lower than other sea lion species, perhaps as a result of low lipid concentration in milk during early lactation (Chilvers 2008). In NZ sea lions, Reduced quantity of prey and low energy content of remaining prey is thought to be responsible for low milk fat content (Chilvers 2008). It was suggested by Chilvers *et al.* (2006) and Chilvers and Wilkinson (2009) that NZ sea lions may be operating at/near their physiological limit, as indicated by long, deep-dives exceeding ADL, and overall poorer condition of sea lions at the Auckland Islands when compared to those at Otago (MPI 2012).

5.1 Limitations

The literature review on dietary methods in chapter 1 discussed the advantages and disadvantages of hard part analysis of scats and regurgitates. Analysis of pinniped scats and regurgitates has been used to determine diet composition via identification of hard parts remaining after digestion, and to estimate the number and size of prey ingested (Tollit, Steward et al. 1997). This technique has advantages over others; it’s non-invasive, uncomplicated and cost-effective. Scat sampling can also deliver sample sizes much larger than techniques requiring capture or by-caught animals. However scat sampling produces biases due to differential erosion and passage rate of prey items in relation to their size, shape and consistency. Larger squid beaks have lower recovery in scats than smaller (Staniland 2002). Smaller fish otoliths are digested faster than larger and so fish with larger otoliths may be overestimated (Browne, Laake et al. 2002; Arim and Naya 2003; Christiansen, Gamst Moen et al. 2005). Recovery rates of prey species in scat and regurgitates vary depending on species, but are increased when all diagnostic structures (such as vertebrae, jaw bones, and teeth) are included in analysis (Orr and Harvey 2001; Cottrell and Trites 2002; Staniland 2002; Tollit, Wong et al. 2003; Phillips and Harvey 2009). These biases can hinder accurate diet quantification, but do not prevent spatial or temporal comparisons (Tollit, Heaslip et al. 2006). In chapter 2 I excluded the data from the 2012/2013 season, which was not validated by prey accumulation curves constructed in chapter 2 due to small sample size. In chapter 3 I included raw data from 1995 to 1997 and 2013 to extend the timeframe to better examine long term trends (Childerhouse, Dix et al. 2001). However, sample sizes in these years were small (n = around 30), so estimates were less precise than in years with larger scat collections. In Chapter 3 I used CPUE as a proxy for true abundance of prey in the environment. Although CPUE is an indirect measure of abundance it is useful in that it does not interfere with harvesting and data are easily collected (Maunder, Sibert et al. 2006). Decreases in CPUE over time can signify overexploitation, while stable CPUE implies sustainable harvesting. CPUE can sometimes be used to estimate true abundance, but in this study it is used to infer trends in abundance over time. When correlating occurrence of a species in diet with abundance in the environment, I assume that occurrence is independent of the occurrence of other species. Scats collected in this study are male-biased since many were collected on the grassy sward on Sandy Bay, where there are more male sea lions. Female sea lions are more likely to spend time on the beach, where scats are harder to collect (Augé, Chilvers et al. 2009). In contrast, all survival and breeding probabilities in Chapter 4 were estimated using tag-resight data of female sea lions tagged on Enderby Island. The diet of female and male sea lions differ in that females consume a greater amount of opalfish according to stomach contents (Meynier, Mackenzie et al. 2009); and more arrow squid, and less red cod and scampi according to QFASA (Meynier, Morel et al. 2010). Scats collected are also likely to be biased towards adult sea lions. However we can still gain valuable information by comparing male biased diet data with survival and breeding of females since fluctuations in prey species over time is still documented. Likewise the impacts on survival and breeding of females is relevant to males even though they are not constrained in their foraging as females are, they are still susceptible to nutritional stress and would demonstrate lowered survival and breeding probability as females do.

5.2 Diet composition over 13 years at Enderby Island

Common prey of New Zealand sea lion based on scat samples collected at Enderby Island, from 1999/2000 to 2012/2013, were opalfish, rattail, red cod, octopus, arrow squid, ling, smallscaled cod, hoki, triplefin, fur seals and giant octopus (Chapter 2). Most of these are demersal species, and NZ sea lions feed on or near the sea floor at depths more than 200 m. Inter-annual variation is evident, mainly due to fluctuations in dominant species opalfish, rattail, red cod, fur seal and octopus.

Differences in important prey species between scat and regurgitate collections show biases these two methods produce. Both scat and regurgitate samples confirm important prey types that appear in both types of samples. Prey taxa found here are in line with recent studies of diet in the Auckland islands, with some notable differences from an earlier study (Childerhouse, Dix et al. 2001). This study of 13 years of routine sampling represents the longest time series of diet data available for this or any pinniped species.

Resource competition between NZ sea lions and commercial fishery operations is a possibility and could have flow on effects for the breeding population at the Auckland islands. Red cod, arrow squid, ling and hoki are harvested commercially (MPI 2013), and are main prey species of NZ sea lions from 1999/2000 to 2012/2013. These fish accounted for 29.2% and 30.8% of total prey by occurrence, and 11.6% and 29.1% by abundance in scats and regurgitates respectively (Table 2; Table 7). The Auckland Islands has been suggested as marginal habitat for NZ sea lions, which operate at their physiological limit while diving (Chilvers, Wilkinson et al. 2006). New Zealand sea lions are generalist feeders, taking prey opportunistically based on what is available in the environment (Lalas 1997; Meynier, Mackenzie et al. 2009). This leads to direct interactions with fisheries in the form of incidental deaths, and likely indirect resource competition for the aforementioned important prey species. The edges of the Auckland Islands shelf are highlighted in this study as important foraging grounds for NZ sea lions, where prey resources can be found reliably and in high abundance. This key area is outside the protected area and is open to commercial fishery operations (MPI 2013). However the shelf is key for NZ sea lions too, as is evident by their consistent travel to forage there, despite being far from rookeries and females having dependant pups onshore (Chilvers, Wilkinson et al. 2005). This area may contain the only prey resources rich enough in this marginal habitat to provide for the energy requirements of the deepest diving, slowest breeding, and only endemic otariid of NZ (Gales and Mattlin 1997; Chilvers, Wilkinson et al. 2010).

5.3 Long-term trends in the diet and functional response to changes in prey availability

Results from this research show clear long-term trends in main prey species that may be influencing the decline of this population (Figure 3-1). There has been a marked decline in the occurrence of giant octopus in the diet over time. Reduction in large prey types such as giant octopus and hoki and may force sea lions to take more readily available prey. This could explain the observed increase in less energetically rewarding prey types such as smaller *Octopus* spp and opalfish (Figure 3-1). Lowered fish:cephalopod ratio in the diet and increased contribution of cephalopod species such as arrow squid and *Octopus* sp. may lower the overall quality of diet when compared to a diet higher in fish species (Figure 3-2). Arrow squid and hoki are both targeted commercially in the Auckland Islands region during the breeding season of NZ sea lions (MPI 2013).

The best models for functional response by sea lions to increased prey density were those that incorporated random annual variation (Table 3-2). This suggests that abundance of prey species is not the only variable affecting intake of prey by sea lions. Arrow squid and hoki were best represented by Type II models indicating that foraging by sea lions is not unrestricted. Foraging of prey at high densities may indicate a satiation response, preference for an alternate species, or competition imposed by fisheries take. Resource competition imposed by fisheries could restrict intake by sea lions, or force prey shifts to species not commercially harvested. Uncertainty in resource availability puts pressure on an already stressed population that may be operating at its physiological limit (Chilvers, Wilkinson et al. 2006). Lactating females and dependent pups are particularly vulnerable to changes in resource availability (Meynier, Morel et al. 2010). A shortage of high quality or abundant food could lead to reduced reproductive output and survival, with no behavioural means to buffer the impacts on the population.

5.4 Effects of diet on survival and breeding for female NZ sea lions

I investigated survival and breeding probability of NZ sea lions with reference to the amount of main prey species in the diet from 1997/1998 to 2009/2010. Survival probability is best explained by the null model (Table 4-1), indicating that survival is not significantly affected by the amount of any one prey type in the diet. Smallscaled cod and hoki have the best predictive capacity after the null model; hoki was correlated with an increase in survival for all age groups, while smallscaled cod predicted an increase in survival for all age classes except individuals over 15 years (Figure 4-2). In contrast, breeding probability is better explained by the amount of hoki and ling in the diet than by the null model (Table 4-1), perhaps giving a clue to the decline in pup production in the last 20 years. The null models predict that prey types will show no relationship with breeding/survival probability. The greater effect of diet on breeding than survival makes biological sense when resources may be limiting population growth. Adult female NZ sea lions limited by prey availability may have enough food to survive but may choose not to invest in energetically expensive breeding. This would buffer the observed effect on survival since we would re-sight individuals that are alive but perhaps not in body condition to breed. The declining pup production in the Auckland islands (Chilvers, Wilkinson et al. 2010) is in line with this reasoning. If valuable prey stocks like ling and hoki continue to decline in the diet we may see a significant impact on survival not seen here. Reduction in prey stocks by fishery operations via targeted removal, by-catch or destruction of habitat can lead to nutrient stress in NZ sea lions (Robertson and Chilvers 2011). Population stability may then be affected by reduced survival and reproductive output as a result of nutrient stress; this can lead to population decline.

Hoki increases probability of both survival and breeding so that the finite rate of increase surpasses 1 and the population begins to grow when the hoki occurs in 35% of scats (PO = 0.35) (Figure 4-1).

The PO value required for hoki to produce λ≥1 is twice that seen in the 13 year study period examined in Chapter 2 (%F0 >15%) but this level may have been reached historically (pre 1988), when CPUE data shows that hoki were much more abundant in the environment (Chapter 3; Figure 3-4). Ling is an extremely energetically valuable prey item that increases breeding probability and is predicted to allow the NZ sea lion population to grow at PO of >0.3 (Figure 4-1). These important prey types are threatened by fishery operations which target hoki and ling, and by-catch smallscaled cod in the squid and scampi trawl fisheries operating in the Auckland Islands region.

5.5 Conclusions and recommendations

To quantify potential resource competition, we need further studies into the relationship between fisheries catch and occurrence in the diet. Fisheries remove a significant quantity of resources from the environment; I recommend future studies where fisheries catch is examined with reference to sea lion diet. Monitoring important prey types like hoki and ling in the Auckland islands region is important to reduce the competitive effects of fisheries operations on NZ sea lions. Squid and scampi trawl fisheries are also likely to have an impact on the decline of NZ sea lion population by removing prey biomass via by-catch of main prey types. To reduce the indirect effects of fisheries on the decline of NZ sea lions we need to re-evaluate current methods, and take more extreme action. Changing fishing methods from trawling to jigging would reduce by-catch, habitat modification and mortality of sea lions. Alternately extending the marine reserve to the edge of the Auckland islands' shelf where sea lions forage would dramatically reduce overlap between fisheries and sea lions. Restrictions on fisheries so that operations are suspended during the breeding season would reduce temporal overlap. The indirect impacts of fishing operations need to be considered along with the more obvious direct impacts. For instance monitoring female body condition, in addition to survival, may help to validate the theory that females may choose not to breed in some years. The effects of any management changes, such as an increase in the marine reserve, should be estimated to ensure management is effective. It is without question that more research is needed as the NZ sea lion population continues to decline, and greater measures must be put in place for their conservation.

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APPENDICES

Appendix 3-1: WinBUGS code for fitting model to the diet PO and CPUE data. Comments in WinBUGS are in blue and indicated by hashes.

Scat models

```
Model # unconstrained estimates of proportion of species x in scats for each year

{
    for (i in 1:n.years) {
        p[i] <- 1-q[i]
        logit.q[i] ~ dnorm(0,0.001)
        logit(q[i]) <- logit.q[i]
        abs[i] ~ dbin(q[i],n.scat[i])
    }
}


Model # Type I model
{

    log.a ~ dnorm(0,0.01)
    a <- exp(log.a)
    b ~ dnorm(0,0.01)
    sd ~ dunif(0,10)
    tau <- pow(sd,-2)

    for (i in 1:n.years) {
        re[i] ~ dnorm(0,tau)                        # random variation among years
        abs[i] ~ dbin(q[i],n.scat[i])
        log(q[i]) <- min(0,-(a*CPUE[i])+0*re[i])    # Type I without random effect
        # the "min" is necessary to avoid probabilities > 1 (problem with log link)
    }
}

Model # Type I with random effect
{

    log.a ~ dnorm(0,0.01)
    a <- exp(log.a)
    b ~ dnorm(0,0.01)
    sd ~ dunif(0,10)
    tau <- pow(sd,-2)

    for (i in 1:n.years) {
        re[i] ~ dnorm(0,tau)                        # random variation among years
        abs[i] ~ dbin(q[i],n.scat[i])
        log(q[i]) <- min(0,-(a*CPUE[i])+re[i])      # Type I with random effect
        # the "min" is necessary to avoid probabilities > 1 (problem with log link)
    }
}
```

```
Model # Type II model
{

    log.a ~ dnorm(0,0.01)
    a <- exp(log.a)
    b ~ dnorm(0,0.01)
    sd ~ dunif(0,10)
    tau <- pow(sd,-2)

        for (i in 1:n.years) {
            re[i] ~ dnorm(0,tau)                    # random variation among years
            abs[i] ~ dbin(q[i],n.scat[i])
                        log(q[i]) <- min(0,-(a*CPUE[i])/(b+CPUE[i])+0*re[i]) # Type II without random effect
            # the "min" is necessary to avoid probabilities > 1 (problem with log link)
        }
}

Model # Type II with random effect
{

    log.a ~ dnorm(0,0.01)
    a <- exp(log.a)
    b ~ dnorm(0,0.01)
    sd ~ dunif(0,10)
    tau <- pow(sd,-2)

    for (i in 1:n.years) {
        re[i] ~ dnorm(0,tau)                        # random variation among years
        abs[i] ~ dbin(q[i],n.scat[i])
        log(q[i]) <- min(0,-(a*CPUE[i])/(b+CPUE[i])+re[i]) # Type II with random effect
        # the "min" is necessary to avoid probabilities > 1 (problem with log link)
    }
}


#Raw data for %FO of species and CPUE
#Hoki
list(
n.years=14,
CPUE=c(34.4,181.9,55.5,24.6,31.9,6.7,13.4,34.4,34.5,36.5,84.8,105.2,32.7,38.3),
n.scat=c(43,62,34,62,112,112,102,67,102,66,86,97,64,67),
abs=c(43,56,30,57,108,106,94,67,93,61,79,86,61,61)      # number with no hoki
)

#Red cod
list(
n.years=15,
CPUE=c(49.0,17.0,26.7,80.6,34.0,41.8,56.7,64.5,26.7,11.9,56.2,12.8,46.7,44.6,59.2),
n.scat=c(43,62,34,62,52,112,112,102,67,102,66,86,97,64,67),
```

```
abs=c(39,57,32,35,34,69,65,73,56,67,55,58,69,45,38)      # number with no Red cod
)

#Arrow squid
list(
n.years=15,
CPUE=c(7340.0,2642.0,4396.1,3590.0,3236.5,4919.0,3450.4,9168.9,3744.9,8454.9,10612.6,10724.3,
6776.0,8335.3,6556.1),
n.scat=c(43,62,34,62,52,112,112,102,67,102,66,86,97,64,67),
abs=c(42,62,34,54,42,89,91,91,59,80,53,79,86,55,52)      # number with no arrow squid
)
```

Appendix 4-1: Construction of a Cormack-Jolly-Seber (CJS) model adapted from McCarthy (2007) with likelihood calculations done in two parts; 1) the surveys up to the last time the animal was encountered alive; and 2) subsequent surveys.

Part 1

It is known that animal *i* is alive on each occasion *j* until it was last encountered alive. However, it might be either detected ($Y_{i,j}$ = 1) or not detected ($Y_{i,j}$ = 0) on each occasion. The likelihood of each of these observations is,

$$\Phi_{i,j}\,(Y_{i,j}P_{i,j} + (1\text{-}Y_{i,j})(1\text{-}P_{i,j}))$$

where $\Phi_{i,j}$ is the animal's survival probability for the interval from *j*-1 to *j*, *Pi,j* is the probability of it being detected on occasion j, and $Y_{i,j}$ is the encounter probability. These are multiplied together to get the likelihood up to the last encounter. Random effect was incorporated for each year/survey.

Part 2

After the last animal was last encountered alive, the encounter history consists of a string of zeros, so we don't need to have $Y_{i,j}$ in the calculation. However, these zeros can occur in different ways (i.e. through death or non-detection), and this gets progressively more complex with more surveys. The probabilities can be added to obtain the likelihood of one, two, or three zeros occurring,

1: $\Phi_1(1\text{-}P_1) + 1\text{-}\Phi_1$
2: $\Phi_1\Phi_2(1\text{-}P_1)(1\text{-}P_2) + \Phi_1(1\text{-}P_1)(1\text{-}\Phi_2) + 1\text{-}\Phi_1$
3: $\Phi_1\Phi_2\Phi_3(1\text{-}P_1)(1\text{-}P_2)(1\text{-}P_3) + \Phi_1\Phi_2(1\text{-}P_1)(1\text{-}P_2)(1\text{-}\Phi_3) + \Phi_1(1\text{-}P_1)(1\text{-}\Phi_2) + 1\text{-}\Phi_1$

The final steps are to multiply the likelihoods for Part 1 and Part 2 together to get maximum likelihood estimates for the parameters. Inherent in mark-recapture studies, it is not possible to know if an animal is dead or just permanently emigrated out of the population, however permanent emigration is unlikely for NZ sea lions, due to their highly philopatric nature (Chilvers 2008).

Appendix 4-2: WinBUGs code for fitting models for prey types in the diet (PO) to tag-reqight survival data for female NZ sea lions from 1997/1998 to 2009/2010. Comments in WinBUGS are shown in blue and indicated by hashes. Null model hypothesizes that there is no relationship between age related survival and prey types in the diet.

Survival model

```
Model
{
    # Priors for survival parameters
    alpha.s ~ dnorm(0, 1.0E-6)                  # logit(survival) for juveniles
    b.ac2.s ~ dnorm(0, 1.0E-6)                  # effect of being 1+ on survival
    b.ac3.s ~ dnorm(0, 1.0E-6)                  # additional effect of being 4+ on survival
    b.ac4.s ~ dnorm(0, 1.0E-6)                  # additional effect of being 15+ on survival
    b.po ~ dnorm(0, 1.0E-6)                     # effect of prob of occurence of fish species in diet
    b.ac2po.s ~ dnorm(0, 1.0E-6)                # next 3 lines are interactions of age effects and PO
    b.ac3po.s ~ dnorm(0, 1.0E-6)
    b.ac4po.s ~ dnorm(0, 1.0E-6)

    # Priors for re-sighting parameters
    alpha.p ~ dnorm(0, 0.0001)                  # logit(re-sighting prob) for juveniles
    b.ac2.p ~ dnorm(0, 1.0E-6)                  # effect of being 1+ on re-sighting
    b.ac3.p ~ dnorm(0, 1.0E-6)                  # additional effect of being 4+ on re-sighting
    b.ac4.p ~ dnorm(0, 1.0E-6)                  # additional effect of being 15+ on re-sighting
    sd.p.t ~ dunif(0, 100)                      # sd for random variation among surveys
    tau.p.t <- pow(sd.p.t, -2)                  # convert to precision

    # Priors for distribution of binary covariate (allows missing data to be sampled)
    logit.po.c ~ dnorm(0, 0.001)                # overall mean for covariate
    sd.logit.po ~ dunif(0,10)                   # sd among years in for covariate
    tau.logit.po <- pow(sd.logit.po,-2)

    # For each year sample random survey effect and probability of hoki occurring in scat
    for (j in 2:surveys)    {
        logit.po[j] ~ dnorm(logit.po.c,tau.logit.po)
        # annual covariate (logit.po) sampled from distribution
        logit(po[j]) <- logit.po[j]   # convert covariate to real probability rather than logit
        n.pres[j-1] ~ dbin(po[j],n.scat[j-1])   # model po (prob of occurence) from scat data
        re.p.t[j] ~ dnorm(0, tau.p.t)           # assign random survey effect
    }

    # Model survival data
    for (i in 1:n.ind)  { # for each individual...
        for (j in first[i]+1:surveys) {         # for each subsequent survey...
            age[i,j-1] <- age98[i]+j-2          # calculate individual's age at start of interval
            age.effect.s[i,j]<-b.ac2.s*step(age[i,j-1]-1)+b.ac3.s*step(age[i,j-1]-4)+b.ac4.s*step(age[i,j-1]-15)
            age.effect.p[i,j]<- b.ac2.p*step(age[i,j-1]-1)+b.ac3.p*step(age[i,j-1]-4)+b.ac4.p*step(age[i,j-1]-15)
            age.po.int.s[i,j]<-  cut(logit.po[j])*(b.ac2po.s*step(age[i,j-1]-1)+b.ac3po.s*step(age[i,j-1]-4)+b.ac4po.s*step(age[i,j-
1]-15))
            logit(phi[i,j]) <- alpha.s+age.effect.s[i,j]+b.po*cut(logit.po[j])+age.po.int.s[i,j]
            # calc survival prob
            logit(p[i,j]) <- alpha.p+age.effect.p[i,j]+re.p.t[j]# calculate re-sighting probability if alive
```

```
        }

        L1[i,first[i]] <- 1
        for (j in first[i]+1:last[i])
        {
            L1[i,j] <- L1[i,j-1]*phi[i,j]*(p[i,j]*seen[i,j]+(1-p[i,j])*(1-seen[i,j])) # pr of hist when known alive
        }

        L2a[i,last[i]] <- 0          # necessary in case last[i] = surveys
        L2b[i,last[i]] <- 1
        for(j in (last[i]+1):surveys)
        {
            L2b[i,j] <- L2b[i,j-1]*phi[i,j]*(1-p[i,j]) # sum probability missed each time
            L2a[i,j] <- (1-phi[i,j])*L2b[i,j-1] # prob dead this time but missed previously
        }
        L[i] <- L1[i,last[i]]*(sum(L2a[i,last[i]:surveys])+L2b[i,surveys])
        dummy[i] <- 1
        dummy[i] ~ dbern(L[i])

    }

    for (i in 1:50)
    {
        po.new[i] <- i/100 # so values of i = 1-50 give po = 0.01-0.5
        logit(phi.new[1,i]) <- alpha.s + b.po*logit(po.new[i])
        logit(phi.new[2,i]) <- logit(phi.new[1,i]) + b.ac2.s+ b.ac2po.s*logit(po.new[i])
        logit(phi.new[3,i]) <- logit(phi.new[2,i]) + b.ac3.s+ b.ac3po.s*logit(po.new[i])
        logit(phi.new[4,i]) <- logit(phi.new[3,i]) + b.ac4.s+ b.ac4po.s*logit(po.new[i])
    }

}

.
```

Appendix 4-3: WinBUGs code for fitting models for prey types in the diet (PO) to breeding probability for female NZ sea lions from1997/1998 to 2009/2010. Comments in WinBUGS are shown in blue and indicated by hashes. Null model hypothesizes that there is no relationship between age related survival and prey types in the diet.

Breeding Model

```
Model
{
    # Priors for breeding parameters
    alpha.b ~ dnorm(0, 0.001)            # logit(breeding) for juveniles
    b.ac4.b ~ dnorm(0, 0.001)            # effect of being 4+ on breeding
    b.po.b ~ dnorm(0, 0.001)             # effect of prob of occurence of fish species in diet
    b.ac4po.b ~ dnorm(0, 0.001)                    # next 3 lines are interactions of age effects and po
    sd.fem ~ dunif(0, 10)                          # sd for random variation among surveys
    tau.fem <- pow(sd.fem, -2)           # convert to precision

    # Priors for distribution of binary covariate (allows missing data to be sampled)
    logit.po.c ~ dnorm(0, 0.001) # overall mean for covariate
    sd.logit.po ~ dunif(0,10)            # sd among years in for covariate
    tau.logit.po <- pow(sd.logit.po,-2)

    # For each year sample random survey effect and probability of hoki occuring in scat
    for (j in 1:surveys)    {
        logit.po[j] ~ dnorm(logit.po.c,tau.logit.po)  # annual covariate (logit.po) sampled
        logit(po[j]) <- logit.po[j]   # convert covariate to real probability rather than logit
        n.pres[j] ~ dbin(po[j],n.scat[j])      # model po (prob of occurence) from scat data
    }

    #Model breeding data
    for (i in 1:n.fem)      # for each adult female...
    {
        re.fem[i] ~ dnorm(0,tau.fem)      # assign random effect to each female
        for (j in 1:surveys)   {          # for each year...
            age[i,j] <- age98[i]+j-1      # calculate individual's current age
            age.effect.b[i,j] <- b.ac4.b*step(age[i,j]-15) + cut(logit.po[j])*b.ac4po.b*step(age[i,j]-15)
            logit(pb[i,j]) <- alpha.b + age.effect.b[i,j] + cut(logit.po[j])*b.po.b + re.fem[i]
            # calc prob of breeding use 0* cut if we want to run null model
            breed[i,j] ~ dbern(pb[i,j])       # sample whether breeding or not
        }
    }   # need to close loops for sampling data, and make calculation bit separate

    # Calculations for graphing
    for (i in 1:10) # Loop needs integars but you can divide by 100 below to get 0.01 to 0.11
    {
    po.new[i] <- i/100 # so values of i = 1-11 give po = 0.01-0.11
    logit(pb.new[3,i]) <- alpha.b + b.po.b*logit(po.new[i])  # calc breeding prob for 4-14 year olds
    logit(pb.new[4,i]) <- logit(pb.new[3,i]) + b.ac4.b+ b.ac4po.b*logit(po.new[i]) # for 15+
    }

}
```

Appendix 4-4: Tables showing the models results for each prey type and survival of NZ sea lions from 1997/1998 to 2009/2010. Each table shows model results for each prey type comparing age classes. Prey types shown are main prey types (>%10 of samples) from 1998 to 2010. Each node is a parameter representing the effect of PO on the survival or resighting probability, for that age group. See Footnote 1 for notation. The logit of survival and resight probability for <1 year olds is the intercept term, and the additional effect of aging is cumulative for older age classes. E.g. for age class 2, the intercept (logit of annual survival probability when logit(PO) = 0) is given by alpha.s + b.ac2.s, and the estimated change in logit survival when logit(PO) is increased by one unit is given by b.po + b.ac2po.s.

Arrow squid					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.94	0.28	-2.56	-1.93	-1.47
alpha.s	-0.16	0.36	-1.03	-0.14	0.40
b.ac2.p	1.37	0.14	1.07	1.37	1.64
b.ac2.s	-0.62	0.90	-2.52	-0.46	0.67
b.ac2po.s	-2.47	0.64	-3.80	-2.34	-1.57
b.ac3.p	1.54	0.08	1.40	1.54	1.70
b.ac3.s	2.56	0.71	1.41	2.51	3.84
b.ac3po.s	2.07	0.52	1.27	1.98	3.13
b.ac4.p	-0.43	0.30	-1.11	-0.41	0.11
b.ac4.s	-4.15	2.80	-10.94	-3.07	-1.09
b.ac4po.s	-2.04	1.83	-6.70	-1.33	-0.12
b.po	0.27	0.21	-0.21	0.29	0.59

Fur seal					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-2.06	0.23	-2.52	-2.05	-1.67
alpha.s	-0.73	0.30	-1.42	-0.70	-0.24
b.ac2.p	1.36	0.14	1.11	1.36	1.66
b.ac2.s	1.54	0.50	0.57	1.54	2.59
b.ac2po.s	-0.71	0.17	-1.04	-0.73	-0.36
b.ac3.p	1.55	0.07	1.41	1.55	1.69
b.ac3.s	1.21	0.45	0.28	1.22	1.99
b.ac3po.s	0.77	0.19	0.38	0.77	1.13
b.ac4.p	-0.42	0.26	-0.94	-0.41	0.07
b.ac4.s	-3.12	1.12	-6.34	-2.99	-1.34
b.ac4po.s	-0.93	0.50	-2.39	-0.88	-0.15
b.po	-0.04	0.10	-0.25	-0.03	0.12

Giant octopus					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.86	0.31	-2.43	-1.92	-1.23

alpha.s	-0.65	0.47	-1.44	-0.72	0.29
b.ac2.p	1.31	0.14	1.06	1.31	1.59
b.ac2.s	1.65	0.48	0.59	1.68	2.60
b.ac2po.s	-0.63	0.17	-0.97	-0.64	-0.32
b.ac3.p	1.54	0.07	1.40	1.54	1.68
b.ac3.s	1.82	0.67	0.70	1.84	3.34
b.ac3po.s	0.93	0.24	0.50	0.95	1.41
b.ac4.p	-0.36	0.25	-0.84	-0.35	0.13
b.ac4.s	-1.17	1.08	-3.22	-1.29	1.29
b.ac4po.s	-0.09	0.35	-0.77	-0.13	0.68
b.po	0.00	0.16	-0.29	-0.02	0.33

Hoki					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.89	0.26	-2.41	-1.91	-1.28
alpha.s	-0.35	0.37	-1.13	-0.28	0.24
b.ac2.p	1.36	0.15	1.08	1.36	1.69
b.ac2.s	4.03	1.00	2.37	3.97	6.23
b.ac2po.s	0.24	0.33	-0.29	0.24	0.96
b.ac3.p	1.54	0.07	1.40	1.54	1.69
b.ac3.s	-1.28	0.84	-2.78	-1.12	0.33
b.ac3po.s	-0.18	0.28	-0.70	-0.13	0.31
b.ac4.p	-0.39	0.25	-0.88	-0.39	0.10
b.ac4.s	-1.50	1.57	-4.48	-1.49	1.91
b.ac4po.s	-0.22	0.58	-1.32	-0.21	0.98
b.po	0.11	0.13	-0.17	0.13	0.32

Ling					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.81	0.21	-2.21	-1.82	-1.33
alpha.s	0.04	0.38	-0.84	0.09	0.69
b.ac2.p	1.33	0.13	1.06	1.33	1.61
b.ac2.s	2.85	1.28	0.42	2.85	4.81
b.ac2po.s	-0.24	0.55	-1.26	-0.22	0.60
b.ac3.p	1.55	0.07	1.40	1.55	1.69
b.ac3.s	-0.40	1.34	-2.48	-0.05	1.59
b.ac3po.s	0.17	0.58	-0.69	0.28	1.02
b.ac4.p	-0.38	0.27	-0.92	-0.37	0.12
b.ac4.s	-0.48	2.04	-4.69	-0.35	3.71
b.ac4po.s	0.15	0.81	-1.59	0.23	1.75
b.po	0.29	0.16	-0.08	0.31	0.56

***Octopus* sp.**					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-2.00	0.36	-2.80	-1.97	-1.37
alpha.s	-1.30	0.56	-2.87	-1.19	-0.59
b.ac2.p	1.31	0.14	1.04	1.32	1.59

b.ac2.s	0.97	0.67	-0.15	1.00	2.18
b.ac2po.s	-2.45	0.60	-3.61	-2.34	-1.51
b.ac3.p	1.55	0.08	1.40	1.54	1.69
b.ac3.s	1.50	0.74	-0.06	1.56	2.68
b.ac3po.s	2.29	0.79	0.75	2.44	3.53
b.ac4.p	-0.40	0.27	-0.97	-0.38	0.09
b.ac4.s	0.99	1.65	-2.20	0.86	4.42
b.ac4po.s	1.82	1.60	-1.36	1.74	5.09
b.po	-0.54	0.46	-1.83	-0.46	0.03

Opalfish

node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.88	0.20	-2.24	-1.90	-1.43
alpha.s	-0.71	0.44	-1.82	-0.63	-0.07
b.ac2.p	1.30	0.14	1.05	1.30	1.57
b.ac2.s	3.97	1.20	1.79	4.03	5.88
b.ac2po.s	0.73	1.60	-2.12	0.56	3.22
b.ac3.p	1.54	0.07	1.39	1.54	1.69
b.ac3.s	-1.07	1.08	-3.02	-0.85	0.71
b.ac3po.s	-0.29	1.53	-3.14	0.07	2.15
b.ac4.p	-0.40	0.26	-0.89	-0.40	0.11
b.ac4.s	-0.49	1.17	-2.73	-0.49	1.91
b.ac4po.s	0.60	1.68	-2.74	0.65	4.25
b.po	-0.09	0.63	-1.69	0.01	0.86

Rattail

node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.93	0.27	-2.47	-1.93	-1.49
alpha.s	-0.32	0.21	-0.72	-0.33	0.10
b.ac2.p	1.31	0.14	1.03	1.31	1.55
b.ac2.s	2.57	0.72	1.30	2.59	3.79
b.ac2po.s	-1.42	1.37	-4.09	-0.98	0.37
b.ac3.p	1.55	0.08	1.40	1.55	1.69
b.ac3.s	0.00	0.71	-1.32	0.07	1.26
b.ac3po.s	1.32	1.31	-0.63	1.09	4.13
b.ac4.p	-0.55	0.45	-1.80	-0.50	0.19
b.ac4.s	3.36	4.98	-1.85	1.29	16.20
b.ac4po.s	3.76	3.91	-1.37	2.27	11.93
b.po	0.47	0.29	-0.11	0.45	1.04

Red cod

node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.82	0.19	-2.16	-1.83	-1.40
alpha.s	-0.54	0.22	-0.92	-0.56	-0.01

b.ac2.p	1.26	0.14	1.02	1.25	1.52
b.ac2.s	9.40	2.00	5.86	9.14	12.88
b.ac2po.s	4.13	1.03	2.18	4.08	6.09
b.ac3.p	1.55	0.07	1.41	1.55	1.70
b.ac3.s	-6.73	1.89	-10.09	-6.42	-3.37
b.ac3po.s	-4.15	0.92	-5.86	-4.12	-2.35
b.ac4.p	-0.49	0.36	-1.38	-0.46	0.10
b.ac4.s	1.90	3.03	-1.42	0.79	9.91
b.ac4po.s	2.28	2.28	-0.56	1.50	7.90
b.po	0.26	0.26	-0.18	0.24	0.96

Smallscaled cod					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-1.88	0.27	-2.45	-1.87	-1.37
alpha.s	0.02	0.47	-0.73	0.05	0.81
b.ac2.p	1.33	0.14	1.09	1.32	1.65
b.ac2.s	3.37	0.45	2.71	3.24	4.31
b.ac2po.s	-0.01	0.20	-0.33	-0.04	0.43
b.ac3.p	1.54	0.07	1.40	1.54	1.68
b.ac3.s	-1.21	0.65	-2.35	-1.27	0.31
b.ac3po.s	-0.18	0.27	-0.68	-0.18	0.45
b.ac4.p	-0.37	0.25	-0.86	-0.37	0.12
b.ac4.s	-2.94	1.22	-5.59	-2.74	-1.07
b.ac4po.s	-0.87	0.52	-1.93	-0.80	-0.04
b.po	0.29	0.20	-0.04	0.29	0.65

Triplefin					
node	**mean**	**sd**	**2.50%**	**median**	**97.50%**
alpha.p	-2.08	0.17	-2.38	-2.07	-1.80
alpha.s	-0.43	0.17	-0.74	-0.42	-0.11
b.ac2.p	1.36	0.11	1.14	1.36	1.57
b.ac2.s	2.71	0.73	1.48	2.98	3.84
b.ac2po.s	-0.30	0.31	-0.87	-0.18	0.15
b.ac3.p	1.55	0.09	1.36	1.55	1.71
b.ac3.s	-0.46	0.38	-1.04	-0.56	0.38
b.ac3po.s	0.16	0.22	-0.19	0.11	0.61
b.ac4.p	-1.61	0.40	-2.08	-1.69	-0.47
b.ac4.s	33.48	5.98	22.25	33.34	43.46
b.ac4po.s	6.39	2.31	1.38	6.84	9.46
b.po	0.08	0.06	-0.03	0.08	0.19

Appendix 4-5: Tables showing the models results for each prey type and breeding of NZ sea lions from 1997/1998 to 2009/2010. Each table shows model results for each prey type comparing age classes. Prey types shown are main prey types (>%10 of samples) from 1998 to 2010. Each node is a parameter representing the effect of PO on the breeding probability for that age group. See Footnote 2 for notation. The logit of breeding probability for 4-14 year old females is the intercept term, and the additional effect of aging is cumulative for older age classes. E.g. for age class 4, the intercept (logit of annual breeding probability when logit(PO) = 0) is given by alpha.b + b.ac4.b, and the estimated change in logit survival when logit(PO) is increased by one unit is given by b.po.b + b.ac4po.b.

Hoki **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	0.93	0.32	0.27	0.92	1.55
b.ac4.b	-1.63	1.00	-3.84	-1.58	0.35
b.ac4po.b	-0.50	0.39	-1.34	-0.47	0.27
b.po.b	0.40	0.12	0.15	0.40	0.63

Triplefin **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	-0.47	0.24	-0.95	-0.47	0.00
b.ac4.b	-0.11	1.06	-2.30	-0.10	1.86
b.ac4po.b	0.08	0.36	-0.68	0.08	0.75
b.po.b	-0.13	0.08	-0.30	-0.13	0.03

Opalfish **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	-0.19	0.21	-0.59	-0.20	0.27
b.ac4.b	-0.14	0.79	-1.70	-0.18	1.60
b.ac4po.b	0.27	1.27	-2.29	0.24	3.02
b.po.b	-0.15	0.34	-0.79	-0.17	0.63

Rattail **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	0.10	0.19	-0.25	0.11	0.46
b.ac4.b	-0.58	0.64	-1.93	-0.56	0.58
b.ac4po.b	-0.36	0.79	-2.08	-0.34	1.09
b.po.b	0.29	0.27	-0.21	0.30	0.79

Red cod **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	0.23	0.17	-0.07	0.22	0.58
b.ac4.b	-0.81	0.59	-2.03	-0.79	0.35
b.ac4po.b	-0.60	0.60	-1.83	-0.58	0.56
b.po.b	0.39	0.20	0.05	0.38	0.82

***Octopus* sp.** **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	-0.85	0.28	-1.44	-0.84	-0.28
b.ac4.b	0.63	1.18	-1.75	0.64	3.09
b.ac4po.b	0.83	1.10	-1.39	0.86	3.10
b.po.b	-0.68	0.24	-1.16	-0.68	-0.18

Arrow squid **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	-0.13	0.33	-0.85	-0.11	0.48
b.ac4.b	-1.51	1.15	-3.85	-1.50	0.66
b.ac4po.b	-0.70	0.66	-2.02	-0.69	0.55
b.po.b	-0.02	0.19	-0.44	-0.01	0.32

Ling **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	1.18	0.29	0.63	1.18	1.76
b.ac4.b	-0.82	1.08	-2.91	-0.81	1.26
b.ac4po.b	-0.22	0.45	-1.09	-0.21	0.65
b.po.b	0.56	0.12	0.32	0.55	0.80

Smallscaled cod **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	-0.36	0.41	-1.07	-0.37	0.47
b.ac4.b	-0.87	1.89	-3.79	-1.14	3.46
b.ac4po.b	-0.23	0.78	-1.44	-0.34	1.56
b.po.b	-0.11	0.17	-0.40	-0.12	0.24

Fur seal **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	0.02	0.18	-0.34	0.02	0.39
b.ac4.b	-0.82	0.57	-1.92	-0.83	0.33
b.ac4po.b	-0.18	0.19	-0.56	-0.18	0.22
b.po.b	0.04	0.06	-0.08	0.04	0.16

Giant octopus **node**	**mean**	**sd**	**2.5%**	**median**	**97.5%**
alpha.b	0.66	0.43	-0.30	0.66	1.43
b.ac4.b	-2.02	1.49	-4.97	-2.01	0.89
b.ac4po.b	-0.57	0.48	-1.49	-0.57	0.40
b.po.b	0.25	0.14	-0.07	0.25	0.52

***Footnote 1*:**

alpha.p: The intercept for logit(re-sighting probability); for animals <1 year old.
b.ac2.p: The effect of being > 1 year old on logit(re-sighting probability).
b.ac3.p: The additional effect of being > 3 years old on logit(re-sighting probability).
b.ac4.p: The additional effect of being > 14 years old on on logit (re-sighting probability).
alpha.s: The intercept for logit(survival probability); for animals <1 year old.
b.ac2.s: The effect of being > 1 year old on logit(survival probability).
b.ac3.s: The additional effect of being > 3 years old on logit(survival probability).
b.ac4.s: The additional effect of being > 14 years old on on logit (survival probability).
b.po: Effect of logit(PO) on logit(survival probability) of animals < 1 year old, where PO is the probability of occurrence of a prey type in scat samples.
b.ac2po.s: The additional effect of logit(PO) on logit(survival probability) for animals > 1 year old.
b.ac3po.s: The additional effect of logit(PO) on logit(survival probability) for animals > 3 years old.
b.ac4po.s: The additional effect of logit(PO) on logit(survival probability) for animals > 14 years old.

***Footnote 2*:**

alpha.b: The intercept for logit(breeding probability), here for females aged 4 – 14 years old.
b.ac4.b: The effect of being >14 years old on logit(breeding probability), where PO is the probability of occurrence of a prey type in scat samples.
b.po.b: Effect of logit(PO) on logit(breeding probability) for females 4-14 years old.
b.ac4po.b: The additional effect of logit(PO) on logit(breeding probability) for females > 14 years.