Investigating variation in the diet and foraging ecology of the long-finned pilot whale (*Globicephala melas edwardii*) in Aotearoa New Zealand waters

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Abstract

Knowledge of foraging ecology is essential to understanding how species interact with the ecosystem they inhabit. Foraging variation due to ontogenetic and/or anthropogenic factors can affect individual body condition, which could have implications for reproductive fitness and survivorship. Despite a high stranding frequency, limited knowledge is available on the foraging ecology of long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) within New Zealand waters. To address these knowledge gaps, multiple methods of dietary analysis (stomach content analysis, n = 283; stable isotope analysis, n = 125; and fatty acid analysis, n = 15) were performed on samples collected from carcasses of LFPWs stranded along the New Zealand coast between 2009 and 2017. Six new taxa contributed to LFPW diet, including the first report of fish consumption for this population. Whilst arrow squid *Nototodarus* spp. was determined to be the most important prey, both ontogenetic and spatiotemporal variation were noted in prey consumption. Stomach content, stable isotope and fatty acid investigations all supported a preference for pelagic feeding. However, both stomach content and stable isotope investigations also documented occasional benthic/coastal foraging, especially for mature male LFPWs and in the year 2017. Biochemical dietary tracers examined in five of the top prey species to LFPW diet at Farewell Spit suggested that prey investigated were not chemically similar and/or at least one key prey species was missing from analysis. Initial insights gained from morphometric body condition measurements signalled that axillary girth may explain some variation in the proportion of saturated, polyunsaturated fatty acids and dietary fatty acid C20:1n9 in the inner layer of dorsal blubber, though sample sizes were small. Given the sustained reliance on arrow squid in the diet of this species, monitoring of overlap between regions of commercial fisheries and LFPW foraging in these waters, in part through continued support of long-term data sets, is recommended. Furthermore, the importance of accurate body condition measurements and their potential for use in welfare assessment and strandings situations is discussed. Recommendations for future research, include telemetry studies, further investigation of fatty acid and body condition biomarkers in LFPWs and prioritisation of analysis of LFPW dietary samples collected during the austral winter.

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List of Abbreviations

AICc	Akaike information criterion (corrected)
ANOVA	Analysis of Variance
BCI	Body condition index
C:N	Carbon:Nitrogen stable isotope ratio
cm	Centimeter
cos2	Co-sign^2
ctr	Contribution to data variance
df	Degrees of freedom
Dim 1	Dimension 1
Dim 2	Dimension 2
Dim 3	Dimension 3
DNA	Deoxyribonucleic acid
e.g.,	exampli gratia
et al.	et alli
FO	Frequency of occurrence
FWS	Farewell Spit
GAM	Generalised additive model
GLG	Growth layer group
GLM	Generalised linear model
IRI	Index of relative importance
LFPW	Long-finned pilot whale
lm	Linear model
m	meter
mm	millimeter
MSE	Mass-stranding event
mNDS	multi-dimensional scaling
MUFA	Monounsaturated fatty acid

NIWA	National Institute of Water and Atmospheric Science
PERMANOVA	Permutational analysis of variance
PUFA	Polyunsaturated fatty acid
SEA	Standard ellipse area
SEAc	Standard ellipse area (corrected)
SFA	Saturated fatty acid
SI	Stewart Island
SIMPER	Similarity percentage
sp.	Genus, unspecified species
spp.	Genus, multiple species
TA	Total area
TBL	Total body length
VIF	Variation inflation factor
°C	Degrees Celsius
Δ	Delta
%	Parts per hundred
‰	Parts per thousand
±	Plus or minus, standard deviation
$\bar{x}$	Mean

Chapter 1 — Introduction

Long-finned pilot whales *Globicephala melas edwardii* refloated after stranding at Onetahua Farewell Spit, New Zealand in 2021. Photo credit: Rebecca Boys.

1.1. Introduction

Dietary studies include investigations from the specifics of what an individual consumes, to the behaviours displayed when sourcing that nutrition. Analysis of these dietary behaviours, which differ between species, geographies, and even cultures of the same species, can contribute to the understanding of life history, spatial distribution, trophic interactions, and relationships with local ecological food webs (Schoener 1987; Nakano and Murakami 2001; Braga et al. 2012). Changes to an ecosystem can be associated with temporal or spatial changes in target prey species, which are particularly useful in environments that are difficult to monitor such as the ocean (Pierce and Boyle 1991; Phillips and Gregg 2003; Chiu-Werner et al. 2019). Such changes can occur through trophic cascades altering species abundance, which may affect prey selection and thus impact predator fitness based on optimal nutrient intake (Maklakov et al. 2008; Deans et al. 2015). Hence, having baseline information on the prey species and a comprehensive knowledge of their diet holds significant conservation and management implications (Sinclair et al. 2018; Findlay and Hill 2021; Frank et al. 2021; Pachomski et al. 2021), particularly in areas where the prey species overlap with commercially targeted species.

Attempts to explain and describe foraging behaviours can be categorised broadly within two main concepts: foraging for the benefit of the group (social foraging theory, e.g., Giraldeau and Caraco 2000) or foraging for the benefit of the individual (optimal foraging theory). The most well-known theory is optimal foraging theory (Emlen 1966; MacArthur and Pianka 1966). According to optimal foraging theory, an organism will target the prey that provides the most energy for the least energetic expense. Several energetic expenses may be considered, including location, size, and the behaviour of prey species (e.g., Emlen 1966; MacArthur and Pianka 1966; Kramer 1988; Doniol-Valcroze et al. 2011; Langerhans et al. 2021). However, this theory has been criticised as "optimal"

is difficult to test and uncommon in nature (Pyke et al. 1977; Pierce and Ollason 1987). Therefore, additions have been suggested in the recent literature, including the consideration of nutritional components of target prey (MacArthur and Pianka 1966; Hill 1988; Hughes 2009; Raubenheimer and Simpson 2018).

Energetic expenses associated with marine environments differ from those in the terrestrial environment due to factors such as depth and pressure changes of the ocean (Doniol-Valcroze et al. 2011; Beltran et al. 2021). For example, additional energetic considerations have been described for air breathing marine species such as oxygen depletion affecting search time (Tyson et al. 2016). These expenses have then been connected to diving behaviour (Stephens et al. 2008; Doniol-Valcroze et al. 2011) and assessment of prey quality (Thompson and Fedak 2001; Thums et al. 2013), and therefore specifics of the prey species and size which is consumed in each foraging trip. Optimal foraging theory predicts that the optimal depth of foraging for air breathing marine predators is relative to body size, and therefore may not correspond with the depth of maximum target prey density (Mori 1998). Hence, foraging ecology encompasses much more than just identification of predator and prey, often combining several analyses to understand what individuals are feeding on, and where.

1.2. Methods used to study foraging ecology

In order to study foraging ecology, several methods have been developed including traditional methods such as stomach content, regurgitate and scat analysis (e.g. Hyslop 1980; McIntosh et al. 2006; Klare et al. 2011; Rodrigues et al. 2020), biochemical methods such as isotopic analysis (Hobson 1999; Codron et al. 2018; Le-Alvarado et al. 2021; Ishikawa et al. 2022), and fatty acid analysis (e.g., Iverson et al. 2004; Galicia et al. 2015), GPS tracking (e.g., Allan et al. 2013), and behavioural observation (e.g., Quigley et al. 2022). Behavioural observation studies have gained popularity with emerging technologies such as unmanned aerial systems (UAS; Christie et al. 2016; Wang et al. 2019).

However, these technologies can be expensive, and behavioural studies require baseline information on movement patterns and feeding locations in order to place UAS in the correct location, making this an impractical option where these factors remain unknown. Utilisation of tracking technologies such as tracking and data relay satellite has also increased in the literature over recent years (e.g., Ryan et al. 2004; Kuhn et al. 2010; Dragon et al. 2012; Posen et al. 2021; Fijn et al. 2022) as tags have been developed to be smaller and less intrusive to individuals being studied. Moreover, success in locating feeding habitat and also dive depths (and therefore likely prey species) in the marine environment has been reported using tags (Volpov et al. 2016; Bestley et al. 2019). However, tagging of a live animal has important ethical and local cultural considerations so may not be possible in all areas.

1.2.1. Stomach content analysis

Stomach content analysis is the process of analysing the contents of an individual's stomach to identify sources of prey, prey size, their relative importance to diet, and therefore where a species fits into an ecological system (Hyslop 1980; Hall et al. 1995; Amundsen and Sánchez-Hernández 2019). Identification of prey tends to focus on diagnostic hard part remains as these are more difficult to digest and are therefore digested slower, so are retained in the stomach for a longer time period than other tissues. Identification of diagnostic hard parts is carried out through observation of morphometric characteristics, comparison to reference collections and measurements of specific features (Hyslop 1980). Molecular techniques such as DNA barcoding of the recovered prey items can also be used to aid with accurate taxa identification (e.g., Moran et al. 2016; Aguilar et al. 2017; Hacker et al. 2021; Roffler et al. 2021).

Once prey identification has been confirmed, stomach content investigations tend to focus on analysing the frequency of occurrence of each prey species and proportional contribution of each

prey species to overall predator diet by number and/or weight (see Hyslop 1980, Pierce and Boyle 1991; Amundsen et al 2019 for detailed overview of techniques). Often analysis techniques are combined for a comprehensive understanding of diet, providing information on prey contribution by number and/or weight of each prey group. Where regression equations exist for prey species, hard part remains can also be individually measured to reconstruct estimated length and mass of prey items at the time of ingestion (e.g., Clarke et al. 1986; Härkönen 1986). The prey counts and reconstructed prey size measurements can be used in combination to calculate the relative importance of each prey group to diet, informing both conservation and management of a species.

Stomach content analysis has been adapted to studies of wild individuals extensively over the past century (Costello 1990; Amundsen et al. 1996; Amundsen and Sánchez-Hernández 2019). This established technique is widely used in feeding ecology research, especially when working with highly mobile species where direct observation of feeding can be difficult e.g., in the marine environment. Stomach contents are thought to reflect the diet from a period of minutes to days before examination (Sekiguchi and Best 1997; Young et al. 2018) depending on the species being investigated. Stomach contents can be obtained from live individuals through gastric lavaging, a process involving flushing the stomach with water (e.g., Fraser 1976, Wilson 1984). Analysis is also often carried out post-mortem through removal of stomach contents in-situ or excising the intact stomach from a carcass (e.g., Pusineri et al. 2007; Sakyi et al. 2019; Foskolos et al. 2020). Recent developments in molecular studies have found that faecal and gastric samples from free-swimming bottlenose dolphins *Tursiops truncatus* showed very similar dietary findings to the stomach contents of stranded individuals (Dunshea et al. 2013), suggesting that the analysis of stomach contents is likely to be representative of the diet of free-swimming cetacean populations in at least some cetacean species. Stomach contents can also be a useful indicator of foraging habitat or feeding depth

(Fitch and Brownell Jr 1968; Sparrevohn and Støttrup 2008), especially when juveniles with known nursery grounds (James et al. 2019) or which habituate specialised environments such as benthos (Weltz et al. 2018) are reported in stomachs. Indeed, it has suggested that stomach contents analysis from stranded individuals could even serve as a useful guide for species composition in the local area (Maldini et al. 2005).

Key caveats of stomach content analyses often centre around species identification such as: 1) erroneous identification and 2) reporting only hard part remains. These can be due to either to digestive loss or erosion or difficulty in identifying soft tissue, therefore causing a bias in stomach content data (Stapp 2002; Dehn et al. 2007; Meckstroth et al. 2007) towards hard-part remains that are retained.

1.2.2. Stable isotope analysis

Carbon and nitrogen stable isotopes are most frequently used to infer dietary and trophic information about a species, as these stable isotope values have been found to be related to that of prey organisms (DeNiro and Epstein 1978). Stable isotope values of sulphur are also increasingly utilised, often alongside carbon, to infer foraging habitat (e.g., DeNiro and Epstein 1978; Yamanaka et al. 2000; McCutchan Jr et al. 2003; Bearhop et al. 2004; Newsome et al. 2010; Fry and Chumchal 2011; Szpak and Buckley 2020), whilst nitrogen stable isotope values have been used to infer trophic interactions of a species (e.g., DeNiro and Epstein 1981; Oelbermann and Scheu 2002; Meckstroth et al. 2007; Marshall et al. 2019). Furthermore, stable isotope analysis of prey can give insights into contribution to diet (Phillips et al. 2014), often after prey species have been identified using a different dietary method such as scat or stomach content analyses (e.g., Gerringer et al. 2017; Antón-Tello et al. 2021; Takahashi et al. 2022).

When used in ecological studies, measuring stable isotope values assimilated from prey to predator provides dietary information on different timescales depending on the turnover time of the tissue selected for analysis. Turnover times refer to the time an isotopic value is retained post-feeding, with different tissues providing information for differing timescales in an individual's diet (Vander Zanden et al. 2015). For example, skin can be used for dietary analysis on a scale of hours to weeks (e.g., Watt et al. 2019), muscle from a week to a month (e.g., McNicholl et al. 2018) and blood on a scale of months (e.g., Bontempo et al. 2016). For extended temporal timescales, bones are often used in archaeological dietary studies (e.g., Somerville et al. 2017) and teeth have been used for bulk stable isotope analysis (analysis using the full tissue) of diet over a full lifetime in sperm whales *Physeter macrocephalus* (Zupcic-Moore et al. 2017). Serial sampling of stable isotopes from growth layers in teeth can also provide time-series data, as reported in multiple species including elephants *Elephas maximus* and *Stegadon orientalis* fossils (Ma et al. 2019) and bottlenose dolphins *Tursiops truncatus* (Pereira et al. 2020). Although samples from most tissues are only able to be collected post-mortem, stable isotopes can be examined in live individuals through biopsy skin and blubber collections (e.g., Todd et al. 2010), sloughed skin (e.g., Steinitz et al. 2016) and scat (e.g., Montanari and Amato 2015). Turnover rates are further reported to differ between species, though actual data on species-specific tissue turnover time is scarce; often only available from studies of captive animals such as brown bears *Ursus arctos yesoyensis* (Narita et al. 2006), West-Indian manatees *Trichechus manatus* (Ortiz and Worthy 2006), bottlenose dolphins (Caut et al. 2011; Browning et al. 2014a) and killer whales *Orcinus orca* (Caut et al. 2011).

Tissue choice in studies using stable isotopes therefore relates to both turnover time and logistics of sample collection. Long-term dietary analyses require tissues with a longer turnover time such as bone (Tieszen et al. 1983; Vales et al. 2020; Teixeira et al. 2021) or teeth (Walker and Macko 1999;

Shipley et al. 2021), whereas short-term trophic analyses can be conducted on tissues with minimal turnover time such as skin (Hobson et al. 1996; Todd et al. 2010; Giménez et al. 2016). Studies of captive bottlenose dolphins suggested a timeframe of just 20–32 days for skin tissue turnover (Browning et al. 2014a). However, whilst stable isotope studies that focus on bone and/or teeth of marine mammals (e.g., Hirons et al. 2001; Riccialdelli et al. 2013; Becker et al. 2021) have the advantage of providing a lifelong isotopic signature, they require access to carcasses and analysis can be heavily resource intensive. The interpretation of stable isotope data has caused some uncertainty in marine mammal studies to date due to 1) tissue choice, 2) sample integrity and 3) discrimination factor, which are described in more detail below.

Sample integrity is an important factor to consider when analysing stable isotope data (Durante et al. 2020). In ecological studies especially, there is often a time lag between collection and analysis of the sample, which creates the need for preservation. The time lag could be anywhere from days to many years if samples are used from tissue archives such as museum collections (Edwards et al. 2002). Taxon-specific effects on isotope values have been reported in various tissues based on storage method applied. Examples include turtles (Barrow et al. 2008), reef fish (Stallings et al. 2015), rainbow trout *Oncorhynchus mykiss*, zooplankton, and shrimp *Mysis diluviana* (Wolf et al. 2016), brown bears *Ursus arctos* (Javornik et al. 2019), and skin of multiple cetacean species including beluga whales *Delphinapterus leucas*, harbour porpoise *Phocoena phocoena*, minke whales *Balaenoptera acutorostrata*, fin whales *Baleanoptera physalus*, and humpback whale *Megaptera novaeangliae* (Lesage et al. 2002; Lesage et al. 2010; Kiszka et al. 2014a; Newsome et al. 2018).

Also known as fractionation factor, the discrimination factor refers to the difference in a specific isotope value in a prey species in comparison to its value after it has been incorporated into predator tissue (Caut et al. 2009). Although essential for considering trophic interactions, discrimination

factors are not well defined in cetaceans (Borrell et al. 2012; Teixeira et al. 2022). Species that are closely related are widely thought to have similar degrees of isotopic "tissue enrichment", a term which refers to the quantity of isotope incorporated into predator tissue from prey. Therefore, historical marine mammal literature tended to use a standard 2-4% enrichment factor for nitrogen values between trophic levels (DeNiro and Epstein 1981). Recently, predictions of trophic discrimination factors estimated from phylogenetically similar species using Bayesian inference through the R package "SIDER" (Healy et al. 2018) are becoming more commonly used in literature (e.g., Lerner et al. 2018; Jones et al. 2020). The lack of certainty surrounding which trophic discrimination factors to utilise has led to calls for caution when interpreting differences in nitrogen isotope values (e.g., Bond and Jones 2009; Hussey et al. 2010). Indeed, the trophic enrichment factor for nitrogen was reported as 1.57% for skin in captive bottlenose dolphins *Tursiops truncatus* (Giménez et al. 2016). These lower-than-expected trophic discrimination factors may lead to errors when assessing of trophic level of predators (McCormack et al. 2019).

Advances in methodology for stable isotope studies such as compound-specific isotope analysis (CSIA) and compound-specific analysis of amino acids have allowed more certainty in the interpretation of nitrogen values (e.g., Ishikawa 2018; McMahon and Newsome 2019; Troina et al. 2021; Harada et al. 2022). For example, CSIA revealed that a temporal change in the isotopic values of bowhead whale *Balaena mysticetus* skin was also apparent at the base of the food web, suggesting that the trophic level of bowhead whales remained stable despite variability in ice cover and temperature in Western Greenland (Pomerleau et al. 2017).

1.2.3. Fatty acid analysis

While fatty acids are essential components of many biochemical processes, certain types of fatty acids tend to accumulate and persist as they move up the food chain from one trophic level to the

next (e.g., Alfaro et al. 2006). There is growing interest in the use of fatty acids as biochemical tracers, which are sometimes referred to as fatty acid trophic markers, in studies of foraging ecology (Dalsgaard et al. 2003). As these fatty acids are incorporated into adipose tissue, they can be compared to fatty acid profiles in prey to help identify and understand dietary source (e.g., Auel et al. 2002; Iverson et al. 2004; Happel et al. 2016b; Choy et al. 2020). When assessing diet using analysis of fatty acids, three key groups of fatty acids are often presented: saturated fatty acids (SFAs; those with no double bonds), monounsaturated fatty acids (MUFAs; those with a single double bond), polyunsaturated fatty acids (PUFAs, those with multiple double bonds). Predators struggle to biosynthesize certain fatty acids which are therefore thought to be accumulated through diet and classed as "dietary fatty acids" (Iverson et al. 2004).

Qualitative comparisons of fatty acid values from individuals of a particular species can be used to look for dietary variation within or between populations (e.g., Stowasser et al. 2012). Further to this, qualitative analysis has also been applied to compare fatty acid profiles of predators with those of prey to distinguish likely trophic interactions (e.g., Bradshaw et al. 2003; Grahl-Nielsen et al. 2010a). In diet manipulation experiments of sandpipers *Calidris mauri*, fatty acid composition of the predator adipose tissue has been reported to reflect that of its prey (Egeler et al. 2003). As the roles and metabolisms of individual fatty acids are being investigated more fully, it appears that organisms feeding in terrestrial systems have a lower reported proportion of the PUFA docosahexaenoic acid (DHA) than those feeding in marine systems, with purely marine feeders having the highest DHA/linolenic acid ratio (Koussoroplis et al. 2008).

Increasingly, quantitative methods such as the Quantitative Fatty Acid Analysis (QFASA; Iverson et al. 2004) model and Bayesian mixing models are being applied to ecological studies to statistically determine dietary composition (e.g., Galloway et al. 2015; Happel et al. 2016a; Choy et al. 2019;

Thiemann et al. 2022). The QFASA method uses calibration coefficients (CCs) to account for metabolism of each fatty acid from prey to predator, which is thought to be species-specific. As calculating accurate CCs can currently only be achieved through captive feeding trials, CCs have been estimated only for a small number of species. These CC estimates have been used to allow quantitative analyses in other similar species (e.g., Xie et al. 2022). However, a lack of known species-specific CCs combined with the large amount of prey needed for both QFASA and Bayesian modelling has resulted in some studies still focussing on using qualitative rather than quantitative methods (e.g., Jackson et al. 2021; Segura-Cobeña et al. 2021; Jackson et al. 2022).

Analyses of dietary fatty acids have been especially beneficial in marine studies, as PUFAs are more commonly found in phytoplankton than in terrestrial producers (Williams and Buck 2010; Colombo et al. 2017). Thus, much of the dietary fatty acid research to date has been focused on organisms within aquatic systems (e.g., Vlieg and Body 1988; Sargent et al. 1999; Alkanani et al. 2007; Stowasser et al. 2009; Prato and Biandolino 2012; Murillo et al. 2014; Susanto et al. 2016; Bromaghin et al. 2017; Parzanini et al. 2020; McMullin et al. 2021) such as several marine mammal species including pinnipeds (Iverson et al. 1997; Grahl-Nielsen O et al. 2005; Tucker et al. 2008; Meynier et al. 2010; Lambert et al. 2013; Knox et al. 2019), mysticetes (Grahl-Nielsen et al. 2011; Waugh et al. 2014; Meier et al. 2016) and odontocetes (Williams et al. 1977; Guitart et al. 1999; Samuel and Worthy 2004; Herman et al. 2005; Smith and Worthy 2006; Loseto et al. 2009; Grahl-Nielsen et al. 2010a; Choy et al. 2020).

Although many tissues contain fatty acids, samples of blubber are used most often to study fatty acid profiles in marine mammals (e.g., Meynier et al. 2008a; Skoglund et al. 2010; Guerrero and Rogers 2017; Guerrero et al. 2020). Whilst studying fatty acids in only one tissue may not be fully representative of the full fatty acids content of an individual, fatty acids from prey which are

incorporated into blubber tissue (Borobia et al. 1995) can provides dietary data on a timescale of weeks to months (e.g., Beck et al. 2007; Tucker et al. 2008; Loseto et al. 2009; Knox et al. 2019). Interestingly, tissues sampled from different sites on the body of bottlenose dolphins (Samuel and Worthy 2004) and sea lions *Phocarctos hookeri* (Lambert et al. 2013) did not differ significantly by fatty acid composition. However, there has been some evidence of stratification within the vertical blubber layers of marine mammals (Krahn et al. 2004; Smith and Worthy 2006; Strandberg et al. 2008; Lambert et al. 2013; Jackson et al. 2022), with the proportion of dietary fatty acids increasing towards the deepest blubber layer for species such as common dolphins *Delphinus* spp. and bottlenose dolphins. The high variability of fatty acid composition in this inner blubber layer has been linked to dietary and metabolic differences (Strandberg et al. 2008). Interestingly, no vertical stratification of fatty acids was observed in the blubber layers of stranded long-finned pilot whales (Walters 2005). Nevertheless, it is recommended that fatty acid analysis in marine mammals is performed on the deepest blubber layer (closest to the muscle) to obtain the most accurate readings for dietary studies (Smith and Worthy 2006; Guerrero et al. 2016).

1.2.4. Use of multiple methodologies

Using multiple methodologies concurrently is thought to detect foraging complexities that individual methodologies alone would not decipher (Young et al. 2018; Hoenig et al. 2021). For example, values of $\delta^{15}N$ often overlap in prey species, so the use of isotope analysis alone would not be able to identify prey consumed without utilising a secondary method such as stomach content analysis. Stomach contents analysis and stable isotope analysis have been combined to research diet of a diverse range of species. For example, combining stomach content and stable isotope analyses in snow crabs *Chionoecetes opilio* (Divine et al. 2017) allowed importance of both size and sex-specific dietary differences noted by only one of the methodologies to be contextualised. Similarly, stable

isotope analyses of feral cats *Felis silvestris* revealed the contribution of items such as human refuse to diet that was not noted in stomach contents (Meckstroth et al. 2007). Additionally, the use of a further biochemical method such as fatty acid analysis provides a more thorough understanding of diet (Herman et al. 2005; Allan et al. 2010; O'Donovan et al. 2018). Indeed, stomach content, stable isotope and fatty acid analyses were all considered individually imperfect methods to study foraging of double-crested cormorants *Phalacrocorax auratus,* but authors were able to elucidate diet when these methods were combined (King et al. 2017).

Studies encompassing combinations of approaches to research foraging are increasingly common in the marine environment where organisms are difficult to access. The combination of stable isotope and fatty acid analyses was able to confirm feeding strategies of intertidal barnacles (Puccinelli et al. 2016) and elasmobranchs (Every et al. 2019). In addition, fatty acid analysis revealed a differentiation of producer contribution to diet in sargassum associated fishes, even when isotope values of their prey overlapped (Rooker et al. 2006). Such multi-method approaches have also been recommended for future dietary studies of marine mammals (e.g., Bowen and Iverson 2013).

1.2.5. Dietary studies of cetacea

Combining multiple methodological approaches is increasingly used to discern dietary variation in cetacean research (e.g., Gibbs et al. 2011; Madgett et al. 2019; McCluskey et al. 2021). For example, stomach content together with stable isotope analyses revealed the first report of cephalopods as the primary food source of dwarf minke whales, *Balaenoptera acutorostrata* (Milmann et al. 2019*)*. The joint use of stomach content, stable isotope and fatty acid analyses also confirmed a high prevalence of squid in Canadian bottlenose whale *Hyperoodon ampullatus* diet (Hooker et al. 2001). Similarly, cephalopods have been reported as the most important prey group to the diet of sperm whales *Physeter macrocephalus* (Evans and Hindell 2004; Chua et al. 2019), Pacific white-sided dolphins

Lagenorhynchus obliquidens (Lee et al. 2019) and Risso's dolphins *Grampus griseus* (Öztürk et al. 2007), though these studies only used single methodologies.

Conversely, stomach contents analysis has shown that some species, such as Guiana dolphins *Sotalia guianensis*, consumed high numbers of fish prey (Rodrigues et al. 2020). However, diet composition may change along with local prey abundance (Evans 1994; Young and Cockcroft 1994; Santos et al. 2013), as is predicted by optimal foraging theory. For example, fish were the most important prey in the diet of striped dolphins *Stenella coeruleoalba* in the Eastern Mediterranean Sea (Dede et al. 2016) while fish and cephalopods were equally important to the diet of striped dolphins in the Ligurian Sea (Würtz and Marrale 1993).

Dietary differences between spatially segregated feeding populations of the same species have also been demonstrated in bottlenose dolphins *Tursiops truncatus* (Barros et al. 2010) and killer whales (Foote et al. 2012). Feeding differences have not only been documented at the population level — variability in stable isotopes (carbon, nitrogen, and sulphur) within the same population of southern right whales *Eubalaena australis* were attributed to differences in prey consumption (Valenzuela et al. 2018). Likewise, opportunistic feeding in south Australian sperm whales (Evans and Hindell 2004) is also reported to cause individual dietary variation.

Ontogenetic variability in cetacean diet has also been reported. For example, lactating females feed differently in spotted dolphins *Stenella attenuata* (Bernard and Hohn 1989) and *S. frontalis* (Malinowski and Herzing 2015), whilst older individuals were found to feed at higher trophic levels in both right whales *Eubalaena australis* (Valenzuela et al. 2018) and beluga whales *Delphinapterus leucas* (Marcoux et al. 2012). In contrast, ontogenetic variation was not observed in captured fin whales, with all individuals over four years of age showing similar isotopic values (Borrell et al. 2012).

Studies focussing on large scale temporal differences can present logistical difficulty, but long-term temporal studies are useful in identifying changes in the marine environment, which are not as easily observed as in the terrestrial environment. For example, comparisons of carbon and nitrogen isotope values between temporally distinct samples have been able to show trophic changes to food webs that have been associated with fishing activity (Wiley et al. 2013) and climate change (Bond and Lavers 2014). Temporally decreasing isotopic values in beluga whales in the Cook Inlet, USA (Nelson et al. 2018) and Cumberland Sound, Canada (Marcoux et al. 2012) have also indicated dietary shifts in these regions.

Dietary shift can also be noted seasonally, alongside changing prey resources. Seasonal differences in beluga whale distribution at the Cook Inlet, USA are suspected to be caused by dietary change, corresponding with local prey abundance (Castellote et al. 2020). Similarly, prey abundance appears to influence resident killer whale movements, where seasonal presence of the whales in the Johnstone Strait, Canada was revealed to be positively associated with occurrence of local salmon species (Nichol and Shackleton 1996).

1.3. Diet and body condition

Diet not only affects predator movements but is also linked to fat stores of an individual. For example, seasonal dietary differences were found to correlate with variation in both axillary girth and blubber thickness measurements in sei *Balaenoptera borealis* and fin whales (Lockyer et al. 1985). Blubber thickness has also been reported to vary with diet in several cetacean species such as the harbour porpoise (Kastelein et al. 2019), North Atlantic fin whale (Lockyer 1986; Williams et al. 2013) and North Atlantic right whale (Miller et al. 2011b). Furthermore, blubber thickness can also affect fatty acid profiles in harbour porpoises (Learmonth 2006).

Attempts have been made to classify the energetic reserves of an animal to provide information on health. Often, these have concentrated around fat reserves of an individual, such as blubber, and have been referred to as "body condition measurements". However, there is uncertainty over the suitability of blubber measurements alone as indicators of energy reserves in cetaceans (e.g., Joblon et al. 2014; Castrillon and Bengtson Nash 2020; Derous et al. 2020). For example, the lipid content of blubber provided no indication of physical conditions such as cause of death or morphometric body condition in stranded ziphiid and balaenopterid species (Kershaw et al. 2019). Yet in a delphinid species, the striped dolphin, the lipid content of blubber was found to be the most accurate indicator of nutritional health; while neither blubber thickness nor girth could explain nutritional condition (Gómez-Campos et al. 2011).

As previously described, the links between blubber, energy storage and prey consumption are complex. Complicating matters, blubber also has multiple functions in the marine mammalian body, including thermodynamics and buoyancy (Lockyer 1993). Changes in blubber composition and condition may be reflective of other processes, such as metabolism or ontogeny (Grahl-Nielsen et al. 2011). Therefore, investigation into cetacean body condition is advised to incorporate multiple morphometric and blubber measures for validation (Castrillon and Bengtson Nash 2020).

1.4. Focal species – the long-finned pilot whale, *Globicephala melas*

Long-finned pilot whales *Globicephala melas* (herein LFPWs) are one of two species of pilot whale, the other being the short-finned pilot whale *G. macrorhynchus.* Whilst *G. macrorhynchus* are observed more commonly in warmer waters (e.g., Van Waerebeek et al. 2009; Buden and Bourgoin 2018; Costa et al. 2020a; Plön et al. 2020; Ramírez-León et al. 2020; Coché et al. 2021;; Sankalpa et al. 2021 Bouslah et al. 2022), *G. melas* are predominantly found in the cooler temperate waters, including the Mediterranean Sea and even around the sub-Antarctic and Arctic regions (e.g., Notarbartolo di

Sciara 2002; Olson 2009; Di Tullio et al. 2016; Buscaglia et al. 2020; Correia 2020; de Lima et al. 2021; Félix et al. 2021; Skern-Mauritzen et al. 2022).

Two geographically separated sub-species of LFPW are described; *G. melas melas* is found in Northern Hemisphere waters around Europe and North America, whereas *G. melas edwardii* (Davies 1960) occurs in waters off southern Chile, South Africa, southeast Australia and around New Zealand (Table 1.1, Table 1.2). Fewer studies have been conducted on the southern ranging sub-species *G. m. edwardii* despite extensive distribution across the Southern Hemisphere (Kraft et al. 2020). Considered as internationally "least concern" (IUCN Red List, updated 2018) and nationally in New Zealand as "not threatened" with a qualification of "data poor" (Baker et al. 2019), Southern Hemisphere LFPWs are minimally represented in the scientific literature.

Pods of LFPWs are typically formed of matrilineal societies (Augusto et al. 2017; Boran and Heimlich 2019), with social linkages even suggested during diving behaviour. The deepest LFPW dives are proposed to occur over 1000 m, yet despite this extensive diving capability, LFPWs have been more frequently recorded in relatively shallower waters (up to 650 m, Table 1.2) during telemetry studies. Tagging studies in the Norwegian and Ligurian Seas have recorded a wide range of possible LFPW foraging dive depths, from 24 – 648 m (Baird et al. 2002; Isojunno et al. 2017), often diving to benthic regions and with 10 m of the sea floor (Isojunno et al. 2017). These diving behaviours along with wider movement and dispersal observed in LFPWs are considered highly related to prey distribution (Olson 2009). Knowledge of key LFPW prey species and their distribution is therefore vital to understanding drivers of LFPW movement patterns, depth ranges and suitable habitat. Thus, understanding of local LFPW foraging ecology and target prey is critical data for ecosystem-based conservation and management efforts.

The diet of both LFPW sub-species appear to comprise predominantly of cephalopods (see Table 1.1) of varying species. In the Northeast Atlantic, *G. m. melas* stomach contents have been reported to contain mostly oceanic and pelagic cephalopods (Gannon et al. 1997a; Spitz et al. 2011; Santos et al. 2014). However, in Northwest Iberia, inshore and benthic cephalopods were more important to diet (Santos et al. 2014). Secondary in importance to cephalopods, a variety of fish species have been recovered from the stomachs of *G. m. melas* including pelagic (Overholtz and Waring 1991; Abend and Smith 1997; De Pierrepont et al. 2005), and benthopelagic (Spitz et al. 2011; Ijsseldijk et al. 2015; Santos et al. 2014) species. However, reports of fish in the diet of *G. m. edwardii* populations are not as common (Gales et al. 1992; Chalcobsky et al. 2021). To date, there are no published reports of fish remains from stomach contents of LFPWs in New Zealand waters (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009). Diet in this sub-species therefore appears to be dominated by cephalopods (Table 1.1).

Dietary stable isotope comparisons of *G. m. melas* and other cetaceans in the Alboran Sea suggested that LFPWs may have a smaller isotopic dietary niche than other pelagic feeders habituating a similar area, such as Risso's and bottlenose dolphins (Giménez et al. 2018). Interestingly, muscle tissue of *G. m. melas* in the North Atlantic revealed a higher contribution of fish within the diet compared with skin tissue (Abend and Smith 1997), indicating possible dietary changes over a small temporal scale in the sub-species. This stable isotope data from *G. m. melas* supports the presence of seasonal feeding differences suggested by stomach contents analysis (Overholtz and Waring 1991). However, a lack of isotopic differentiation within the population of *G. m. edwardii* in Kerguelen waters of the southern Indian Ocean was taken to indicate no significant short-term dietary changes in the southern sub-species (Table 1.1; Fontaine et al. 2015). Moreover, no isotopic differentiation was reported by age, sex, or lactation status from stranded *G. m. edwardii* in Southeast Australia

(Jackson 2017). Similarly, fatty acid profile analysis of LFPWs stranded in a similar area observed little ontogenetic variation in fatty acid profiles (Walters 2005).

Few studies have examined temporal and spatial variation in LFPW diet (Table 1.1). Longitudinal isotopic studies in the Strait of Gibraltar reported seasonal variation in nitrogen but not carbon stable isotopes from skin of *G. m. melas* (de Stephanis et al. 2008). However, stomach contents analysis showed seasonal differences in the diet of LFPWs from the Faroe Islands (Desportes and Mouritsen 1993) and annual differences in diets of LFPWs in the North Atlantic (Gannon et al. 1997b). Analysis of populations from differing geographic locations suggest that the eastern and western North Atlantic populations may not be feeding at the same trophic level, with isotopic differences in teeth suggesting differing movement patterns (Abend and Smith 1995). Indeed, global literature suggests that LFPW distribution could be characteristic of prey location (Cañadas et al. 2002; Table 1.2). For example, high LFPW occurrence around Iceland tends to follow seasonal squid distribution (Selbmann et al. 2022). Distribution of the northern sub-species *G. m. melas* in Iberian waters appears to coincide with shallower more coastal prey that this population is feeding on (Table 1, 2). However, LFPWs are recorded mainly offshore in the Alboran Sea, Northwest and Northeast Atlantic, Norwegian Sea, and Southern Ocean (Table 1.2). Spatial distribution studies of the southern sub-species are scarce, and it is recognised that further research is required to understand distribution of *G. m edwardii* in the Southern Hemisphere (Kraft et al. 2020).

Investigation into dietary fatty acid profiles is especially limited for LFPWs (Walters 2005; Monteiro et al. 2015b). Similarly, multi-method approaches to dietary studies are not common in the LFPW literature (Table 1.1), studies linking diet and body condition are rare. A single stranded male LFPW in Denmark had a blubber thickness of 51-103 mm across different body sections, which was considered a sign of moderate-good condition (Alstrup et al. 2022), whilst a single stranded animal

in Iceland had a blubber thickness of 31.3 mm and was considered to be in poor nutritional state (Davison et al. 2015). The mean blubber thickness of LFPWs mass-stranded on the Scottish coast was reported at 36.7 mm (Brownlow et al. 2015) and ranged between 30.7 and 74 mm in LFPWs stranded in Australia (Walters 2005). No link to body condition or nutritional state was suggested in these studies. In fact, the lack of relationship between blubber thickness and the total lipid content of blubber in Australian LFPWs (n = 63) suggested that blubber thickness may not be a good indicator of energy reserves (i.e., body condition) in this species (Walters 2005). Indeed, body condition was judged by "total length at age" rather than blubber measurements in studies of the costs of raising males to Faroese LFPW mothers (Nichols et al. 2014).

1.4.1 LFPWs in New Zealand

In New Zealand waters, the distribution of pilot whales (including both LFPWs and short-finned pilot whales) has been modelled from sightings data and categorised as offshore (>25km from the coastline) with a preference for deep waters (Stephenson et al. 2020), though pods clearly also move through coastal waters resulting in their high propensity to strand in New Zealand.

Mass-standings of LFPWs are relatively frequent on the New Zealand coast and occur mainly during the austral summer (Ogle 2017; Betty et al. 2020). Studies of LFPWs in New Zealand waters have so far concentrated on life history, genetics, social structure, persistent contaminants, and welfare (Brabyn 1990; Oremus et al. 2009; Betty 2019; Betty et al. 2019; Betty et al. 2020; Meyer 2020; Lischka et al. 2021; Betty et al. 2022; Boys et al. 2022). Additionally, stomach contents have been explored in a total of 37 animals stranded in three stranding events in New Zealand (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009). The small sample sizes of these previous studies also did not permit either ontogenetic or spatiotemporal analysis of LFPW dietary variation.

Known prey recovered from stomach contents of LFPWs stranded on the New Zealand coast include arrow squid, of which two species (*Nototodarus sloanii* and *N. gouldii*) are reported in local waters (Uozumi and Forch 1995). Additionally, the common New Zealand octopus *Pinnoctopus cordiformis* has been described as of secondary dietary importance to LFPWs in this region (Beatson and O'Shea 2009). Whilst other pelagic squid have been noted in low numbers (Beatson et al. 2007b), fish have not been recorded in the diet of LFPWs in New Zealand waters. Additionally, no examination of stable isotopes, fatty acids or body condition has been published for LFPWs in this region. The high frequency of LFPW mass strandings on the New Zealand coast therefore presents an opportunity to assess the little-known feeding ecology of the southern sub-species, *G. m. edwardii*.

Table 1.1 Dietary and trophic data for long-finned pilot whales (*Globicephala melas*). SCA = stomach content analysis, SIA = stable isotope analysis, FA = fatty acid analysis, TBL = total body length. Cephalopod, Fish and Other columns refer to number of unique species. Only stable isotope values for LFPW skin are included in this table.

Species	Location	*n*	Methods	Cephalopod	Fish	Other	Dominant prey	Dietary variation	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
G. m. melas (Northern)	Scotland	1	SCA	2	2	0	Cephalopod	N/A	N/A	N/A	Ritchie 1924
	Newfoundland	29	SCA	1	1	0	Fish	N/A	N/A	N/A	Sergeant 1962
	Western mid-Atlantic	4	SCA	1	2	0	N/A	N/A	N/A	N/A	Overholtz and Waring 1991
	Faroe Islands	720	SCA	9	14	>1	Cephalopod	TBL, season	N/A	N/A	Desportes and Mouritsen 1993
	Western North Atlantic	30	SCA	6	7	0	Cephalopod	N/A	N/A	N/A	Gannon et al. 1997a
	Western North Atlantic	8	SCA	6	6	0	Cephalopod	N/A	N/A	N/A	Gannon et al. 1997b
	Northeast Atlantic	11	SCA	12	8	1	Cephalopod	N/A	N/A	N/A	Spitz et al. 2011
	Northeast Atlantic	48	SCA	18	4	>1	Cephalopod	Spatial, temporal, ontogenetic	N/A	N/A	Santos et al. 2014
	Southern North Sea	2	SCA	2	5	2	N/A	N/A	N/A	N/A	Ijsseldijk et al. 2015
	Cape Cod	3	SIA	N/A	N/A	N/A	N/A	Spatial	N/A	13.8 ± 0.36	Abend and Smith 1995
	Mid-Atlantic Bight	3	SIA	N/A	N/A	N/A	N/A	Spatial	N/A	13.9 ± 0.36	Abend and Smith 1995
	Faroe Islands	3	SIA	N/A	N/A	N/A	N/A	Spatial	N/A	11.7 ± 0.45	Abend and Smith 1995

Table 1.1 continued

Species	Location	*n*	Methods	Cephalopod	Fish	Other	Dominant prey	Dietary variation	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
	Western North Atlantic	6	SIA	>1	>1	0	N/A	By tissue	-18.75 ± 0.143	13.88 ± 0.130	Abend and Smith 1997
	Strait of Gibraltar	5	SIA	N/A	N/A	N/A	N/A	None found	-16.20 ± 0.22	12.70 ± 0.32	de Stephanis et al. 2008
	Strait of Gibraltar	51	SIA	N/A	N/A	N/A	N/A	None found	-16.37 ± 0.40	11.29 ± 0.38	de Stephanis et al. 2008
	Northern Ireland	22	SIA	N/A	N/A	N/A	Cephalopod	Spatial	-17.7 ± 0.7	12 ± 0.7	Monteiro et al. 2015a
	Scotland	46	SIA	N/A	N/A	N/A	Cephalopod	Spatial	-18.7 ± 0.7	11.3 ± 0.6	Monteiro et al. 2015a
	North Atlantic	114	SIA	N/A	N/A	N/A	Cephalopod	TBL, Spatial	-18.3 ± 0.8	12.0 ± 1.0	Monteiro et al. 2015b
	Mediterranean Sea	15	SIA	N/A	N/A	N/A	N/A	N/A	-17.8 ± 0.3	10.5 ± 0.7	Pinzone et al. 2015
	Mediterranean Sea	21	SIA	N/A	N/A	N/A	N/A	N/A	-17.7 ± 0.6	10.5 ± 0.5	Pinzone et al. 2019
	North Atlantic	56	FA	N/A	N/A	N/A	N/A	Spatial	N/	N/A	Monteiro et al. 2015b
G. m. edwardii (Southern)	Tasmania	2	SCA	14	>1	0	Cephalopod	N/A	N/A	N/A	Gales et al. 1992
	South Africa	5	SCA	23	>1	0	Cephalopod	Cephalopod	N/A	N/A	Sekiguchi et al. 1992
	Northeast New Zealand	16	SCA	5	0	0	Cephalopod	N/A	N/A	N/A	Beatson et al. 2007b
	Farewell Spit, New Zealand	21	SCA	2	0	0	Cephalopod	N/A	N/A	N/A	Beatson and O'Shea 2009

Table 1.1 continued

Species	Location	*n*	Methods	Cephalopod	Fish	Other	Dominant prey	Dietary variation	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
	Southern Chile	7	SCA	3	0	0	Cephalopod	N/A	N/A	N/A	Mansilla et al. 2012
	Tasmania	114	SCA	26	>2	0	Cephalopod	Spatial, TBL	N/A	N/A	Beasley et al. 2019
	Chile	28	SCA	7	5	5	Cephalopod	N/A	N/A	N/A	Chalcobsky et al. 2021
	Tasmania	94	SIA	N/A	N/A	N/A	N/A	N/A	-19.6 ± 0.4	10.7 ± 0.9	Davenport and Bax 2002
	Kerguelen waters	65	SIA	65	0	0	N/A	N/A	-18.4 ± 0.5	12.2 ± 0.3	Fontaine et al. 2015
	Southeast Australia	147	SIA	N/A	N/A	N/A	Cephalopod	N/A	-17.6 ± 0.4	12.2 ± 0.6	Jackson 2017
	Western South Atlantic	1	SIA	N/A	N/A	N/A	N/A	N/A	-16.3	13	Troina et al. 2020
	Chile	54	SIA	N/A	N/A	N/A	Cephalopod	N/A	-14.5 ± 0.8	13.6 ± 1.3	Becker et al. 2021
	Australia	63	FA	N/A	N/A	N/A	Cephalopod/ Fish	None	N./A	N/A	Walters 2005

Table 1.2. Distribution and depth data for long-finned pilot whales (*Globicephala melas*) globally, and their known prey in New Zealand. * indicates mean water depth at time of sighting

Species	Location	*n*	Distribution	Depth (m)	Method	Paper
Global studies	North Atlantic	*N/A*	Variable	N/A	Review	Buckland et al. 1993
G.m.melas	Northeast Atlantic	*N/A*	Offshore, shelf break	N/A	Review	Abend and Smith 1999
	Alboran Sea	*N/A*	Mostly deepwater	848 ± 281.2*	Survey/Video	Canadas and Sagarminaga 2000
	Ligurian Sea	*171*	Offshore, deep diving	300 – 800	Survey	Cañadas et al 2002
	Ligurian Sea	*5*	Offshore	72 – 648	Tagging	Baird et al. 2002
	Mediterranean Sea	*N/A*	Deep water	N/A	Survey	Mangion and Gannier 2002
	Faroe Islands	*3*	Variable	< 500	Tagging	Bloch et al. 2003
	Northeast Atlantic	*2*	N/A	< 510	Tagging	Nawojchik and Aubin 2003
	Mediterranean Sea	*N/A*	Mostly deepwater	2,056 ± 403*	Survey	Gannier 2005
	Northwest Atlantic	*1*	Offshore, deep diving	> 1,500	Tagging	Mate et al. 2005
	Scotland	*54*	Deepwater	< 1,951	Survey	MacLeod et al. 2007
	Ligurian Sea	*N/A*	Pelagic	> 1,000*	Survey	Azzellino et al. 2008
	North Norwegian Sea	*7*	N/A	> 600	Tagging	Sivle et al. 2012
	North Norwegian Sea	*2*	N/A	13 – 513	Tagging	Aoki et al. 2013

Table 1.2. continued

Species	Location	*n*	Distribution	Depth (m)	Method	Paper
	North Norwegian Sea	*11*	Deep diving	4 – 617	Tagging	Visser et al. 2014
	Southwestern Atlantic	*10*	Outer continental slope/shelf	500 – 1,000	Survey	Di Tullio et al. 2016
	North Norwegian Sea	*19*	N/A	24.7 – 617.4	Tagging	Isojunno et al. 2017
	Alboran Sea	*50*	Offshore, deep diving	500 – 2,500	Modelling	Giménez et al. 2018
	North Atlantic	*N/A*	Mostly offshore		Review	Pike et al. 2019
	Iceland	*N/A*	Offshore, continental edge		Observation	Selbman et al. 2022
G. m. edwardii	South Africa	*N/A*	Offshore, continental slope	N/A	Observation	Sekiguchi et al. 1992
	South Africa/Namibia	*N/A*	Offshore, continental shelf	N/A	Observation	Findlay et al. 1992
	Australia	*5*	Variable	< 60	Tagging	Gales et al. 2012
	Southern Ocean	*3*	Offshore, continental slope	NA	Acoustic detection	Barlow et al. 2021
New Zealand studies						
G. m. edwardii	New Zealand	*N/A*	Offshore, deep diving	N/A	Spatial distribution models	Stephenson et al. 2020
Nototodarus spp.	Southeast New Zealand	*N/A*	N/A	< 600	Fisheries observations	Uozumi and Forch 1995
	New Zealand	*N/A*	N/A	17 – 1,146	Fisheries observations	Anderson et al. 1998

Table 1.2. continued

Species	Location	*n*	Distribution	Depth (m)	Method	Paper
	Southeast New Zealand	*N/A*	N/A	Highest density at < 300	Fisheries observations	Jackson et al. 2000
Pinnoctopus spp.	New Zealand	*N/A*	Coastal	< 300		Carrasco et al. 2014

1.5. Study rationale

Despite such a high stranding frequency, there is currently limited knowledge of the foraging ecology and potential fisheries overlap of LFPWs within New Zealand waters. Currently, knowledge of diet and foraging of LFPWs in this region is based on the stomach contents of a limited number of individuals ($n = 37$) from three stranding events (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009). Prior to this PhD study, no analysis had been conducted to corroborate insights from these stomach contents studies, or to explore isotopic niche or longer-term diet. Moreover, no research has previously been conducted to understand dietary variability within this species within New Zealand waters. Whilst overseas populations of LFPWs have displayed dietary variation spatially, both temporal and ontogenetic differences have also been noted (Table 1.1). Within the LFPW population in New Zealand waters, it is unclear if any ontogenetic, spatial, or temporal foraging differences occur. Furthermore, there has been little exploration into the relationship between diet, fatty acid profiles, blubber thickness, and blubber lipid content within LFPWs. Therefore, it is unknown whether changes in target prey species influence individual body condition, which could have implications for reproductive fitness and survivorship.

1.5.1. Thesis aims, objectives and structure

This thesis addresses critical gaps in our knowledge of the foraging ecology of LFPWs within New Zealand waters, using samples collected from carcasses involved in mass-strandings along the New Zealand coast between 2009 and 2017 (see Appendix 1.1 for further details). As the first investigation of intraspecific dietary variation of LFPWs from New Zealand waters, this study aims to provide insights into LFPW diet composition, variation, and potential links between diet and individual body condition.

To achieve this aim, there are four research objectives:

Objective 1: Investigate intraspecific variation in the prey composition of LFPWs stranded on the New Zealand coast.

Objective 2: Assess ontogenetic, spatial, and temporal isotopic niche dynamics within the LFPW population.

Objective 3: Evaluate the use of biochemical tracers in key prey species to quantify LFPW dietary variation.

Objective 4: Explore possible linkages between chemical dietary tracers and individual LFPW body condition.

Studies of foraging ecology in marine mammals integrating methodology can help to understand 1) the dietary composition of a species in a particular location and 2) observations of possible ontogenetic, spatial, or temporal, changes in diet. Dietary estimates from a single methodology can be difficult to validate (Tucker et al. 2008). This study will therefore apply an integrated approach combining stomach content, stable isotope, and fatty acid analyses to gain a better understanding of the diet and foraging interactions of LFPWs in New Zealand waters. Moreover, this research seeks to explore relationships between foraging and body condition of LFPWs through comparison of dietary data to common body condition measurements: girth, TBL:girth ratio, blubber lipid content and blubber thickness. Specifically, this study will comprise six chapters (Table 1.3), an introductory chapter (this chapter), four data chapters with associated literature reviews (Chapters 2-5) and an overarching discussion and synthesis of the combined thesis findings (Chapter 6; Table 1.3).

Table 1.3. Overview of thesis by chapter, questions, and analyses. LFPW = long-finned pilot whale (*Globicephala melas edwardii*), SCA = stomach contents analysis, CA = correspondence analysis, GAMs = generalised additive models, SIA = stable isotope analysis, FA = fatty acid analysis, n-MDS = non-parametric multidimensional scaling, PERMANOVA = permutational multivariate analysis of variance, SIMPER = similarity percentages, GLMs = generalised linear models

Chapter	Topic	Questions	Methods
1	Introduction and literature review	1.1 What does the published and grey literature tell us about the diet and foraging ecology of cetaceans and specifically LFPWs?	Literature review
2	Intraspecific dietary variation of long-finned pilot whales LFPWs stranded on the Aotearoa New Zealand coast.	2.1. What is the prey composition of LFPW stomach contents? 2.2. Are there ontogenetic, differences in LFPW diet, as revealed by stomach contents? 2.3. Are there spatial or temporal differences in LFPW diet, as revealed by stomach contents?	SCA Index of relative importance Bray-Curtis CA GAMs
3	Isotopic niche analysis of LFPWs in Aotearoa New Zealand waters	3.1. What are the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of LFPW skin? 3.2. Are there ontogenetic, spatial, or temporal differences in LFPW trophic dynamics, as revealed by stable isotopes?	SIA GAMs NicheRover

Table 1.3. continued

Chapter	Topic	Questions	Methods
4	Comparative analysis of LFPWs and their primary prey: insights from stable isotope and fatty acid analyses	4.1. Can LFPW prey species be distinguished via SI ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) analysis? 4.2 What are the dietary fatty acid profiles of potential LFPW prey from the Golden Bay/Tasman Bay region? 4.3. What do biochemical profiles of LFPW prey species tell us about their relative importance to LFPW diet?	FA SIA n-MDS PERMANOVA SIMPER Prey polygons
5	Body condition measurements and fatty acid profiles from LFPWs stranded on the Aotearoa New Zealand coast	5.1 What is the total lipid content of LFPW blubber? 5.2. Are there ontogenetic variations in body condition measurements of LFPWs? 5.3. Is there variation in the fatty acid profile of LFPW blubber in relation to body condition measurements?	Body condition indices FA PERMANOVA GLMs
6	Discussion and conclusions	6.1. What insights has this thesis provided towards likely diet and foraging ecology of LFPWs in New Zealand waters?	Literature review Self-critique

Chapter 2 — Intraspecific dietary variation of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the Aotearoa New Zealand coast.

A squid beak from the stomach of a long-finned pilot whale *Globicephala melas edwardii* stranded on the Aotearoa New Zealand coast. Photo credit: Bethany Hinton.

In this chapter, an investigation of the stomach contents recovered from 283 long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast (2009 – 2017) is presented to address the first research objective:

Objective 1: Investigate intraspecific variation in the prey composition of LFPWs stranded on the New Zealand coast.

This chapter is a re-formatted version of the manuscript:

Hinton et al. (*in prep*). Intraspecific dietary variation of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the Aotearoa New Zealand coast.

2.1. Abstract

Dietary studies can give important information on species interaction within their environment. Long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) strand frequently on the Aotearoa New Zealand coast, yet little is known of their diet. Stomach contents were examined from 283 LFPW carcasses stranded across eight locations in New Zealand between 2009 and 2017. Of the stomachs examined, 74% (n = 210) contained remains of cephalopods, 18% (n = 52) contained fish remains, and 16% (n = 44) of stomachs were empty. Percentage index of relative importance (%IRI) was calculated for remains of each identifiable prey group, revealing that *G. m. edwardii* in New Zealand waters rely heavily on arrow squid (*Nototodarus* spp.), at least in the immediate days prior to stranding. Generalised additive models (GAMs) indicated that total body length, sex and location were important predictors of variation in the percentage number (%N) of arrow squid consumed. Bray-Curtis dissimilarity matrices and correspondence analysis were further used to investigate ontogenetic (sex, maturity status, reproductive group) and spatiotemporal (year, location, stranding event) factors affecting variation in prey consumed. Whilst immature and mature individuals showed similarity in prey composition, fish remains were more frequently found in mature male stomachs than in those of mature females. Spatiotemporal variation in prey composition and diversity was noted by year, location, and stranding event. The findings of this study confirm that LFPWs are a predominantly teuthophagus predator, supplementing their cephalopod-dominated diet with fish. Whilst the diet of other LFPW populations appears to vary by total body length and location, dietary variation by sex is less commonly reported elsewhere, suggesting that this population may be demonstrating a different approach to feeding than overseas.

2.2. Introduction

Dietary studies are fundamental to understanding species function and their ecological interactions (Bowen 1997; Jory et al. 2021), offering insights into both predator behaviour and distribution (Trainor et al. 2014; Abrams 2019). Studies of dietary plasticity have garnered widespread interest in particular (Spitz et al. 2006; Santos et al. 2015; Costa and Angelini 2020). Factors affecting diet are not mutually exclusive and include social status (Metcalfe et al. 1992; Chen et al. 2010), morphological variation (Rincón et al. 2007) and local ecological conditions (Tollit et al. 1998; Palm et al. 2013; Marklund et al. 2018) and individual specialisation (Estes et al. 2003; Araújo et al. 2011). Optimal foraging theory (OFT) suggests that any of these differences in phenotype or prey availability may cause an individual to target a different prey species (e.g., Werner and Hall 1974; Pyke et al. 1977).

While dietary variation has been described both within (intra-) and between (inter-) populations, factors influencing this variation can be complex to determine. For example, ecological factors could influence foraging of a population over various temporal scales (Bassoi and Secchi 2000). These can include prey availability (Choy et al. 2020), climate/temperature (Rupil et al. 2018; Esteban et al. 2020) and habitat differences (Pusineri et al. 2007), which may cause dietary changes at the wider population level. From a functional perspective, dietary variation may be expected to vary during life stages (ontogeny) with increased nutritional demands, at times such as pregnancy and lactation (Bernard and Hohn 1989; Rechsteiner et al. 2013). Further to this, learned behaviours and foraging techniques may change or improve over time, resulting in dietary changes with increasing age (Kidawa and Kowalczyk 2011; Patterson et al. 2015) and/or body size (Lucifora et al. 2009). Such individual dietary variation, although often overlooked (Vander Zanden et al. 2010), has been noted in multiple marine species (Koen Alonso et al. 2002; Ward et al. 2006; Marcus et al. 2016; Kim et al.

2020), recognising that organisms may be responding simultaneously to a multitude of environmental stressors (Griffen et al. 2016; Gunderson et al. 2016; Hewitt et al. 2016; Chapman 2017).

Intraspecific dietary variation has been described for several marine species (Vogt and Guzman 1988; Schafer et al. 2002; Mills et al. 2021), including marine mammals (Clarke and Pascoe 1985; Pierce and Boyle 1991; Pauly et al. 1998; Santos et al. 1999; Lowry et al. 2004; Sheffield and Grebmeier 2009; Pomerleau et al. 2011), using stomach content analysis; the most enduring form of dietary study in marine mammal research (Hyslop 1980; Pierce and Boyle 1991; Bowen and Iverson 2013). Prey tissue is thought to digest within hours to days in delphinid stomachs (Sekiguchi and Best 1997). Conversely, fish otoliths remain in marine mammal stomachs for approximately 7-24 hours (McMahon and Tash 1979; Jobling and Breiby 1986; Sekiguchi and Best 1997), whereas cephalopod beaks are more resistant to digestion so are retained for longer (Bigg 1985; Harvey 1989; Santos et al. 2001).

Stomach content research can identify spatially diverse diet from the same species feeding at regionally distinct sites (Gannon and Waples 2004; Miller et al. 2013; Viola et al. 2017), as well as temporal changes that may result from natural or anthropogenic fluctuations in prey availability (Rupil et al. 2018; Ning et al. 2020). Analysis of stomach contents has been useful in gaining insight into dietary variation in the Northern Hemisphere long-finned pilot whale (*Globicephala melas melas*) in the Bay of Biscay, English Channel, Faroe Islands, and Atlantic (Overholtz and Waring 1991; Clarke 1994; González et al. 1994; Gannon et al. 1997b; Aguiar dos Santos and Haimovici 2001; Aguiar dos Santos and Haimovici 2002; De Pierrepont et al. 2005; Santos et al. 2014), and the Southern Hemisphere sub-species *G. m. edwardii* in Chile (Mansilla et al. 2012; Chalcobsky et al. 2021) and Tasmania (Gales et al. 1992; Beasley et al. 2019). Globally, the diet of the long-finned pilot whale

(herein: LFPW) predominantly comprises cephalopods (González et al. 1994; Beatson and O'Shea 2009; Spitz et al. 2011; Santos et al. 2014; Beasley et al. 2019). Global literature suggests that LFPW distribution could be characteristic of high productivity and prey density (Cañadas et al. 2002; Hamilton et al. 2019) as expected in optimal foraging theory. In the North Atlantic, temporal dietary fluctuations were reported for the Northern Hemisphere subspecies of LFPWs (*G. m. melas*) at both annual and seasonal timescales (Gannon et al. 1997b; Santos et al. 2014). In addition, ontogenetic dietary variation was observed for *G. m. melas* captured in drive fisheries off the Faroe Islands, with larger individuals found to be eating larger squid (Desportes and Mouritsen 1988). In contrast, a recent examination of the diet of the Southern Hemisphere sub-species (*G. m. edwardii*) stranded on the coast of Tasmania, Australia revealed smaller animals were consuming larger squid (Beasley et al. 2019).

In New Zealand, provisional stomach content analysis of 37 LFPWs (*G. m. edwardii*) sampled from three mass stranding events (MSEs; Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009) suggested a cephalopod-dominated diet. Here, the diet of *G. m. edwardii* is explored further by examining intraspecific variation in stomach contents recovered from individuals stranded on the New Zealand coast. Specifically, this chapter aims to (1) describe overall prey composition, and relative importance of each prey group to diet, (2) assess ontogenetic variation in prey consumption and (3) assess spatiotemporal variation in prey consumption.

2.3. Materials and methods

2.3.1. Sample collection

Morphometric data and stomach contents were opportunistically sampled from 283 LFPWs (*G. m. edwardii*) across 14 stranding events (10 MSEs and four singletons) on the New Zealand coast between 2009 and 2017 (Table 2.1, Figure 2.1). Samples were taken from strandings in the North Island (Raglan, Wairoa, Waimārama), South Island (Farewell Spit, Spencer Park Beach, Port Levy,

Te Oka) and Stewart Island (West Ruggedy, Mason Bay; Table 2.1, Figure 2.1). As many individuals as logistically possible were sampled from each stranding event, with no intentional size or sex bias. The only exception was the 2017 MSE at Farewell Spit, where stomachs were sampled from only freshly dead individuals (n = 3). Total body length (TBL, n = 278) and anatomical sex assessment (n = 282) were recorded on gross examination (Geraci and Lounsbury 2005). The abdominal cavity was subsequently opened to access the gastrointestinal tract, where the forestomach, main stomach and pyloric stomach were independently sampled *in-situ* to extract contents, following standard sampling protocols (Geraci and Lounsbury 2005). Stomach contents were carefully removed from each stomach chamber and placed into separate labelled bags. All stomach contents were stored frozen at -20 ℃ until subsequent analysis.

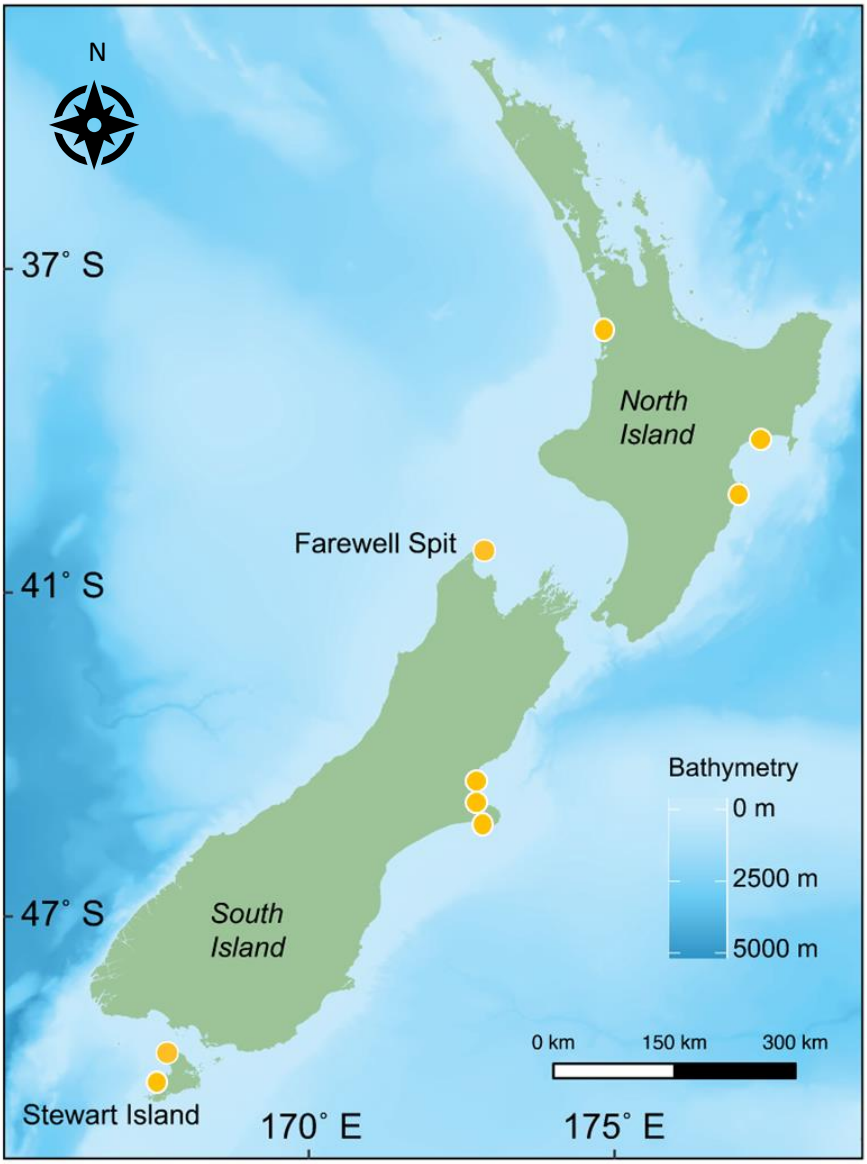

Figure 2.1. Locations of long-finned pilot whale (*Globicephala melas edwardii*) strandings on the New Zealand coast from which stomach contents were collected for this study, 2009–2017. From North to South in the north island: Raglan, Wairoa, Waimārama. From North to South in the South Island: Farewell Spit, Spencer Park Beach, Port Levy, Te Oka. From North to South in Stewart Island: West Ruggedy, Mason Bay. Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted from National Institute of Water and Atmospheric research (NIWA) under a creative commons by license (CANZ 2008), with permission from NIWA original copyright.

2.3.2. Age, sexual maturity, and reproductive group

Teeth were collected to assess age via dentinal growth layer groups (GLGs) as detailed in Betty et al. (2022). In summary, the least worn teeth were extracted from carcasses and a 3–5 mm section from the middle of the tooth was attained through grinding both sides, using a 600-grit wheel on a faceting machine. Mid-sections were then decalcified using hydrochloric acid (RDO, Apex Engineering Products Corporation, Aurora, Illinois), and 25 μm sections were taken on carbon a dioxide freezing stage of a sledge microtome. Each mid-section was stained using Ehrlich's haematoxylin and weak ammonia solution (Betty et al. 2022). All age estimations were made by at least two experienced readers and were performed in the absence of any further biological information, so as not to bias age estimates. Age estimates were available for 95% (n = 269) of individuals included in this study.

Reproductive status was assessed from histological examination of testes and gross examination of ovaries (see Betty 2019) and was available for 70% (n = 199) of individuals in the current study. Males were categorised into three reproductive groups: (1) immature, (2) maturing, (3) mature; defined by the relative proportion of mature seminiferous tubules in testes (Betty et al. 2019). Females were categorised into four reproductive groups, where possible: (1) immature, (2) pregnant, (3) lactating, (4) resting (Betty 2019). Immature females were defined by a lack of ovarian corpora scars, pregnant females by the visible presence of a foetus (but absence of milk in the mammary glands), lactating by the presence of milk in the mammary glands, and resting by the presence of at least one *corpus luteum* or *corpus albicans* scar indicating previous ovulation, but with no indication of pregnancy or lactation. Mature females that were not able to be confidently classified into a reproductive group due to state of decomposition (n = 11) were classified as "indeterminate mature". Both indeterminate females and males classified as "maturing" (n = 3) were excluded from reproductive group analyses.

Maturity status was classified by pooling reproductive groups as follows: "mature" status included all mature males as well as indeterminate, pregnant, lactating, and resting females; "immature" status included immature males and females. Where reproductive status was not available, body length was used as a predictor of sexual maturity using estimations presented by Betty (2019) and Betty et al. (2019) for the same population.

2.3.3. Stomach content analysis

Stomach contents were analysed following standard methods (Geraci and Lounsbury 2005). First, prey remains were thawed, rinsed through a 1 mm sieve, sorted into prey groups based on visual similarity (e.g., cephalopod eye lenses, squid beaks, fish bones, freshly ingested prey) and photographed. Hard-part remains were stored dry (fish bones and otoliths) or in 70% ethanol (cephalopod beaks), while fresh prey items were stored frozen at -20˚C.

Intact prey species were photographed and identified to the lowest taxonomic level possible using identification guides (e.g., Roberts et al. 2015; McMillan et al. 2019; Appendix 2.1). Hard part remains were counted, and diagnostic components used for identification. For cephalopods, diagnostic remains included lower cephalopod beaks, which were identified to the lowest possible taxonomic level using published guides (Clarke et al. 1986; Xavier and Cherel 2009) and reference collections of cephalopod beaks commonly found in New Zealand waters (curated by Massey University and National Institute of Water and Atmospheric Science, Taihoro Nukarangi; NIWA, respectively). Sub-samples of cephalopod beaks were further verified by an independent squid beak expert (Dr. Yves Cherel, National Centre for Scientific Research, Paris) during a squid identification workshop held at NIWA, Wellington (September 2019). Lower beaks that could not be identified due to degradation or breakage or were too small for identification were classified as "lower cephalopod beaks".

Fish otoliths and jaw bones containing teeth were used to identify fish prey species with reference to published literature and guides (Smale et al. 1995; Leach 1997; Furlani et al. 2007). Counts of fish represented by the hard part remains were determined by sagittal otolith counts divided by two, and jaw bone counts divided by four, respectively. Where there were co-occurring remains e.g., three jaw bones and two otoliths, this was counted as one fish, whereas five jaw bones and one otolith was counted as two fish. All fish otolith identifications were verified using national fish reference collections (Massey University and NIWA). If fish eye lenses were present without any further identifiable remains, the count of fish eye lenses was divided by two to determine fish count and categorised as "unidentifiable fish".

Table 2.1. Number and percentage of long-finned pilot whales (*Globicephala melas edwardii*) sampled for stomach content, TBL (total body length), age, sex, maturity status, and reproductive group following stranding events on the New Zealand coast, 2009–2017. Data as presented by stranding event. "Stranded (*n*)" = total number of individuals that stranded in that particular event, "Deceased (*n*)" = number of individuals that during the stranding event, "Stomach (*n*)" = number of individuals examined for stomach contents, IM = sexually immature, MM = mature male, P = pregnant female, L = lactating female, R = resting female, IN = indeterminate mature female, U – denotes reproductive group was not able to be assessed. "SC (*n*)" = number of pilot whales with prey remains recovered from stomachs.

										Reproductive Group							
Stranding	**Stranded**	**Deceased**	Stomach	TBL	Age	Male	Female	Immature	Mature	IM	MM	P	L	R	IN	U	SC
	(*n*)	**(*n*)**	**(*n*)**	(*n*)	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**	**(*n*)**
Christchurch 2009	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0
Farewell Spit 2009	105	105	49	49	49	21	28	18	31	0	0	2	0	0	0	47	42
Port Levy 2010	50+	17	16	16	16	5	11	12	4	10	0	0	0	0	2	4	10
Stewart Island 2010	28	28	16	16	16	9	7	9	7	9	2	2	0	0	3	0	14
Te Oka 2010	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	1
Raglan 2010	20	20	20	20	20	8	12	7	13	5	0	0	0	0	4	11	6
Wairoa 2011	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1
Farewell Spit 2011a	84	17	7	7	7	5	2	3	3	3	1	0	1	1	0	1	7
Stewart Island 2011	107	107	77	74	69	25	52	23	54	22	8	8	4	25	1	9	66
Farewell Spit 2011b	65	56	49	49	48	22	27	15	33	12	2	1	11	11	0	11	49
Wairamārama 2013	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Farewell Spit 2014a	39	39	36	35	36	15	21	15	20	15	3	4	10	3	0	1	35
Farewell Spit 2014b	99	50	6	6	3	3	3	1	5	1	2	1	2	0	0	0	6
Farewell Spit 2017	400+	252	3	3	3	0	3	1	2	1	0	1	0	1	0	0	2
Total	1,001+	694	283	278	269	115	168	105	174	79	18	19	28	41	10	87	239

2.3.4. DNA barcoding

Visual identification was inconclusive for some prey. Thus, a 5 mm^3 subsample of muscle tissue from the anguilliformes (n = 11) and elasmobranchs (n = 4) that had soft tissue present was sent for DNA barcoding to discern species. Additionally, subsamples of 10 arrow squid from LFPWs involved in this study had also previously been barcoded using the same methodology (Lischka et al. 2021). All muscle tissue had DNA extracted using QIAGEN reagents (QIAGEN) and EconoSpin columns (Epoch Life Science) using protocols for the animal tissues in the Dneasy Blood and Tissue Handbook (QIAGEN® 2006). The 648–bp barcode region cytochrome c oxidase, subunit I (COI) gene (Hebert et al. 2003; Hebert et al. 2004). Was amplified using C_FishF1t1/C_FishR1t1 (Ivanova et al. 2007) as described in Braid et al. (2014). If a single clean band appeared on PCR products, these were sequenced at Macrogen (Korea) using M13 primers, which were edited using CodonCode Aligner (ConCode Corep., USA). The identification engine Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007; August 2022) was used to compare sequences to relevant reference barcodes.

2.3.5. Prey length and mass reconstruction

To estimate the length and mass of prey at the time of ingestion, measurements of lower rostral length (LRL) of squid beaks, lower hood length (LHL) of octopus beaks (Clarke et al. 1986) and otolith length (Furlani et al. 2007) were recorded. All measurements were taken to the nearest 0.1 mm using digital callipers. Prey mass and length reconstruction estimation equations were applied from Clarke (1986), Lu and Ickeringill (2002), Furlani (2007), Horstkotte (2008), Bolstad (2008), Miller et al (2013), Horn (2016), Northern (2017) and Blasina et al. (2018). Where intact cranial remains and vertebral columns were recovered, these were not included in length or mass reconstruction due to damage.

2.4. Statistical analysis

2.4.1. Overall prey composition, and relative importance to diet

To investigate appropriate sample sizes for detection of prey groups, a cumulative prey curve was created in R package "vegan" (Oksanen et al. 2013). Raw counts of each identifiable prey group were used in curve construction. Sample order of individuals was randomised across 10,000 iterations to avoid sampling bias (e.g., Miller et al. 2013).

To assess prey contribution to diet, percentage index of relative importance (%IRI) was calculated using:

$$\%\mathrm{IRI}_i = \mathrm{FO_i}(\%\mathrm{N_I} + \%\mathrm{M}_i)$$

where prey group = i, the frequency of occurrence = FO, percentage number = %N and the percentage mass = %M (Cortés 1997).The FO was calculated as the number of LFPWs each prey species was recorded in, divided by the total number of stomachs containing identifiable prey; %N as the total number of each prey species, divided by the total number of all prey species found, expressed as a percentage; and the %M as the total reconstructed mass of each prey species, divided by the total estimated mass of all prey species found, expressed as a percentage. The %IRI aids comparison of prey contribution across multiple studies (Cortés 1997) and is used increasingly in stomach content studies (e.g., Medina et al. 2015; Rodrigues et al. 2020; Gonzalez-Pestana et al. 2021; Lin et al. 2021). Only identifiable hard part remains that were 1) able to be accurately measured and 2) had species regression equations available were included in %N, %M and %IRI calculations.

2.4.2. Ontogenetic and spatiotemporal variation in prey consumption

The total counts of prey items recovered for each identifiable prey species consumed were used to calculate approximate prey diversity using the Shannon diversity index (e.g., Dolar et al. 2003) with equation:

$$H' = -\sum[(\frac{n_i}{N})ln(\frac{n_i}{N})]$$

where n_i = count of prey species and N = total count of all prey species combined. Prey diversity was calculated by the following groups: sex, maturity status, reproductive group, stranding year, stranding location, and stranding event to allow comparison of prey diversity among groups.

Differences in LFPW diet composition were assessed between sex, maturity status, reproductive group, stranding year, stranding location, and stranding event using the Bray-Curtis similarity index on percentage FO data (%FO; e.g., Rodrigues et al. 2020; Lin et al. 2021). The % FO was calculated as:

$$\frac{PWP}{PWS} * 100$$

where PWP = number of individual LFPWs the prey group was recorded in, and PWS = the number of stomachs containing identifiable prey. The %FO is considered less ambiguous than other measures (e.g., %M) when using large sample sets; it does not rely as heavily on how digested prey is, hence is more reliable, though less informative, when attempting to quantify diet across timeframes and studies (Buckland et al. 2017; Amundsen and Sánchez-Hernández 2019). As only data over 10% FO can be used in Bray-Curtis calculations (e.g., Rodrigues et al. 2020; Lin et al. 2021), all squid species other than arrow squid were combined into the group "other squid" and all fish species combined to form the group "fish". This resulted in four taxonomic groups for analysis: arrow squid, octopus, other squid, and fish. Whilst using broad taxonomic groups of "fish" and "other squid" does not allow the comparative resolution that identifying specific prey species does, these groups were used in order not to lose information from unidentifiable remains. The Bray-Curtis index was presented as a similarity (rather than dissimilarity) percentage by using the following equation:

$$(1 - bray\ curtis\ index) * 100$$

The Bray-Curtis matrices and cluster heatmaps were produced using the "vegdist" and "heatmap" functions in R package "vegan" and are available in Appendices 2.2 and 2.3. Correspondence analysis was used to visualise dietary variation (e.g., García-Berthou 2001; Gebert and Verheyden-Tixier 2001; Gobel et al. 2019), using %FO data (e.g., Lagos and Bárcena 2018). Chi-squared tests resulting from correspondence analysis were used to assess variation in prey composition by reproductive group, stranding year, location, and event. The R packages FactormineR and FactoShiny (Lê et al. 2008; Husson et al. 2016) were used together to run correspondence analysis on data and generate graphs.

All further analyses were performed on the two main prey species, as chosen by high %IRI values (Table 2.2), of arrow squid and octopus. Non-parametric Kruskal-Wallis tests were applied to assess the number of main prey items consumed as these do not assume a normal data distribution. It is important to note that this comparison of hard parts requires remains to be sufficiently undigested for identification (Buckland et al. 2017). The relationship between beak size (LRL for arrow squid and LHL for octopus) and LFPW age and body length, respectively was assessed using Spearman rank sum tests (e.g., Santos et al. 2007; Beasley et al. 2019). Correlations were presented by sex and maturity status using the R package "ggplot2" (Wickham 2011). Beak size was used rather than reconstructed length to avoid reliance on accuracy of the regression equations used, which would add a further layer of uncertainty to data.

Finally, the variation in the number of prey consumed per individual was assessed through generalised additive models (GAMs), fitted for the main prey species only (e.g., Santos et al. 2013). The relationship between prey number (%N) against a range of variables: body length, sex, maturity status, location, year, and stranding event using GAMs (e.g., Santos et al. 2013; Marçalo et al. 2018).

Age was not included as a factor due to significant correlation between age and body length (Pearson, t = 10.51, correlation = 0.60, p = < 0.001) and reproductive group was also excluded as it was only available for 70% of data. Models were built with binomial distribution with data weighted equal to the number of prey items in each stomach. Gamma set to 1.4 to prevent overfitting (Wood 2017) with all possible combinations of variables. Akaike's information criterion adjusted for small sample size (AICc; Burnham et al. 2011) was used to select the best fitting model. Models within three AICc units of the optimum model were deemed equally likely, and the top three were reported. Models were tested for interactions for the three top-ranked models. Final models were checked for normality and obvious patterns in the residuals. As data was not normally distributed and contained high numbers of zeros, non-parametric Kruskal-Wallis tests were used (e.g., Santos et al. 2007) to measure the mean number of prey species ingested between ontogenetic (sex, maturity status, reproductive group) and spatiotemporal (stranding year, location, event) variables of significance retained in the top three GAM models.

2.5. Results

Stomachs contents collected historically through the long-finned pilot whale project across New Zealand over an eight-year period (2009–2017, Table 2.1) and stored at Massey University were investigated from a total of 10 mass and four single strandings.). Across all stranding events, 283 LFPW carcasses were investigated for stomach contents (Table 2.1). Of those, stomach contents were successfully collected from 239 (84%, Table 2.1) individuals, while 44 stomachs were empty (16%; see Appendix 2.4 for further breakdown of empty stomachs). Of the 239 LFPWs with stomach contents, 90% (n = 214) contained identifiable prey remains including cephalopod beaks and identifiable fish otolith and bones. A further 10% (n = 25) individuals contained only unidentifiable

remains (e.g., eye lenses, unidentifiable fish bones, eroded or broken cephalopod beaks; Appendix 2.5).

2.5.1. Overall prey composition, and relative importance to diet

A total of 24,369 prey items was recovered from 239 individuals for identification. Across all stranding events and years, 13 taxa were identified from stomach contents, including eight squid, four fish and a single octopus taxon (Table 2.2). Of these, six taxa were newly recorded to the diet of LFPWs in New Zealand waters. Identifiable prey items included intact cephalopods, fish bones, fish otoliths, fish egg cases, and lower cephalopod beaks. Unidentifiable prey remains included upper or broken cephalopod beaks, both cephalopod and fish eye lenses, unidentifiable fish bones, and miscellaneous tissue (Appendix 2.5). A single fish otolith could not be identified due to lack of corresponding otoliths within reference collections. Similarly, tooth plates were noted in on stomach that were believed to belong to the New Zealand eagle ray (*Myliobatis tenuicaudatus;* Leach 1997), but without further remains this could not be confirmed. However, identification of conger eel (*Congridae* sp.) and carpet shark (*Cephoscyllium* sp.; see Appendix 2.6) was confirmed through DNA analysis. Finally, *Nototodarus* spp. (herein referred to as arrow squid) were likely *Nototodarus sloanii* based on DNA barcoding completed on a subset of fresh squid recovered from the same stomachs (Lischka et al. 2021).

The cumulative prey curve did not reach a plateau, indicating that it is unlikely that the full prey diversity was sampled. Still, the curve showed that that approximately 20 animals were needed to sample 50% of the prey diversity, 60 animals needed to be sampled in order to record about 70% of prey diversity and 250 animals were needed to record 90% of the prey diversity (Figure 2.2).

When stomach content data were pooled for all LFPWs examined, cephalopods were the most common prey by both number (98.67%) and reconstructed mass (91.98%). The top five prey taxa to

contribute to LFPW diet were arrow squid (92.81%N, 87.36%M 98.77%IRI), *Pinnoctopus cordiformis* (herein referred to as octopus; 4.32%N, 6.69%M, 1.01%IRI), conger eel (0.36%N, 2.94%M, 0.12%IRI), carpet shark (0.28%N, 1.72%M, 0.02%IRI) and *Lycoteuthis lorigera* (0.73%N, 0.37%M, 0.03%IRI, Table 2.2). The youngest individual with prey remains observed in the stomach (minimum of 16 arrow squid) was an immature female (217 cm TBL, <1 year old) stranded at Rakiura (Stewart Island).

Table 2.2. Frequency of occurrence (FO), total number, total mass, % number, % mass, index of relative importance (IRI) and % index of relative importance (%IRI) of prey species recovered from stomach contents of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast, 2009–2017 (*n* = 239).

Species	FO	Total number	Total mass (g)	% Number	% Mass	IRI	% IRI
Cephalopods							
Chiroteuthis veranyi	0.05	21	1,065	0.33	0.06	0.02	0.01
Histioteuthis atlantica	0.06	28	3,173	0.45	0.17	0.04	0.02
Lycoteuthis lorigera	0.05	46	6,931	0.73	0.37	0.06	0.03
Moroteuthopsis ingens	0.05	24	1,391	0.43	0.11	0.03	0.02
Nototodarus spp.	0.96	5,404	1,601,839	92.81	87.36	172.87	98.77
Octopoteuthis spp.	<0.01	1	543	0.02	0.03	<0.01	<0.01
Pholidoteuthis massayae	0.01	2	951	0.03	0.05	<0.01	<0.01
Pinnoctopus cordiformis	0.16	274	119,774	4.32	6.69	1.79	1.01
Teuthowenia pellucida	0.01	3	35	0.05	0.00	<0.01	<0.01
Fish							
Arripis trutta	<0.01	1	1,419	0.02	0.08	<0.01	<0.01
Congridae. sp	0.06	38	53,974	0.36	2.94	0.21	0.12
Cephoscyllium sp	0.02	17	31,502	0.28	1.72	0.04	0.02
Macruronus novaezelandiae	0.02	22	7,456	0.19	0.41	0.01	0.01

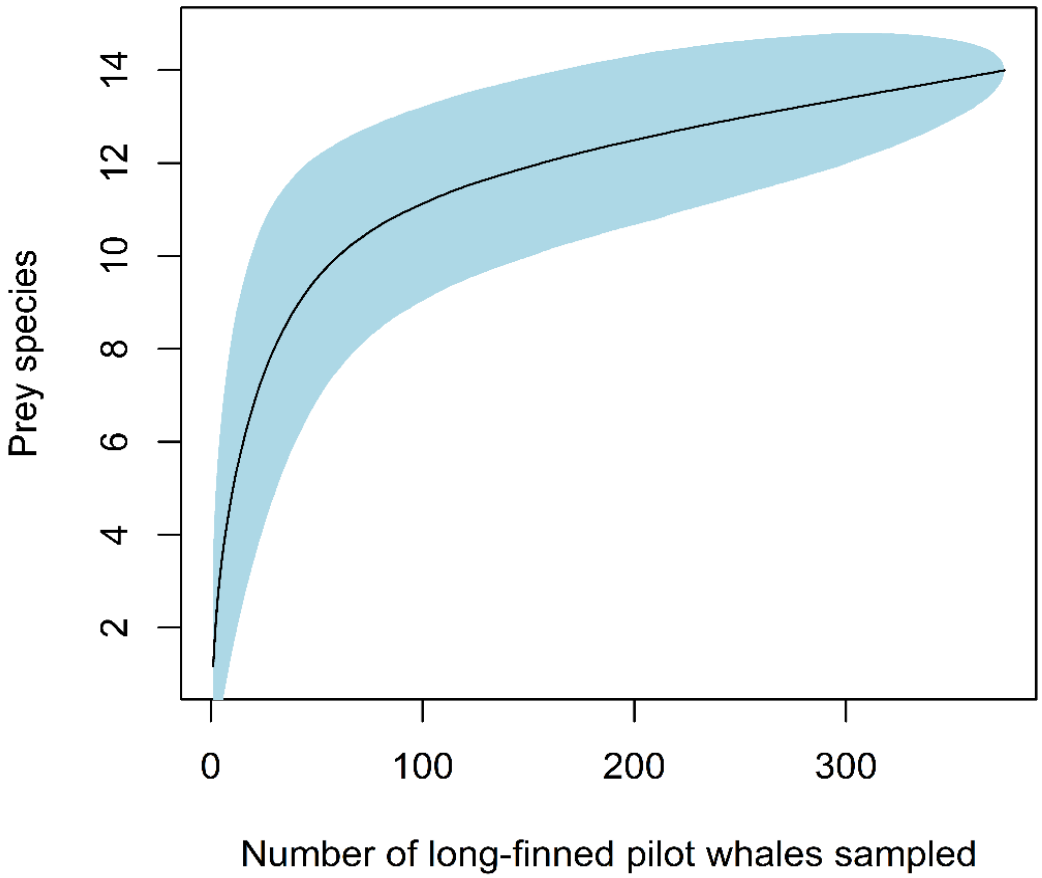

Figure 2.2. Cumulative curve of prey species recovered from the stomach contents of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast, 2009–2017 (*n* = 239). The order of individuals sampled was randomised across 10,000 iterations.

This was the only individual yearling with prey remains detected, though prey remains were recovered from 69% of the stomachs of immature individuals aged 1 year or older (n = 72). The average LRL for arrow squid beaks recovered from LFPW stomach contents was 4.52 mm, equating to a median reconstructed length of approximately 173 mm and mass of 211 g. The length of arrow squid beaks ingested increased significantly with both increasing LFPW age and body length, but both showed only a weak positive correlation (age: rho = 0.18, p = <0.001; body length: rho = 0.25, p = <0.001; Figure 2.3). The median LHL of octopus beaks averaged 4.13 mm, equating to a reconstructed length of approximately 767 mm and mass of 296g. The LHL decreased significantly with increasing LFPW body length and age, respectively (Age: rho = -0.28, p = <0.001; body length: rho = -0.18, p = 0.002; Figure 2.3). However, when assessing females alone, a positive correlation between octopus LHL and LFPW age was shown (Figure 2.3D).

2.5.2. Ontogenetic and sex variation in prey consumption

The %FO of prey groups consumed was similar between immature (n = 76) and mature (n = 159) individuals (96.3%), showing dietary homogeneity between LFPWs of differing maturity status. A lower level of similarity was recorded between males (n = 99) and females (n = 140; 70.2%), showing a degree of heterogeneity between male and female diet.

The %FO of prey groups consumed differed significantly by reproductive group (x^2 = 158.7, p = <0.001), with the first and second dimensions of correspondence analysis explaining 96.21% and 2.97% of the variance, respectively (Figure 2.4A). Fish contributed highly to variance, being found more frequently in stomachs of mature males than in those of other reproductive groups. Arrow squid also contributed highly to variance and were observed more commonly in mature females (pregnant, lactating and resting). Furthermore, both resting females and mature males more frequently consumed "other squid" (Figure 2.4A). Bray-Curtis indices indicated similarity in %FO

of prey groups consumed between mature females of differing reproductive status, i.e., lactating females (n = 28) vs. resting females (n = 39) = 91.6%, pregnant females (n = 18) vs. lactating females = 89.6%, and pregnant vs. resting females = 89.1%. The least dietary similarity was recorded between lactating females and mature males (n = 18; 54.87%). Immature individuals (n = 57) were most similar to pregnant females (89.5%). Consistently, the diversity index showed mature males had the largest prey diversity ($H' = 1.01$) followed by resting females ($H' = 0.18$), pregnant females ($H' = 0.05$) and lactating females ($H' = 0.04$).

2.5.3. Spatiotemporal variation in prey consumption

The %FO of prey groups also differed significantly by year stranded (x^2 = 161.5, p = <0.001) with the first and second dimensions of correspondence analysis explaining 59.02% and 38.97% of variance, respectively (Figure 2.4B). The "other squid" category contributed most to data variation, where LFPWs more frequently consumed "other squid" in 2010 (n = 30) than any other year. All LFPWs showed a high level of similarity in %FO of prey groups consumed between years, as evidenced by Bray-Curtis indices above 70%. However, LFPWs stranded in 2017 (n = 3) were the most unique compared to 2009 (n = 42; 69.8%), 2010 (69.2%), 2011 (n = 123; 69.2%) or 2014 (n = 41; 78.7%). Indeed, arrow squid were found exclusively within all examined stomachs from 2017 (n = 3). Correspondingly, 2017 was the year with the least diversity of species consumed ($H' = 0$) followed by 2014 ($H' = 0.19$), 2010 ($H' = 0.36$), 2009 ($H' = 0.39$) and 2011 ($H' = 0.55$).

The %FO of prey groups differed significantly by location stranded (x^2 = 491.1, p = <0.001), with the first and second dimensions of correspondence analysis explaining 81.06% and 17.72% of variance, respectively (Figure 2.4C). Arrow squid consumption contributed highly to variance, which was grouped mostly with individuals stranded at Raglan, Stewart Island and Port Levy. Furthermore,

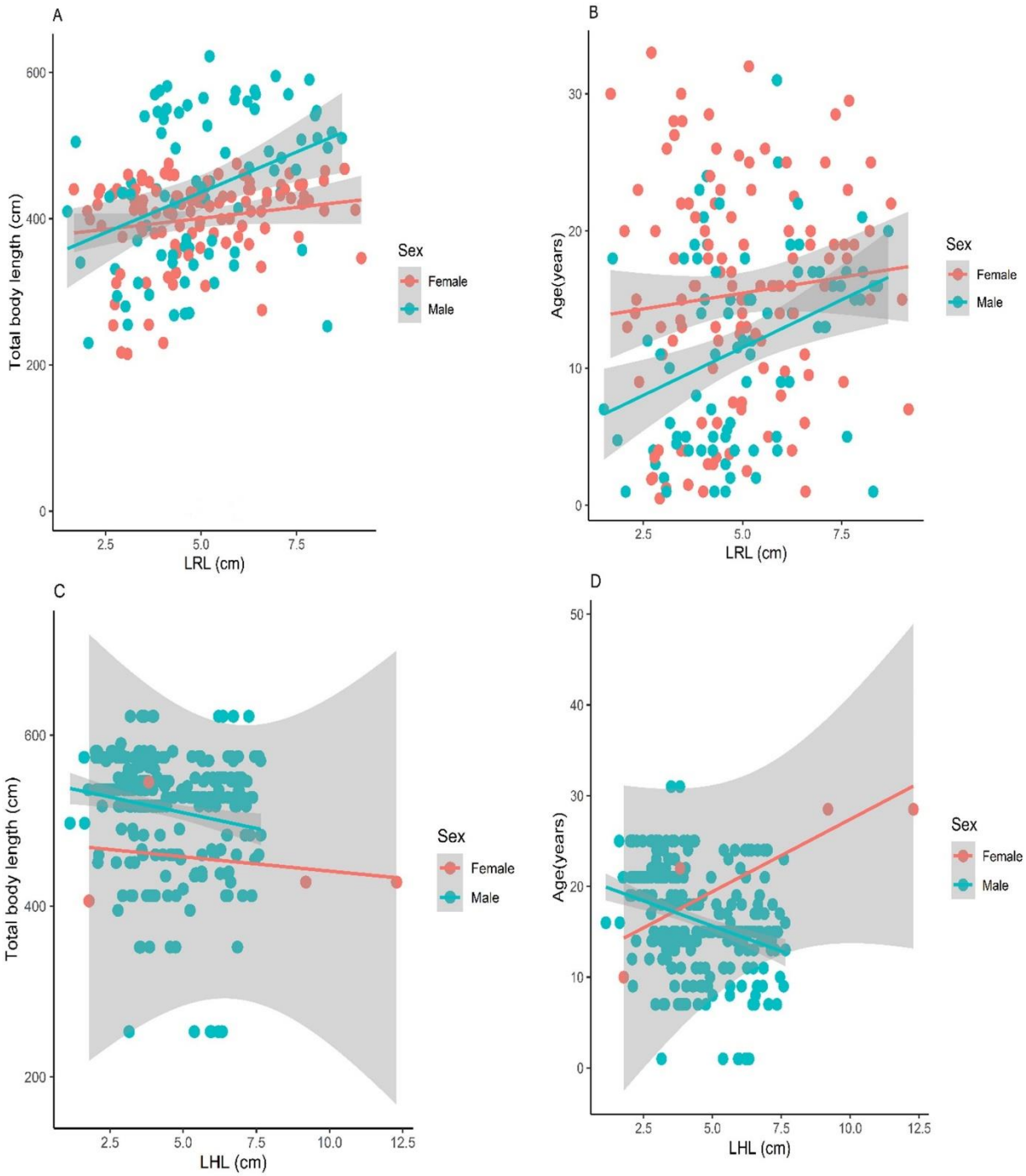

Figure 2.3. Relationships between (A) lower rostral length (LRL) of arrow squid (*Nototodarus* spp.) ingested, and long-finned pilot whale (*Globicephala melas edwardii;* LFPW) total body length (TBL), (B) LRL of arrow squid and LFPW age, (C) lower hood length (LHL) of octopus (*Pinnoctopus cordiformis*) ingested with LFPW TBL, and (D) LHL of octopus and LFPW age. LRL and LHL measurements were taken from prey recovered from stomachs of LFPW carcasses from strandings on the New Zealand coast, 2009 – 2017.

octopus was more frequently detected in stomachs of stranded individuals at Farewell Spit (Figure 2.4C), whilst the %FO of other squid was associated with Stewart Island and Te Oka, and fish with Wairoa. Pairwise similarity in prey groups consumed by LFPWs was high between Stewart Island (n = 79) and Port Levy (n = 10; 83.7%), and between Stewart Island and Farewell Spit (n = 141; 75.8%). Conversely, %FO of prey groups consumed was most unique at Wairoa (n = 1), which shared dietary similarity to Te Oka (80.0%), but not Farewell Spit (21.3%), Stewart Island (29.1%) or Port Levy (25.8%). Correspondingly, LFPWs stranded at Stewart Island ($H' = 0.24$) consumed the most diverse set of prey groups.

Finally, differences in %FO of prey groups consumed between stranding events were deemed significant (x^2 = 908.8, p = <0.001), with the first dimension of correspondence analysis explaining 65.81% of variance and the second dimension explaining 29.64%. The "other squid" prey group contributed highly to variance, which was associated with the Stewart Island 2010 and Te Oka 2010 stranding events (Figure 2.4D). In general, more individuals involved in the Farewell Spit stranding events (other than Farewell Spit 2014a or Farewell Spit 2017) demonstrated octopus consumption than other events (Figure 2.4D), whereas Farewell Spit 2014a, Farewell Spit 2017 (n = 3), Stewart Island 2010 and Raglan (n = 7) stranding events were more associated with arrow squid consumption. Finally, the Wairoa 2011 (n = 1) stranding had the largest %FO of fish consumption, due to only one animal involved in that event. Similarity in %FO of prey groups consumed varied highly between stranding events (Figure 2.4D). For example, LFPWs stranded at Farewell Spit 2014a (n = 35), and Wairoa 2011 showed little similarity through Bray-Curtis indices. Still, stranding events at Farewell Spit generally showed high homogeneity in prey groups consumed. For example, stranding events at Farewell Spit 2009 (n = 42) and Farewell Spit 2011b (n = 49) recorded Bray-Curtis

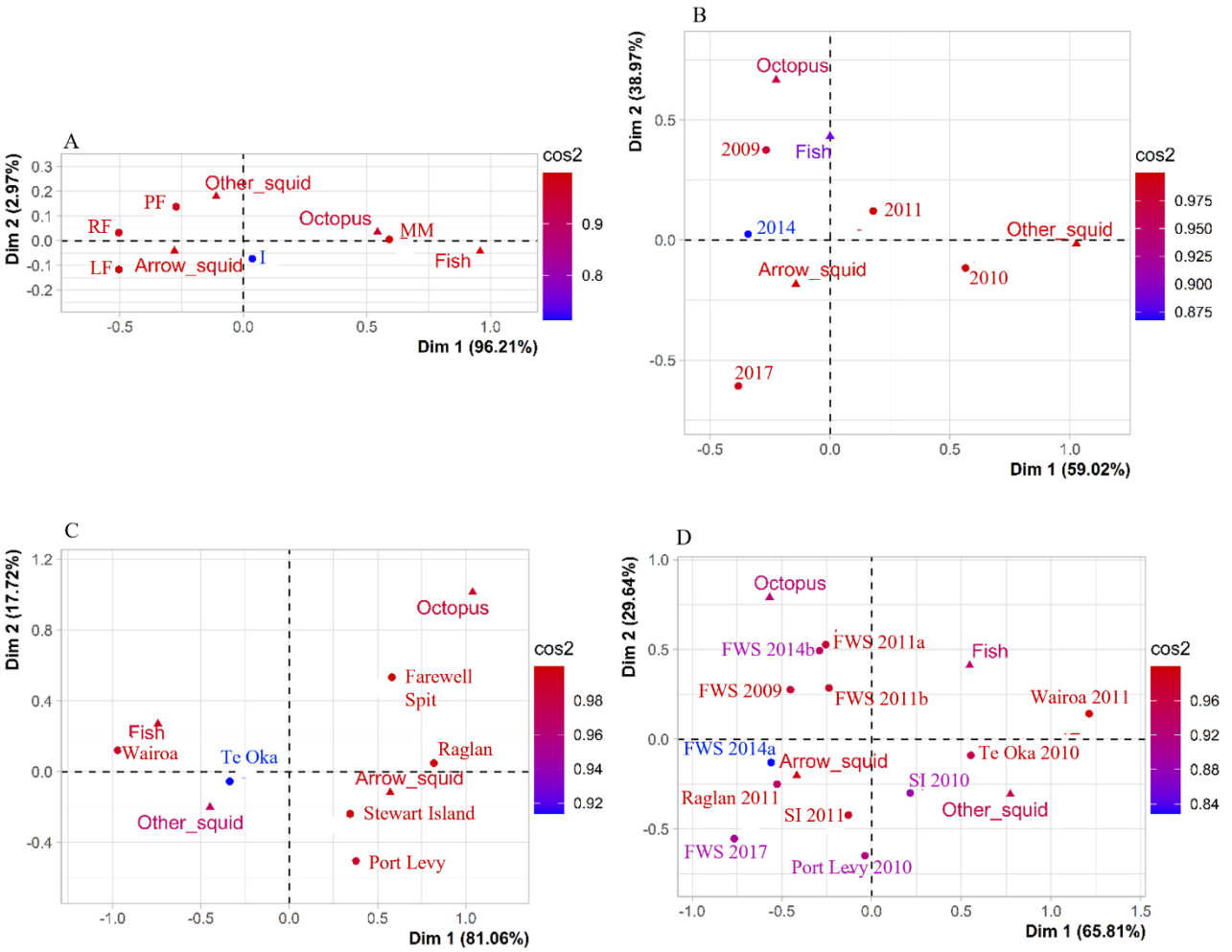

Figure 2.4. Correspondence analysis of variation in prey consumption of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast, 2009–2017. Percent frequency of occurrence of stomachs containing arrow squid (*Nototodarus* spp.), octopus (*Pinnoctopus cordiformis*), fish or "other squid" are used for data construction. Graphs explore variation by (A) reproductive group (n = 160), (B) stranding year (n = 239), (C) location stranded (n = 239), and (D) stranding event (n = 239). FWS = Farewell Spit, SI= Stewart Island. All graphs are coloured according to Cos^2 (cosign^2) where red is high, and blue is low. A: LF = lactating female, PF = pregnant female, R = resting female, 4 = immature and 5 = mature male.

similarity of 92.3%. Interestingly, strandings at Stewart Island 2010 (n = 13) and Port Levy 2010 (n = 7), which occurred only three weeks apart, also showed high dietary homogeneity in %FO of prey groups consumed (88%).

2.5.4. GAM analysis

For arrow squid, the model that best fit variation in %N consumed retained TBL, sex, maturity status, year and location as significant covariates and explained 60.4% of the deviance (Table 2.3, Figure 2.5). No difference in the number of arrow squid consumed between immature (mean = 29) and mature (mean = 28) LFPWs was detected. However, females (mean = 30) ate significantly more arrow squid then males (mean = 26; H = 5.28, p = 0.02), the mean number of arrow squid consumed also varied by location (H = 11.8, p = 0.035), and was significantly lower in 2011 than 2009 (H = 2852, p = <0.001). Although age had no clear relationship with number of arrow squid consumed, LFPW TBL was significantly correlated with the total number of arrow squid ingested per individual (rho = -0.14, p = 0.04).

For octopus, the model that best fit variation in the %N consumed retained sex as the only covariate and explained 14.9% of the deviance. Males consumed significantly more octopus (mean = 9; H = 5.15, p = 0.02) than females (mean = 2). Neither LFPW age nor TBL showed a significant relationship with number of octopus consumed (p > 0.05).

Table 2.3. Summary statistics of the top three generalised additive models selected based on Akaike Information Criterion corrected for small samples sizes (AICc) of the two most important prey (by % number) to diet of long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) stranded on the New Zealand coast, 2009 – 2017. % DE: % deviance explained; LL: log-likelihood; wAICc = aAICc weight; δAIC: difference in Akaike's Information Criterion (AICc) of the current and top-ranked model; TBL: total body length of LFPWs. Significant variables are given in bold; arrow squid: *Nototodarus* spp.; octopus: *Pinnoctopus cordiformis*. %N = percentage number

Response variable	Model; gamma = 1.4	AICc	% DE	LL	wAICc	δ AIC
%N Arrow squid	~ s(TBL, by Sex) + **sex** + maturity*year + **location**	957.17	60.4	1.00	0.70	-
	~ s(TBL, by Sex) + **sex** + year + **location**	958.88	59.6	0.43	0.30	1.72
	~ s(TBL, by = Sex) + **sex** + year* **location**	974.30	59.6	0.19	<0.01	17.12
%N Octopus	~ **sex**	45.15	14.9	1.00	0.19	-
	~ location	45.77	11.4	0.73	0.14	0.62
	~ sex + location	46.85	21.0	0.43	0.08	1.70

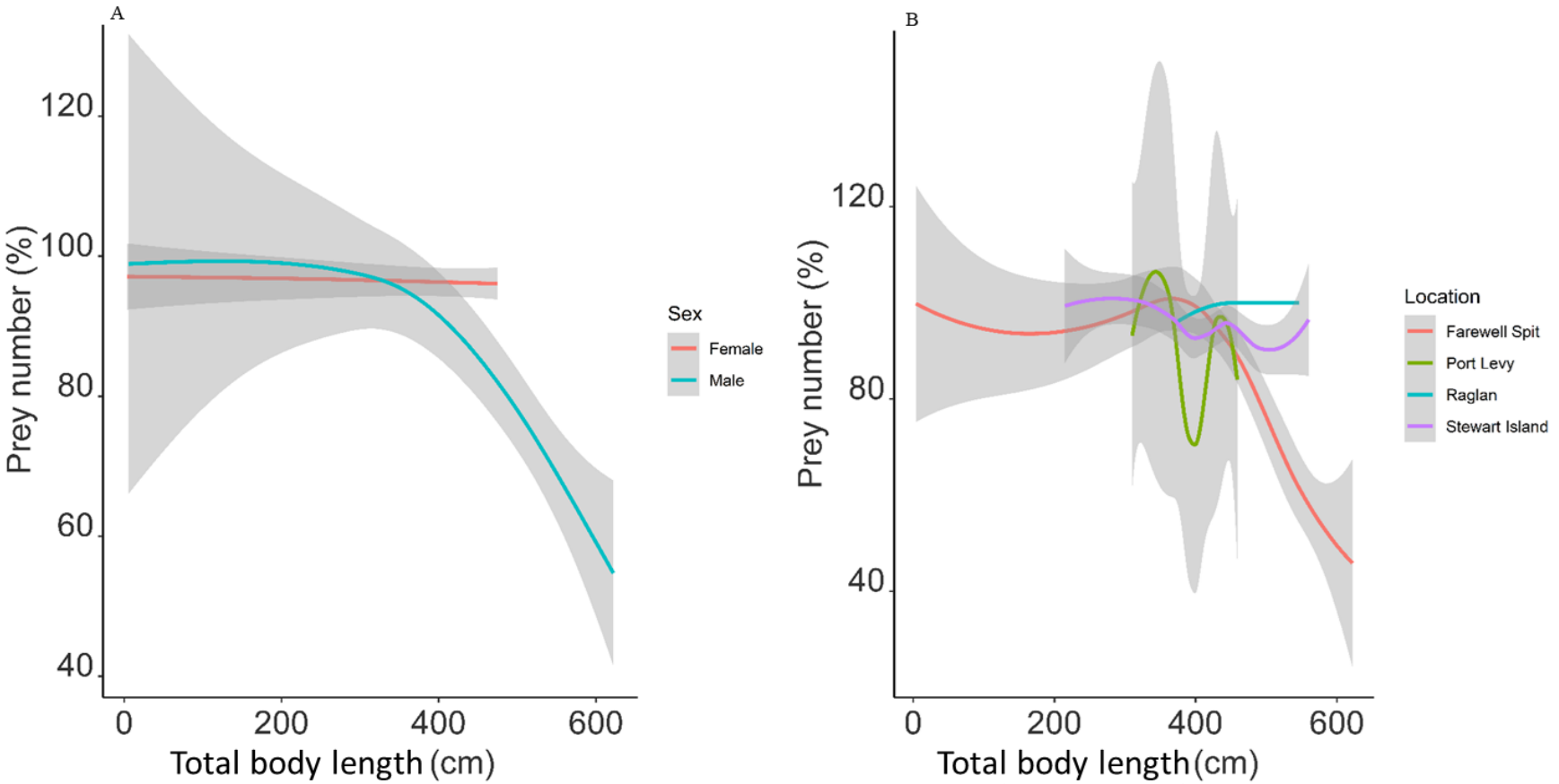

Figure 2.5. General additive models of the relationship between % number of arrow squid (*Nototodarus* spp.) in the diet of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast (2009–2017) and their total body length (TBL), displayed by sex (A) and location (B).

2.6. Discussion

The research from this chapter confirms that LFPWs are a teuthophagus species, targeting arrow squid (*Nototodarus* spp.) and common octopus (*Pinnoctopus cordiformis*) in New Zealand waters, and additionally supplementing diet with fish and other pelagic squid. Though the majority of prey remains recorded belonged to pelagic species, prey remains found from carcasses at Farewell Spit suggest that male LFPWs may spend at least some of their time feeding demersally, which could have implications for strandings. Variation in the size of both arrow squid and octopus consumed was positively correlated with increased LFPW body length, but not necessarily age, suggesting the targeting of prey with higher energy values from larger rather than older individuals. Furthermore, variation in prey diversity and composition was evident by both ontogenetic and spatiotemporal factors, whereby the larger and/or mature males ate a more diverse diet including more commonly consuming fish species compared to females. Additionally, the %FO of each prey group consumed differed by location stranded and stranding event, indicating a level of spatial plasticity in foraging.

Identification of target prey species may help to inform where LFPWs are foraging prior to stranding. Thus, the presence of both fish remains and prey tissue found in stomachs from multiple stranding events in this study suggests that at least some LFPWs may be feeding within the day prior to stranding and are therefore likely feeding within New Zealand waters. Though it is not currently clear where LFPWs forage within New Zealand, the distribution of *Globicephala* spp. (including both LFPWs and short-finned pilot whales *G. macrorhynchus*) in this area has been categorised as offshore (>25km from the coastline) with a preference for deep waters (Stephenson et al. 2020). As the overall percentage of individuals found with empty stomachs in this study was small (16%), and there was a high contribution of pelagic species to diet, it is suggested LFPW foraging mainly occurs in pelagic waters around New Zealand. However, the presence of demersal

species such as kahawai and carpet shark in both the forestomach and main stomach of male LFPWs suggests at least some time feeding demersally prior to stranding.

2.6.2. Overall prey composition and relative importance to diet

This study revealed 13 prey taxa, six of which were previously unknown to the diet of LFPWs in New Zealand waters. Cephalopods, more specifically squid (n = 8 species), dominated diet by both FO and %N, though this is a small proportion of the >86 squid species currently identified in New Zealand waters (Bolstad 2007). The findings in this study agree with previous international studies that concluded LFPWs rely mainly on a diet of cephalopods and can supplement this with fish (Overholtz and Waring 1991; Gannon et al. 1997b; Giménez et al. 2018; Becker et al. 2021; Chalcobsky et al. 2021). Furthermore, this study agrees with previous stomach content analysis of LFPWs in New Zealand waters, revealing arrow squid (*Nototodarus* spp.) and octopus (*Pinnoctopus cordiformis*) as the main target prey species (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009).

Secondary in importance to cephalopods, remains of fish from the Merluccidae (hoki; *Macruronus novaezelandiae*), *Arripidae* (kahawai; *Arripis trutta*), *Cephoscyllium* (carpet shark) and Congridae (conger eel) families were recorded in LFPW stomachs for the first time in New Zealand waters. Hoki are a benthopelagic species that are caught commercially in mid-water and bottom trawls at around 300–750 m (McClatchie et al. 2005; Bowden et al. 2021) whilst conger eels are reported bycatch in deepwater trawls (Finucci et al. 2019) indicating that LFPWs that strand on the New Zealand coast forage in waters of this depth. However, whilst kahawai are also a pelagic species, they tend to be more common in shallower coastal areas, with commercial catch around 100 – 200 m (Bradford 1999; Armiger et al. 2019). Carpet sharks are also more common in inshore waters, but are a demersal species found around New Zealand up to 500 m depth (Horn 2016), suggesting at least some degree of plasticity in foraging habitat for the New Zealand LFPW population. Similarly, both

benthopelagic, demersal fish and pelagic fish species have been recovered from LFPWs from the North Sea and Northeast Atlantic (Overholtz and Waring 1991; Spitz et al. 2011; Ijsseldijk et al. 2015).

The international differences in number of fish remains reported could be due to local differences in prey availability. Alternatively, this could also signify a larger reliance on cephalopods for LFPWs *G. m. edwardii* than northern sub-species *G. m. melas,* or potential changes in diet over time. Still, it was noted that fish are likely underrepresented in this study due to lack of intact fish prey remains in comparison to cephalopods. Accordingly, strandings with a high %FO of empty stomachs appeared to consistently co-occur with low %FO of fish (Appendix 2.4). Caution is advised when assessing contribution to diet of hard part remains in stomach contents as this method can overestimate cephalopod contribution to diet (Gannon et al. 1997a). Unlike fish otoliths, cephalopod beaks cannot be fully digested (Jackson et al. 1987) and are therefore retained in stomachs for longer timescales. As such, fish are likely to be underestimated in estimations such as %IRI and %M when using only "identifiable prey remains" (Santos et al. 2014). It is therefore possible that fish could contribute more to diet than suggested in this analysis. Overall, fish accounted for 1.3 %N and 0.97 %IRI of the identifiable prey species in this study, though the %FO of fish did also vary on both ontogenetic and spatial scales (Figure 4.4).

2.6.3. Ontogenetic and sex variation in prey consumption

Sex was included as a covariable in four out of six of the top GAM models, suggesting sex contributes highly to variation in %N of arrow squid and octopus consumed by LFPWs in New Zealand waters. When examining %FO of prey remains in males and females, nearly half of the males (n = 50) recorded fish remains of some description, but only three females. Octopus was also reported more frequently in male stomachs. Both *P. cordiformis* and many of fish species consumed (e.g., conger eels and carpet sharks) were benthic inhabitants. Combined, this could suggest a possible difference

in feeding habitat between sexes, with males more often foraging in benthic environments, which could have implications for strandings. A difference in foraging habitat between males and females has been recorded in other odontocetes including Franciscana dolphins (*Pontoporia blainvillei*; Bassoi et al. 2021) and bottlenose dolphins (*T. truncatus*; Hernandez-Milian et al. 2015) and could help in reducing intraspecific competition for food.

Whilst variation in prey diversity between sexes was noted, the contribution to diet of each individual species other than arrow squid was low (≤ 1 %IRI, Table 2.2). However, %IRI does not account for calorific content or nutritional composition of prey. As male LFPWs grow to a larger maximum size than females (Betty et al. 2022), males of increased body size may be targeting more diverse, higher calorie prey to sustain their larger energetic needs. Indeed, mature males recorded a higher prey diversity index and were also more associated with lower arrow squid and higher fish consumption than mature females (Figures 2.4 and 2.5). Studies on comparative energetics suggest that fish of the Congridae family have an increased calorific and energetic value compared to squid (Lockyer 2007; Santos et al. 2014; Malinowski and Herzing 2015; Spitz et al. 2018). Of the prey species recorded in this study, eel remains belonged to the high calorie Congridae family and were found more frequently in stomachs of males (Figure 2.4), supporting the idea that males may supplement their diet with higher energy prey.

Mature females in all reproductive groups displayed a lower prey diversity than mature males. Lactating females recorded the lowest prey diversity, possibly due to avoidance of risky feeding (Srinivasan et al. 2017). However, lactating females may simply be targetting prey that were easiest to catch, therefore expending less energy feeding, as all individuals as expected to by OFT. Furthermore, lactating females were also highly associated with arrow squid, but none were discovered with empty stomachs (Appendix 2.4). Given that lactation necessitates a 32–63% increase

in food consumption (Lockyer 1993), lactating females may be feeding more regularly to sustain the increased energy demands of lactation (Rechsteiner et al. 2013; Hin et al. 2019). Indeed, tagging studies of LFPWs (*G. m. melas*) in Norwegian waters found that lactating females spent more time foraging than other mature individuals (Isojunno et al. 2017). Conversely, resting females displayed an increased prey diversity in comparison to lactating and pregnant females, driven by more frequent consumption of "other squid", such as *C. veranyi*, *L. loirgera*, and *Moroteuthopsis ingens* (warty squid). It is possible that these oceanic cephalopods (Clarke 1966; Jackson et al. 2000; Hoving et al. 2007) are more energetically costly to feed upon, and so are not favoured during pregnancy/lactation. It would be beneficial to employ further techniques, including nutritional analysis, to establish a better understanding of drivers behind dietary variation in LFPWs of different reproductive groups within New Zealand waters.

Overall, no difference was found in the number of arrow squid consumed between immature and mature individuals, possibly due to mature individuals consuming a larger number of prey items overall than immature LFPWs. Furthermore, the Bray-Curtis Index showed that dietary similarity was high between the two maturity states, but that immature individuals were more highly associated with empty stomachs. This could have been due to age of the immature individuals, which may still have been weaning (Gannon et al. 1997b; Betty 2019), and therefore had fewer hard part remains in stomachs.

Furthermore, LFPWs with a larger body length (and therefore mature individuals) consumed fewer arrow squid (Figure 2.5) but with a larger LRLs (Figure 2.3A). In accordance with OFT, the energetic gain of arrow squid consumption may only outweigh the energetic cost of foraging for larger LFPWs if larger arrow squid are consumed, due to the greater energetic needs for LFPWs with greater body length. In general, larger individuals may be expected to consume larger prey as this is generally

common in the marine environment (Weise et al. 2010; Juanes 2016), including in LFPWs in the Northeast Atlantic (Desportes and Mouritsen 1993; Santos et al. 2014). Age, however, displayed a stronger correlation with the size of arrow squid LRLs recovered from males than females (Figure 2.3B). This suggests that dietary variation between larger and smaller females is likely a function of body size rather than other ontogenetic changes or experience, though these may not always be mutually exclusive for males. Dietary variation may therefore be a function of both the energetic needs and the greater foraging capabilities e.g., utilising deeper dives (Kooyman 1988), that come with larger body size (Benoit-Bird 2004; Allen et al. 2022).

2.6.4. Spatiotemporal variation in prey consumption

Dietary variation was also recorded across different spatiotemporal scales. Only two of the four single stranded LFPWs had remains in their stomachs, which had a similar diet composition. However, remains in the stomachs from these two single stranded individuals but had a different composition to all other strandings (Figure 2.4D). Both occurred off the east coast of New Zealand (Te Oka and Wairoa; Figure 2.1), which could suggest a level of geographic heterogeneity in diet. However, if this were the case, it would also be expected that the individual from Te Oka would still show some similarity in diet to nearby Port Levy (Figure 2.4D), which was not the case. Alternatively, as are LFPWs are expected to show long-term social stability (Amos et al. 1993; de Stephanis et al. 2008; Augusto et al. 2017), individuals that stranded alone may have separated from their social groups due to being sick or injured (Dailey and Walker 1978; Cordes 1982). It is possible that the single stranded individuals may not have been feeding typically prior to stranding, therefore demonstrating a difference in prey composition in comparison to mass stranded LFPWs. The addition of post-mortem analysis to conclude cause of death may help to understand this further in the future.

Dietary composition was relatively similar between the mass stranded LFPWs stranded across other locations, especially between Stewart Island and Port Levy as well as Farewell Spit, respectively. However, LFPWs stranded at Farewell Spit did consume significantly more octopus but were less associated with oceanic "other squid" than those stranded at Stewart Island. This could perhaps indicate a difference in foraging area prior to stranding between these two locations. Similar spatial changes in diet have been recorded in other LFPW populations from the North Atlantic (Santos et al. 2014) and Tasmania (Beasley et al. 2019) and could indicate a level of dietary plasticity when travelling through different ocean habitats (Becker et al. 2021). Indeed, prey diversity varied considerably across stranding locations in this study and was higher in the colder regions of Stewart Island than in the warmer waters of Farewell Spit (Chiswell 1994), possibly due to increasing coastal productivity in areas around Stewart Island (Pinkerton et al. 2019). Mapping of prey distribution against LFPW distribution and stranding events could help with understanding what, if any, role prey has within LFPW stranding events. Both Port Levy and Raglan presented a larger proportion of LFPWs with empty stomachs compared to the other locations, both strandings also occurred in the year 2010. The dietary composition of LFPWs stranded in 2010 was the most unique in comparison to other years. As the stranding events occurring in 2010 involved fewer than the 30 animals needed to obtain half the species diversity according to the cumulative prey curve (Table 2.1, Figure 2.2), this may have confounded the data. Still, using correspondence analysis, the year 2010 was grouped more closely with "other squid" than the rest of the strandings tested, which could be due to 2010 including the only stranding in this study from the austral winter season which occurred in Raglan in the year 2010. It has been previously suggested that LFPWs in New Zealand waters may vary their foraging areas dependant on seasonal productivity (Hamilton et al. 2019). Similarly, LFPW populations in the Northern Hemisphere have also shown evidence of seasonal

dietary change (Abend and Smith 1997; de Stephanis et al. 2008; Santos et al. 2014). Furthermore, consumption of high numbers of arrow squid in summer and more fish in winter has also been noted in pinnipeds in New Zealand waters (Fea et al. 1999; Harcourt et al. 2002). Therefore, LFPWs in New Zealand waters may also target abundant arrow squid in the warmer months, and switch to a different dietary composition over the winter. Analysis of further stomach content samples collected from the austral winter season are recommended to help elucidate possible seasonal dietary change in LFPWs from New Zealand waters.

Whilst seasonal comparisons were not possible in this study, temporal comparisons showed that numbers of arrow squid differed significantly by year. The lowest numbers of arrow squid were recorded in 2011, when the greatest prey diversity was recorded. As 2011 was also the year that the most LFPWs were sampled (n = 116), temporal differences in diet diversity may reflect sampling bias. Temporal comparisons were also possible at stranding hotspot Farewell Spit (Betty et al. 2020), revealing that the earlier stranding events in 2009 and 2011 were associated with a higher %FO of octopus, than in later years (Figure 2.4). Correspondingly, strandings at Farewell Spit in 2014 and 2017 showed high similarity in %FO of prey groups consumed (Bray-Curtis = 80%) and recorded the least dietary diversity compared to earlier years. This could indicate a change in target prey species over time. Indeed, hoki, conger eels, kahawai, carpet sharks and *L. lorigera* were all absent from the stomachs of LFPW stomachs at Farewell Spit after 2011. However, unidentifiable fish and cephalopod remains were recorded in 2014, which could have belonged to any of the aforementioned species. Furthermore, stomach contents of LFPWs stranded at Farewell Spit in 2005 and 2008 also recorded low prey diversity, including no remains of fish (Beatson et al. 2007b; Beatson and O'Shea 2009).

Alterations to target prey species could be indicative of local changes in prey abundance (Lin et al. 2021). Regular consumption of different target prey species is typically associated with a generalist foraging style (Cloyed et al. 2021). Indeed, populations of LFPWs have been described in the literature as both opportunistic/generalist feeders (Nøttestad et al. 2015; Pinzone et al. 2019) in the Norwegian Sea and Mediterranean Sea, and, in contrast, have been described as having a restricted prey niche specialising mainly in cephalopods (Mansilla et al. 2012; Skern-Mauritzen et al. 2022) in the Southern Atlantic and Nordic Sea. Stable isotope analysis of *G. m. edwardii* in Chile revealed LFPWs relied heavily on oceanic squid such as the Ommastrephid *Matialia hyadesi* as well as *Kondakovia longimana* (closely related to *M. ingens*) and *Histioteuthis* sp., and less so on neritic squids or fish (Becker et al. 2021). Thus, LFPWs stranded at Farewell Spit, and more widely across New Zealand, are likely demonstrating a similar foraging style to *G. m. edwardii* in Argentina; typically displaying a specialist feeding style targeting mainly oceanic Ommastrephid squids and octopus, but with the ability to diversify target prey when necessary.

Studies of nutritional composition of prey are recommended to aid explanations of dietary variation. Additionally, a focus on stomach content recovery during the austral winter is recommended to assess potential seasonal variation in target prey, whilst longer-term dietary techniques such as stable isotope and fatty acid analysis would be beneficial to aid understanding of LFPW dietary trends over longer timescales.

Chapter 3 — Isotopic niche analysis of long-finned pilot whales (*Globicephala melas edwardii*) in Aotearoa New Zealand waters

A box of long-finned pilot whale *Globicephala melas edwardii* skin samples for stable isotope samples. Photo credit: Bethany Hinton.

In this chapter, stable isotope analysis of skin samples collected from long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast (2009–2017; n = 125) are presented to address the second research objective:

Objective 2: Assess ontogenetic, spatial, and temporal isotopic niche dynamics within the LFPW population.

This chapter is a re-formatted version of the following published manuscript:

Hinton B, Stockin KA, Bury SJ, Peters KJ, Betty EL (2022). Isotopic Niche Analysis of Long-Finned Pilot Whales (*Globicephala melas edwardii*) in Aotearoa New Zealand Waters. *Biology 11*: 1414.

3.1. Abstract
The quantification of a species' trophic niche is important to understand the species ecology and its interactions with the ecosystem it resides in. Despite the high frequency of long-finned pilot whale (LFPW; *Globicephala melas edwardii*) strandings on the Aotearoa New Zealand coast, their trophic niche remains poorly understood. To assess the isotopic niche of *G. m. edwardii* within New Zealand, ontogenetic (sex, total body length, age, maturity status, reproductive group) and spatiotemporal (stranding location, stranding event, and stranding year) variation were investigated. Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) were examined from skin samples of 125 LFPWs (67 females and 58 males) collected at mass-stranding events at Onetahua Farewell Spit in 2009 ($n = 20$), 2011 ($n = 20$), 2014 ($n = 27$) and 2017 ($n = 20$) and at Rakiura Stewart Island in 2010 ($n = 19$) and 2011 ($n = 19$). Variations in δ^{34}S values were examined for a subset of 36 individuals. Generalised additive models revealed that stranding event was the strongest predictor for δ^{13}C and δ^{15}N values, whilst sex was the strongest predictor of δ^{34}S isotopic values. Although similar within years, δ^{13}C values were lower in 2014 and 2017 compared to all other years. Furthermore, δ^{15}N values were higher within Farewell Spit 2017 compared to any other stranding event. This suggests that the individuals stranded in Farewell Spit in 2017 may have been feeding at a higher trophic level, or that the nitrogen baseline may have been higher in 2017 than in other years. Spatiotemporal differences explained isotopic variation of LFPWs in New Zealand waters better than ontogenetic factors.

3.2. Introduction

Stable isotope analysis has steadily grown as an ecological tool over recent years (Newsome et al. 2010), with the method now commonly applied to trophic analysis and foraging ecology (Bearhop et al. 2004; Crawford et al. 2008). For example, stable isotopes have been used to determine dietary niche and relative prey contribution to diet for a wide range of marine and freshwater species (Newsome et al. 2007; Boecklen et al. 2011; Gillespie 2013; Navarro et al. 2013; Jackson and Britton 2014), including cetaceans (whales, dolphins, and porpoises; e.g., Mendes et al. 2007; Giménez et al. 2017b; Borrell et al. 2021).

Multiple isotopes have been used in foraging research including isotopes of carbon (McCutchan Jr et al. 2003; Cherel and Hobson 2007), nitrogen (DeNiro and Epstein 1981; Matthews and Ferguson 2014), oxygen (Balasse et al. 2005), sulphur (Hoekstra et al. 2002; McCutchan Jr et al. 2003; Duffill Telsnig et al. 2019), and strontium (Crowley et al. 2017). Isotopic values of carbon are typically used to infer information relating to foraging habitat (Hobson 1990; Cherel and Hobson 2007; Kiszka et al. 2011), whereas nitrogen isotopes have been linked to protein quantity, quality, and trophic feeding level (Peterson and Fry 1987; Oelbermann and Scheu 2002). Sulphur isotopes ($\delta^{34}S$) combined with carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, are now increasingly being used to provide clarity around prey source pathways, e.g., estuarine, or marine (Fry 2002; Connolly et al. 2004b; Duffill Telsnig et al. 2019). The combination of these isotopes can elucidate approximate feeding habitats, trophic level source and food web pathways, and provide information on the isotopic niche of an animal. Triple isotope studies have been successfully used in studies of marine ecosystems (Connolly et al. 2004; Cardona et al. 2009), including those involving cetacea (Matthews and Ferguson 2015; Wilson et al. 2017; Valenzuela et al. 2018), especially to describe isotopic niche. Whilst isotopic niche should be considered as a distinct entity from trophic niche (Hette-Tronquart

2019; Shipley and Matich 2020), the two are likely correlated (Jackson et al. 2011). Hence, isotopic niche can be used to help describe trophic niche, given correct consideration of the ecological context (Marshall et al. 2019).

Trophic niche partitioning between species is a common strategy to reduce resource competition (Hutchinson 1957). Isotopic niche differences have been observed between different cetacean species inhabiting the same geographical area (Gibbs et al. 2011; Praca et al. 2011; Giménez et al. 2018; Costa et al. 2020b; Borrell et al. 2021; Durante et al. 2021). This reduction in foraging competition could also be driving isotopic niche differences within socially distinct populations of the same species (Nicholson et al. 2021a) and even between individuals within the same population (Rossman et al. 2015). Isotopic variation within a population has been linked to ontogenetic factors such as age (Marcoux et al. 2012; Valenzuela et al. 2018), sex (Reisinger et al. 2016), total body length (herein referred to as "TBL"; (Meissner et al. 2012; Riccialdelli and Goodall 2015), life stage (Jackson-Ricketts et al. 2019), or sexual maturity status (Riccialdelli et al. 2013). Although some species have shown isotopic homogeneity within a population (Borrell et al. 2012), diet may still change between spatially or socially distinct populations of the same species as is observed in killer whale *Orcinus orca* (Reisinger et al. 2016), bottlenose dolphins *Tursiops truncatus* (Gannon and Waples 2004) and Northern Hemisphere LFPWs *G. m. melas* (LFPWs; Abend and Smith 1995).

Whilst both spatial and seasonal differences in *G. m. melas* isotopic values have been noted (Abend and Smith 1995; de Stephanis et al. 2008), dietary differences have also been reported to be related to body size (Desportes and Mouritsen 1988). In New Zealand, the Southern Hemisphere LFPW subspecies *G. m. edwardii* is the most frequently stranded cetacean by number and several locations have been identified as local stranding hotspots (Betty et al. 2020). Stomach content analyses of 37 LFPWs from three stranding events in New Zealand described six cephalopod species present in

their stomachs (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009). Whilst stomach content analysis provides important short-term dietary insights (Hyslop 1980; Sekiguchi and Best 1997), it does not give information on diet that has already been assimilated over a longer timescale, which can be provided through isotopic investigation (Post 2002). Furthermore, insights to intraspecific dietary or trophic variation and local isotopic niche of this sub-species are also lacking. This study aimed to address some of these knowledge gaps by exploring ontogenetic and spatiotemporal variation in isotopic niche for LFPWs from two stranding hotspots in New Zealand. Specifically, (1) the isotopic niche of *G. m. edwardii* in New Zealand using carbon, nitrogen, and sulphur isotopes, (2) ontogenetic variation in isotope values by sex, body length, age, maturity status and reproductive group and (3) spatiotemporal overlap in isotopic niche were investigated.

3.3. Materials and Methods

To assess isotopic profiles of LFPWs in New Zealand waters, archived skin samples (*n* = 125) were analysed from individuals collected from stranding events between 2009 and 2017 (Appendix 3.1). Samples of skin were chosen for analysis preferentially from individuals where stomach contents had already been examined (see Chapter 2).

3.3.1 Sampling

Skin was sampled from six stranding events across two *G. m. edwardii* stranding hotspot locations in New Zealand; Onetahua Farewell Spit (FWS; −40.481° S, 172.870° E) and Rakiura Stewart Island (SI; −46.686° S, 167.685° E; Betty et al. 2020; see Figure 3.1). Of these, 87 carcasses were sampled at Farewell Spit during four mass-stranding events (2009, 2011, 2014, 2017) and 38 carcasses at Stewart Island during two mass-stranding events (2010, 2011). All of the mass-strandings sampled occurred during the austral summer between the months of November and February.

Skin sampling, along with measurements of body length and an anatomical assessment of sex, was undertaken in situ at stranding events using standard postmortem procedures (Geraci and Lounsbury 2005). All skin samples were stored at 4 °C in 70% ethanol prior to analysis. Teeth and reproductive organs were sampled where possible, as outlined in Betty et al. (2022), with age data

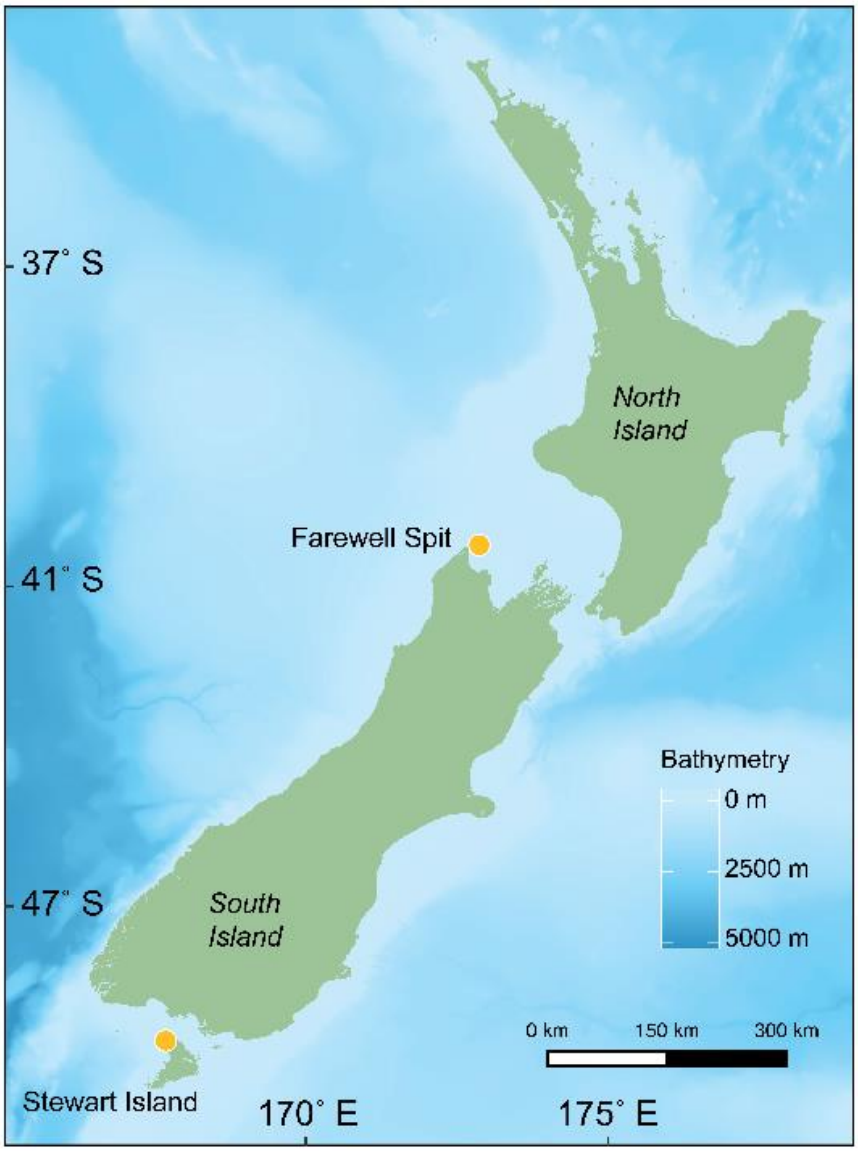

Figure 3.1. Location of sampling sites of long-finned pilot whale (*Globicephala melas edwardii*) carcasses from mass-stranding events at Farewell Spit and Stewart Island, Aotearoa New Zealand. Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted with permission from National Institute of Water and Atmospheric Research (NIWA) under a Creative Commons BY license, with permission from NIWA original copyright (CANZ 2008). Figure reproduced from Hinton et al. (2022).

available for 86% (108 of 125) of individuals and reproductive data available for 82% (102 of 125) individuals. Teeth were used to assess age via dentinal growth layer groups (Betty et al. 2022). Reproductive organs were used to assess sexual maturity status (herein referred to as maturity status) and reproductive group for mature females, where possible (Betty 2019; Betty et al. 2019). Six reproductive groups were defined: immature males, mature males, immature females, pregnant females, lactating females, and resting females. Male maturity was defined by presence/absence of sperm in testes (Betty et al. 2019). Females were defined as "pregnant" by the presence/absence of a foetus, as "lactating" by presence/absence of milk in the mammary glands, and as "resting" by the presence of ovarian corpora indicating previous ovulation, but with no foetus or milk present (Betty 2019). However, if reproductive group and/or maturity status were not available, body length was used as an indicator of maturity status using estimations from the same *G. m. edwardii* population (Betty 2019; Betty et al. 2019). Where sample availability allowed, samples were compared in equal groups of mature males ($n = 5$), mature females ($n = 5$), immature males ($n = 5$) and immature females ($n = 5$) within each stranding event. In one stranding event (FWS2014), more mature females of known reproductive group were available, and these were therefore included in analyses to increase comparative statistical power of mature female reproductive groups (Table 3.1).

Carbon and nitrogen stable isotopes from skin samples ($n = 125$) were analysed to compare ontogenetic and spatiotemporal variation. Additionally, a subset of 36 (13 male and 23 female) samples from sexually mature individuals with the highest, lowest, and median carbon and nitrogen isotope values recorded per stranding event were analysed for sulphur isotope values. Immature individuals were excluded from analyses of sulphur isotopes to avoid confounding the data with individuals that were not fully weaned.

Table 3.1. Ontogenetic characteristics of long-finned pilot whales (*Globicephala melas edwardii*) sampled for stable isotope analysis from mass-strandings on the New Zealand coast, 2009–2017. Unknown refers to individuals where reproductive group was unable to be determined from reproductive organs, but maturity status was instead classified from body length. Table reproduced from Hinton et al. (2022).

Ontogenetic Status	***n***	**Body Length Range (cm)**	**Age Range (Years)**
Maturity status			
Immature	56	168–482	0–13
Mature	69	364–595	6–33
Reproductive group			
Immature male	26	255–482	1–13
Mature male	18	467–581	14–31
Immature female	25	168–375	0–8
Pregnant female	17	364–461	6–33
Lactating female	9	380–446	7–30
Resting female	7	397–453	11–30
Unknown	23	194–595	5–32

3.3.2. Sample preparation

In preparation for stable isotope analysis, skin samples were placed under the fume hood for at least 48 hours (Olin et al. 2014) to evaporate off the storage ethanol. Samples with excess ethanol remaining were further placed under a stream of nitrogen gas (which is not thought to interfere with results) until all ethanol had been removed from the sample. Samples were cut longitudinally to capture all skin layers, as recommended for isotopic studies of cetaceans aiming to consider trophic interactions and diet composition (e.g., Wild et al. 2018). Skin was then homogenized by finely slicing in a glass Petri dish using a clean scalpel blade. Approximately 40 mg of each sample was weighed into Eppendorf tubes and freeze-dried overnight for a minimum of 18 hours or dried in an oven at 60 °C for at least 48 hours.

3.3.3. Carbon and nitrogen isotope analysis

Carbon and nitrogen isotope analysis was carried out at the Environmental and Ecological Stable Isotope Analytical Facility at the National Institute for Water and Atmospheric Research (NIWA), Wellington. Around 1.0 mg of each homogenised skin sample was weighed into tin capsules using a six decimal place (g) microbalance. Tin capsules were formed into balls containing the sample and were analysed by a FLASH 2000 elemental analyser with MAS 200 R autosampler linked to a DELTA V Plus continuous flow isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). Stable isotope values were calculated using ISODAT (Thermo Fisher Scientific) software; $\delta^{13}C$ values were calibrated against Carrara Marble NSB-19 (National Institute of Standards and Technology (NIST), Gaithersburg, MD, USA) and $\delta^{15}N$ relative to Pee Dee Beleminte (PDB) standard followed by correction for O^{17}. International laboratory reference materials from NIST were run at the start and end of every batch of analyses for normalisation (Paul et al. 2007). A working laboratory standard of DL-Leucine (DL-2-Amino-4-methylpentanoic acid, C6H13NO2, Lot 127H1084, Sigma, Melbourne, Australia) and squid were run every 10 samples to correct for machine drift, for quality

control and to report on precision. The international standards USGS65 Glycine was also run every ten samples to check accuracy and precision. Data accuracy was measured to better than 0.15‰ for $\delta^{13}C$ and $\delta^{15}N$ values, whilst precision was measured to better than 0.24‰ for $\delta^{13}C$ and 0.22‰ for $\delta^{15}N$ values. Stable isotope ratios were expressed as delta values (δ) in per mil units (‰), which represent the ratios of heavy to light isotopes within a sample (R_{sample}), relative to the ratio in an international standard ($R_{standard}$) as:

$$\delta = \left(\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right) \times 1000$$

3.3.4. Sulphur isotope analysis

A subset of 36 skin samples from mature individuals was processed for sulphur isotope analysis at IsoTrace Limited, Dunedin (see Appendix 3.3). Samples were analysed using the Carlo Erba NC 2500 elemental analyser coupled to a Europa Hydra isotope ratio mass spectrometer. Stable isotope values were normalised against international standards of Vienna PDB, AIR and Canyon Diablo Troilite for carbon, nitrogen, and sulphur, respectively. Two international reference materials comprising USGS40 mixed with IAEA-S1 (carbon = −26.39‰, nitrogen = −4.52‰, sulphur = −0.30‰), and USGS-41 mixed with IAEA-S2 (carbon = 36.55‰, nitrogen = 47.55‰, sulphur = 22.62‰) used for data normalisation in a three-point system. Replicate analysis of the keratin internal working laboratory standard was used to determine machine drift, and precision of $\delta^{13}C$ (0.08‰), $\delta^{15}N$ (0.04‰) and $\delta^{34}S$ (0.16‰) was assessed from replicates positioned every ten samples.

3.3.5 Correction equations

Lipids are depleted in ^{13}C relative to ^{12}C compared to proteins. The lipid content of ecological samples therefore affects $\delta^{13}C$ values (Focken and Becker 1998). Lipids are thus either removed from the sample before carbon stable isotope analysis, (e.g., Choy et al. 2016; Groß et al. 2021) or a lipid correction equation is applied to samples with C:N mass ratios > 3.5 to correct for the lipid-affected $\delta^{13}C$ values (Logan et al. 2008; Wilson et al. 2014; Giménez et al. 2017c). There is disagreement within published literature regarding the suitability of lipid correction equations being extrapolated to different species for isotopic studies (Arostegui et al. 2019). Therefore, lipids were extracted from a sub-set of 10 LFPW skin samples to check the validity of using published lipid correction equations (e.g., Fry 2002; Post et al. 2007; Logan et al. 2008; Peters et al. 2022; Appendix 3.2). Samples were selected from one location only (FWS) based on, (1) extreme carbon and nitrogen isotope values in comparison to the rest of the dataset and, (2) a wide range of C:N mass ratios. Selected samples had C:N mass ratios ranging from 3.27–4.48 and C:N atomic ratios ranging from 3.81–5.23. The lipid correction equation, which was based on a bootstrapping approach using 74 samples of odontocetes, including LFPWs from Peters et al. (2022), was found to be the best fit for the data. The lipid correction equation:

$$\delta^{13}C_{corrected} = 0.5301486 \times -^{13}C - 7.322335$$

was applied to $\delta^{13}C$ values for samples with a C:N mass ratio over 3.5. Bulk isotope uncorrected $\delta^{13}C$ values were used when C:N mass ratios were <3.5. As lipid extraction can affect nitrogen and sulphur isotope values (Elliott et al. 2014), non-lipid extracted bulk samples were analysed to generate $\delta^{15}N$ and $\delta^{34}S$ values. Additionally, to account for changing carbon dioxide levels in the ocean due to anthropogenic activity (Körtzinger et al. 2003), commonly referred to as the Suess effect,

a correction equation of −0.022% y^{-1} (Quay et al. 2003) was applied to all $\delta^{13}C$ values to the baseline of the most recent sample set collected in 2017.

3.4. Statistical analysis

Following testing assumptions of normality using Shapiro–Wilk tests, Kruskal–Wallis tests were used in the R package "rstatix" (Kassambara 2020) to compare differences in mean $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values both within and among groups defined as: sex, reproductive group, stranding location, stranding event, and stranding year. For $\delta^{13}C$ and $\delta^{15}N$ values, these were also compared among maturity status, which was not an option for $\delta^{34}S$ as $\delta^{34}S$ values were only available for mature animals. Where significant differences occurred, pairwise data were compared using Wilcoxon tests to determine differences between specific groups, (e.g., Fernández et al. 2011; Kiszka et al. 2011). Spearman's correlation coefficient was used to determine if any relationship occurred between body length or age and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values, respectively. The relationship between $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values and a suite of predictive variables was investigated using generalised additive models (GAMs; Hastie and Tibshirani 1990) using the R package "mgcv" (Wood and Wood 2015). Predictive variables were sex, body length, maturity status (only for $\delta^{13}C$ and $\delta^{15}N$ values), stranding location, stranding event, and stranding year. Body length was fitted as a continuous variable, whereas sex, maturity status, stranding location, stranding event, and stranding year were fitted as factors. As body length and age were highly correlated (Spearman rank, rho = 0.85, $p \leq 0.01$), and age was not available for all individuals, body length (n = 125) was included in GAM models as a proxy (with larger animals expected to be typically older) rather than age itself (n = 108). Models were built with Gaussian distribution with gamma set to 1.4 to prevent overfitting (Wood 2017) with all possible combinations of variables. Akaike's information criterion adjusted for small sample size (AICc; Burnham et al. 2011) was calculated using the R package "qpcR" (Ritz and Spiess 2008) to select the

best fitting model. Interactions for the five top-ranked models were also tested. Final models were checked for normality and obvious patterns in the residuals. Models within three AICc units of the optimum model were deemed equally likely, and the top three were reported. Niche partitioning was investigated using Bayesian inference using the R packages "SIBER" (Jackson et al. 2011) and "ggplot2" (Wickham 2011) with ellipses calculated at the 0.40 and 0.95 α level.

Niche regions (NR) were presented in three-dimensions (‰^{3}) using δ^{13}C, δ^{15}N and δ^{34}S data using the R packages "scatterplot3d" (Ligges et al. 2018) and "nicheROVER" (Lysy et al. 2021). Volume of ellipses was set at the 0.40 α level (NR_{40}, e.g., Borrell et al. 2021). Data were split into groups based on ontogenetic variation and stranding event to calculate pairwise isotopic niche overlap. For ontogenetic variation, data were classified as mature males, mature females, and pregnant/lactating females due to data availability. Published methods were followed (Swanson et al. 2015), replacing "Species" with "Group", whereby pairwise niche overlap was defined as the probability (%) of an individual from one group being found within the NR_{40} of another group. Data were presented as a pairwise grid of one-dimensional isotopic density distributions, two-dimensional pairwise isotopic scatter plots and two-dimensional NR_{40} ellipses of five random NR_{40} estimates. Overlap probability was calculated at the 95% level using a Bayesian approach with 10,000 iterations and reported as mean posterior overlap (e.g., Borrell et al. 2021).

The relationship between number of LFPWs stranded and triple isotope niche size was examined through Pearson's correlation analysis both with and without FWS2009 data included. The FWS2009 stranding event appeared anomalous as it had a much larger niche size for the number of animals stranded compared to all other events, and did not fit the trend of the other stranding events. Finally, isotopic range of δ^{13}C using the highest and lowest values were calculated using the formula:

$$\delta y = \delta^{13}C_{ymax} - \delta^{13}C_{ymin}$$

where y = sample size (e.g., Graham et al. 2014). Isotopic ranges of $\delta^{15}N$ and $\delta^{34}S$ were calculated in the same way at the level of (1) the entire dataset, and (2) each stranding event.

All data analysis was completed in R version 4.0.5 (R Core Team 2021).

3.5. Results

Lipid corrections were performed on $\delta^{13}C$ values from 71 (57%) samples, whilst 54 samples (43%) were not lipid-corrected (Appendix 3.4). Following $\delta^{13}C$ corrections for lipid content and Suess effects, $\delta^{13}C$ data were not normally distributed (Shapiro–Wilk, W = 0.96, $p = 0.001$). Overall, neither $\delta^{15}N$ values (Shapiro–Wilk, W = 0.83, $p \leq 0.05$) nor $\delta^{34}S$ values (Shapiro–Wilk, W = 0.94, $p = 0.03$) were normally distributed.

3.5.1. Ontogenetic variation in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values

The mean $\delta^{15}N$ value was 12.59 ± 0.72‰ (Table 3.2), whilst the mean $\delta^{13}C$ value was −17.12 ± 0.73‰ ($n = 125$). No significant correlations were found between $\delta^{13}C$ values and body length (Spearman rank, rho = −0.06, $p = 0.54$) nor age (Spearman rank, rho = −0.12, $p = 0.22$), respectively. Furthermore, no significant differences were found in the $\delta^{13}C$ values between males (−17.04 ± 0.65‰, $n = 57$) and females (−17.20 ± 0.79‰, $n = 68$; Kruskal–Wallis, H = 0.98, $p = 0.32$, Figure 3.2), between immature (−17.00 ± 0.70‰, $n = 56$) and mature (−17.23 ± 0.74‰, $n = 69$) individuals (Kruskal–Wallis, H = 2.89, $p = 0.09$) or among reproductive groups (immature males: −16.79 ± 0.81‰, $n = 26$; mature males: −17.00 ± 0.69‰, $n = 18$; immature females −17.12 ± 0.81‰, $n = 25$; pregnant females: −17.13 ± 0.73‰, $n = 17$; lactating females: −17.40 ± 0.71‰, $n = 9$; resting females: −17.59 ± 1.01‰, $n = 7$; Kruskal–Wallis, H = 9.06, $p = 0.11$, Table 3.2, Figure 3.3).

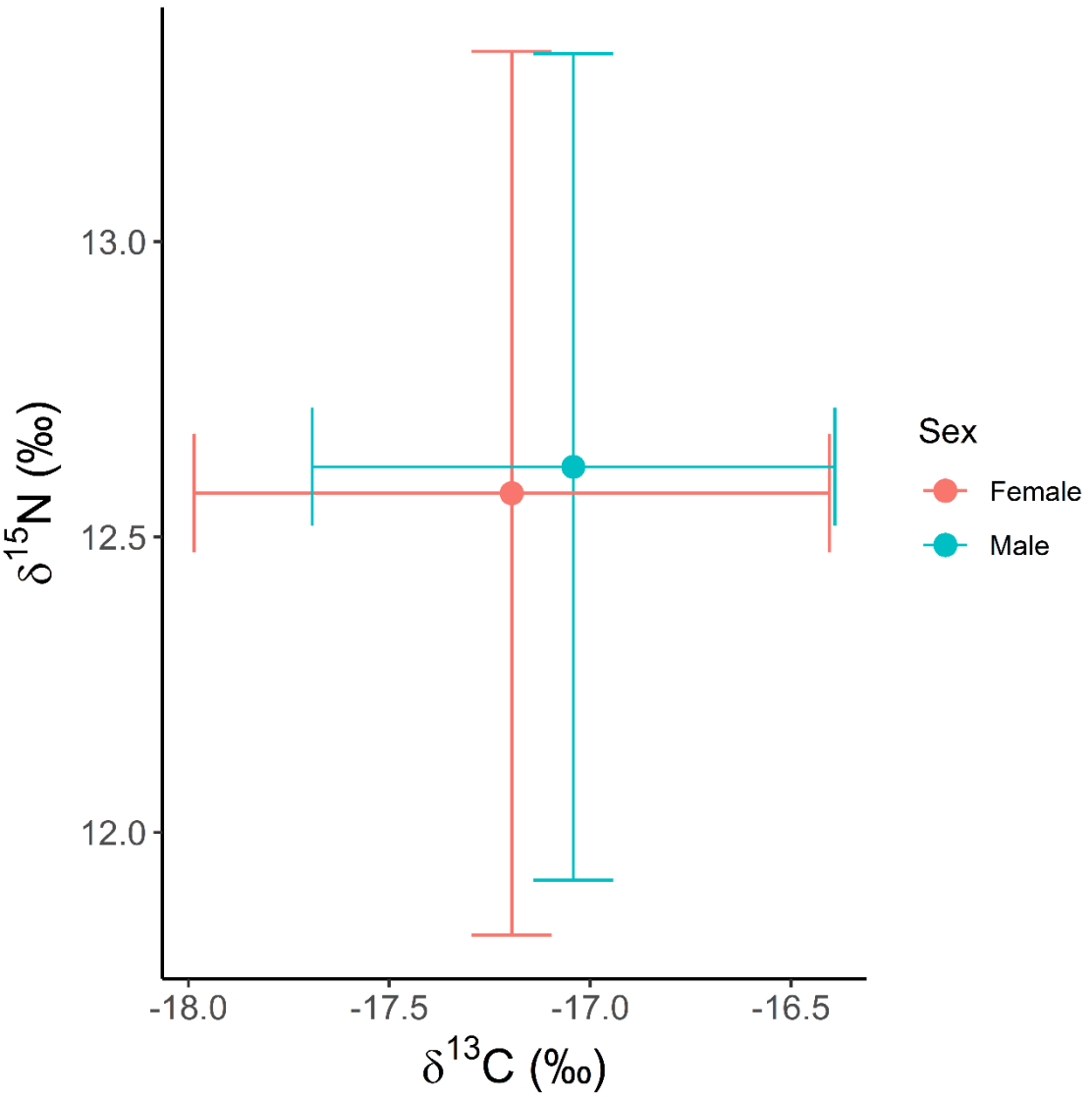

Figure 3.2. Carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) stable isotope biplot from skin samples of male (n = 57) and female (n = 68) long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast between 2009 and 2017. Figure reproduced from Hinton et al. (2022).

Table 3.2. Range, mean and standard deviations (±1 SD) of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) values of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast, 2009–2017, presented by sexual maturity status and reproductive group. Unknown refers to individuals where reproductive group was unable to be determined from reproductive organs, but maturity status was instead classified from body length. Table reproduced from Hinton et al. (2022).

		$\delta^{13}C$ (‰)			**$\delta^{15}N$ (‰)**		
	n	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
All	125	−18.80 to −15.53	−17.12	0.73	11.52 to 16.28	12.59	0.72
Maturity status							
Immature	56	−18.80 to −15.53	−17.00	0.70	11.90 to 15.23	12.59	0.58
Mature	69	−18.77 to −15.82	−17.23	0.74	11.52 to 16.28	12.60	0.82
Reproductive group							
Immature male	26	−18.16 to −16.26	−16.79	0.52	11.97 to 13.27	12.38	0.30
Mature male	18	−18.77 to −16.26	−17.00	0.69	11.52 to 13.27	12.34	0.53
Immature female	25	−18.80 to −15.53	−17.12	0.81	11.90 to 13.93	12.64	0.53
Pregnant female	17	−18.32 to −16.02	−17.13	0.73	11.83 to 14.85	12.53	0.72
Lactating female	9	−18.59 to −16.39	−17.40	0.71	11.70 to 12.85	12.30	0.42
Resting female	7	−18.74 to −15.82	−17.59	1.01	11.72 to 13.37	12.34	0.60
Unknown	23	−18.62 to −15.99	−17.26	0.68	11.75 to 16.28	13.23	1.10

Similarly, no significant correlations were found between $\delta^{15}N$ and body length (Spearman rank, rho = −0.08, $p = 0.36$) nor age (Spearman rank, rho = −0.09, $p = 0.37$), respectively. No differences in the $\delta^{15}N$ values between males (12.62 ± 0.70‰, $n = 58$) and females (12.57 ± 0.75‰, $n = 67$, Kruskal–Wallis, H = 0.41, $p = 0.52$), between immature (12.59 ± 0.58‰, $n = 56$) and mature individuals (12.60 ± 0.82‰, $n = 69$, Kruskal–Wallis, H = 0.53, $p = 0.47$) or among reproductive groups (immature males: 12.38 ± 0.30‰, $n = 26$; mature males: 12.34 ± 0.53‰, $n = 18$; immature females 12.64 ± 0.53‰, $n = 25$; pregnant females: 12.53 ± 0.72‰, $n = 17$; lactating females: 12.30 ± 0.42‰, $n = 9$; resting females: 12.34 ± 0.60‰, $n = 7$; Kruskal–Wallis, H = 6.14, $p = 0.29$) were detected (Table 3.2).

The mean $\delta^{34}S$ value was 21.42 ± 0.91‰ for the pooled dataset ($n = 36$). Sulphur isotope values did not differ significantly between sex (males 21.14 ± 0.99, $n = 13$; females 21.58 ± 0.83, $n = 23$; Kruskal–Wallis, H = 1.87, $p = 0.17$, Table 3.3). Similarly, no significant correlations were found between $\delta^{34}S$ and age (Spearman rank, rho = −0.20, $p = 0.27$) nor body length (Spearman rank, rho = −0.21, $p = 0.22$).

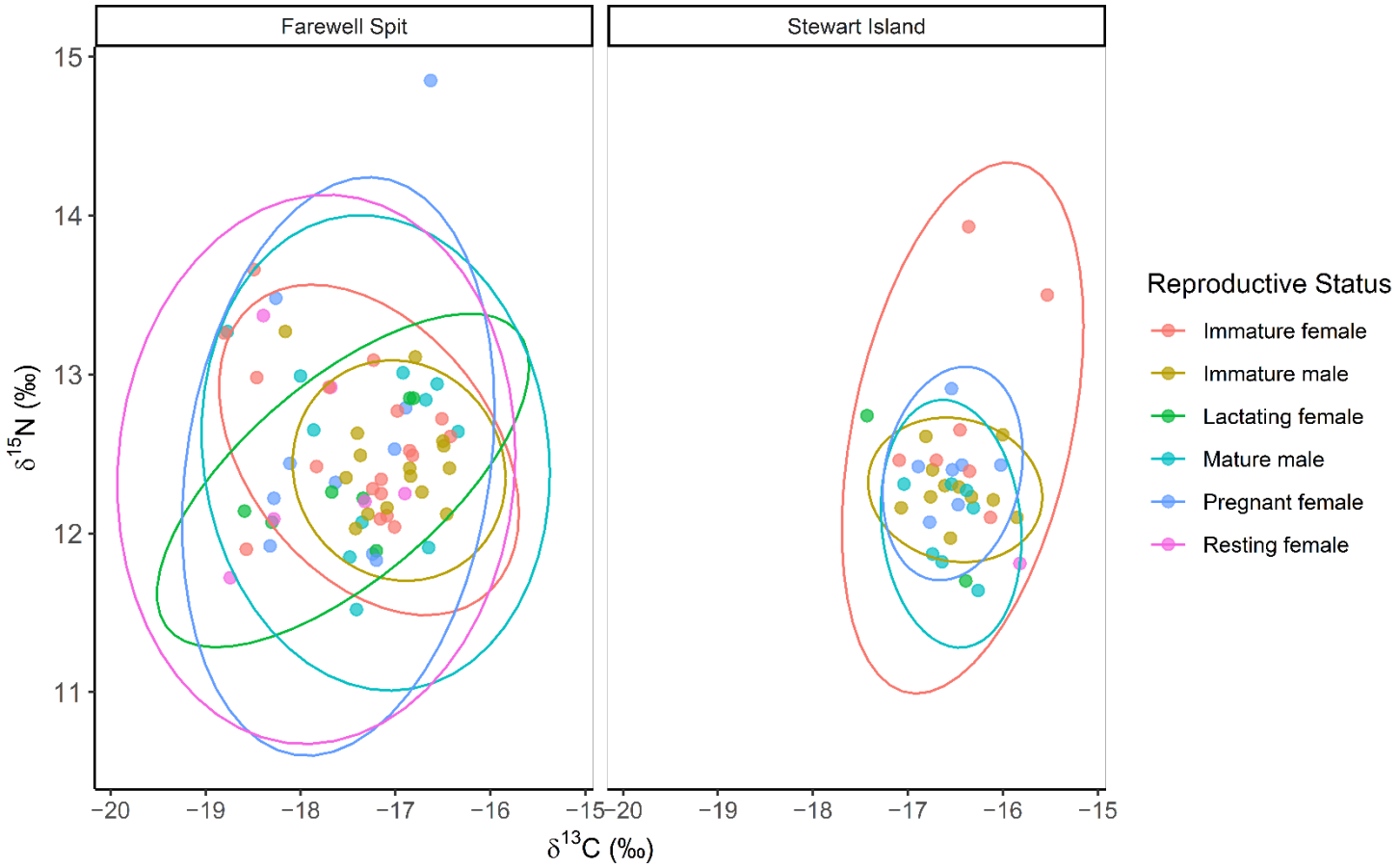

Figure 3.3. Isotopic niche overlap of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) isotopic values of long-finned pilot whales (*Globicephala melas edwardii*) with immature female ($n = 25$), immature male ($n = 26$), lactating female ($n = 9$), mature male ($n = 18$), pregnant ($n = 17$) and resting ($n = 7$) females presented by stranding location on the New Zealand coast, 2009–2017. Ellipses represent 95% of data. Figure reproduced from Hinton et al. (2022).

Table 3.3. Mean and standard deviations (±1 SD) of carbon, nitrogen, and sulphur (δ^{13}C, δ^{15}N and δ^{34}S) values of a subset of 36 mature long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast (2009–2017), presented by sex and reproductive group. Table reproduced from Hinton et al. (2022).

		δ^{13}C (‰)		**δ^{15}N (‰)**		**δ^{34}S (‰)**	
	n	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Male	13	−17.32	0.81	12.59	0.72	21.14	0.99
Female	23	−17.06	0.82	12.70	1.04	21.58	0.83
Pregnant/Lactating female	14	−17.12	0.73	12.68	0.75	21.56	0.90
All	36	−17.14	0.78	12.66	0.93	21.42	0.91

3.5.2. Spatial and temporal variation in δ^{13}C, δ^{15}N and δ^{34}S values

Overall, individuals that stranded at Farewell Spit (n = 87) had significantly lower δ^{13}C and higher δ^{15}N values (δ^{13}C—17.39 ± 0.68‰, δ^{15}N 12.71 ± 0.79‰) compared to those stranded at Stewart Island (δ^{13}C—16.51 ± 0.39‰, n = 38; Kruskal–Wallis, H = 45.6, $p \leq 0.01$; δ^{15}N 12.32 ± 0.44‰, Kruskal–Wallis, H = 8.43, $p \leq 0.01$, Figure 3.4). Total niche area (TA) and corrected standard ellipse areas (SEA_C) were larger for females at both Farewell Spit (female TA = 7.64, SEA_C = 1.89, n = 47; male TA = 4.72, SEA_C = 1.25, n = 40) and Stewart Island (female TA = 2.74, SEA_C = 0.79, n = 20; male TA = 0.83, SEA_C = 0.28, n = 18). The TA and SEAc values were larger at Farewell Spit than Stewart Island for both males and females, respectively. The TA was largest for pregnant females at Farewell Spit (TA = 3.14, SEA_C = 1.96, n = 10), and smallest for mature males at Stewart Island (TA = 0.30, SEA_C = 0.27, n = 7; Appendix 3.5).

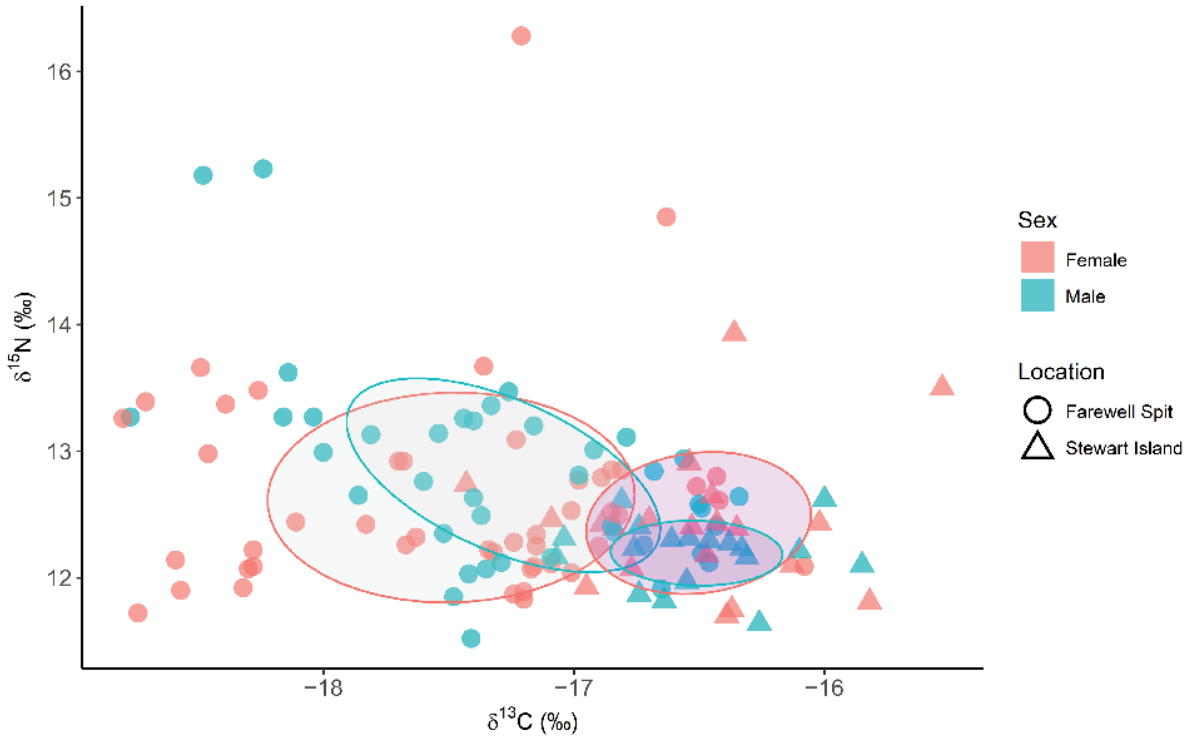

Figure 3.4. Long-finned pilot whales (*Globicephala melas edwardii*) isotopic niche overlap of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) values between males (n = 40) and females (n = 47) stranded at Farewell Spit, and males (n = 18) and females (n = 20) stranded at Stewart Island between 2009 and 2017. Stewart Island is represented as triangles and purple filled ellipses, and Farewell Spit as circles and grey filled ellipses, males are indicated in green and females in peach. Ellipses represent 40% of the data. Figure reproduced from Hinton et al. (2022).

Differences in $\delta^{13}C$ were recorded between stranding events (Kruskal–Wallis, H = 89.7, p = <0.01), with Wilcoxon tests describing four pairs as not significantly different: FWS2014, FWS2017 (p = 0.40); and FWS2009, SI2010 (p = 1); FWS2009, SI2011 (p = 0.25) and SI2010, SI2011 (p = 0.25). Mean $\delta^{13}C$ values were lowest in FWS2017 stranded individuals (mean = −18.04 ± 0.52‰, n = 20), whereas the highest mean $\delta^{13}C$ values were observed in those stranded at FWS2009 (mean = −16.65 ± 0.31‰, n = 20). Nitrogen isotope values differed among stranding events (Kruskal–Wallis, H = 57.1, $p \leq 0.01$), with higher $\delta^{15}N$ values recorded in individuals from FWS2017 (n = 20) than any other stranding event. Nitrogen isotope values were also lower at the FWS2014 stranding event (n = 27) than any other Farewell Spit stranding event.

Sulphur isotope values did not differ significantly between stranding events (Kruskal–Wallis, H = 9.24, p = 0.10) nor stranding location (FWS: 21.33 ± 0.95‰, n = 32; SI: 21.61 ± 0.82‰, n = 18; Kruskal–Wallis, H = 0.65, p = 0.42; Figure 3.5).

3.5.3. GAM analysis

The top three GAMs for $\delta^{15}N$ retained only stranding event, location, and year. The top model retained only stranding event as a covariate, explaining 45% of the deviance (Table 3.4). For $\delta^{13}C$ values, the top two best-fit models retained maturity status, location, year, and stranding event as covariates and explained 69% of the deviance. Sex was also retained as a covariate in the top three GAMs fitted for $\delta^{13}C$ data (Table 3.4). Whilst body length was also fitted to GAMs, this was not retained in the top-ranked models. The top-ranked GAM for $\delta^{34}S$ retained only sex as a covariate. Stranding location and year were also retained, respectively, as covariates in the top three models (Table 3.4). However, the deviation explained was less than 10% for all models (Table 3.4), indicating that the included predictor variables did not explain the data well.

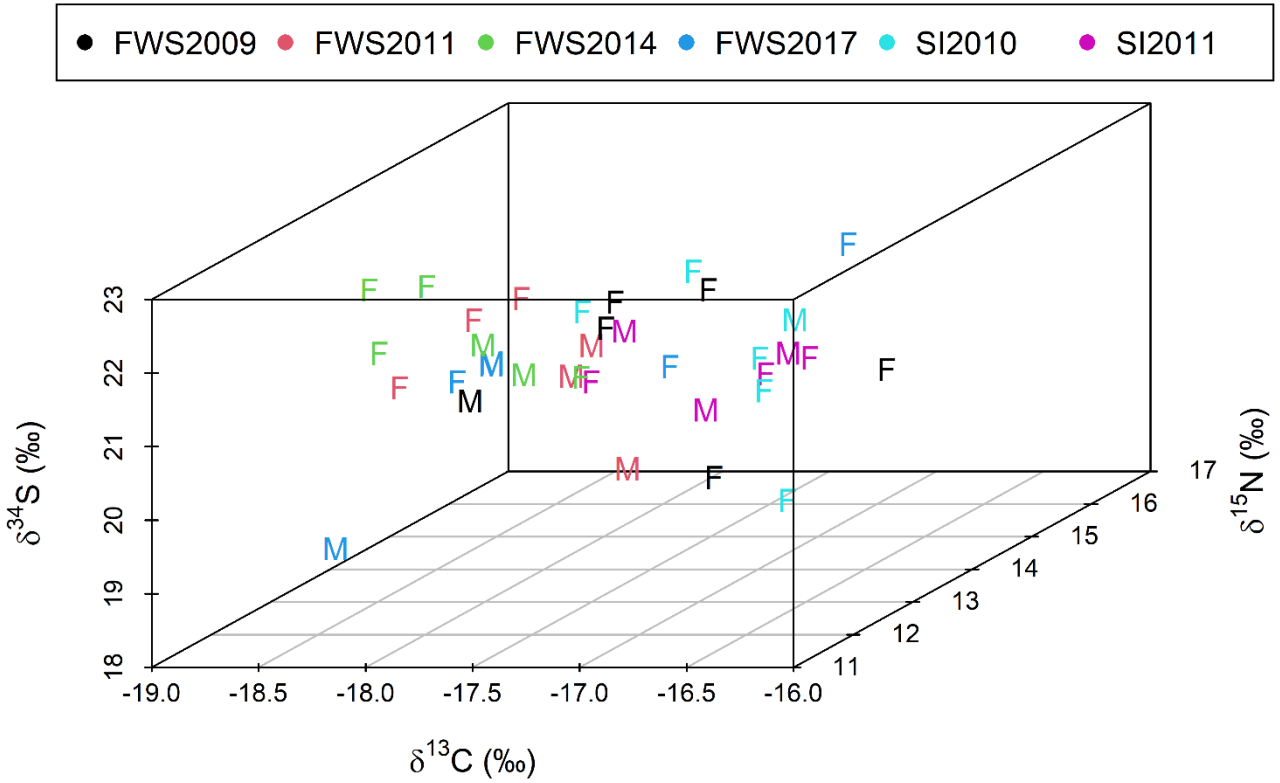

Figure 3.5. Carbon, nitrogen, and sulphur *(δ^{13}C, δ^{15}N and δ^{34}S)* stable isotope triplot of long-finned pilot whale (*Globicephala melas edwardii*) skin samples. Males are represented by "M" and females by "F". Data are presented by stranding event as indicated by colour in the legend. Figure reproduced from Hinton et al. (2022).

Table 3.4. Summary statistics for the top three generalised additive models (GAMs) selected based on Akaike Information Criterion corrected for small samples sizes (AICc) of long-finned pilot whale (*Globicephala melas edwardii*) skin samples, presented by carbon, nitrogen, and sulphur ($\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$) values. LL: log-likelihood; % DE: % deviance explained; δAICc: difference in Akaike's information criterion (AICc) of the current and top-ranked model; wAICc = AICc weight. Significant variables are highlighted in bold. Table taken from Hinton et al. (2022).

Model	**R^2**	**LL**	**% DE**	**δAICc**	**wAICc**
$\delta^{15}N$					
~**Stranding event**	0.431	1.000	45.40	-	0.145
~Location + **Stranding event**	0.431	0.885	45.40	0.250	0.128
~**Year** + Location	0.425	0.553	44.90	1.190	0.080
$\delta^{13}C$					
~**Maturity** + **Stranding event**	0.679	1.000	69.40	-	0.119
~**Maturity** + **Year** + **Location**	0.679	1.000	69.40	-	0.119
~Sex + **Maturity** + **Year** + **Location**	0.680	0.87	69.80	0.284	0.103
$\delta^{34}S$					
~Sex	0.030	1.000	5.59	-	0.211
~Year	0.020	0.885	4.77	0.250	0.186
~Location	0.030	0.486	8.85	1.440	0.102

3.5.4. Triple isotope niche regions

Triple isotope niche regions at the α = 40 level (NR_{40}) were calculated by ontogenetic variation and stranding event. Pairwise comparisons showed the NR_{40} overlaps of individuals from differing ontogenetic groups (Table 3.5A). Females had the most unique isotopic niche space; with only a 48% chance any resting females would be found in the NR_{40} of mature males but a 75% chance they would be found in the NR_{40} of pregnant/lactating females (Table 3.5A). However, there was a high degree of probability that both mature males (82%) or pregnant/lactating females (91%) would be found within the NR_{40} of all females. Likewise, mean niche size was much larger for all females (mean ± SE = 53.58 ± 13.82‰^{3}) than either pregnant/lactating females (33.56 ± 11.24‰^{3}) or males (20.72 ± 7.18‰^{3}). Mean niche size was similar across several stranding events; FWS2011 (6.62 ± 3.60‰^{3}), FWS2014 (4.32 ± 2.27‰^{3}), SI2011 (4.11 ± 2.21‰^{3}) and SI2010 (3.78 ± 2.04‰^{3}). The combined niche width of individuals stranded at FWS2009 (17.62 ± 9.42‰^{3}) and FWS2017 (15.52 ± 8.25‰^{3}) were much larger than those of all other stranding events (Figure 3.6).

There was a 59% chance of an individual from SI2011 being found in the NR_{40} of FWS2009, the highest probability recorded. However, there was only a 1% chance of an individual from FWS2017 being found within the NR_{40} of SI2010. Individuals stranded at Farewell Spit had a 0–36% chance of being found in the NR_{40} of individuals stranded at Stewart Island, whereas there was a much higher chance (0–75%) of an individual from Stewart Island being found in the NR_{40} of an individual stranded at Farewell Spit. Several pairs were considered to have low probability of NR_{40} overlap (<10%), with individuals from FWS2017 seemingly the least likely to be detected within the NR_{40} of any other stranding event (Table 3.5B). The NR_{40} overlap appeared high both between stranding events occurring at the same site (e.g., SI2010 and SI2011) and those that were temporally close (e.g., FWS2009 and SI2010 which occurred only three months apart, Table 3.5B).

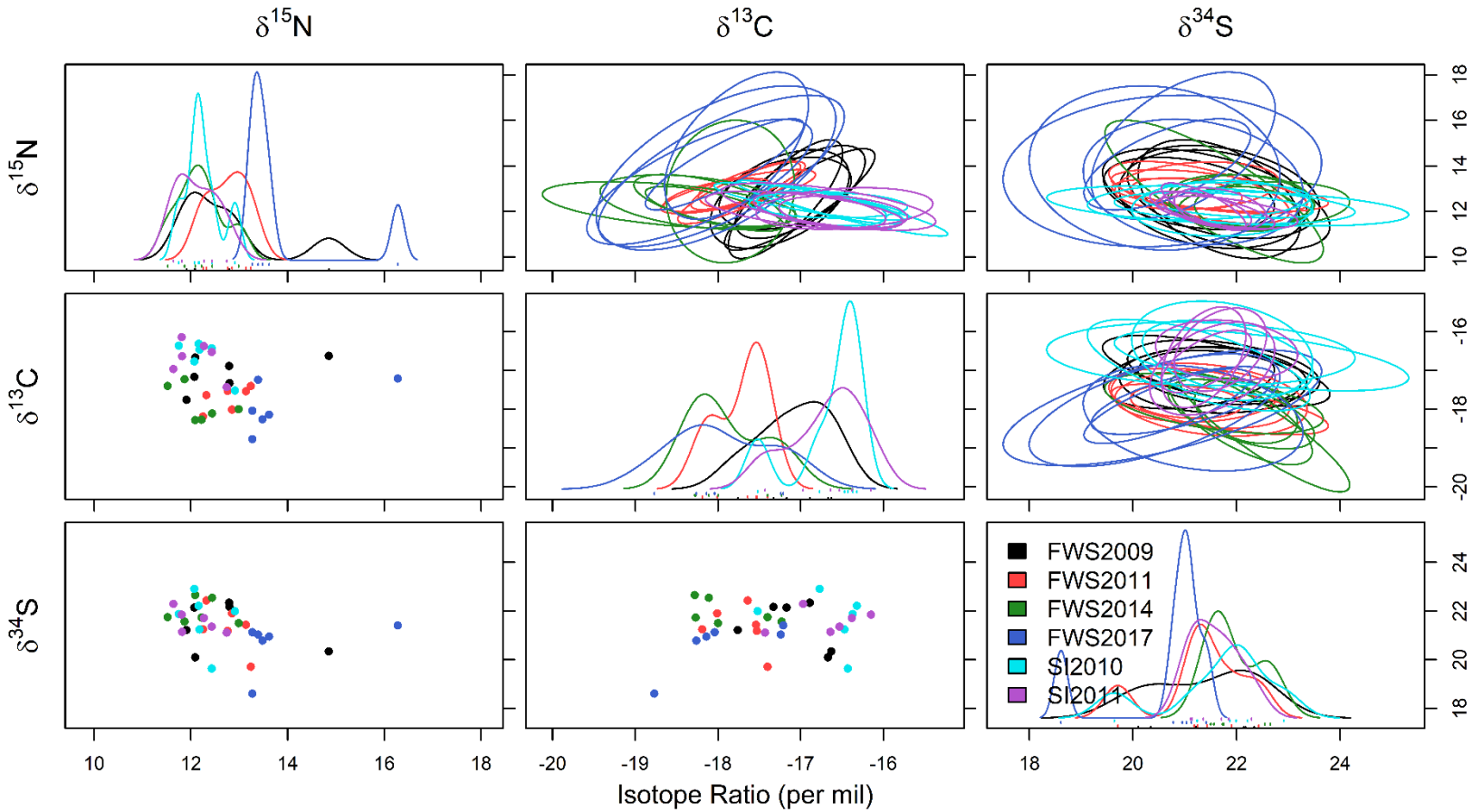

Figure 3.6. Two-dimensional scatterplots, one-dimensional density plots and two-dimensional 95% niche overlap ellipses of five random skin samples of carbon, nitrogen, and sulphur isotopes (δ^{13}C, δ^{15}N and δ^{34}S) of long-finned pilot whales (*Globicephala melas edwardii*) from each of six stranding events on the New Zealand coast, 2009–2017. In the sample identifiers, FWS = Farewell Spit, SI = Stewart Island. Figure taken from Hinton et al. (2022).

Table 3.5. Confusion matrices of triple isotope ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) niche overlap at the 95% confidence level of mature long-finned pilot whales (*Globicephala melas edwardii*) processed from stranding events on the New Zealand coast between 2009 and 2017. Values are the chances (%) that an individual from the group in the left-hand column would be found within isotope niche of any of the other groups in its row. Data presented by (A) maturity status and (B) stranding event. Table taken from Hinton et al. (2022).

(A)

	Mature Male	**Mature Female**	**Pregnant/Lactating Female**
Male		82.14	75.73
Female	48.41		74.90
Pregnant/Lactating female	57.30	91.45	

(B)

	FWS2009	**FWS2011**	**FWS2014**	**FWS2017**	**SI2010**	**SI2011**
FWS2009		21.05	2.65	0.86	25.02	21.11
FWS2011	36.13		17.57	4.07	5.81	27.04
FWS2014	7.94	26.35		9.61	0.38	8.16
FWS2017	1.49	3.51	2.48		0.00	0.75
SI2010	74.78	20.34	1.09	0.01		41.57
SI2011	58.80	29.13	7.26	0.76	37.41	

No significant correlation between stranding group size and niche size (correlation = 0.55, $p = 0.26$) was detected. However, when the FWS2009 stranding event was removed from the dataset, a significant positive correlation was revealed between the number of animals involved in the stranding event and the niche width (correlation = 0.92, $p = 0.03$). Finally, isotopic range was found to be similar between $\delta^{13}C$ (3.27‰), $\delta^{15}N$ (4.75‰) and $\delta^{34}S$ (4.30‰) values for the entire pooled dataset (Table 3.6). The smallest range of $\delta^{13}C$ values was found at the SI2010 stranding event (0.76‰) along with the largest range of $\delta^{34}S$ values (3.27‰). In contrast, the largest range of $\delta^{13}C$ values was recorded at the SI2011 stranding event (1.90‰) and the smallest range of $\delta^{34}S$ values (1.15‰) was recorded at FWS2014. Finally, the largest range of $\delta^{15}N$ values was recorded at the FWS2017 (3.85‰) stranding event, whereas the smallest range was at the FWS2011 stranding (1.20‰).

Table 3.6. Isotopic range expressed as a percentage of carbon, nitrogen, and sulphur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) values of long-finned pilot whales (*Globicephala melas edwardii*) sampled from mass-stranding events on the New Zealand coast, 2009–2017. Data are presented by overall dataset, and by each stranding event: FWS = Farewell Spit, SI = Stewart Island. Table taken from Hinton et al. (2022).

Isotope Range (‰)	**Overall**	**FWS2009**	**FWS2011**	**FWS2014**	**FWS2017**	**SI2010**	**SI2011**
n	125	20	20	27	20	19	19
$\delta^{13}C$	3.27	1.15	0.96	1.64	1.58	0.76	1.90
$\delta^{15}N$	4.76	2.95	1.96	1.47	3.85	2.18	1.86
n	36	6	6	6	6	6	6
$\delta^{34}S$	4.30	2.24	2.72	1.15	2.80	3.27	1.18

3.6. Discussion

Intraspecific variation in isotopic values has been explored in multiple cetacean species (Newsome et al. 2010). Here, ontogenetic, and spatiotemporal effects on the isotopic niche of a single cetacean species, LFPW, were analysed. Overall, isotopic data from this study were characterised by a high level of overlap between the 125 individuals analysed for $\delta^{13}C$ and $\delta^{15}N$ and the 36 individuals analysed for $\delta^{34}S$. Significant differences were found in both $\delta^{13}C$ and $\delta^{15}N$, but not $\delta^{34}S$ values when examined by location stranded and stranding event. No significant differences were found in the univariate comparisons of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values vs. sex, body length, age, maturity status or reproductive group.

In general, mean $\delta^{15}N$ values for LFPWs reported in this study (mean = 12.71‰, n = 125) were lower than mean values reported for other cetacea in New Zealand waters around the same time period, e.g., teuthophagus common dolphins *Delphinus delphis* (female mean = 14.88‰, n = 33; male mean = 14.81‰, n = 23; Peters et al. 2020) and male sperm whales *Physeter macrocephalus* (mean = 15.6‰, n = 37; Guerra et al. 2020). However, mean $\delta^{15}N$ values were still higher than other New Zealand marine mammals with diets that are more focused on copepods and krill, such as blue whales *Balaenoptera musculus* sp. (mean = 11.1‰, n = 8; Torres et al. 2015) and southern right whales *Eubalaena australis* (mean = 8.09‰, n = 18; Torres et al. 2017). Lower $\delta^{15}N$ values were also recorded in *G. m. melas* in the Mediterranean in comparison to other teuthophagus odontocetes such as *P. macrocephalus* and Risso's dolphins *Grampus griseus* (Praca et al. 2011). This could be indicative of offshore feeding (Ward-Paige et al. 2005; Abrantes and Barnett 2011; Troina et al. 2020). Indeed, $\delta^{15}N$ values reported in this study were consistent with those of other LFPW populations globally (Abend and Smith 1995; de Stephanis et al. 2008; Fontaine et al. 2015; Monteiro et al. 2015a; Becker et al.

2021). Similarly, δ^{13}C values recorded here were comparable to those measured in Northern Hemisphere LFPW populations (Abend and Smith 1995; Abend and Smith 1997; Pinzone et al. 2019).

Sulphur isotopes can provide useful information on foraging prey source pathways (Connolly et al. 2004; Duffill Telsnig et al. 2019), LFPW δ^{34}S values from this study were similar to those reported in LFPWs in the Mediterranean (Pinzone et al. 2019). High δ^{34}S ($\bar{x} = 21.52$‰, $n = 36$) values indicated a large contribution to diet from marine sulphate, indicating marine foraging pathways (Connolly et al. 2004; Olin et al. 2012; MacAvoy et al. 2017). The combination of low δ^{13}C values with high δ^{34}S values observed in this study has previously been described as typical of oceanic feeding behaviour (Cardona-Marek et al. 2009), corroborating that LFPWs are primarily an oceanic species (Sekiguchi et al. 1992; Abend and Smith 1999; Giménez et al. 2017a).

3.6.1. Ontogenetic variation in isotope values

No observable differences in isotopic niche among the different ontogenetic groups were detected in this study, aligning with observed isotopic homogeneity of LFPWs in the Strait of Gibraltar (de Stephanis et al. 2008). Whilst sex differences in resource-use have been reported in other cetacean species including bottlenose dolphins *T. truncatus* (Rossman et al. 2015), this has not been recorded in LFPWs previously. Furthermore, higher cadmium levels have been reported in female LFPWs from New Zealand waters than in males (Lischka et al. 2021). Higher cadmium load in females could signify a greater reliance on cephalopod prey (Méndez-Fernandez et al. 2013), as cephalopods are known to accumulate cadmium in their tissues (Bustamante et al. 1998). Females had a larger TA than males when considering only δ^{13}C and δ^{15}N values and were less likely to be found in the triple isotope niche of males (56%) than the other way around (79%, Table 3.5A). Yet, no differences were detected in mean δ^{13}C, δ^{15}N or δ^{34}S values between males and females. Whilst sex was retained as a

predictor in the top-ranked GAM for $\delta^{34}S$ (Table 3.4), the deviance explained was very low (6%), indicating that there are likely other factors that determine $\delta^{34}S$ values.

Like many cetacean species, *G. m. edwardii* displays sexual dimorphism with males being larger than their female counterparts (Jefferson et al. 2011; Betty et al. 2022). It is possible that increased overall body size, rather than sex, could be driving the small isotopic niche differences reported here. However, body length was not retained as a predictor in the top-ranked models for $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ (Table 3.4) nor significantly correlated with isotopic values. Whilst maturity status was retained as a predictor explaining $\delta^{13}C$ variation, this was not the case for $\delta^{15}N$ or $\delta^{34}S$ data. Hence, this study did not reveal a link between consumption of prey from higher trophic levels and body length. Similarly, no relationship was evident between stable isotope values and body length in *P. macrocephalus* (Guerra et al. 2020; Palmer et al. 2022), or $\delta^{34}S$, sex and body size in *T. truncatus* (MacAvoy et al. 2017).

An increased reliance on higher trophic levels with increased body length has been reported in weaned striped dolphins *Stenella coeruleoalba* (Meissner et al. 2012; Giménez et al. 2017a), whilst studies of *P. macrocephalus*, Commerson's dolphins *Cephalorhynchus commersonii*, common dolphins *D. capensis* and *T. truncatus* all reported an increase in $\delta^{15}N$ with age (Niño Torres et al. 2006). Though no statistical relationship was apparent between isotope values and body length or age in this dataset, high $\delta^{15}N$ values were recorded in some of the smallest and youngest LFPWs, which is consistent with reliance on lactation in young cetacea (Knoff et al. 2008; Viola et al. 2017; Gelippi et al. 2020).

The effect of reproduction on stable isotope values in cetaceans has not been well studied, but it has been suggested that energetic demands and nutrient intake of mature females can differ due to reproductive status (Bernard and Hohn 1989; Rechsteiner et al. 2013; Malinowski and Herzing 2015).

In this study, pregnant females had the largest isotopic niche of all reproductive groups. It has been suggested that the specific stage of pregnancy could affect isotope values of humpback whales *Megaptera novaeangliae* (Clark et al. 2016), so further distinction in reproductive groups, including pregnancy stage, may be necessary to elucidate isotopic variability. Furthermore, lactating LFPWs often had higher δ^{15}N values than resting females, though this difference was not statistically significant. In general, older females that are no longer reproductively active may target riskier prey (Engen and Stenseth 1989), causing a change to their isotopic niche. However, resting LFPWs in this study were not necessarily of advanced age. Overall, isotopic homogeneity among reproductive groups could be due to trophic similarity within the population, lack of sufficient samples within each stranding event or indeed, varying stages of pregnancy. A similar lack of variation in isotope values by reproductive group has been reported in sei whales, *B. borealis* and Bryde's whales, *B. edeni* (Takahashi et al. 2022). Differences in isotopic values that do not meet the threshold for statistical significance have been previously proven ecologically significant through the use of complementary dietary analysis methods such as fatty acid analysis (Browning et al. 2014). Accordingly, future examination of fatty acid profiles for the New Zealand *G. m. edwardii* population could shed further light on their foraging ecology.

3.6.2. Spatial and temporal variation in stable isotope values

Spatial differences in isotopic composition within a population are well recorded in cetacea, including *G. melas* (Abend and Smith 1995; Monteiro et al. 2015a). For example, spatial differences in δ^{15}N values have been attributed to prey selection and trophic breadth, whilst differences in δ^{13}C have been linked to feeding area (e.g., offshore, or coastal) and latitude (Newsome et al. 2007; Newsome et al. 2010). It was predicted that stable isotope strandings events would have lower δ^{13}C values compared to Farewell Spit due to the more southerly location (Rau et al. 1982), however the

opposite was true (Figure 3.4). Furthermore, δ^{15}N values were consistently lower in Stewart Island than Farewell Spit. The lack of significant differences in sulphur isotope values suggests that these carbon and nitrogen isotopic variances are likely due to variation in primary productivity and baseline isotope values between the two locations rather than differences in diet or food web pathways. Future studies would benefit from baseline isotopic information obtained from either: (1) sampling suspended particulate organic matter in surface waters or a sessile primary consumer; or (2) employing compound specific isotope analysis to tease out confounding baseline versus trophic level drivers of elevated δ^{15}N values (Chikaraishi et al. 2009; Hannides et al. 2009; Chikaraishi et al. 2014).

The isotopic ranges of values per stranding event for carbon, nitrogen and sulphur were much smaller than those observed in the overall dataset. Furthermore, stranding event was retained in three of the top six GAMs reported for δ^{13}C and δ^{15}N, indicating that stranding event was an important driver of variation for carbon and nitrogen isotopic values. Individuals involved in the SI2010 mass-stranding had the smallest niche size of all the stranding events, which indicates little inter-individual difference in prey and foraging locations for animals involved in this stranding event. However, SI2010 was also the event with the smallest number of overall individuals stranded (Appendix 3.1) which may confound the results. The widest NR_{40} was recorded at FWS2009 even though this stranding did not comprise the most animals stranded. When FWS2009 was removed from the dataset, a positive correlation was seen between niche size and the total number of LFPWs from all other stranding events. Although LFPWs are generally believed to live in matrilineal pods (Foote 2008; Whitehead et al. 2017), mass-stranding events of LFPWs on the New Zealand coast have been reported to involve individuals from many different maternal lineages (Oremus et al. 2013). This wider NR_{40} and isotopic variability could therefore signify multiple groups that have

previously been dispersed from each other (Dammhahn et al. 2017), but have fused to form a "super pod" shortly prior to stranding. With little other information available, such as genetic barcoding for individuals within stranding events, it is impossible to assume the genetic or social composition of the FWS2009 stranding event. It could be that the individuals stranded in FWS2009 represented a single pod. If that were the case, a wide NR could indicate a more heterogeneous feeding strategy or utilisation of more varied resources (Scholz et al. 2020). Both a wide isotopic niche and heterogeneity of isotopic niche within a population can indicate a generalist feeding strategy, diversified diet, or a degree of individual dietary specialization (Vander Zanden et al. 2010; Jourdain et al. 2020; Källberg Normark et al. 2022).

The large niche size recorded in FWS2009 appeared to be driven by a larger range of δ^{15}N values compared to other stranding events (Table 3.6). The individuals stranded in the FWS2017 event also recorded a large niche size, driven by both the largest range of δ^{15}N values and second largest range of δ^{34}S values compared to other stranding events (Table 3.6). This indicates that individuals in these two stranding events had a more varied diet. This could be due to ingestion of a mixture of different trophic level prey which themselves feed in a variety of benthic/pelagic, and coastal/oceanic habitats. Isotopic density plots for both FWS2011 and SI2010 (Figure 3.6) also had lower δ^{34}S values, suggesting an inshore or benthic component to feeding prior to these stranding events (Connolly et al. 2004; Barros et al. 2010). Globally, LFPWs have been recorded as having some dietary plasticity, either following prey that have migrated due to changes in oceanic currents and water temperatures or adapting their diet to locally available prey (Gannon et al. 1997b; Cañadas et al. 2002; de Stepahais et al 2008; Chalcobsky et al. 2021). Indeed, observations of a single captive LFPW showed a preference shift to the more abundant prey when prey proportions were varied (Kritzler 1952).

Stomach content studies of LFPWs from New Zealand waters suggest a large dietary reliance on arrow squid *Nototodarus* spp. (Chapter 2; Beatson 2007; Beatson et al. 2007a; Beatson et al. 2007b).

It is difficult to ascertain whether changes such as a widening NR_{40} are indicative of a temporal niche change since the data in this study only span a few years. Whilst $\delta^{15}N$ values were highest in 2009 they were also high in 2017, suggesting there is not a linear temporal pattern in $\delta^{15}N$ values. However, a temporal decline in $\delta^{13}C$ values at Farewell Spit was noted between 2009 and 2017 (Figure 3.6), echoing similar findings from marine predators such as tuna (*Tunnus albacares*, *T. obesus* and *T. alalunga*; Lorrain et al. 2020) and *D. delphis* (Peters et al. 2020) across the Pacific Ocean in recent years. Whilst seasonal differences in prey have been recorded in LFPW populations in the northern hemisphere (Santos et al. 2014)], data in this study are exclusively from mass-strandings that occurred during the austral summer (November to February) in New Zealand, preventing seasonal comparisons.

Resource partitioning of socially and spatially distinct groups has been noted in other cetacea (Giménez et al. 2017b; Nicholson et al. 2021b). Although stranding records and sightings data show that *G. m. edwardii* strand all around New Zealand, only two stranding hotspot locations (Betty et al. 2020) were explored here. Despite the geographic separation of Stewart Island and Farewell Spit (~800 km apart) there was little isotopic variability between stranding events at the two locations when strandings occurred within the same year. In the absence of tracking, genetic, or migratory data, it is not known whether any surviving members of the FWS2009 stranded pod were involved in the stranding event three months later at Stewart Island.

Population homogeneity has been recorded in northern hemisphere LFPW populations (Gannon et al. 1997a), suggesting that individuals in the same pods may feed in similar environments. As stranding event appeared to be the most prominent predictor of niche, a degree of individual/group

specialisation (de Stephanis et al. 2008) or cooperative foraging may exist, as has been observed in other odontocetes (Ruiz-Cooley et al. 2021). Multiple feeding techniques have been observed in LFPW populations, including both shallow and deep foraging dives (Sivle et al. 2012; Isojunno et al. 2017) and nocturnal (Robin et al. 2002; Mengual et al. 2015) and suction feeding (Werth 2000) in captive animals. Satellite tagging of the closely related short-finned pilot whales *G. macrorhynchus* in the northeastern Atlantic revealed that individuals may be able to adapt foraging states and behaviour per dive in response to immediate physiological and environmental constraints (Quick et al. 2017). However, it is not clear what foraging strategy *G. m. edwardii* utilise in New Zealand waters due to a lack of tagging, video, or distribution data for this species.

This study was the first to investigate isotopic variation of *G. m. edwardii* in New Zealand waters. Overall, spatiotemporal variation appeared to have a greater effect on isotopic values than ontogenetic variation, with significant differences in $\delta^{13}C$ and $\delta^{15}N$ values detected between stranding location and event. Whilst $\delta^{34}S$ values did not directly relate to ontogenetic or spatiotemporal factors, incorporating sulphur isotope data improved isotopic niche calculations and provided insight into drivers of other isotopic differences. In particular, $\delta^{34}S$ values determined possible drivers of isotopic niche differences between stranding events, which were not easily identified using just $\delta^{13}C$ and $\delta^{15}N$ values. Finally, this study showed the benefits of long-term tissue archiving when supported by robust life history datasets. Further sampling of *G. m. edwardii* and their associated prey from additional locations over multiple seasons would improve understanding of spatial and seasonal niche changes for *G. m. edwardii*. In addition, satellite tagging of *G. m. edwardii* individuals would provide missing information about their movements, foraging ranges, and habitats.

Chapter 4 — Comparative analysis of long-finned pilot whales (*Globicephala melas edwardii*) and their primary prey: insights from stable isotope and fatty acid analyses

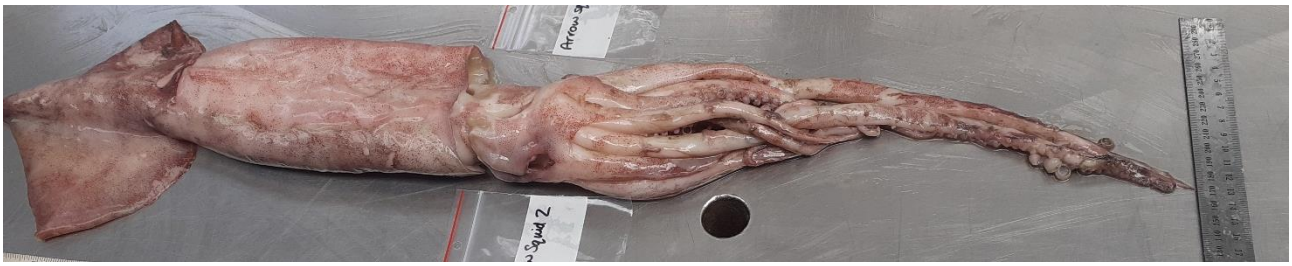

Photo credit: Bethany Hinton. A squid.

In this chapter, stable isotope, and fatty acid values from long-finned pilot whales (*Globicephala melas edwardii*) stranded at Farewell Spit in 2014 (n = 15) were compared to stable isotope and fatty acid values of their five primary prey species at Farewell Spit to address the final research objective:

Objective 3: Evaluate the use of biochemical tracers in key prey species to quantify LFPW dietary variation.

This chapter is a re-formatted version of the manuscript:

Hinton et al (*in prep*). Comparative analysis of long-finned pilot whales (*Globicephala melas edwardii*) and their primary prey: insights from stable isotope and fatty acid analyses.

4.1. Abstract

Knowledge of a species' foraging ecology is essential for understanding its function within the ecosystem and its biological interactions with other species. Multi-method approaches allow validation of dietary findings and account for inherent biases in single-method dietary investigations. A multi-method approach, using both stable isotope and fatty acid analyses was utilised to assess contribution of five key prey species (arrow squid *Nototodarus* spp., common octopus *Pinnoctopus cordiformis*, conger eel *Congridae* sp., carpet shark *Cephoscyllium* sp. and hoki *Macruronus novaezelandiae*) to the diet of long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) in Aotearoa New Zealand waters. Skin and blubber collected from carcasses sampled during a mass-stranding event at Onetahua Farewell Spit in 2014 were used to assess stable isotope and fatty acid variation, respectively. Muscle tissue (n = 15) of prey sourced either from LFPW stomachs or local commercial fisheries were used in assessment of prey. Arrow squid was statistically distinguishable from other prey species through carbon stable isotopes, whilst conger eel had significantly higher nitrogen stable isotopes than other prey. No differences were found in sulphur stable isotopes or overall dietary fatty acids. Although arrow squid showed the most similarity to LFPWs through both stable isotope and fatty acid comparisons, point-to-point prey polygons suggested that key prey species could be missing from this analysis. While LFPWs are likely a teuthophagus predator (cephalopod eater), future research should focus on identifying the missing pelagic squid and/or fish species that this present study has highlighted.

4.2. Introduction

Natural and/or anthropogenic changes to an ecosystem can be associated with temporal or spatial changes in target prey species, thus an understanding of diet has important management implications (Sinclair et al. 2018). Baseline data on target prey species, and any changes to these, are particularly important in environments such as open oceans, which are difficult to monitor (Pierce and Boyle 1991; Phillips et al. 2003; Chiu-Werner et al. 2019). To account for inherent biases in methodology, multidisciplinary combinations of approaches are recommended to address questions of foraging ecology (Nielsen et al. 2018).

One combination of methods used to determine diet is that of stable isotope and fatty acid analyses (Allan et al. 2010; O'Donovan et al. 2018). Stable isotope analysis of carbon and nitrogen has been applied extensively to determine relative prey contribution to diet (Kiszka et al. 2014b; Giménez et al. 2017b; Díaz-Gamboa et al. 2018; Zhang et al. 2019; Borrell et al. 2021; Teixeira et al. 2021; Teixeira et al. 2022) with other stable isotopes such as sulphur included to improve clarity of foraging pathways (Tucker et al. 2014; Matthews and Ferguson 2015; Pinzone et al. 2019; Borrell et al. 2021). However, diet-tissue trophic discrimination factors (TDF; i.e., the difference between the dietary isotope value and the resulting predator tissue value (Caut et al. 2009), key to stable isotope data interpretation, are still to be determined for many species. Although closely related species are widely thought to have similar TDFs, the uncertainty of these values requires caution when interpreting stable isotope results (Wyatt et al. 2010; Bond and Diamond 2011; Kadye et al. 2020).

Similarly, specific fatty acids, such as those synthesised by primary producers and only acquired by diet, are retained between trophic levels (Egeler et al. 2003). Thus, variations in fatty acid profiles can be used as biomarkers of diet within or between populations (Stowasser et al. 2012), or to identify dietary source (Auel et al. 2002; Dalsgaard et al. 2003). Quantitative Fatty Acid Signature Analysis

(QFASA; Iverson et al. 2004) has further been applied to determine dietary composition (Happel et al. 2016). However, the use of calibration coefficients (CCs) is only known for a limited number of species. This makes QFASA an inaccessible analysis for many species, hence literature often still focuses on qualitative methods to distinguish likely trophic interactions (e.g., Bradshaw et al. 2003; Grahl-Nielsen et al. 2010; Guerrero et al. 2020). Accordingly, it is advisable to apply multiple complimentary methodologies to validate dietary findings where possible (e.g., Tucker et al. 2008).

Multi-method approaches are useful to discern foraging complexities that individual methodologies alone would not clarify (Young et al. 2018). This is particularly relevant for marine ecological systems where organisms are difficult to access (Iverson 2009; Bowen & Iverson 2013). Stomach content, stable isotope and fatty acid studies have been used in isolation to elucidate marine mammal diet in Aotearoa New Zealand (e.g., Meynier et al. 2008c; Beatson and O'Shea 2009; Lambert et al. 2013; Miller et al. 2013; Meynier et al. 2014; Guerra et al. 2020; Peters et al. 2020). However, each method has a different capacity to distinguish between prey species. For example, stable isotope values of arrow squid *Nototodarus* spp. overlapped with hoki *Macruronus novaezelandiae* in New Zealand waters, although fatty acid values between the species differ (Vlieg and Body 1988; Meynier et al. 2008b). Therefore, identification of key prey species from stomach contents analysis, in addition to a combination of fatty acid and stable isotope analysis of the same prey specimens, may provide a clearer understanding of the overall diet of a predator.

Within New Zealand, the long-finned pilot whale LFPW; *Globicephala melas edwardii* is the most common cetacean species to mass strand (Betty et al. 2020). Despite this, little is known about the long-term diet, distribution, or foraging behaviour of this species. Whilst diet homogeneity has been noted in the days prior to stranding based on stomach content analysis (Beatson et al. 2007b; Beatson and O'Shea 2009; Chapter 2), long-term dietary trends of LFPWs in New Zealand waters remain

poorly understood. To address this knowledge gap, analyses of stable isotope and fatty acid biomarkers were applied together to explore comparisons between LFPWs and key prey species (Beatson and O'Shea 2009; Chapter 2). Specifically, the aims of this study were to: (1) assess whether LFPW prey can be distinguished via stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) analysis; (2) examine if LFPW prey can be distinguished through analysis of dietary fatty acid profiles; and (3) explore relative importance to LFPW diet of prey species through a combination of stable isotope and fatty acid techniques.

4.3. Methods

4.3.1. Sampling of long-finned pilot whales

Blubber and skin samples (n = 15) were collected from a mass-stranding event of LFPWs on Onetahua Farewell Spit, Golden Bay, New Zealand in January 2014 (Figure 4.1, Table 4.1). Sampling was undertaken *in situ* following standard post-mortem procedures (Geraci and Lounsbury 2005; IJsseldijk and Brownlow 2016). Skin was stored in ethanol and blubber at -20℃ prior to analysis. Whilst care was taken to sample the full skin layer (sampling described in further detail in Chapter 3), only the inner blubber layer was used for fatty acid analysis as is common for dietary studies (Hooker et al. 2001; Krahn et al. 2004; Smith & Worthy 2006; Grahl-Nielsen et al. 2010b).

4.3.2. Sampling of pilot whale prey

Five prey types (arrow squid *Nototodarus* spp., common octopus *Pinnoctopus cordiformis,* conger eel *Congridae* sp., carpet shark *Cephoscyllium* sp. and hoki *Macruronus novaezelandiae*) accounted for 99% of the prey recovered from stomach contents of LFPWs stranded at Farewell Spit, by index of

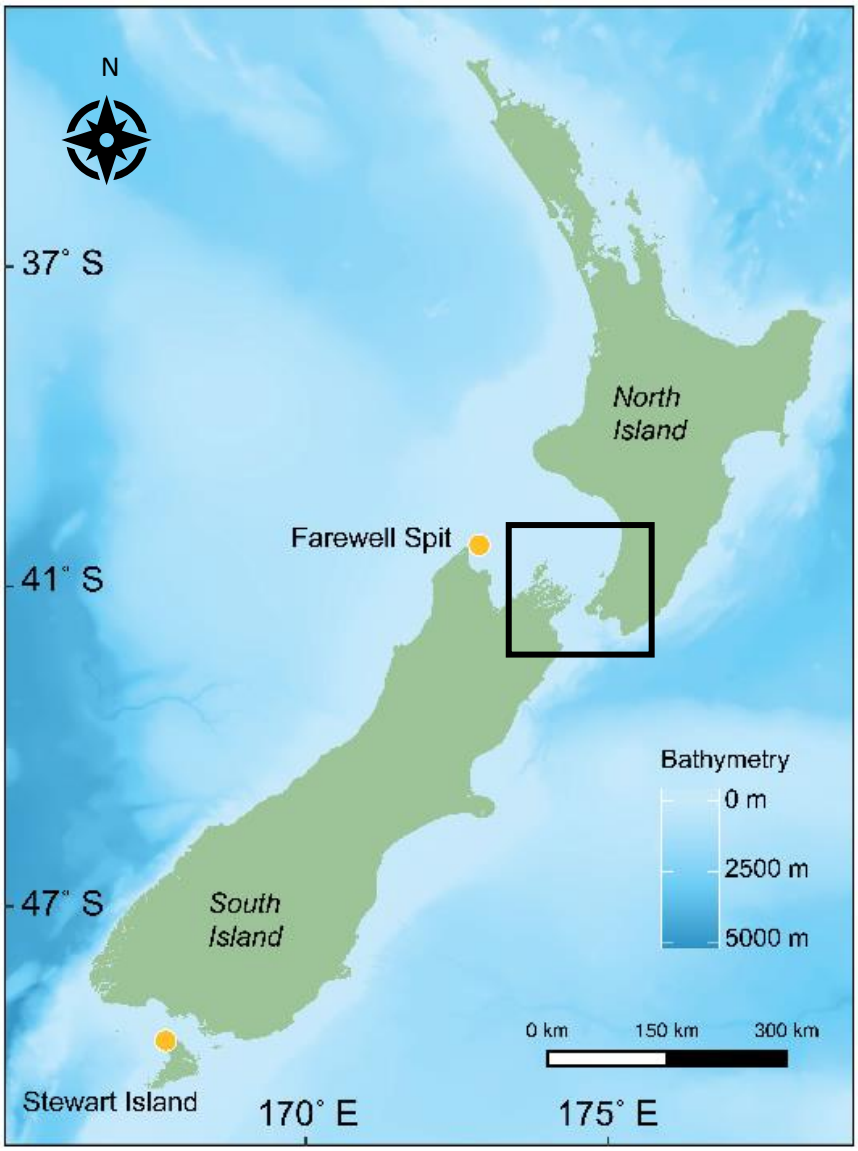

Figure 4.1. Tissue source locations around Aotearoa New Zealand. Prey sourced from vessels within area of the black box (Cook Strait; $n = 9$) in 2021, long-finned pilot whale (LFPW; *Globicephala melas edwardii*) tissue ($n = 15$) in 2014 and prey from LFPW stomachs ($n = 6$) sourced from mass-stranding events at Farewell Spit, in 2011. A single prey specimen was sourced from the stomach contents of a LFPW mass-stranded on Stewart Island in 2010. Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted with permission from National Institute of Water and Atmospheric Research (NIWA) under a Creative Commons BY license, with permission from NIWA original copyright (CANZ 2008). Figure modified from Hinton et al. (2022), Chapter 3.

relative importance (IRI, n = 141; Chapter 2, Appendix 4.1). Representatives of these five prey types were either recovered from the stomach contents of LFPWs mass-stranded in Farewell Spit in November 2011 or Stewart Island in February 2010, or sourced from commercial fishing vessels operating in the Cook Strait in between January and March 2021 (Figure 4.1, Table 4.1). Three individuals of each prey species were selected for stable isotope and fatty acid analysis, in line with previous dietary studies involving stable isotope (e.g., Catry et al. 2019; Krajcarz et al. 2019; McCluskey et al. 2021) and fatty acid data (Tucker et al. 2008; Choy et al. 2019; Madgett et al. 2019). Where possible, three specimens of each prey type were obtained from the same source. This was possible for all prey other than carpet sharks, of which only two specimens were available from a LFPW mass-stranding on Farewell Spit in 2011. The third carpet shark sample was sourced from the mass-stranding at Stewart Island in February 2010 (Figure 4.1, Table 4.1). A 1 cm^3 sample was dissected from lateral muscle of fish and mantle tissue of cephalopods using a scalpel. Samples were subsequently stored frozen at -20 ℃ prior to analysis (e.g., Arriola et al. 2013; Olin et al. 2014).

4.3.3. Stable isotope measurements

Stable isotope measurements were performed on skin tissue of LFPWs that had been stored in 70% ethanol. Skin samples were first placed under the fume hood for at least 48 hours (Olin et al. 2014) to allow all ethanol to evaporate. Lateral muscle tissue of fish and mantle muscle tissue of cephalopods stored frozen were defrosted for at least two hours and prepared whilst partially frozen. Both skin and muscle were sliced finely using a scalpel blade and glass petri dish. All equipment (including glassware, scalpel blade and metal tweezers) was rinsed with distilled water followed by 70% ethanol in between samples to prevent cross-contamination (Levin and Currin

Table 4.1. Source, year sourced, total body length (TBL) and mass of long-finned pilot whale (LFPW; *Globicephala melas edwardii*) prey species arrow squid (*Nototodarus* spp.), carpet shark (*Cephoscyllium* sp.), common octopus (*Pinnoctopus cordiformis*), conger eel (*Congridae* sp.) and hoki (*Macruronus novaezelandiae*) investigated for carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) stable isotopes and fatty acid profiles in New Zealand. Cook Strait refers to the location of the commercial fishery from which prey was sourced. Farewell Spit and Stewart Island refer to location of LFPW mass-strandings; prey with these locations indicated in the "Source" column were taken from the stomachs of LFPW carcasses in those locations. No length or mass measurements were taken from prey sampled from stomachs of carcasses.

Species	ID	Source	Year	TBL (cm)	Mass (kg)
Arrow squid	AS1	Cook Strait	2021	34.5	1.037
Arrow squid	AS2	Cook Strait	2021	39.4	1.342
Arrow squid	AS3	Cook Strait	2021	24.7	4.233
Carpet shark	S1	Farewell Spit	2011	N/A	N/A
Carpet shark	S2	Farewell Spit	2011	N/A	N/A
Carpet shark	S3	Stewart Island	2010	N/A	N/A
Common octopus	O1	Cook Strait	2021	99.2	1.844
Common octopus	O2	Cook Strait	2021	100.6	1.851
Common octopus	O3	Cook Strait	2021	119.3	2.228
Conger eel	CE4	Farewell Spit	2011	N/A	N/A
Conger eel	CE5	Farewell Spit	2011	N/A	N/A
Conger eel	CE6	Farewell Spit	2011	N/A	N/A
Hoki	H1	Cook Strait	2021	81.9	1.505
Hoki	H2	Cook Strait	2021	83.1	1.386
Hoki	H3	Cook Strait	2021	83.0	1.875

2012). Samples were initially sliced longitudinally to capture all skin layers (e.g., Wild et al. 2018). Skin and muscle samples were subsequently transferred into individual labelled Eppendorf tubes, and were oven dried at 60℃ for 48 hours.

All LFPW skin samples were processed at the Environmental and Ecological Stable Isotope Analytical Facility at National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand). Methods described in detail in Chapter 3 and Hinton et al (2022) were followed. Briefly, a MAS 200 R autosampler and analysed by a FLASH 2000 elemental analyser linked to a DELTA V Plus continuous flow isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) was used for sample analysis. Stable isotope ratios were expressed as delta values (δ) in per mil units (‰) as:

$$\delta = \left(\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right) \times 1000$$

All nitrogen values were reported against atmospheric air, and carbon values against a CO_2 reference gas, relative to the international standard Carrara Marble NSB-19 (National Institute of Standards and Technology (NIST), Gaithersberg, MD, USA). This was then calibrated against the original Vienna Pee Dee Belemnite (PDB) limestone standard and was then corrected for ^{17}O. Carbon isotope data were corrected via a two-point normalisation process (Paul et al. 2007) using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{13}C$ = -26.39 ± 0.09 ‰ and NIST 8542 (IAEA-CH-6 Sucrose; certified $\delta^{13}C$ = -10.45 ± 0.07 ‰). Nitrogen isotope data were corrected using the same two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{15}N$ = -4.52 ± 0.12 ‰) and IAEA-N-2 (ammonium sulphate: = +20.41 ± 0.20 ‰). After every ten samples, squid, and a working laboratory standard of DL-Leucine (DL-2-Amino-4-methylpentanoic acid, C6H13NO2, Lot 127H1084, Sigma, Australia) were run to report on precision and to control for quality. Accuracy

and precision were checked by running the international standard USGS65 (glycine: certified $\delta^{15}N$ = 20.68 ± 0.06; certified $\delta^{13}C$ = - 20.29 ± 0.04 ‰) every ten samples also. Data accuracy was measured to better than 0.15 ‰ for $\delta^{13}C$ and $\delta^{15}N$ values, whilst precision was measured to better than 0.24 ‰ for $\delta^{13}C$ and 0.22 ‰ for $\delta^{15}N$ values.

Lateral muscle tissue of fish and mantle tissue of cephalopods, alongside one LFPW skin sample, were processed at IsoTrace Limited, Dunedin following methodology described in Chapter 3 and Hinton et al. (2022), using a Carlo Erba NC 2500 elemental analyser coupled to a Europa Hydra system. Stable isotope values for carbon, nitrogen, and sulphur were calculated and normalised against international standards of Vienna PDB atmospheric air and Canyon Diablo Troilite, respectively. A three-point data normalisation was carried out using two international reference materials containing USGS40 mixed with IAEA-S1 (with certified values of: carbon = -26.39 ± 0.04 ‰, nitrogen = -4.52 ‰ ± 0.06, and sulphur = -0.30 ± 0.03 ‰), and USGS-41 mixed with IAEA-S2 (with certified values of: carbon = 37.63 ± 0.05 ‰, nitrogen = 47.57 ± 0.11 ‰, and sulphur = 22.62 ± 0.08 ‰). Machine drift, and precision of $\delta^{13}C$ (0.08 ‰), $\delta^{15}N$ (0.04 ‰) and $\delta^{34}S$ (0.16 ‰) values were assessed from replicate analysis of a keratin internal laboratory working standard positioned every ten samples.

4.3.4. Fatty acid analysis

Prey muscle and LFPW blubber tissue were sampled semi-frozen immediately prior to analysis. Approximately 2–4 g of each tissue was sub-sampled and individually wrapped in aluminium foil. For blubber, fatty acids were obtained from lipid extracts using standard methodology (Bligh and Dyer 1959). In summary, 3.75 mL of a chloroform: methanol (1:2, v:v) solution was added to approximately 40 mg of sample (Grahl-Nielsen et al. 2010a; Salama et al. 2013), and then vortexed for four minutes. Subsequently, a further 1.25 mL of chloroform was added, and the resulting

solution was vortexed for two minutes. A further 1.25 mL of 8% sodium chloride in milliQ water was next added, which was vortexed for a further minute. After centrifuging at 2,000 rpm for five minutes, the bottom layer, containing all the lipids, was extracted using a double pipette technique. The bottom layer was transferred into a new 15 mL Kimax tube and dried to remove all residues of solvent using a steady stream of nitrogen gas at 40°C. For prey samples, fatty acids were directly methylated (e.g., Parrish et al. 2015) from approximately 40 mg of wet muscle tissue, without extracting the fatty acid (see methylation protocol below).

4.3.5. Fatty acid methylation

The fatty acid methylation procedure is described in detail within Chapter 5. Briefly, 100 µl of C19 internal standard solution (0.5 ml/mL in methanol) was added to samples, and fatty acids were methylated using 2 mL of a methanol:hydrochloric acid:chloroform (10:1:1, v:v:v) solution. Samples were heated at 100 °C in two 45-minute intervals, stopping for 15 minutes of sonification in the middle, totalling 1.5 hours of heating. Samples were then cooled for at least 10 minutes until reaching room temperature, before adding 2 mL of hexane and vortexing. A further 1 mL of milliQ water was added to samples, which were then vortexed again. The hexane (top) layer was transferred to a new Kimax tube, and solutions were placed under nitrogen gas until only fatty acid methyl esters (FAMEs) remained. The FAMEs were resuspended in 2 mL hexane then transferred to a 2 mL amber gas chromatograph (GC) vial. All FAMEs were measured using an Agilent GC- mass spectrometry machine (GC 6890N/MS 5975B, Agilent Technologies Ltd FAs) and were separated on a HP-5 column (5% phenyl methyl siloxane, DB-5MS UI, 30 m x 0.25 mm, 0.25 µm film thickness; Agilent Technologies Ltd). The carrier gas used was helium, and inlet pressure was maintained at 250 °C. All FAME peaks were identified based on their mass spectra, and concentrations of individual fatty

acids were quantified against the C19 internal standard (see Appendix 4.2 for an example of a chromatogram).

4.4. Statistical data analysis

4.4.1. Stable isotope analysis

Only prey samples that had a mass C:N ratio of over 3.5 were lipid corrected (Skinner et al. 2016) using equations for fish from Post et al. (2007). All LFPW samples with a C:N ratio of over 3.5 were also lipid corrected using lipid correction equations from Peters et al. (2022). Carbon isotope data were further corrected for the Suess effect (Quay et al. 2003), accounting for annual oceanic carbon uptake, using 2021 as the baseline as this was the most recent year in the study. Suess-corrected $\delta^{13}C$ values, along with $\delta^{15}N$ and $\delta^{34}S$ values, were tested for normality using Shapiro-Wilk tests. Significant differences in mean isotope values between species were tested using one-way analysis of variance (ANOVA) with post-hoc Tukey test. Non-normally distributed data were tested using Kruskal Wallis with post hoc Wilcoxon test using the base statistics package in R (R Team, 2021). Stable isotope biplots were created using R package "SIBER" (Jackson et al. 2011). To test the effect of different TDFs on $\delta^{15}N$ values, the R package "SIDER" (Healy et al. 2018) was used to estimate TDFs for carbon and nitrogen only using the tissue option "collagen". Additionally, TDF values for $\delta^{15}N$ values calculated for LFPW skin (Abend and Smith 1997) were also used in a comparative analysis. Muscle tissue was analysed to generate stable isotope values for all 15 prey items (Tables 4.2 and 4.3), therefore, SIDER estimates for TDF values of 3.5 ± 1.6‰ were used for nitrogen and 1.6 ± 2.0‰ for carbon. Since $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were normally distributed for all species, ANOVA with post-hoc Tukey tests were applied to compare data.

4.4.2. Fatty acid analysis

Fatty acids were reported using the nomenclature:

CA:B*n*x

where the word 'carbon' is represented by C, A refers to the number of carbon atoms in the chain, the number of double bonds is represented by B, and the placing of the first double bond in relation to the final methyl group in represented as x (Budge et al. 2006). Three key essential polyunsaturated fatty acids (PUFAs) were named in a different way as typical in the literature: C20:5n3, eicosapentaenoic acid = EPA, C22:5n3, docosapentaenoic acid = DPA and C22:6n3, docosahexaenoic acid = DHA.

The mass of each individual fatty acid was calculated first in μg. Duplicate measurements were run per sample, so a mean μg was calculated for each fatty acid. The final individual mass was used to calculate the mean proportion (%) of each fatty acid. Although all fatty acids were reported, only fatty acids with proportions over 0.1% were included in further analysis (Galloway et al. 2014). Therefore, once scarce fatty acids had been removed, proportions were re-scaled to 100% for further analysis (e.g., Thiemann et al. 2022). All proportional fatty acid data were then transformed, using the equation:

$$FA_{transformed} = \ln\left(\frac{FA_{proportion}}{FA_{reference}}\right)$$

where $FA_{transformed}$ is the transformed version of a fatty acid, $FA_{proportion}$ is the original proportional data value, and $FA_{reference}$ is the reference fatty acid (C18:0; Budge et al. 2006). Fatty acids were presented individually and grouped into monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs) and saturated fatty acids (SFAs) . All analyses were carried out on dietary fatty acids only, as defined by Iverson (2004), and comprised: C20:1n9, C20:1n11, C22:1n11, C22:1n13, C18:2n6, C20:4n6, EPA and DHA. Differences in dietary fatty acids amongst prey groups and LFPWs were assessed using one-way ANOVA with post-hoc Tukey tests, using transformed data.

4.4.3. Comparisons of pilot whale and prey biomarkers, and contribution of prey to diet

Permutational ANOVA (PERMANOVA; Anderson 2014) was used on non-transformed fatty acid data (e.g., Guerrero et al. 2020) to assess distance between LFPWs and prey (e.g., Clerc et al. 2017). The normal distribution of data is not a requirement for PERMANOVA analysis. Contribution of each dietary fatty acid to dissimilarity was assessed via similarity percentages (SIMPER) analysis. Variation of fatty acid profiles between prey groups and LFPWs was visualised through non-metric multidimensional scaling (nMDS) of non-transformed data (e.g., Guerrero et al. 2020) using the dietary fatty acid suite.

Predator isotopic values are required to fall within the bounded polygon of prey values for mixing models to be viable (Phillips and Gregg 2003). Prey mixing polygons were created with two combinations using: 1) TDF values for δ^{13}C (1.6 ± 2.0‰) and δ^{15}N (3.5 ± 1.6‰) from SIDER (as no TDF data is available for this species in this area); and 2) TDF values for δ^{13}C from SIDER and for δ^{15}N from Abend and Smith (1997). There were no δ^{13}C TDF values from Abend and Smith (1997, hence the δ^{13}C values from SIDER were compared to the to the values from Abend and Smith (1997) were used to see if TDF values caused different results. Visual inspection of prey polygons and stable isotope biplots (corrected for TDF) was used to determine if data fell within the 95% confidence interval and thus were suitable for Bayesian mixing model analysis (Smith et al. 2013).

4.5. Results

4.5.1. Stable isotope variation of prey

Arrow squid (n = 3, -19.2 ± 0.4‰) were more depleted in δ^{13}C compared to common octopus (n = 3, mean = -17.31 ± 0.05 ‰; p = <0.01), conger eel (n = 3, mean= -17.58 ± 0.19 ‰; p = <0.01), carpet shark (n = 3, mean= -17.58 ± 0.19 ‰; p = <0.01) and hoki (n = 3, mean = -18.09 ± 0.16 ‰; p = <0.01) and hoki were more depleted in δ^{13}C compared to both common octopus (p = 0.02) and carpet shark (p = 0.02, Table 4.2, Figure 4.2). Conger eel (n = 3, mean = 17.31 ± 0.24‰) had significantly higher δ^{15}N values

compared to arrow squid (n = 3, mean = -11.87 ± 1.58 ‰; p = <0.01), common octopus (n = 3, mean = 13.57 ± 0.19‰; p = 0.02) and hoki (n = 3, mean = 13.98 ± 0.17‰; p = 0.03),while carpet shark (n = 3, mean = 15.52 ± 1.21‰) had higher $\delta^{15}N$ values compared to arrow squid (p = 0.01). No differences were observed in $\delta^{34}S$ values among prey species ($F_{4\text{-}8}$ = 1.164, p = 0.395; Table 4.2, Figure 4.2).

Table 4.2. Mean ± standard deviation of carbon, nitrogen, and sulphur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) values of long-finned pilot whales (*Globicephala melas edwardii;* LFPWs) and five of their key prey species arrow squid (*Nototodarus* spp.), carpet shark (*Cephoscyllium* sp.), common octopus (*Pinnoctopus cordiformis*), conger eel (*Congridae* sp.) and hoki (*Macruronus novaezelandiae*). Key prey species were identified from stomach content analyses; Chapter 2) from New Zealand waters. All LFPWs were sampled following a mass-stranding event on Farewell Spit, Golden Bay, New Zealand, in January 2014. *Only one sample available.

Species	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
Arrow squid	3	-19.2 ± 0.5	11.9 ± 1.9	21.0 ± 1.8
Carpet shark	3	-17.5 ± 0.2	15.5 ± 1.2	*20.4
Common octopus	3	-17.3 ± 0.1	13.6 ± 0.2	21.3 ± 0.4
Conger eel	3	-17.6 ± 0.2	17.3 ± 0.3	22.1 ± 1.1
Hoki	3	-18.1 ± 0.2	14.0 ± 0.2	22.4 ± 0.2
Long-finned pilot whale	16	-17.6 ± 0.6	12.1 ± 0.3	*21.8

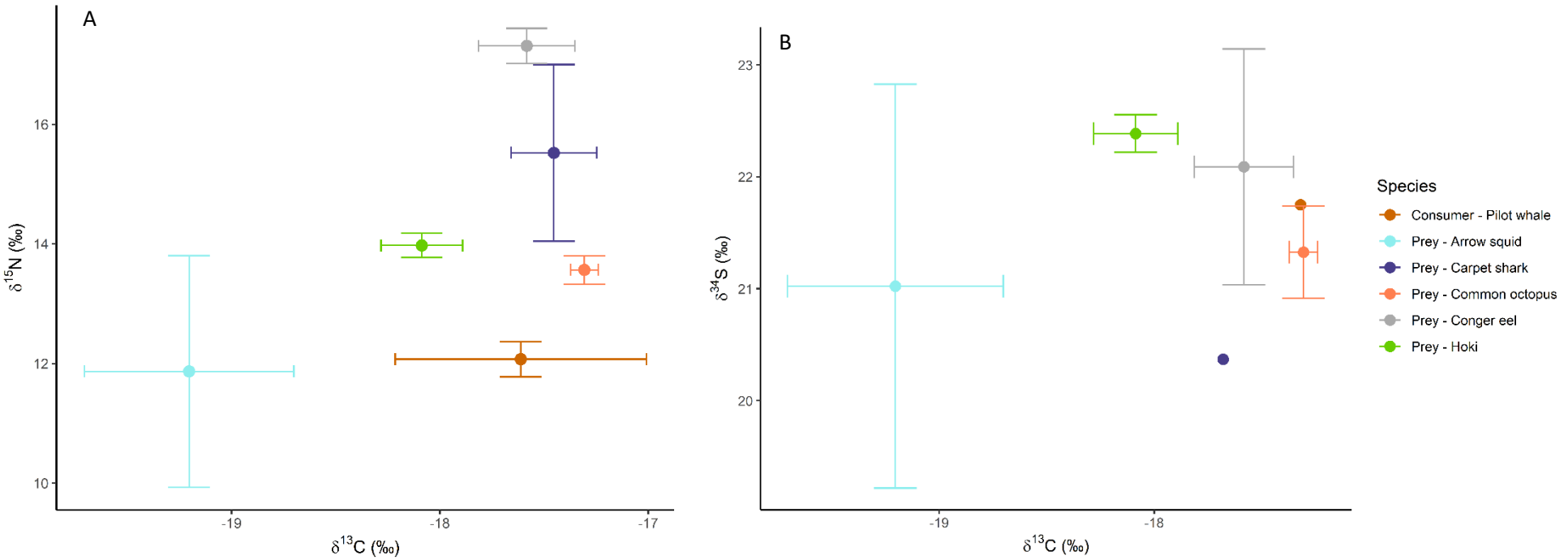

Figure 4.2. A: Stable isotope biplots of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) from skin long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) involved in a mass stranding at Farewell Spit, New Zealand in January 2014, and muscle tissue of five of their key prey species (arrow squid (*Nototodarus* spp.), carpet shark (*Cephoscyllium* sp.), common octopus (*Pinnoctopus cordiformis*), conger eel (*Congridae* sp.) and hoki (*Macruronus novaezelandiae*). Prey species were defined by prior stomach content analyses, Chapter 2). B: Stable isotope biplots of carbon and sulphur ($\delta^{13}C$ and $\delta^{34}S$) from skin of a single long-finned pilot whale, and muscle tissue of the same five of key prey species.

4.5.2. Fatty acid variation within prey

Both conger eel and carpet shark were characterised by similarly high levels of MUFAs, particularly C18:1*n*9 and C18:1*n*7. Conversely, common octopus were characterised by the highest C20:4*n*6 proportions, typical of octopus species. Arrow squid and hoki recorded similar values of most FAs, though hoki displayed higher C16:0 and lower overall PUFA values than arrow squid.

Dietary fatty acids were similar in the three common octopus individuals tested (Figure 4.3), but more variable within all other prey species. Yet, prey species revealed no difference in individual dietary fatty acids other than EPA (ANOVA, F = 19.94, p = <0.01) and DHA (ANOVA, F = 8.80, p = <0.01). Post hoc Tukey tests revealed the proportion of EPA was significantly lower in conger eel (n = 3, mean = 2.97%) compared to arrow squid (n = 3, mean = 11.75%; p = <0.001), common octopus (n = 3, mean = 22.16%; p = 0.001) and hoki (n = 3, mean = 13.52%; p = 0.005). Proportions of EPA were also significantly lower in carpet shark (n = 3, mean = 4.49%) compared to arrow squid (p = <0.001), common octopus (p = <0.001) and hoki (p = 0.003). Similarly, DHA was also lower in conger eel (n = 3, mean = 9.12%) compared to arrow squid (n = 3, mean = 35.91%; p = 0.002). Dietary fatty acids were in the highest proportions in common octopus, at an average of 59.89%, followed by arrow squid (55.09%), hoki (52.42%), carpet shark (32.32%) and conger eel (14.99%), although these differences were not significant (ANOVA, F = 4.34, p = 0.27). Overall, prey species could not be distinguished through dietary fatty acids (PERMANOVA, pseudo-F = 33.23, p = 0.08).

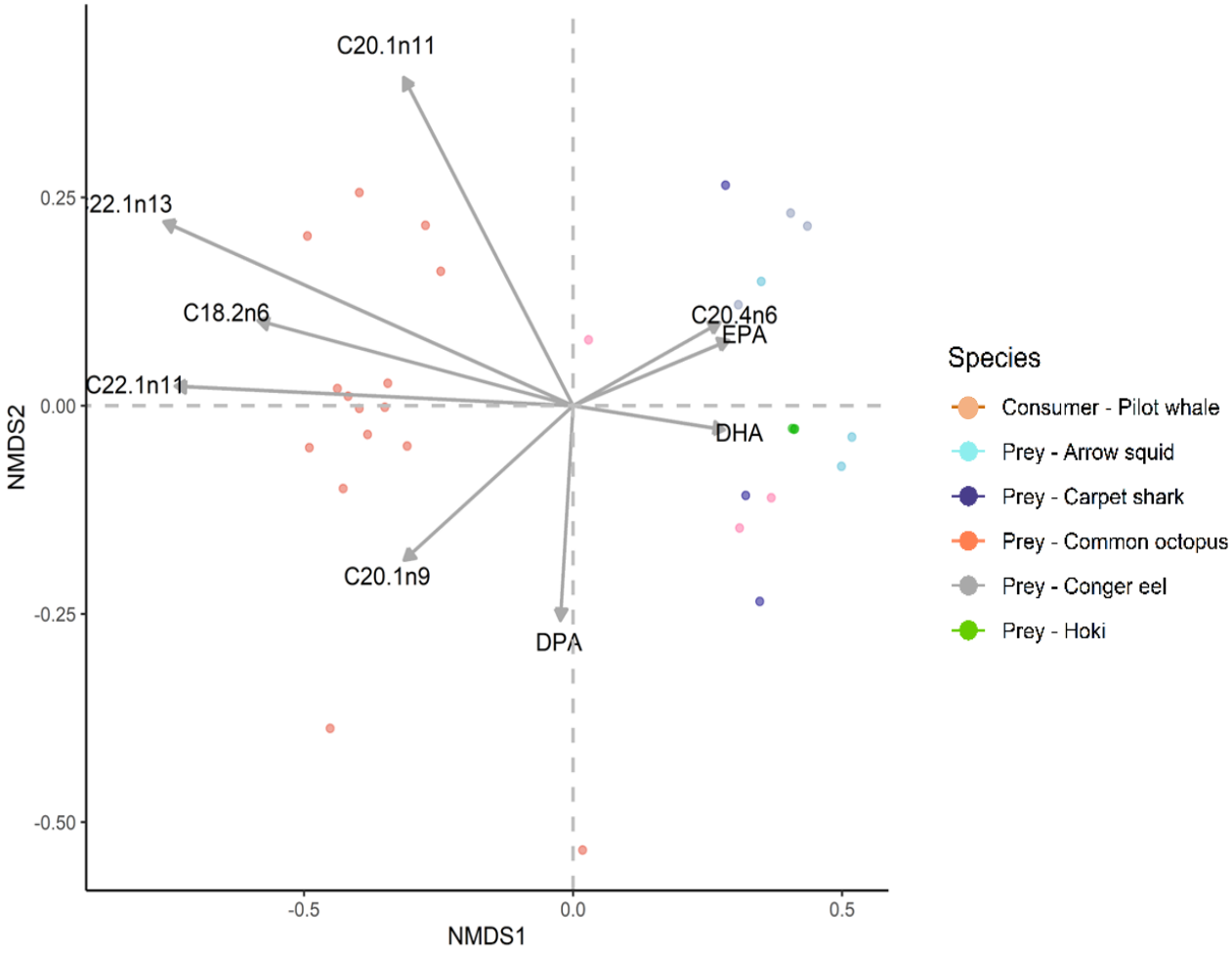

Figure 4.3. Dietary fatty acid profiles of long-finned pilot whales (*Globicephala melas edwardii*, *n* = 15) compared to dietary fatty acid profiles of five prey species (arrow squid *Nototodarus* spp., *n* = 3; carpet shark *Cephoscyllium* sp., *n* = 3; , common octopus *Pinnoctopus cordiformis*, *n* = 3; conger eel *Congridae* sp., *n* = 3; and hoki *Macruronus novaezelandiae n* = 3) as identified by prior stomach content analyses, see Chapter 2, Appendix 4.1. Dietary fatty acids were identified from Iverson (2004). As nMDS plot axes do not have quantitative meaning, arrows are included in the top graph to show fatty acids responsible for the distance.

Table 4.3. Fatty acid profiles of long-finned pilot whales (*Globicephala melas edwardii*) and key prey species (arrow squid *Nototodarus* spp.; carpet shark *Cephoscyllium* sp.; common octopus *Pinnoctopus cordiformis*; conger eel *Congridae* sp., and hoki *Macruronus novaezelandiae*) from New Zealand waters presented as a proportion of total fatty acids. Fatty acids in bold relate to dietary fatty acids as defined by Iverson (2004). Pilot whale = mean values of all 15 long-finned pilot whales tested, SFAs = saturated fatty acid, MUFAs = monounsaturated fatty acids and PUFAs = polyunsaturated fatty acids, and ∑ = total.

	Arrow squid				Common octopus				Conger eel				Carpet shark				Hoki				Pilot whale
ID	AS1	AS2	AS3	Mean	O1	O2	O3	Mean	CE4	CE5	CE6	Mean	S1	S2	S3	Mean	H1	H2	H3	Mean	Mean
C14:0	1.27	2.00	1.33	1.53	0.96	1.02	1.17	1.05	5.28	3.72	2.93	3.98	3.95	0.99	0.84	1.93	1.46	1.35	0.00	1.40	10.84
C15:0	0.66	0.00	0.00	0.66	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.47	0.64	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.99
C16:0	22.95	34.27	32.77	29.99	19.88	17.60	20.91	19.46	23.47	23.30	24.26	23.68	18.08	20.31	22.03	20.14	35.52	25.33	26.01	28.95	20.09
C17:0	1.09	0.00	0.00	1.09	1.19	0.00	0.00	1.19	0.48	0.00	0.00	0.48	0.00	0.00	0.00	0.00	0.00	1.09	0.00	1.09	0.72
C18:0	5.01	5.18	4.59	4.93	10.37	9.25	9.48	9.57	5.81	5.10	4.53	5.15	6.26	10.11	8.20	8.19	4.73	10.79	6.91	7.48	3.76
C16:1n7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00	0.00	0.36	0.67	0.91	0.00	0.79	0.00	0.00	0.00	0.00	4.21
C16:1n9	0.00	0.00	0.00	0.00	0.84	0.65	0.00	0.75	8.94	9.53	10.11	9.53	8.72	4.35	4.74	5.93	0.00	0.00	0.00	0.00	12.69
C17:1	0.73	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.76	0.73	0.00	0.75	1.22	0.00	0.00	1.22	0.00	2.18	0.00	2.18	0.86
C18:1n9	1.01	1.86	2.12	1.66	2.36	2.53	2.47	2.45	32.76	36.56	41.86	37.06	26.21	21.14	18.03	21.79	2.25	2.64	12.32	5.74	25.68
C18:1n7	1.09	1.43	0.00	1.26	2.62	2.63	2.33	2.53	3.70	4.46	4.14	4.10	5.68	6.01	5.68	5.79	1.12	2.91	2.18	1.90	4.01
C18:1n11	0.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.36	0.00	2.36	0.60

Table 4.3. continued

	Arrow squid				Common octopus				Conger eel				Carpet shark				Hoki				Pilot whale
ID	AS1	AS2	AS3	Mean	O1	O2	O3	Mean	CE4	CE5	CE6	Mean	S1	S2	S3	Mean	H1	H2	H3	Mean	Mean
C20:1n11	**6.14**	**0.00**	**0.00**	**6.14**	**0.00**	**0.00**	**0.00**	**0.00**	**1.69**	**0.00**	**0.00**	**1.69**	**2.89**	**0.00**	**0.00**	**2.89**	**4.37**	**5.33**	**1.89**	**3.86**	**1.51**
C20:1n9	**3.97**	**6.14**	**4.75**	**5.15**	**3.61**	**4.36**	**4.25**	**4.07**	**0.00**	**1.94**	**1.88**	**1.92**	**1.12**	**1.62**	**2.62**	**1.79**	**0.00**	**3.56**	**0.00**	**3.56**	**5.25**
C22:1n11	**4.94**	**0.00**	**0.00**	**4.94**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.42**	**0.00**	**0.00**	**0.42**	**0.00**	**0.00**	**0.00**	**0.00**	**1.47**
C22:1n13	**0.50**	**0.00**	**0.00**	**0.50**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.36**	**0.00**	**0.00**	**0.36**	**0.00**	**0.00**	**0.00**	**0.00**	**0.82**
C18:2n6	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.55**	**0.00**	**0.00**	**0.55**	**1.00**	**0.90**	**0.00**	**0.95**	**0.00**	**0.00**	**0.00**	**0.00**	**1.20**
C20:4n6	**1.16**	**1.19**	**1.38**	**1.24**	**5.33**	**5.27**	**5.01**	**5.20**	**1.46**	**1.16**	**0.00**	**1.31**	**1.86**	**4.08**	**4.75**	**3.56**	**1.39**	**0.00**	**2.88**	**2.13**	**0.57**
EPA	**10.59**	**12.94**	**11.73**	**11.75**	**20.89**	**23.27**	**22.31**	**22.16**	**3.36**	**2.82**	**2.74**	**2.97**	**3.78**	**3.04**	**6.66**	**4.49**	**11.12**	**21.39**	**8.06**	**13.52**	**1.27**
DHA	**31.69**	**34.70**	**41.33**	**35.91**	**24.48**	**30.75**	**30.13**	**28.45**	**10.53**	**9.29**	**7.54**	**9.12**	**14.41**	**25.43**	**22.03**	**20.63**	**36.34**	**23.28**	**37.65**	**32.42**	**3.48**
DPA	29.50	0.00	0.00	29.50	2.02	2.66	1.94	2.21	0.37	1.76	1.89	1.23	2.74	1.12	4.41	2.76	1.69	1.95	2.11	1.91	2.09
∑SFAs	37.63	41.44	38.69	39.58	27.22	27.87	31.56	28.88	35.51	32.13	31.73	33.75	22.67	21.30	22.87	22.28	41.71	38.01	32.91	37.55	35.80
∑MUFAs	5.03	9.44	6.87	7.11	9.43	10.18	9.05	9.55	48.21	52.84	57.05	55.40	46.93	34.02	31.07	37.34	7.75	16.34	16.39	13.49	55.84
∑PUFAs	57.74	48.82	54.44	53.67	52.71	61.95	59.39	58.02	16.28	15.03	11.23	15.18	23.78	34.57	37.86	32.07	50.54	45.64	50.70	48.96	8.00
∑Dietary FAs	58.99	54.97	59.19	57.72	54.31	63.65	61.70	59.89	17.59	15.21	12.16	14.99	25.84	35.07	36.06	32.32	50.88	53.56	50.48	51.64	15.57

4.5.3. Comparisons of pilot whale and prey biomarkers, and contribution of prey to diet

The LFPWs displayed a higher proportion of C14:0, C16:1*n*9, and C17:1, and a lower proportion of PUFAs, when compared to any of the prey species tested. The fatty acid profiles of prey species were characterised by high individual variation, but all had elevated levels of C16:0 compared to other fatty acids (Table 4.3), as is common in marine animals. Differences in dietary fatty acids were observed between predator and prey species (PERMANOVA, pseudo-F = 2.82, $p = 0.04$). Post-hoc Tukey tests showed that dietary fatty acids in LFPWs were significantly different to carpet sharks only ($p = 0.02$). Finally, SIMPER analysis revealed the three dietary fatty acids with most contribution to dissimilarity between LFPWs and carpet sharks were C22:1*n*11, C20:1*n*11 and C18:2*n*6 (Appendix 4.3).

As the prey groups in the study sample could only be separated isotopically and not by fatty acid profiles, only mixing polygons were carried out for stable isotope data. The mixing polygon demonstrated that none of the LFPW stable isotope values fell within 95% mixing region of the prey using SIDER values only (Figure 4.4), indicating that those data were not suitable for mixing models. However, when substituting TDF values for nitrogen from SIDER for those in Abend and Smith (1997), some of the consumers ($n = 6$) fell within the 95% confidence polygon (Figure 4.4, Appendix 4.5). However, none of the consumers fell within the inner contours, indicating (1) a low probability that they occurred within the prey mixing polygons, and (2) that they were unsuitable for Bayesian mixing model analysis (see Appendix 4.7 for further exploration).

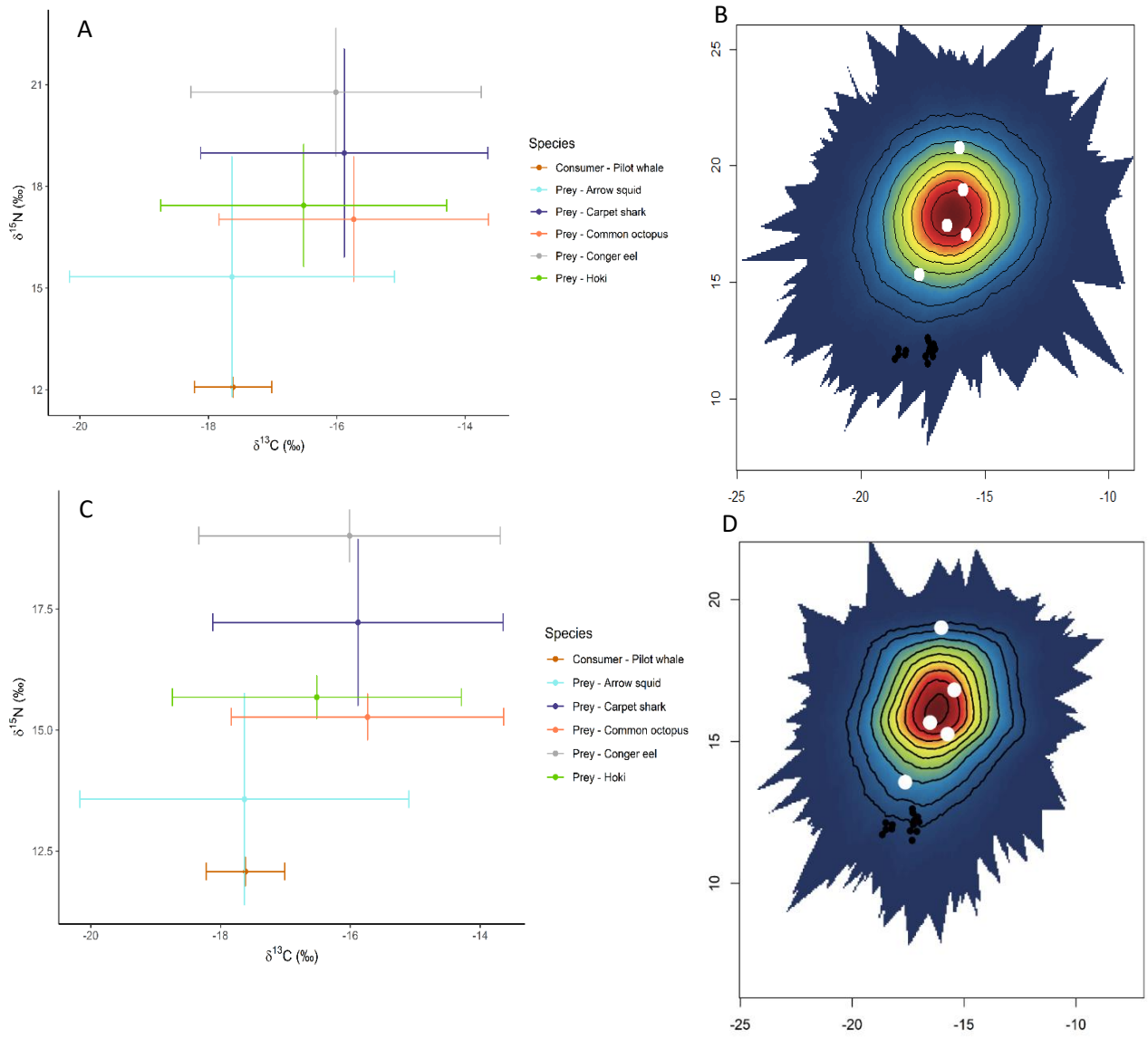

Figure 4.4. Isotope biplots (A and C) and point-to-point polygons (B and D) of carbon and nitrogen (δ^{13}C and δ^{15}N) values from skin of long-finned pilot whales (LFPWs; *Globicephala melas edwardii*; *n* = 15) and muscle of five key prey species (arrow squid *Nototodarus* spp. *n* = 3; carpet shark *Cephoscyllium* sp., *n* = 3; common octopus *Pinnoctopus cordiformis n* = 3; conger eel *Congridae* sp., *n* = 3; and hoki *Macruronus novaezelandiae*, *n* = 3) as defined by prior stomach content analyses (Chapter 2) from New Zealand waters. All LFPWs were sampled following a mass-stranding event on Farewell Spit New Zealand in January 2014. White dots in the plots B and D represent mean prey values and black dots represent consumers (LFPWs), each line represents 10% confidence interval. Prey data in all plots are corrected for trophic discrimination factors (TDF) δ^{13}C values (δ^{13}C 1.57 ± 2.03) from R package SIDER. The TDF correction in for δ^{15}N values in A and B was from SIDER (δ^{15}N 3.46 ± 1.60) and C and D used LFPW specific TDFs (δ^{15}N 1.7 ± 0.24) from Abend and Smith (1997).

4.6. Discussion

Overall, prey species showed a high level of similarity with each other for both stable isotope and fatty acid biomarkers. Overlap was highest between stable isotope values of arrow squid and LFPWs, indicating that arrow squid were an important component of LFPW diet, as previously demonstrated by stomach contents analysis (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009; Chapter 2). Conversely, fatty acid analysis showed LFPWs and carpet sharks had differences in dietary fatty acids, suggesting that carpet sharks contribute little to LFPW diet.

4.6.1. Stable isotope variation within prey

Several of the prey species (common octopus, conger eel, carpet shark and hoki) displayed large similarity in $\delta^{13}C$ values, whilst all prey species demonstrated high overlap in $\delta^{34}S$ values, indicating that over the timeframe of isotopic tissue equilibrium, they had resided in similar marine habitats. Arrow squid, however, recorded statistically lower $\delta^{13}C$ values than other prey, consistent with their deep-sea, pelagic habitat (Jackson et al. 2000; McClatchie et al. 2005). In addition, arrow squid demonstrated a large variation in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values, suggesting the derivation of prey from multiple source pathways (Vander Zanden et al. 2010; Codron et al. 2012; Duffill Telsnig et al. 2019; Scholz et al. 2020). This aligns with the reported generalist feeding behaviour of arrow squid (Braley et al. 2010). Both common octopus and carpet sharks displayed the highest mean $\delta^{13}C$ values along with low mean $\delta^{34}S$ values, suggesting a reliance on benthic food source pathways (Duffill Telsnig et al. 2019; Figure 4.2). This aligns with known distribution of these species; common octopus and carpet sharks occur mainly in coastal waters around New Zealand, in depths of up to 300 m and 500 m, respectively (Carrasco 2014; Horn 2016). Similarly, carpet shark $\delta^{15}N$ and $\delta^{34}S$ values were very variable, as might be expected from a scavenging species (Horn 2016).

Common octopus exhibited the narrowest overall within-species overlap for stable isotopes of all prey species (Figure 4.2), which suggests a degree of dietary homogeneity among individuals tested (Flaherty and Ben-David 2010). More unexpectedly, only modest isotopic variation was noted in hoki, which is known to be an opportunistic pelagic feeder (Clark 1985; Connell et al. 2010). Given hoki diet is thought to vary by factors such as individual specimen size, foraging location (i.e., longitude) and water depth (Connell et al. 2010), the low variation in stable isotope values could reflect just a subset of the population. Indeed, all hoki specimens examined in this study were obtained from the same source, so could have originated from one catch.

4.6.2. Fatty acid variation within prey

Dietary fatty acid profiles of prey species had a high degree of overlap, which can indicate a food chain where multiple prey species are also interacting with each other. Indeed, fatty acids of arrow squid have previously been grouped with mesopelagic fish due to similarities in fatty acid profiles (Pethybridge et al. 2012), although some differences were noted. For example, a single arrow squid, along with a single carpet shark, were the only two of the 15 prey specimens tested that included the long-chain dietary MUFAs C22:1*n*11 and C22:1*n*13 (Table 4.3). The fatty acids derived from C20:0 and C22:0 are characteristic of food chains based on calanoid copepods (Pascal and Ackman 1976; Stowasser et al. 2012) from marine pelagic environments (Stibor et al. 2004; Turner 2004). Furthermore, *n*-3 PUFAs (represented by EPA and DHA in this study) were significantly increased in all arrow squid (Table 4.3), consistent with previous studies of fatty acids in arrow squid in New Zealand waters (Meynier et al. 2008b) and are indicative of oceanic phytoplankton (Sargent 1987). As arrow squid demonstrate foraging pathways from both phytoplankton and copepods, this provides further evidence of a pelagic feeding pattern.

Conversely, common octopus and conger eel demonstrated the highest and lowest proportions of PUFAs recorded in prey, respectively. Studies examining the effect of water depth on fatty acid profiles from multiple shrimp species found higher levels of PUFAs in shallow water individuals (Yerlikaya et al. 2013). This would suggest that common octopus and conger eel were the shallowest and deepest dwelling of the prey species analysed, respectively. However, this does not align for conger eel given their isotopic values (Figure 4.2) or what is known about the habitats and distribution of conger eels in the marine environment (Cau and Manconi 1984; Anderson 2005). Nevertheless, no difference was detected in fatty acid profiles of corals growing at different depths (Meyers et al. 1978), and lower levels of PUFAs have also been attributed to fish rich in lipids (Prato and Biandolino 2012), and those living in decreased light or cooler waters (Dalsgaard et al. 2003; Burgess et al. 2018). Thus, a combination of high fat content and nocturnal feeding (Correia et al. 2009), rather than depth, could be driving the low PUFA levels reported here in conger eels.

4.6.3. Comparisons of long-finned pilot whale and prey biomarkers, and contribution of prey to LFPW diet

The fatty acid values of LFPWs in this study aligned with those reported for *G. m. edwardii* stranded on the Australian coast (Walters 2005). However, a larger number of dietary fatty acids (n = 10) were reported in the Australian LFPWs compared to this study (n = 8), which could relate to the larger number of LFPWs sampled (n = 63, Walters 2005). Even so, the number of dietary fatty acids recorded was larger still (n = 14) in a Northern Hemisphere study of 56 *G. m. melas* across four locations (Monteiro et al. 2015b). A greater range of fatty acids in Northeast Atlantic LFPW populations may indicate a diverse diet (Guest et al. 2010) or foraging over a wider spatial area. Indeed, stomach content and stable isotope studies suggest that fish are a more abundant dietary component for Northeast Atlantic LFPWs than those foraging in waters around Argentina, Australia, or New Zealand (Gales et al. 1992; Beatson and O'Shea 2009; Beasley et al. 2019; Becker et

al. 2021). Similar spatial variability in diet has been recorded in the bottlenose dolphin *Tursiops truncatus*, as well as grey *Halichoerus grypus*, harp *Pagophilus groenlandicus*, and hooded seals *Cystophora cristata* (Samuel and Worthy 2004; Beck et al. 2007; Tucker et al. 2009). The extended dietary fatty acid suite and spatial variation in dietary fatty acids noted in the Northeast Atlantic (Monteiro et al. 2015b) could alternatively be a function of multiple sampling sites, with variation resulting from different baseline foraging pathways between locations (Rooker et al. 2006). Therefore, it is tentatively suggested that the small number of dietary fatty acids noted in the current study is a function of the single site sampled, which indicates that the LFPWs sampled in this study foraged in similar habitats, consuming a similar diet prior to stranding.

Overall, $\delta^{13}C$ values of LFPWs overlapped with those of common octopus, conger eel, carpet shark and hoki, indicating a similar foraging habitat for all these species. Only arrow squid and hoki displayed a lower mean $\delta^{13}C$ value (Figure 4.2). Given the TDF value of 1.57 ± 2.03% used for $\delta^{13}C$ values, only arrow squid looked to contribute highly to LFPW diet. However, these results must be interpreted with the understanding that LFPW $\delta^{13}C$ values may have been affected by ethanol storage (Hidalgo-Reza et al. 2019; Durante et al. 2020).

Further isotopic analysis of sulphur values revealed similar results to $\delta^{13}C$ values. Though the $\delta^{34}S$ value was only obtained for one LFPW in this study, the value of 21.8 ‰ was very similar to the mean value of 21.42 ± 0.91 ‰ recorded in 36 LFPWs stranded on the New Zealand coast between 2009 and 2017 (Hinton et al 2022; Chapter 3). Sulphur values of LFPWs also appear to overlap with $\delta^{34}S$ values for both octopus and arrow squid (Table 4.2, Appendix 4.4). As $\delta^{34}S$ values fractionate little through the food chain (McCutchan Jr et al. 2003), it would be expected for predators to display very similar $\delta^{34}S$ values to their prey, providing further evidence that arrow squid remain a key prey species for LFPWs. This would be consistent with stomach contents analysis of LFPWs in New

Zealand waters, which revealed a high contribution of both arrow squid and octopus to diet (Beatson and O'Shea 2009; Chapter 2).

Furthermore, LFPWs also had lower δ^{15}N values than all prey other than arrow squid, which could indicate a low to zero contribution to LFPW diet from all other prey species. However, previous studies of investigating the stable isotope values of LFPW and their prey have also found similar δ^{15}N values between LFPW skin and their cephalopod prey (Jackson 2017, Praca et al 2011). It could be that the TDF values between LFPWs and their prey are low, although further studies would be required to confirm this. Still, it must be noted that δ^{15}N values could be confounded by decomposition of prey tissue that was sourced from stomach contents (i.e., conger eel and carpet shark; Table 4.1). Mean δ^{15}N values of LFPWs were similar to those reported for the dusky dolphin *Lagenorhynchus obscurus*, Risso's dolphin *Grampus griseus*, and Gray's beaked whale *Mesoplodon grayi* in New Zealand, which are all known to predate on a mixture of pelagic fish and squid (Vaughn et al. 2007; Loizaga de Castro et al. 2015; Peters et al. 2022). This may suggest that LFPWs are feeding further offshore, where δ^{15}N values are thought to be lower due to fewer anthropogenic influences (Hobson 1999; Gaston et al. 2004; Ward-Paige et al. 2005; Sabadel et al. 2020). Indeed, a preference for offshore waters has been reported in other LFPW populations from multiple locations (Findlay et al. 1992; Buckland et al. 1993; Shane 1995; Cañadas et al. 2002; Heide-Jørgensen et al. 2002; Mate et al. 2005; Azzellino et al. 2008; Pinzone et al. 2015). It is possible that the prey specimens sourced from fisheries for this study (i.e., arrow squid, common octopus and hoki) may not have been from waters far enough offshore to be representative of LFPW diet, thus restricting this study's ability to elucidate true contribution to diet.

As mixing polygons indicated that some key dietary species could remain missing (Figure 4.4), Bayesian analyses were not able to be applied in this study. This was despite key species (99% IRI)

found in stomachs of LFPWs stranded on Farewell Spit being included (Chapter 2; Appendix 4.1). However, global studies have concluded that LFPWs forage on multiple cephalopod species (Gannon et al. 1997b; Mansilla et al. 2012; Santos et al. 2014; Monteiro et al. 2015a; Beasley et al. 2019; Becker et al. 2021). Indeed, squid of the families Lycoteuthidae, Moroteuthidae, Chiroteuthidae, Cranchiidae, Pholidoteuthidae, and Histioteuthidae were also detected in stomachs of stranded LFPWs from wider New Zealand waters, accounting for up to 34% of the diet, by IRI, dependant on location stranded (Beatson et al. 2007b; Chapter 2). These additional squid species could account for missing prey species in this study, since only one species of squid (arrow squid) was sampled.

Qualitative analysis of fatty acids revealed that DHA was one of the most prominent dietary fatty acids in LFPW blubber, which is typical of a diet high in squid (Guerrero et al. 2020). Arrow squid was the prey species that contained the highest proportions of DHA also, suggesting a key importance of arrow squid to LFPW diet. Arrow squid also contained the highest proportions of C20:1*n*9 and C20:1*n*11, the two most abundant dietary fatty acids detected in LFPWs in this study. Studies from Southeastern Australia listed C20:1*n*9 and C20:1*n*11 as markers of bathypelagic squid and fish, respectively (Pethybridge et al. 2010). It is therefore recommended to conduct further stable isotope and fatty acid analyses on a range of squid and fish as potential LFPW prey species (e.g., Riccialdelli et al. 2013), which may further elucidate missing prey items.

If indeed prey items were missing from stomach contents analysis, this could signify dietary change either seasonally or as a function of stranding events. This is because stable isotope and fatty acid biomarkers assimilate into cetacean tissue over a period of weeks to months (Newsome et al. 2010; Watt et al. 2019), whereas stomach contents analysis only investigates feeding from the previous day/s (Sekiguchi and Best 1997) and is therefore, biased towards prey that preserve well or have hard parts. Seasonal dietary change has been recorded in *G. m. melas* from the Faroe Islands

(Desportes and Mouritsen 1993). Furthermore, *G. m. edwardii* stranded in the South Atlantic displayed foraging plasticity by consuming neritic prey when in coastal waters (Becker et al. 2021), a strategy that LFPWs in New Zealand may use when in coastal areas prior to stranding. Still, it is not currently understood where LFPWs that strand from New Zealand waters forage. As LFPWs can travel up to 200 km within 24 hours (Bloch et al. 2003; Gales et al. 2012), there is a wide range of potential foraging areas available to these individuals in the weeks to months prior to stranding. A better understanding of how, where and what LFPWs forage on in New Zealand waters, possibly via telemetry studies, would help elucidate if changes in target prey are occurring either over time, by season or immediately prior to stranding.

Additionally, temporal differences in stable isotope and fatty acid baseline values may partially explain differences noted among LFPW and prey biomarkers. To account for isotopic differences in species between sites and seasons (Dethier et al. 2013; Teixeira et al. 2022), prey samples were taken preferentially from stomachs of LFPWs stranded at Farewell Spit, or from fisheries operating within a nearby area during the austral summer months. However, prey tissue was not able to be obtained from LFPWs and prey during the same year, due to a lack of fresh intact prey tissue available in stomachs (Appendix 4.6). Given that several of the prey species are generalist feeders (Cau and Manconi 1984; Braley et al. 2010; Connell et al. 2010), source pathways for both stable isotope and dietary fatty acids could have varied between sampling years dependent on prey consumed. Indeed, variation in both stable isotope and fatty acids of fish have been described by season, location and even size (Guest et al. 2010; Britton et al. 2021), whilst seasonal fatty acid variation has also been noted for arrow squid *Nototodarus gouldi* in Australian waters (Pethybridge et al. 2012). An assessment of baseline stable isotope and fatty acid variation via analysis of suspended particulate organic matter, or through compound-specific isotope analysis of fatty acids and/or amino acids

from LFPW tissue (e.g., McClelland and Montoya 2002; Chikaraishi et al. 2009; Hannides et al. 2009; Chikaraishi et al. 2014; Sabadel et al. 2019; Guerra et al. 2020) is therefore recommended in future studies to uncover drivers behind stable isotope and fatty acids variation.

Finally, this study displayed the influence of TDF values on trophic studies. The δ^{15}N TDF value for LFPWs estimated at 3.5 ± 1.6 ‰ in SIDER has also been used in studies of LFPWs *G. m. edwardii* in the Southern Atlantic (Becker et al. 2021), whilst marine mammal literature historically uses a 2–4‰ TDF for δ^{15}N values between trophic levels (e.g., DeNiro and Epstein 1981; Bentaleb et al. 2011). However, uncertainty surrounding specific δ^{15}N enrichment factors has led to calls for caution when interpreting differences in δ^{15}N values (Bond and Diamond 2011) as, although essential for considering trophic interactions, TDF values are not well-defined in cetaceans (Borrell et al. 2012). In the western North Atlantic, the δ^{15}N enrichment factor was only 1.57 ‰ in skin of captive bottlenose dolphins *T. truncatus* (Giménez et al. 2016), whilst the mean value was 1.4 ‰ for multiple cetaceans in the Mediterranean (Mèndez-Fernandez et al. 2012), and a similar 1.7 ± 0.24 ‰ for skin of LFPWs *G. m. melas* in the Atlantic (Abend & Smith 1997). Using the revised δ^{15}N TDFs of 1.7 ± 0.2 from Abend and Smith (1997), rather than those from SIDER, resulted in more LFPWs falling within the prey polygon (Figure 4.4, Appendix 4.5). This indicates that the Abend and Smith (1997) value may be more accurate and highlights the need for robust and accurate species-specific TDFs within trophic analyses.

Whilst quantitative contribution to LFPW diet using stable isotope and fatty acid analysis was not able to be assessed in this study, qualitative methods provided novel stable isotope and fatty acid data of known LFPW prey in New Zealand waters. Indeed, results presented here broadly agree with previous studies, suggesting that LFPWs are likely to rely on oceanic prey, in particular squid, with the ability to also forage coastally (demonstrating plasticity in their diet), possibly prior to

strandings. Future studies utilising larger sample sizes of LFPWs, and potential prey are recommended to elucidate dietary importance of oceanic squid species and the effects of life history on diet. Combining stable isotope and fatty acid analyses provided greater interpretive power to qualitatively assess LFPW diet. Therefore, this work highlights the benefits of using multiple methodologies to better elucidate drivers of variation when comparing predator with prey biomarkers (e.g., Tucker et al. 2008; Kelly and Scheibling 2012; King et al. 2017; Young et al. 2018), particularly given the constraint of relatively small sample sizes.

Chapter 5 — Body condition measurements and fatty acid profiles from long-finned pilot whales (*Globicephala melas edwardii*) stranded on the Aotearoa New Zealand coast.

Long-finned pilot whales *Globicephala melas edwardii* refloated after stranding at Onetahua Farewell Spit, New Zealand in 2021. Photo credit: Rebecca Boys.

In this chapter, fatty acid analysis from blubber samples of long-finned pilot whales (*Globicephala melas edwardii*) stranded at Farewell Spit in 2014 (n = 15) were compared to body condition measurements of the same individuals to address the third research objective:

Objective 4: Explore possible linkages between chemical dietary tracers and individual LFPW body condition.

This chapter is a re-formatted version of the manuscript:

Hinton et al (*in prep*). Body condition measurements and fatty acid profiles from long-finned pilot whales (*Globicephala melas edwardii*) stranded on the Aotearoa New Zealand coast.

5.1. Abstract

Body condition measurements are widely used to assess marine mammal health and nutritional status, though little agreement exists as to which measurements are the most informative across species. This study aimed to understand what relationships, if any, occur between body condition measurements and fatty acid profiles in long-finned pilot whales, LFPWs; *Globicephala melas edwardii*. Fatty acid profiles and six body condition measurements, including % blubber lipid content and five morphometric measurements (dorsal, lateral, and ventral blubber thickness, axillary girth, body length:girth ratio [body condition index; BCI]), were assessed in 15 carcasses originating from a mass-stranding on Onetahua Farewell Spit, Aotearoa New Zealand in 2014. Age was a good predictor of variation in axillary girth only, likely due to increased body size in older individuals. Fatty acid profiles were characterised by high levels of monounsaturated fatty acids (MUFAs), which was most likely due to insulation, and/or relative fatty acid profiles of local primary producers. Notably, no variation was recorded in fatty acid profiles by sex or maturity status, and none of the body condition measurements were able to consistently predict relative fatty acid proportions in examined LFPWs. However, axillary girth was able to explain some variation in saturated fatty acids, polyunsaturated fatty acids, and dietary fatty acid C20:1*n*9, though sample sizes were low. Further investigation into the links between body condition measurements, particularly axillary girth, and fatty acids on a larger sample of *G. m. edwardii* is recommended. This would be helpful when attempting to quantify individual condition and nutritional status at stranding events.

5.2. Introduction

It is important to understand the factors that influence health, reproductive fitness, and survivorship of a species to ensure effective conservation management (Deem et al. 2001; Reed 2005; Beausoleil et al. 2018). Body condition measurements attempt to gather information through measurable morphometric or chemical indicators of energy reserves (e.g., lipid content), therefore providing standardised information on an animal's individual condition (Hanks 1981; Loudon et al. 1983; Clutton-Brock and Sheldon 2010; Castrillon and Bengtson Nash 2020; Christiansen et al. 2020; Dalle Luche et al. 2021). A multitude of body condition measurements are currently in use, including measurements of adipocyte number, cortisol, or body/fat mass/volume (Lockyer et al. 1985; Oregui et al. 1997; Bengoumi et al. 2005; Alapati et al. 2010; Cook et al. 2012; Castrillon et al. 2017; Pearson et al. 2018; Carbajal et al. 2021; Ogloff et al. 2022).

Body condition measurements have been applied as stand-alone indicators or calculated as measurements relative to frame size (Audige et al. 1998; Vargas et al. 1999; Joblon et al. 2014; Wijeyamohan et al. 2015). Although factors such as sex, body size, maturity stage, or reproductive status may affect body condition and/or composition (Bearhop et al. 2004b; Nielsen et al. 2013; Adamczak et al. 2021), there is also evidence of environmental and anthropogenic impacts (Reading and Clarke 1995; Gibson et al. 2018). Whilst external disturbances are thought to affect food intake (Kastelein et al. 2019), the effect of dietary change on body condition is less clear. Though dietary change has little consequence for the body condition of some species (Severud et al. 2013; Yeung and Yang 2017), in some taxa, such as convict cichlids *Archocentrus nigrofasiatus* diet does impact individual condition (Brown et al. 2004). Thus, it is important to understand, on a species-specific level what effects, if any, dietary change has on individual body condition.

Fatty acid analysis is an effective means of studying dietary change (Couturier et al. 2020), widely applied across several species of marine mammals (Williams et al. 1977; Iverson et al. 1997; Guitart et al. 1999; Herman et al. 2005; Smith and Worthy 2006; Meynier et al. 2008a; Loseto et al. 2009; Tucker et al. 2009; Grahl-Nielsen et al. 2010a; Williams and Buck 2010; Lambert et al. 2013; Meier et al. 2016; Haug et al. 2017; Knox et al. 2019; Kolodzey et al. 2021; Meyers et al. 2022a). For marine mammals, fatty acids are sampled across various tissues, though most commonly blubber (e.g., Borobia et al. 1995; Brenna et al. 2018; Guerrero et al. 2020) which presents in three key layers (Samuel and Worthy 2004), with stratification of fatty acids (i.e., varying compositions and concentrations of individual fatty acid) across these different layers (Aguilar and Borrell 1990; Krahn et al. 2004; Lambert et al. 2013). The inner blubber layer is the most metabolically active within marine mammals (Ellisor et al. 2013), so dietary fatty acids are thought to assimilate to the inner blubber layer first (Lockyer et al. 1984). The inner blubber layer is therefore predicted to be most indicative of diet on a scale of weeks-months (Smith and Worthy 2006; Strandberg et al. 2008a; Guerrero and Rogers 2017).

Blubber fatty acid profiles, prey availability and nutritional status have all been linked to body condition measurements of blubber across a variety of marine mammals (Learmonth 2006; Miller et al. 2011a; Hart et al. 2013; Williams et al. 2013; Kastelein et al. 2019; Bernier-Graveline et al. 2021; Stewart et al. 2021). Multiple blubber metrics have been applied as body condition measurements including mass, thickness, weight, and lipid content (Lockyer 1986; Koopman et al. 2002; Evans et al. 2003; Marón et al. 2021). Yet, despite blubber lipid content commonly being linked to body shape and condition in cetacea (Lockyer 1986; Aguilar and Borrell 1990; Read 1990; Evans et al. 2003; Miller et al. 2012), recent studies suggest blubber lipid content provides little indication of body condition (Kershaw et al. 2019; Christiansen et al. 2020).

As there are contrasting reports on the validity of different body condition measurements among cetacean species, the relationship between measurements of body condition and fatty acid profiles was investigated for a single cetacean species; long-finned pilot whales (LFPWs; *Globicephala melas edwardii*). Specifically, the aims of this study were to: (1) assess variation in body condition measurements (dorsal, lateral, and ventral blubber thickness, axillary girth, body length:girth ratio [body condition index; BCI]), and % blubber lipid content) by ontogenetic factors (age, sex, maturity status), (2) assess variation in blubber fatty acid profiles by ontogenetic factors (sex, maturity status), and (3) calculate the predictive power of body condition measurements on the proportion of fatty acid classes present in the inner blubber layer from LFPWs stranded on the Aotearoa New Zealand coast.

5.3. Materials and methods

5.3.1. Sample collection

Standardised external morphometric measurements were taken from carcasses originating from a mass-stranding on Farewell Spit, New Zealand in January 2014 (n = 15; Figure 5.1), following Geraci and Lounsbury (2005). The sample size used in this study is small but aligns with similar dietary fatty acid studies in Atlantic walruses *Odobenus rosmarus rosmarus* in Norway (Skoglund et al. 2010; n = 18), as well as Northern bottlenose whales *Hyperoodon ampullatus* and ground squirrels *Ictidomys tridecemlineatus* in Canada (Hooker et al. 2001; Price et al. 2013; n = 12). Five morphometric measurements were used to assess body condition (Figure 5.2); blubber thicknesses from the A) axillary dorsal, B) lateral, and C) ventral areas, D) the axillary girth (herein referred to as girth, used to calculate body length:girth ratio), and E) the total body length (herein referred to as body length, used to calculate body length:girth ratio; Figure 5.2). All measurements were taken to the nearest millimetre. Carcass decomposition state was assessed using standard scoring, where 1 = Freshly dead, 2 = Fresh, 3 = Moderate decomposition , 4 = Advanced decomposition and 5 = Skeletal remains

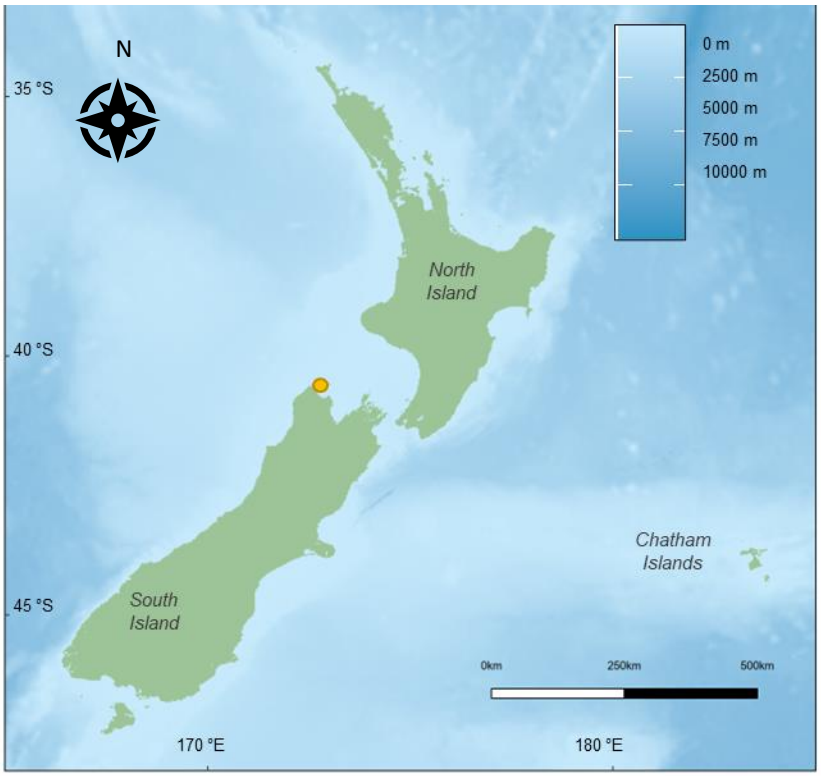

Figure 5.1. Location of stranding site (Farewell Spit, Golden Bay, South Island, New Zealand) from which long-finned pilot whales (*Globicephala melas edwardii*, *n* = 15) were sampled for body condition measurements and fatty acid profiles for this study. Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted from National Institute of Water and Atmospheric Research (NIWA) under a Creative Commons BY license (CANZ 2008), with permission from NIWA original copyright.

(for more detailed descriptions, see Geraci and Lounsbury (2005) and IJsseldijk et al. (2019)). All carcasses selected for analysis were deemed to be in a similar decomposition state (between scores 2-3; (IJsseldijk et al. 2019) to minimise any effects of decomposition on analytical results. Sex was determined anatomically based on visual inspection of reproductive organs *in situ*.

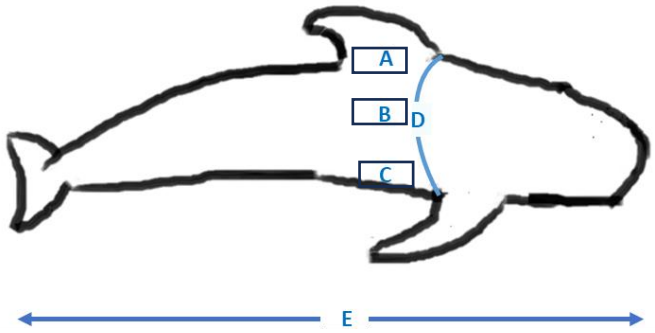

Figure 5.2. Representation of locations of long-finned pilot whale (*Globicephala melas edwardii*) blubber measurements dorsal (A), lateral (B) and ventral (C) and measurements of axillary girth (D) and total body length (E).

5.3.2. Sampling of blubber for fatty acid analysis

A full depth blubber sample approximately 10 cm x 10 cm was extracted from the axillary dorsal region (Figure 5.2, location A) of each individual for chemical analysis. A small layer of skin and muscle remained on the sample in order to distinguish blubber alignment at later subsampling. The inner blubber was sub-sampled, foil-wrapped, then stored frozen at -20℃ until further analysis.

5.3.3. Age, sexual maturity, and reproductive status

The ages of LFPWs were estimated from dentinal growth layer groups in teeth, as outlined by Betty et al. (2022). Sexual maturity and reproductive status were determined based on histological

examination of testes (Betty et al. 2019) and gross examination of ovaries (Betty 2019). Six reproductive groups were defined as: immature male, mature male, immature female, pregnant female, lactating female, and resting female, following Chapter 2. Male maturity was defined by presence/absence of sperm in testes (Betty et al. 2019). Females were defined as 'pregnant' by the presence/absence of a foetus, as 'lactating' by presence/absence of milk, and as 'resting' by the presence of ovarian corpora scarring indicating previous ovulation, but with no foetus or milk observed (Betty 2019).

5.3.4. Chemical analysis of blubber samples

Immediately prior to chemical analysis, 2–4 g of blubber from the inner layer were sub-sampled from semi-frozen tissue for ease of sampling, using a scalpel blade. Equipment was cleaned using an 80% ethanol solution and distilled water between each sample. Sub-samples were subsequently re-wrapped in foil and transported frozen to the Environmental and Ecological Stable Isotope Analytical Facility at the National Institute for Water and Atmospheric research, Wellington, New Zealand (NIWA) for lipid content analysis and fatty acid profiling.

Table 5.1. Summary of ontogenetic and body condition measurements of long-finned pilot whales (*Globicephala melas edwardii*) stranded on Farewell Spit, New Zealand in 2014 (*n* = 15). Body condition measurements are blubber lipid content (inner layer, %) dorsal, lateral, and ventral blubber thickness (mm) and body length:girth ratio (BCI). TBL = total body length.

Sex	*TBL (cm)*	*Maturity status*	*Reproductive status*	*Estimated Age*	*Lipid content (%)*	*Girth (cm)*	*Dorsal (mm)*	*Lateral (mm)*	*Ventral (mm)*	*BCI*
F	326	Immature	Immature	4	N/A	170	36	18	27	0.52
F	360	Immature	Immature	8	55	176	32	23	32	0.49
F	324	Immature	Immature	5	82	178	28	15	21	0.55
F	406	Mature	Lactating	10	68	19	29	18	27	0.47
F	423	Mature	Lactating	30	59	234	20	19	36	0.55
F	396	Mature	Pregnant	7	N/A	194	32	22	32	0.49
F	460	Mature	Pregnant	22	55	210	38	22	22	0.46
F	397	Mature	Resting	11	31	204	32	16	42	0.51
F	410	Mature	Resting	13	53	248	36	24	36	0.60
M	276	Immature	Immature	2	85	160	32	19	26	0.58
M	433	Immature	Immature	10	55	214	32	19	32	0.49
M	340	Immature	Immature	4	50	184	29	23	28	0.54
M	545	Mature	Mature	22	N/A	230	45	27	46	0.42
M	556	Mature	Mature	15	82	220	31	31	46	0.40
M	496	Mature	Mature	17	70	230	32	20	34	0.46

5.3.5. Lipid extraction

Lipids were extracted from blubber samples following Bligh and Dyer (1959; see Appendix 5.1 for exploration of appropriate methodology for these samples), approximately 40 mg (Grahl-Nielsen et al. 2010b; Salama et al. 2013) wet blubber tissue was weighed using weighing paper and transferred using clean dissecting forceps into individual 15 mL Kimax tubes. To extract lipids, 3.75 mL of a chloroform:methanol (1:2, v:v) solution was added to each sample, which was subsequently vortexed for four minutes. A further 1.25 mL of chloroform was added before vortexing for an additional two minutes. Then, 1.25 mL of 8% NaCl in milliQ water was added to the sample followed by a final vortex of one minute. The samples were subsequently centrifuged at 2,000 rpm for five minutes to separate lipids. After clear phase separation, the bottom layer, containing all the lipids, was extracted using a double pipette technique, whereby a short Pasteur pipette was inserted into the sample to the bottom of the tube, and the bottom layer was then collected using a long Pasteur pipette inside the short one. This lipid phase was transferred into a second clean, pre-weighed, screw top, 15 mL Kimax tube and dried using a steady stream of nitrogen gas at 40 ℃ to remove all residues of solvent. The Kimax tube containing the lipid was subsequently weighed to the nearest 0.001 mg. The weight of the Kimax tube was subtracted from the weight of tube plus lipid sample to obtain the weight of the lipids. The lipid content was reported against the wet weight of the original blubber tissue as a percentage (%). Lipid content was estimated for a subset of 12 individuals (Clavijo et al. 1999) and was used as the sixth measurement of body condition.

5.3.6. Fatty acid profiling

The fatty acids contained in the extracted lipid fraction of the LFPW blubber were derivatised into fatty acid methyl esters (FAMEs) prior to measurement via gas chromatography-mass spectrometry (GC-MS). After the addition of 100 μL of C19 internal standard solution (0.5 mL/mL in methanol), fatty acids were methylated using 2 mL of a methanol:hydrochloric acid:chloroform (10:1:1, v:v:v)

solution. Samples were then heated at 100℃ for 1.5 h in two 45-minute intervals, with 15 minutes of sonification in the middle. Samples were cooled to room temperature for 10 minutes before adding 2 mL of hexane. After vortexing for two minutes, 1 mL of milliQ water was added and samples were vortexed for a further one minute. After waiting for one minute for the solution to settle, the hexane layer (top layer) was transferred into a new Kimax tube. These final steps were repeated twice more to recover as many fatty acids as possible. Solutions were placed under a stream of nitrogen gas until only FAMEs remained. FAMEs were resuspended in 2 mL hexane then transferred to a 2 mL amber GC vial. FAMEs were measured using an Agilent gas chromatograph (GC 6890N) connected to a mass spectrometer (MS 5975B; Agilent Technologies Ltd, California). Individual FAMEs were separated on a HP-5 column (5% phenyl methyl siloxane, 30 m x 0.25 mm, 0.25 μm film thickness: Agilent Technologies Ltd California). Helium was used as the carrier gas. The inlet temperature was maintained at 250°C. The oven temperature programme began at 70°C, was held for one minute, ramped to 250°C at 5.0°C minute^{-1}, held for 6 minutes, ramped to 320°C at 10°C minute^{-1} and held for 10 minutes. All fatty acids were identified based on their mass spectra. Relative weights of individual fatty acids were quantified against C19, the internal standard, using percentage relative area method (e.g., Monteiro et al. 2021; see Appendix 4.2 for example chromatogram).

5.4. Statistical analysis

5.4.1. Body condition measurements

The BCI was calculated for all LFPWs by dividing the girth by the body length (Raverty et al.,2020) where:

$$BCI = \frac{axillary\ girth}{total\ body\ length}$$

In total, six body condition measurements were assessed: dorsal, lateral, and ventral blubber thicknesses, girth, lipid content, and BCI, selected based on a review of cetacean body condition measurements by Castrillon and Bengston-Nash (2020).

Normality of data was first tested using Shapiro-Wilk tests. Due to small sample size, models with a single explanatory variable were selected for the analysis. To test for relationships between morphometric measurements as described in objective one, general linear models were used to investigate the relationships between all six body condition measurements and age. The relationships between TBL and girth, dorsal, lateral, and ventral blubber thickness, and lipid content, respectively, were also assessed using general linear models whereas the non-linear relationship between BCI and TBL was assessed by Spearman rank coefficients (e.g., Raverty et al. 2020). Models were tested in both directions, but as results were the same, only one direction is reported. Variation in blubber fatty acid profiles by ontogenetic factors described in objective two was also tested. Where significant relationships were found between the TBL and body condition measurements, analysis of covariance (ANCOVA) was used to test for variation by sex and maturity status, respectively, whereas analysis of variance (ANOVA) was used where no significant relationship was found (see Appendix 5.2). Significance was tested to the 0.05 level.

5.4.2. Fatty acid profiles

Individual fatty acids were reported using the nomenclature:

$$\mathrm{CA{:}B}n\mathrm{x},$$

whereby ***C*** refers to 'carbon', **A** gives the number of carbon atoms in the FA, **B** gives the number of double bonds in the chain, and **x** gives the positioning of the first double bond, in relation to the final methyl group. Three fatty acids were named differently: EPA (C20:5*n*3, eicosapentaenoic acid),

DPA (C22:5*n*3, docosapentaenoic acid) and DHA (C22:6*n*3, docosahexaenoic acid), all considered essential polyunsaturated fatty acids (PUFAs).

The mass of individual fatty acids was stated in μg. As samples were analysed in duplicate, mean mass of each fatty acid was calculated along with mean total fatty acids. These values were then used to calculate the proportion (%) of each fatty acid within a sample. Although all fatty acids were reported, those recording a value under 0.1% were excluded from further analysis (Galloway et al. 2014). The proportion of fatty acids were therefore re-scaled to 100% for use in further analysis once low proportion fatty acids were eliminated (e.g., Thiemann et al. 2022).

For univariate analyses, fatty acid proportion data were normalised according to the data transformation in Budge et al. (2006) whereby:

$$FA_{transformed} = ln\,(FA_{proportion}/FA_{reference})$$

where $FA_{transformed}$ is the transformed value of the fatty acid in question, $FA_{proportion}$ is the original datum and $FA_{reference}$ is the reference fatty acid. The $FA_{reference}$ used in this study is C18:0, as suggested in Budge et al (2006). The transformed fatty acid data were grouped into classes of saturated fatty acids (SFAs), MUFAs, and PUFAs. One-way ANOVAs were used to investigate differences in SFAs, MUFAs and PUFAs respectively with both sex and maturity status (e.g., Guzmán-Rivas et al. 2022).

A one-way permutational analysis of variance (PERMANOVA; Anderson 2014) was performed on non-transformed data as this is the most appropriate analysis for ecological data including fatty acid studies (see Couturier et al. 2020 for a review of fatty acid analyses for use in marine studies). PERMANOVAs were used to check for dissimilarity in fatty acid values between sex and maturity status. A similarity percentage (SIMPER) analysis was performed to establish which fatty acids contributed the most to dissimilarity (e.g., Ricardo et al. 2015; Couturier et al. 2020; Fonseca et al.

2022). Though no statistical tests were performed on reproductive status due to small sample size, dissimilarity was visualised by reproductive groups using nMDS plots, with ellipses calculated by sex at the 90% level. Significance for all statistical tests was set at the 0.05 level.

5.4.3. Predictive power of morphometric body condition measurements on fatty acid classes

To assess whether any of the morphometric measurements were able to predict variation in lipid content or fatty acid concentrations as described in objective 3, generalised linear models (GLMs) were applied to non-transformed data. Following methods used in Kershaw et al. (2019) modified for fatty acids rather than lipid content, data were modelled with GLMs rather than GLMMs as there were no repeat measurements being tested. GLMs were modelled along with variation inflation factors (VIFs) and the dredge function in R package "vegan" (Oksanen et al. 2013). In summary, collinearity od regression coefficients was first checked using VIFs were. If strong co-linearity was detected, then covariates were removed from analysis using a stepwise technique, with the covariate showing highest VIF score removed at each stage. This continued until all covariate values were less than three (Zuur et al. 2010). The dredge method ran all possible combinations of remaining covariables, and the optimal model was selected using small-sample size corrected Akaike Information Criterion (AICc; Burnham et al. 2011). The lower the AICc score, the better fit the model is, but models within three AICc units of the optimum model were deemed equally likely to reflect the true situation. Model weight scores were also reported: the closer to one that a model weight is, the higher the predictive power of that model. If the optimum model includes the intercept only, this indicates that none of the covariables or interactions between those factors had predictive power of the variable under investigation.

Modelling was performed to establish any relationships between morphometric measurements and proportions of: 1) C20:1*n*9, 2) DHA, 3) C20:1*n*11, 4) SFAs, 5) MUFAs and 6) PUFAs in LFPWs. The

three dietary fatty acids included (C20:1*n9*, DHA and C20:1*n*11) were all identified in the top ten fatty acids to contribute to dissimilarity in SIMPER analysis. Covariables for all models were defined as: dorsal, lateral, and ventral blubber thicknesses, body length, girth and BCI. Body length and age were both also added to GLMs as covariables for comparison of effects.

Data analysis and graphical visualisations were performed in statistical software R (R Core Team, 2021). All computation of nMDS was completed in R package "vegan" (Oksanen et al. 2013), VIFs were calculated using R packages "tidyverse" (Wickham and Wickham 2017) and "caret" (Kuhn et al. 2020), AICc was calculated in R package "MuMIN" (Barton and Barton 2015). The R packages "ggplot2" (Wickham 2011), "ggpubr" (Kassambara and Kassambara 2020) and "ggvegan" (Simpson 2021) were used for data visualisation.

5.5. Results

5.5.1. Variation in body condition measurements

Dorsal blubber thickness was most commonly the largest of the blubber thickness measurements (mean = 32.27, SD = 5.44; Table 5.1). Dorsal blubber thickness did not vary with sex, maturity status or age. Conversely, lateral blubber thickness was the lowest of the blubber thickness measurements and ranged between 16–27 mm (mean = 21.07; SD = 4.20; Table 5.1), whilst ventral blubber thickness ranged between 21 and 46 mm (mean = 32.47; SD = 7.78; Table 5.1). No significant differences were observed between either lateral or ventral blubber thicknesses and sex or maturity status respectively, nor age.

The BCI ranged from 0.40 to 0.58 (mean = 0.50; SD = 0.06; Table 5.1). However, BCI was not significantly different by sex or maturity status, nor correlated with age. Lipid content ranged from 31 to 85% (mean = 62.08%; SD = 15.87; Table 5.1). The highest lipid contents were observed in the smallest immature male (85%, body length: 276 cm), smallest immature female (82%, body length:

324 cm) and largest male (82%, body length: 556 cm) investigated. No effects of sex, maturity status or age were detected on blubber lipid content.

Table 5.2. Pairwise general linear models of body condition measurements taken from the carcasses of long-finned pilot whales (*Globicephala melas edwardii*) stranded on Farewell Spit, New Zealand in 2014. General linear models with t- statistic (t) and *p*-values are reported. Significant *p*-values are given in bold. BCI = body condition index, girth = axillary girth, Dorsal = dorsal blubber thickness, Lateral = lateral blubber thickness, Ventral = ventral blubber thickness and Lipid = % blubber lipid content.

Measurement	Variable	t	*p*-value
Age	Girth	4.607	**<0.01**
	Dorsal	0.002	0.998
	Lateral	1.086	0.297
	Ventral	1.756	0.103
	BCI	-1.329	0.207
	Lipid	-0.570	0.581
Girth	Dorsal	0.448	0.661
	Lateral	1.600	0.134
	Ventral	2.765	**0.016**
	BCI	-0.821	0.427
	Lipid	-0.877	0.401
Dorsal	Lateral	1.526	0.151
	Ventral	0.778	0.450
	BCI	-1.387	0.189
	Lipid	-0.508	0.623
Lateral	Ventral	2.570	**0.023**
	BCI	-2.149	0.051
	Lipid	0.478	0.643
Ventral	BCI	-1.734	0.107
	Lipid	-0.821	0.431
BCI	Lipid content	-0.344	0.738

Finally, girth ranged from 160 to 248 cm (mean = 202.80; SD = 26.47; Table 5.1). Whilst girth showed no significant differences by sex or maturity status it was correlated with age ($t = 4.607$, $p < 0.01$). The only body condition measurements that were significantly positively correlated with one another were: girth and ventral blubber thickness ($p = 0.004$; Table 5.2), ventral and lateral blubber thickness ($t = 2.510$, $p = 0.02$)

5.5.2. Variation of fatty acid profiles

A total of 21 fatty acids were detected in LFPW blubber (Table 5.3). The fatty acids with the highest proportions were C18:1*n*9 (Oleic acid), C16:0 (Palmitic acid), C16:1*n*9 (Palmitoleic acid) and C14:0 (Myristic acid). All 21 fatty acids were present across all sex and maturity status classifications apart from C20:4*n*6 (Eicosadienoic acid) which was not reported in mature males. Although males displayed a higher SFA content (Table 5.3, Figure 5.3), differences were not significant. In fact, no significant difference was found in the proportions of SFAs, MUFAs and PUFAs respectively, by either sex or maturity status (Figure 5.3).

Table 5.3. Fatty acids (FAs) from the inner blubber layer of long-finned pilot whales (*Globicephala melas edwardii*) stranded on Farewell Spit, New Zealand in 2014. Values for each fatty acid are presented as a proportion (%) of total fatty acids reported. SD = standard deviation, ∑SFAs refers to total proportion of saturated fatty acids, ∑MUFAs to total proportion of monounsaturated fatty acids, ∑PUFAs to total proportion polyunsaturated fatty acids, EPA = eicosapentaenoic acid C20:5n3, DPA = docosapentaenoic acid C22:5n3 and DHA = docosahexaenoic acid C22:6n3. Dietary fatty acids (Iverson, 2004) are given in bold.

	Female				Male			
Fatty Acid	Immature	SD	Mature	SD	Immature	SD	Mature	SD
C14	7.89	0.83	11.18	1.71	11.64	1.93	13.57	2.90
C15	0.80	0.31	1.03	0.30	1.20	0.17	0.84	0.14
C16	16.11	3.16	20.75	5.15	19.20	1.58	25.04	2.17
C17	0.38	0.15	0.55	0.15	0.56	0.27	0.30	0.28
C18	2.66	0.62	3.98	1.10	3.68	0.23	3.25	1.14
C16:1*n*7	2.90	0.19	3.47	0.80	8.84	8.08	2.63	0.20
C16:1*n*9	18.41	3.35	13.16	3.28	10.04	7.73	9.50	0.88
C17:1	1.09	0.57	0.71	0.44	0.29	0.06	0.27	0.23
C18:1*n*9	27.25	3.08	25.07	1.90	24.16	1.00	26.25	0.55
C18:1*n*7	3.61	0.47	3.87	0.43	4.18	0.33	4.38	0.04
C18:1*n*11	0.14	0.20	0.25	0.16	0.70	0.55	0.07	0.10
C20:1*n*11	**0.43**	**0.47**	**1.60**	**1.00**	**2.36**	**1.57**	**0.62**	**0.33**
C20:1*n*9	**4.34**	**1.92**	**5.17**	**2.32**	**4.28**	**2.84**	**6.35**	**1.53**
C22:1*n*11	**0.48**	**0.35**	**1.40**	**0.22**	**1.16**	**0.90**	**0.69**	**0.53**
C22:1*n*13	**0.37**	**0.31**	**0.61**	**0.15**	**0.81**	**0.16**	**0.85**	**0.32**
C18:2*n*6	**1.21**	**0.06**	**1.14**	**0.35**	**0.97**	**0.36**	**0.46**	**0.37**
C20:4*n*6	**0.75**	**0.24**	**0.42**	**0.37**	**0.47**	**0.10**	**0.00**	**0.00**
EPA	**1.14**	**0.45**	**0.70**	**0.39**	**1.19**	**0.33**	**0.63**	**0.31**
DHA	**3.91**	**1.42**	**3.74**	**0.88**	**2.99**	**1.95**	**3.46**	**0.38**
DPA	5.58	6.15	0.94	0.32	1.20	0.19	0.53	0.36
SFAs	27.84	2.79	37.49	7.54	36.28	3.00	43.00	0.57
MUFAs	59.03	9.34	55.32	6.55	56.81	1.33	51.60	0.74
PUFAs	12.59	7.32	6.94	1.35	6.81	1.98	5.08	1.12

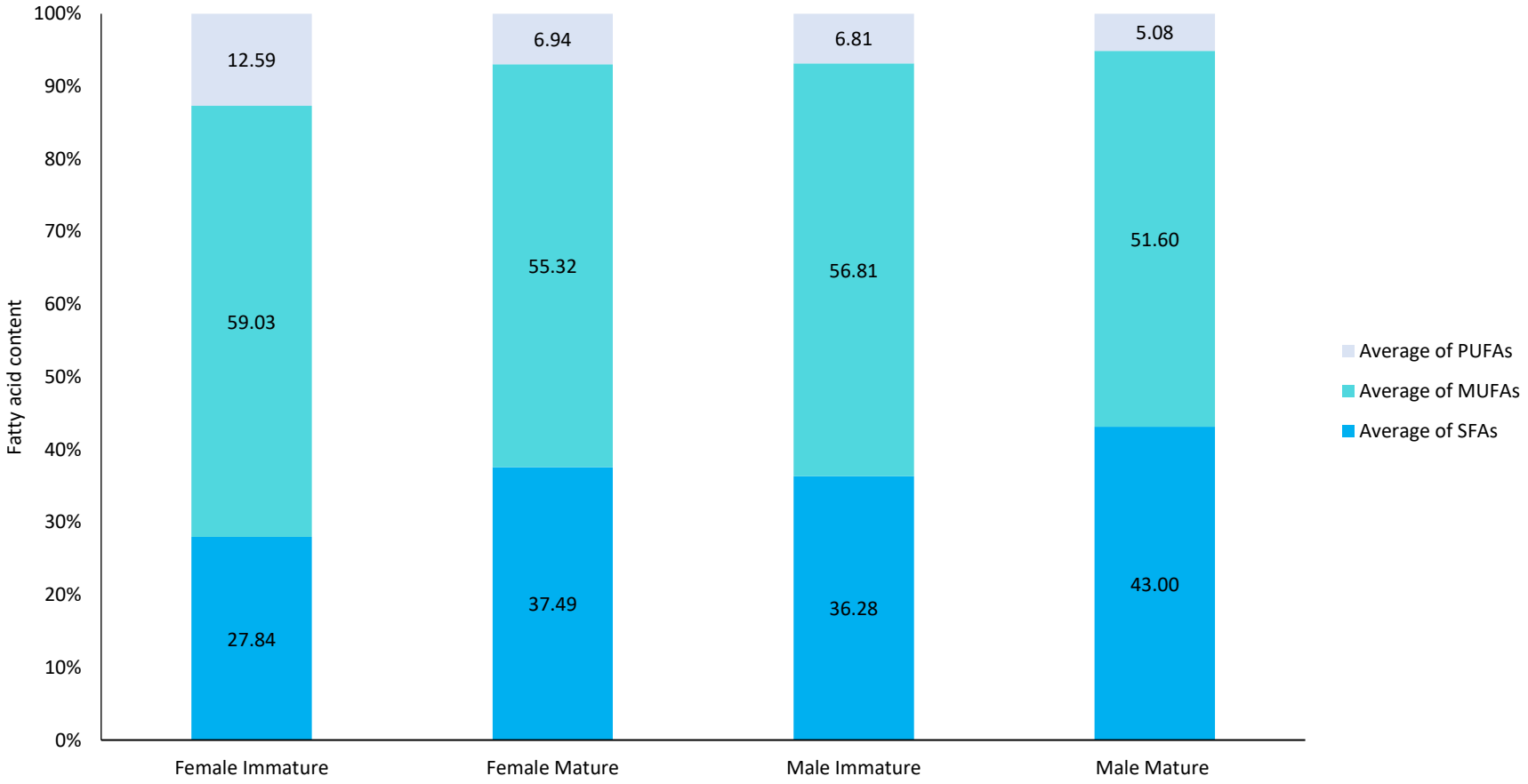

Figure 5.3. Mean proportions (%) of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) from the inner blubber layer of long-finned pilot whale (*Globicephala melas edwardii*) stranded on Farewell Spit, New Zealand in 2014. Fatty acid content is presented using the following sex/maturity groups: Female Immature, Female Mature, Male Immature, Male Mature (see Chapter 2 for sex/maturity group definitions).

Neither maturity status, nor sex, had a significant impact on fatty acid profiles. Fatty acids contributing most to dissimilarity between males and females were: C16:1*n*9, C16:0, C14:0, C20:1*n*9, DPA, C18:1*n*9, C16:1*n*7, DHA, C18:0, C20:1*n*11, whilst fatty acids that contributed most to dissimilarity between mature and immature individuals were: C16:0, C16:1*n*9, C14:0, C20:1*n*9, C18:1*n*9, C16:1*n*7, DPA, DHA, C18:0, C20:1*n*11. A high degree of individual variability in fatty acid profiles was evident, with males exhibiting a larger range of dissimilarity compared to females (Figure 5.4).

5.5.3. Predictive power of morphometric body condition measurements on fatty acids

The intercept was retained as the only covariate in the optimum GLM for lipid content and two of the dietary fatty acids (C20:1*n*11 and DHA), respectively (Table 5.4). Weight was under 0.50 for both models, suggesting a relatively low level of data variance explained. The girth was retained as the only covariable in the optimum GLMs for C20:1*n*9, SFAs and PUFAs respectively, where girth increased with increasing C20:1*n*9 and SFAs but decreased with increasing PUFAs. The MUFA variation was best explained by ventral blubber thickness (Table 5.4). The model with the highest weight (0.51), and therefore best explained data variation was SFA ~ girth.

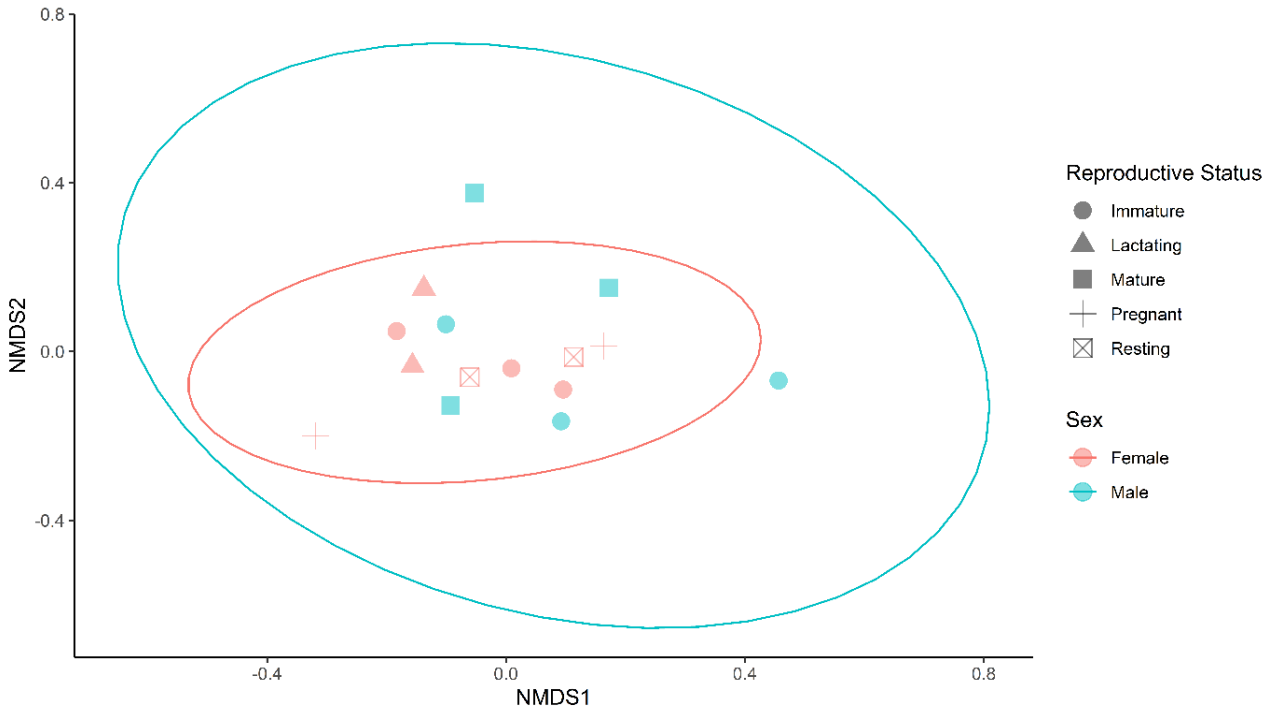

Figure 5.4. Non-parametric multidimensional scaling (nMDS) plot of dissimilarity in fatty acid profiles of long-finned pilot whales (*Globicephala melas edwardii*). Shapes relate to reproductive status and colours relate to sex. Ellipses are calculated by sex at the 95% level.

Table 5.4. Summary table of generalised linear model and small-sample size corrected Akaike Information Criterion (AICc) model selection results investigating predictive power of various body condition measurements on fatty acid (FA) classes and dietary fatty acids C20:1*n*11, C20:1*n*9 and docosahexaenoic acid (DHA) C22:6*n*3 of long-finned pilot whales (*Globicephala melas edwardii*). logLiK = log likelihood, SFAs = saturated fatty acids, MUFAs = monounsaturated fatty acids, PUFAs = polyunsaturated fatty acids. The top models within three AICc points are presented, with the optimal model given in bold.

	Model	AICc	Weight	logLik
SFAs	**~ girth**	**100.9**	**0.51**	**-46.37**
	~ girth + ventral blubber thickness	103.9	0.11	-45.96
MUFAs	**~ ventral blubber thickness**	**102.6**	**0.17**	**-47.22**
	~ intercept only	103.2	0.13	-49.12
	~ age	103.6	0.11	-47.70
PUFAs	**~ girth**	**91.4**	**0.26**	**-41.62**
	~ intercept only	91.7	0.22	-43.37
	~ age	93.7	0.08	-42.75
C20:1*n*9	**~ girth**	**72.1**	**0.29**	**-31.96**
	~ intercept only	73.2	0.17	-34.11
	~ ventral blubber thickness	74.2	0.10	-33.00
C20:1*n*11	**~ intercept only**	**53.2**	**0.35**	**-24.12**
	~ BCI	54.8	0.16	-23.19
	~ girth	55.3	0.12	-23.56
DHA	**~ intercept only**	**54.7**	**0.37**	**-24.87**
	~ BCI	55.9	0.21	-23.85
	~ dorsal blubber thickness	57.3	0.11	-24.54

5.6. Discussion

This study offers the first insights into blubber measurements and fatty acid composition of LFPWs in New Zealand waters. Whilst stomach content analysis (Beatson et al. 2007b; Beatson and O'Shea 2009; Chapter 2) and stable isotope analysis (Hinton et al. 2022; Peters et al. 2022; Chapter 3) of the same population offer short-term dietary insights, this qualitative fatty acid analysis investigates longer-term diet and how this may relate to individual body condition.

5.6.1. Variation in body condition measurements

Overall, blubber thickness measurements were generally consistent with other odontocetes, with lateral and dorsal blubber measurements being the thinnest and the thickest for each individual, respectively (e.g., Konishi 2006; Marón et al. 2021). Significant pairwise correlations were recorded between two sets of body condition measurements only: ventral and lateral blubber thickness, and girth and ventral blubber thickness, respectively (Table 5.3). Mysticetes considered visually "fat" had large lipid deposits in the ventral region (Ackman et al. 1975), while thicker ventral blubber in mature sei *Balaenoptera borealis* and fin whales *B. physalus* was attributed to enhanced energy storage in the ventrum (Lockyer et al. 1985). An increase in ventral blubber thickness may, therefore, have a particular impact on girth. As dorsal and ventral blubber thicknesses were also reported to increase in minke whales *B. acutorostrata* during the feeding season (Niæss et al. 1998), this suggests a link between increased food intake and thicker blubber, which would logically increase girth. Therefore, girth may be a useful non-invasive measurement of nutritional state in LFPWs, though investigations using a larger sample size are recommended to validate this suggestion.

Interestingly, girth was also the only measurement correlated positively with age, which could be a function of increasing TBL (see Appendix 5.2). Overall, no differences were found between body condition measurements and sex or maturity respectively, even when the effects of TBL were

removed. Notably, this is unlike the larger blubber thickness found in in younger bottlenose dolphins *Tursiops truncatus* thought to be due to increased buoyancy and thermodynamic requirements of immature marine mammals (Adamczak et al. 2021). Furthermore, adipocyte number and density were found to be higher in the middle blubber layer of immature than mature Indo-Pacific bottlenose dolphin *Tursiops aduncus* (Roussouw et al. 2022*)* and all layers of bowhead whales *Balaena mysticetus* blubber *(*Ball et al. 2015). However, increased energy demands of growth (Read et al. 1993) could cause decreased body condition (Russell et al. 2022) or quicker mobilisation of fatty acids in immature LFPWs, leading to a reduced blubber thickness than may be expected. Alternatively, lack of foraging experience in immature individuals may lead to fewer successful feeding events (Aoki et al. 2021), which may be further compounded during summer, when recovery from nutritional stress is thought to be more difficult (Jeanniard du Dot et al. 2008). As noted by Rosen et al. (2007), failure to ingest prey may cause catabolism of blubber in marine mammals, which is likely enhanced during stranding events, especially in smaller individuals with fewer energy reserves to draw upon. Whilst it is difficult to conclusively prove, starvation effects from protracted stranding events, where whales remain in shallow waters for several days prior to stranding, could explain why a larger blubber thickness was not reported here in younger LFPWs.

The range of lipid content reported for LFPWs in New Zealand waters is consistent with ranges recorded in other odontocetes (Aguilar and Borrell 1990). The mean lipid content (62%) of LFPW blubber from this study was typical of cold water cetacea (mean = 60%; Koopman 2007) and was comparable to *G. m. edwardii* from Australian waters (range = 34.6 – 87.9%; Walters 2005). Though a higher mean lipid content was recorded in *G. m. melas* from the Northeast Atlantic and Faroe Islands (Lockyer 1993; Borrell et al. 1995; Koopman 2007), lower lipid content levels have also been reported in blubber of *G. m. edwardii* from the South Atlantic, and *G. m. melas* from the Northwest Atlantic

and Mediterranean (Weisbrod et al. 2000; Pinzone et al. 2015; Garcia-Cegarra et al. 2021). Lipid levels of LFPWs appear to show spatial variability which could represent environmental factors including latitude. Furthermore, the inner region of blubber may contain a lower lipid content than other blubber layers due to higher metabolic activity (e.g., Bagge et al. 2012). Decreased lipid content could therefore indicate a degree of emaciation (Kajiwara et al. 2001), as lipid is replaced with water in the blubber of emaciated cetacea to retain structural integrity (Dunkin et al. 2005; Agusti et al. 2022). However, no pathological examination of carcasses was undertaken to confirm this in the present study.

5.6.2. Variation of fatty acid profiles

All fatty acid profiles were characterised by high total MUFA proportions, especially C16:0, C18:0, C18:1n7, C18:1n9 and C16:1n7, as is typical in marine mammals (Käkelä and Hyvärinen 1996; Smith and Worthy 2006; Waugh et al. 2014; Guerrero et al. 2020), including comparable studies involving LFPWs (Walters 2005; Monteiro et al. 2015b). Overall, fatty acid profiles did not differ significantly by maturity status or sex, although males did show a larger dissimilarity range than females (Figure 5.5). As fatty acids from the inner blubber layer most closely reflect the composition of prey, this could indicate a wider range of diet consumed by males. However, dietary homogeneity of LFPWs within New Zealand waters (Chapter 2, Beatson and O'Shea 2009) are likely to result in minimal dietary fatty acid differences between sexes.

Elevated concentrations of SFAs were recorded across all examined animals, accounting for 36% of total fatty acids (Table 5.2, Figure 5.4). Notably, SFA proportions were also higher than has been previously reported for other odontocetes (e.g., Guitart et al. 1999; Ko et al. 2016; Tang et al. 2021). This may be partially explained by stratification of both lipid and fatty acids within marine mammal blubber (Strandberg et al. 2008), resulting in higher SFA concentration in the inner blubber layer.

Such stratification has been recorded in multiple species, including elephant seals *Mirounga leonina* (Guerrero and Rogers 2017) and common dolphins *Delphinus* spp. (Smith and Worthy 2006). However, stratification of lipids has not been previously recorded in the blubber of LFPWs (Lockyer 1993; Walters 2005; Koopman 2007). The values of two specific SFAs (C14:0 and C16:0) were found to be more elevated in *G. m. edwardii* from this study compared to those sampled from Australia (Walters 2005) or *G. m. melas* in the Northeast Atlantic (Monteiro et al. 2015b). Both C14:0 and C16:0 have been identified as "phase change" fatty acids which have thermodynamic functions (Dunkin et al. 2005). Indeed, environmental differences have explained fatty acid de-saturation across multiple marine mammal species (Guerrero and Rogers 2019), and fatty acid de-saturation has also been recorded in multiple marine organisms towards the poles (Guerrero & Rogers 2019; Parzanini et al. 2020). This suggests that elevated SFA values from LFPWs in New Zealand waters could be related to lower latitude. However, Iverson et al. (2004) noted that both C14:0 and C16:0 accumulate in marine mammals through a mixture of biosynthesis and diet, so could therefore be reflective of local food webs. Indeed C14:0 and C16:0 were the most abundant SFAs recorded in zooplankton from New Zealand waters (Meyers et al. 2022). Hence, raised levels of C14:0 and C16:0, and consequently elevated SFAs, in LFPW blubber are likely due to a combination of local dietary and environmental inputs.

The mean proportion of PUFAs reported in LFPWs was lower than in previous odontocete studies (Grahl-Nielsen et al. 2010; Koopman 2007; Smith & Worthy 2006; Strandberg et al. 2008). Higher consumers are unable to biosynthesize PUFAs (Zhang et al. 2020) and obtain all PUFAs from prey (Castro et al. 2016), consumer PUFA levels therefore reflect those found in their prey. Conversely, prior metabolisation of PUFAs results in lower proportions recovered (Grahl-Nielsen et al. 2010) possibly indicating disease or starvation, which could be a function of the stranding events that

samples were obtained from (Hart et al. 2013). Additionally, low PUFA content in organisms has been linked to feeding in low light conditions (Burgess et al. 2018), suggesting New Zealand LFPWs feed either at depth, at night, or both. Indeed, nocturnal feeding has been noted in *G. m. melas* from the Ligurian Sea (Baird et al. 2002). Knowledge of the fatty acid concentrations of prey would, therefore, be beneficial to help confirm drivers behind low PUFA proportion.

5.6.3. Predictive power of morphometric body condition measurements on fatty acid proportions

None of the body condition measurements succeeded in consistently predicting dietary fatty acid variation via GLM models. In fact, the intercept was retained as the only covariate in optimal GLMs for two of the three dietary fatty acids (Table 5.4). One explanation for this is the influence of TBL, though this was removed from GLMs due to high correlation (see Appendix 5.3). Alternatively, the relationships between morphometric measurements and dietary fatty acid proportions in the inner blubber layer may not be linear as was tested here. This could be tested with larger sample sizes in the future using other statistical measures such as generalised additive models. Varied functions of each fatty acid within the predator may have a large influence on body condition measurements. Indeed, low C17:0 levels have potentially been linked to metabolic syndrome in bottlenose dolphins *T. truncatus* (Venn-Watson et al. 2015); although this is not a dietary fatty acid, it does show that individual differences in fatty acid function occur.

Girth was retained as a covariable in the optimal model for variation in dietary fatty acid C20:1*n*9, PUFA and SFA proportions, respectively (Table 5.4). C20:1*n*9 is a long-chain PUFA typical to marine pathways (Parzanini et al. 2020). Long-chain PUFAs are preferentially deposited in the inner blubber layer due to relative low melting point and therefore ease of mobilisation (Lockyer et al. 1984; Grahl-Nielsen et al. 2005). The increased PUFAs in the inner blubber layer of LFPWs with decreased girth shown in this study may therefore be due to increased need for PUFA mobilisation, possibly during

times of stress. As girth also increased with increased SFA levels, girth may, therefore, be a good predictor of variation in fatty acid deposition in LFPWs.

There is debate as to the ability of either fatty acids or body condition to reflect dietary intake in marine mammals. For example, in harp seal *Pagophilus groenlandicus* a weak correlation between prey and predator fatty acids is noted, concluding that fatty acids may be more reflective of metabolism (Grahl-Nielsen et al. 2011). However, a collection of five fatty acids was able to separate the odontocetes killer whales *Orcinus orca* by ecotype (Herman et al. 2005). However, body condition measurements have been linked to prey more commonly for mysticetes; body condition correlated with prey abundance per capita in fin whales *B. physalus* (Williams et al. 2013), nutrition in right whales *Eubalaena glacialis* and *Eubalaena australis* (Miller et al. 2011), and foraging success in North Pacific gray whales *Eschrichtius robustus* (Soledade Lemos et al. 2020). In contrast, polar bear *Ursus maritimus*, body condition was not correlated with any particular prey consumption (Florko et al. 2021). These disparities between taxa would suggest that body condition measurements and prey consumption may be more closely linked in fully aquatic marine mammals, possibly due to differences in blubber function, such as temperature regulation and buoyancy needs. Indeed, blubber is known to be a multi-faceted organ capable of several functions including structural integrity, thermoregulation, buoyancy, and energy storage (Biuw et al. 2003; Iverson 2009; Ball et al. 2017; Davis 2019). Therefore, investigations into cetacean body condition are now advised to incorporate multiple morphometric and blubber measures for validation (Castrillon and Bengtson Nash 2020), and studies into the relationships between morphological parameters, feeding behaviours and health status have been proposed as a priority for future research (Sharp et al. 2014).

Even if not related to diet, body condition measurements may provide useful information to interpret overall fatty acid composition, and therefore, still have implications for understanding

individual condition. Reliance on BCI over blubber thickness alone has been suggested as a better proxy for individual condition in killer whales (Raverty et al. 2020). However, there was not one morphological measurement, or set of measurements, that consistently predicted the fatty acid variation recorded in New Zealand LFPWs, although it is acknowledged that the small sample size may in part, explain this finding.

Overall, both body condition measurements and fatty acid profiles of LFPWs in this study were comparable to those of other odontocetes, especially LFPW populations from Australian waters (Walters 2005). Significant differences in girth with age suggested that older LFPWs in New Zealand have larger girth than younger individuals, though this may be a function of increasing body size. A larger sample size to investigate the effects of reproductive status and season on body condition measurements is recommended to help elucidate drivers behind variation.

Fatty acid profiles presented in this chapter were characterised by high levels of MUFAs, particularly C16:1*n*9 and C18:1*n*9, as is typical in cetacea. A high SFA content was also noted in comparison to other LFPW populations, most likely due to thermoregulatory response, or relative to the fatty acid profiles of local primary producers. Reported fatty acid variation was not able to be explained by one body condition measurement alone, although this study has shown that girth holds the most promise in its ability to predict relative fatty acid proportions of *G. m. edwardii*. Further work is recommended to elucidate how body condition measurements relate to fatty acid composition in this species, which would be helpful when attempting to quantify individual condition and nutritional status at stranding events. Specifically, a larger sample size of both LFPW body condition indices and fatty acids should be explored throughout all blubber layers.

Chapter 6 – General Discussion

Long-finned pilot whales *Globicephala melas edwardii* refloated after stranding at Onetahua Farewell Spit, New Zealand in 2021. Photo credit: Rebecca Boys.

6.1. General discussion

This thesis has presented new insights into long-finned pilot whale (LFPW; *Globicephala melas edwardii*) foraging ecology in Aotearoa New Zealand waters. Differences in diet composition were observed on both ontogenetic and spatiotemporal scales, with isotopic investigations supporting the tendency for pelagic feeding observed from stomach content analysis. Both stomach contents and isotopic investigations noted the ability to forage benthically/coastally, especially in mature males and in the most recent year investigated, 2017. Although six new taxa were discovered in the diet of LFPWs in this study, biochemical dietary tracers examined in five of the top prey species to LFPW diet revealed that at least one key prey species was missing from analysis. Regardless, arrow squid (*Nototodarus* spp.) contributed most to LFPW diet in all methods explored. In addition, an initial exploration into potential insights gained from morphometric body condition measurements signalled that relationships between girth, ventral blubber thickness and fatty acids would be worth exploring further. Overall, this thesis has provided novel contributions to, and improved understanding of, the foraging ecology of LFPWs in New Zealand waters. This chapter outlines the key research contributions to science, and management implications resulting from themes explored within this thesis. Furthermore, recommendations for future research are discussed.

6.2. Summary of main results and scientific contributions

This thesis addressed gaps in knowledge of the foraging ecology of LFPWs in New Zealand waters by investigating samples collected from carcasses involved in mass strandings along the New Zealand coast. To do this, research focussed on assessing diet composition, variation, and its effect on individual body condition in New Zealand waters, using multiple complementary methodologies to address the four thesis objectives outlined in Chapter 1:

Objective 1: Investigate intraspecific variation in the prey composition of LFPWs stranded on the New Zealand coast.

Objective 2: Assess ontogenetic, spatial, and temporal isotopic niche dynamics within the LFPW population.

Objective 3: Evaluate the use of biochemical tracers in key prey species to quantify LFPW dietary variation.

Objective 4: Explore possible linkages between chemical dietary tracers and individual LFPW body condition.

Variation in the prey composition of LFPWs stranded on the New Zealand coast was investigated in Chapter 2. Whilst the contents of LFPW stomachs were dominated by arrow squid *Nototodarus* spp., dietary composition varied by sex and body size (Chapter 2). This differed from previous international studies of LFPWs in the literature (e.g., Gannon et al. 1997b; Santos et al. 2014), where no differences in diet have been determined between sexes. Furthermore, six new taxa were discovered in the diet of LFPWs in this region. New taxa were primarily fish species, whereas no fish species had previously been identified within the diet of LFPWs in this New Zealand region (Beatson et al. 2007a; Beatson et al. 2007b; Beatson and O'Shea 2009). Fish have been described in the diet of Northern Hemisphere *G. m. melas* (Overholtz and Waring 1991; Spitz et al. 2011; Nøttestad et al. 2015), but the incidences of fish in the diet of Southern Hemisphere *G. m. edwardii* are less common (e.g., Chalcobsky et al. 2021), possibly indicating a level of geographic variation in diet reflecting abundance and availability of local prey species.

The first investigation of LFPW isotopic niche in New Zealand waters was conducted in Chapter 3. Spatiotemporal factors had a larger effect than ontogenetic factors on intraspecific isotopic variation,

consistent with overseas studies (de Stephanis et al. 2008; Monteiro et al. 2015a). Sulphur was used for the first time in isotopic studies of Southern Hemisphere LFPWs, elucidating drivers of isotopic variance both in temporal and ontogenetic variation (Chapter 3).

Following this, Chapter 4 evaluated the use of biochemical tracers in key prey species to quantify LFPW dietary variation. Complimentary methodologies of stable isotope and fatty acid analyses were applied to quantify the dietary importance of five key prey species (identified from Chapter 2) to LFPWs stranded at Farewell Spit. Qualitative analysis of both stable isotope and fatty acid data suggested that arrow squid were an important component of diet, consistent with stomach contents findings from Farewell Spit (Chapter 2, Beatson et al. 2009). Overall, however, analysis revealed that key prey species tested may not have been isotopically matched to LFPWs, inappropriate trophic discrimination factors used or missing key species from the study, supported by the much wider range of species reported in stomachs of LFPWs overseas (Gannon et al. 1997b; Mansilla et al. 2012; Beasley et al. 2019). This was likely because only the top five dietary species were selected for their stable isotope and fatty acid profile analyses and sample sizes were small. This could be improved by examining a larger sample and wider range of potential prey species than reported herein.

The potential linkages between the proportion of fatty acids from the inner dorsal blubber and body condition measurements of LFPWs were explored in Chapter 5. Measurements of girth increased significantly with total body length and age, consistent with Northern Hemisphere LFPWs off the Faroe Islands (Lockyer 1993). Furthermore, axillary girth explained some variation in the proportion of 1) saturated, 2) polyunsaturated fatty acids and 3) dietary fatty acid C20:1*n*9 in the inner layer of dorsal blubber. Whilst no single body condition measurement was consistently linked to all dietary fatty acids studied, a larger sample size than was used in this exploratory chapter would be required to make any firm conclusions.

Finally, this thesis utilised a long-term, archived collection of samples, from LFPWs that stranded on New Zealand shores between 2009 and 2017. Long-term datasets are integral to the understanding changes in the marine environment (Wolfe et al. 1987), and their benefits should not be underestimated.

6.3. Key research findings

6.3.1. Reliance on arrow squid

Arrow squid were consistently considered an important prey species to the diet of LFPWs stranded in New Zealand between 2009 and 2017, across all chapters and methodologies explored: stomach content, stable isotope, and fatty acid analyses. This concurs with stomach content analysis of a smaller subset (n = 37) of LFPWs examined from New Zealand strandings between 2005 and 2008 (Beatson et al. 2007; Beatson and O'Shea 2009). These findings are most consistent with the trace prey (defined as hard part remains only) analysed by Gannon et al (1997b) who reported a single squid species accounted for 70% by number, 83.9% by mass and 86% by index of relative importance (IRI) of trace prey with 100% frequency of occurrence in LFPWs. Similarly, individual LFPW stomachs have been reported to contain remains of only one squid species in stranding studies (Overholtz and Waring 1991). Comparisons of prey from 13 cetacean species classified LFPWs as "specialist" feeders in (MacLeod et al. 2006) and their diet has also been described as "restricted" in comparison to other marine mammals in the Norwegian Sea (Skern-Mauritzen et al. 2022).

Arrow squid are part of the Ommastrephidae family (Dunning and Förch 1998; Wakabayashi et al. 2012). Whilst most studies have not indicated one species to be so overwhelmingly important to LFPW diet, a reliance on Ommastrephid squids has been widely reported elsewhere, especially at higher latitudes (Santos et al. 2014). Within other odontocetes, dietary specialists have been identified in particular geographic areas. For example, gadids were reported to account for 98% of the weight of white-beaked dolphins *Lagenorhynchus albirostris* diet in the North Sea only (Jansen et

al. 2010). Similarly, killer whales *Orcinus orca* in the northwest Pacific are the only killer whale population known to rely heavily on a diet of various salmonids (Ford and Ellis 2006). Furthermore, an environmental difference in dietary plasticity is noted, with subantarctic ecotypes the most reliant on a singular prey species (Foster 2019). Therefore, LFPWs could be targeting fewer species in New Zealand waters because of local environmental conditions.

The reliance on arrow squid noted in this thesis may alternatively be due to assessments being carried out primarily on samples collected from LFPWs stranded within the austral summer, which could be reflecting seasonal dietary preference. As noted in Chapter 2, this is an important consideration when interpreting these data as other marine mammals in local waters have been shown to rely heavily on arrow squid in summer only (Fea et al. 1999). Optimal foraging theory would predict that LFPWs, and other local marine mammal predators, may simply be feeding on abundant, energy-rich prey, implying neither specialisation nor opportunism. Indeed, all three methodologies explored (Chapter 2, 4) indicated that arrow squid may be overestimated in diet. From stomach contents in Chapter 2, the prey curve did not reach an asymptote indicating that not all prey groups were detected. Furthermore, fish number often could not be accurately estimated due to lack of identifiable remains, leading to a suspected underestimation of fish importance to diet. Similarly, both stable isotope and fatty acid analyses of prey in Chapter 4 could be interpreted to suggest that some key prey species were omitted, consistent with the suggestion that fatty acid and stable isotope nitrogen data suggest a lesser importance of cephalopods to diet than stomach contents (Rodhouse 2013).

Whilst there is a reported reliance of LFPWs on cephalopods in other areas of the world (Gannon et al. 1997b; Aguiar dos Santos and Haimovici 2001; Beasley et al. 2019), the potential underestimation of fish to the diet of LFPWs in New Zealand waters cannot be excluded. As there was high overlap

in biochemical data of LFPW prey species (see Chapter 4), LFPW prey species are likely to occupy similar habitats within New Zealand waters. Therefore, fisheries data may provide insight into possible prey species missing from diet. Whilst 347 species were bycaught in the arrow squid trawl between 1990 and 2017 (Finucci et al. 2019), only two of the top 30 most frequently bycaught species were detected in stomachs of LFPWs examined in Chapter 2; hoki *Macruronus novaezelandiae* (number 8) and carpet shark *Cephaloscyllium* sp (number 30). Furthermore, of the commercial fisheries recorded to have incidentally captured LFPWs, hoki is the only prey species that has been reported in the stomachs of LFPWs to date (Chapter 2). The fact that LFPWs were captured by vessels targeting other fish (jack mackerel *Trachurus declivis* and *T. novaezelandia*, ling *Genypterus blacodes*, bluefin *Thunnus maccoyi* and bigeye tuna *T. obesus*, school shark *Galeorhinus galeus*, hake *Merluccius australis* and tarakihi *Nemadactylus macropterus*; Fisheries New Zealand Protected Species Bycatch Open Database) raises the potential that some or all of these fish could be the prey species missing from LFPW diet (Chapter 2, 4). Investigations of bycaught LFPW stomach contents would be helpful to help clarify this uncertainty and should be considered a priority for LFPW dietary research going forward.

Still, the vast number of arrow squid identified in LFPW stomachs from all stranding events indicate that arrow squid is a key prey species of LFPWs, at least over the summer months. Furthermore, the similarities of both chemical tracers (stable isotopes and fatty acids, see Chapter 4) from LFPWs to those of arrow squid indicated that LFPWs may be feeding on arrow squid for at least several weeks prior to stranding.

6.3.2. Dietary variation

The samples examined in this thesis were taken exclusively from stranded individuals. The use of samples from strandings could confound data, as stranded animals may display irregular feeding

patterns due to illness or injury (Praca et al. 2011). However, this is considered more of an issue in events involving a single stranded animal, rather than the mass-stranding events (MSEs) that involve a large pod, which for the most part represent healthy individuals (Betty et al. 2020). Furthermore, previous reports on stranded cetacea have indicated that one sex may strand more frequently (e.g., Silva and Sequeira 2003) which can introduce bias in results and not consider certain ontogenetic traits. The effects of this were somewhat minimised through the study design; whilst all LFPWs in the dataset were analysed for stomach contents in Chapter 2, samples used in Chapters 3, 4 and 5 were selected from larger MSEs to allow for intraspecific analysis and to cover a range of reproductive groups, maturity status, ages, body lengths, and sex.

Although arrow squid was identified as the key prey species overall, this thesis revealed for the first time, that variation in other species ingested was apparent on both ontogenetic and spatiotemporal scales. Notably, diet varied with stranding location in both stable isotope and stomach content analyses (Chapter 2, 3), suggesting a level of spatial variability in diet. Indeed, there were a higher number of fresh tissue remains in the stomachs of LFPWs from Stewart Island (Chapter 2) indicating very recent feeding in comparison to other areas. Furthermore, LFPWs stranded at Stewart Island had a higher diversity of prey in stomachs (Chapter 2) in comparison to other locations, which may indicate a degree of spatial variance in feeding. This has also been recorded internationally, where key prey species in LFPW populations varied spatially (Overholtz and Waring 1991; Gales et al. 1992b; Clarke 1994; Gannon et al. 1997b; Aguiar dos Santos and Haimovici 2001; De Pierrepont et al. 2005; Santos et al. 2014).

Sex was also a key driver in variation of stomach contents (Chapter 2) and sulphur isotopes (Chapter 3), though not carbon and nitrogen isotopes (Chapter 3). Both sulphur isotopes and stomach contents indicated that mature males displayed a more benthic/coastal foraging pattern compared to female

counterparts, although the explanatory power of this finding was low (Chapter 3). Similarly in Chilean waters, diet between sexes was notably different, but not statistically, as males consumed larger *Ilex argentinus* squid than females (Chalcobsky et al. 2021). Although males also demonstrated a wider range of dissimilarity in their fatty acid profiles than females within this thesis, this analysis included all fatty acids, not just those linked to diet (Chapter 5). In fact, two of the top three fatty acids contributing to dissimilarity between males and female were C16:1*n*9 and C14, both of which were noted as considerable higher in LFPWs than any of their key prey species tested in Chapter 4. One explanation is this represents further evidence of a key prey species missing from analysis (see Chapter 4). Conversely, since C14 is obtained from biosynthesis as well as diet (Iverson et al. 2004), variation in C14 may not accurately reflect dietary variation intake between males and females at all. Instead, differences in fatty acids may reflect metabolism and ontogeny, as has been suggested in odontocetes generally (Koopman 2007) and in individual species such as sperm whales *Physeter macrocephalus* (Jackson et al. 2022) and bottlenose dolphins (Samuel and Worthy 2004).

Indeed, it was the larger, mature males that were found to have the most unique diet and isotopic niche in this study (Chapter 2, 3). This trend may also be true for fatty acids, but due to the small sample size (n = 15, Chapter 4), a comparison between the dietary fatty acids of mature males and other reproductive groups could not be confirmed. Nonetheless, these first insights still suggest that ontogeny or even body size, rather than sex alone, may be the driver behind variation recorded between both diet and biochemical tracers in LFPWs in New Zealand.

6.3.3. Insights into long-finned pilot whale foraging

Whilst the foraging locations around New Zealand are currently unknown, knowledge could be improved by utilising telemetry, which has helped reveal foraging areas and depths for a range of marine mammal species (e.g., Hooker et al. 2002; Abecassis et al. 2015; Arranz et al. 2019; Benoit-

Bird et al. 2019; Visser et al. 2021). In the meantime, the distribution of key prey species and carbon stable isotope analysis can provide insights into the likely foraging locations and habitats of predators (e.g., Burton and Koch 1999; Aurioles et al. 2006; Rossman et al. 2010; Szpak and Buckley 2020).

Distribution of arrow squid, the primary LFPW prey species identified in this thesis, is thought to be ubiquitous across New Zealand waters. Arrow squid have been reported to occur up to 1000 m depth but are more commonly reported at depths less than 500 m (Anderson et al., 1998). Sampling from the southern waters of New Zealand revealed negligible numbers of arrow squid deeper than 500 m, with the highest density of arrow squid shallower than 300 m depth (Jackson et al. 2000). Indeed, commercial catch of this species in New Zealand is focussed at around 150–400 m depths (Anderson and Edwards 2018). Studies in the Chatham Rise, New Zealand determined arrow squid to be shallow shelf dwellers during both larval and adult life stages (Uozumi and Forch 1995). Other LFPW prey species identified such as *Moroteuthopis ingens*, *Lycoteuthis lorigera* and hoki (Chapter 2) are all described as deep-water species inhabiting the continental shelf and slope seas (Jackson et al. 2000; McClatchie et al. 2005; Hoving et al. 2007; Fontaine et al. 2015). Furthermore, carbon and sulphur isotope values of arrow squid, hoki and LFPWs (Chapter 3, 4) in New Zealand indicated that marine rather than coastal food source pathways were commonly utilised.

It is plausible, therefore, that LFPWs in New Zealand waters are currently feeding off the continental slope. Specifically, the abundance of squid and hoki reported around the Stewart Snares shelf (Roberts et al. 2018), and Chatham Rise (Dunn 2009; O'Driscoll et al. 2011) would appear good potential feeding locations. Telemetry studies suggest that LFPWs can dive as deep as 2000 m in the Ligurian Sea but spend the majority of their time in shallower waters (Robin et al. 2002; Sivle et al. 2012). Given the depth of their known prey in New Zealand waters and the isotopic values recorded

from LFPW skin between 2009 and 2017, LFPWs are likely feeding down to 500 m depth in this region.

All dietary investigations in this thesis indicated a level of plasticity in foraging (Chapters 2, 3, 4). The consumption of more coastal prey species such as conger eel *Congridae* sp., octopus *P. cordiformis* and carpet shark was more commonly associated with mature male LFPWs (Chapter 2). However, sulphur stable isotope values suggested that benthic/coastal feeding was also more common in the year 2017 (Chapter 3), even when the number of mature males sampled was similar, indicating a possible temporal shift in foraging area to more coastal regions for either LFPWs or their prey. Plasticity in coastal feeding has also been attributed to LFPWs in Chilean waters (Becker et al. 2021), and around Canada, where nearshore foraging hotspots have been identified (McComb-Turbitt et al. 2021). The PUFA levels in coastal species conger eel *Congridae* sp. (Chapter 4) corroborated with reports *Congridae* sp. are nocturnal feeders (Levy et al. 1988; Choi et al. 2008; Shoji et al. 2017). The presence of conger eels and nocturnal octopus (Bassett et al. 2008; Hesse et al. 2016) in small numbers in LFPW diet (Chapter 2, 4) therefore, indicates an element of nocturnal feeding within coastal New Zealand waters. Indeed, long, deep LFPW dives recorded at night were assumed to be foraging trips (Shane 1995; Robin et al. 2002; Nawojchik et al. 2003; Mate et al. 2005), showing a likely diurnal foraging strategy for LFPWs.

6.3.4. Diet and body condition

No single body condition measurement was found to consistently explain variation in all three of the dietary fatty acids tested (Chapter 5). However, girth did increase with increasing dietary fatty acid C20:1*n*9. This fatty acid was in higher proportions in arrow squid than any of the other prey tested (Chapter 4) and is further considered a marker of bathypelagic squid in the Southern Ocean (Pethybridge et al. 2010). Whilst this could suggest a degree of increased girth with squid

consumption, the explanatory power of girth on C20:1*n*9 variation was low in this study. Still, insights agreed with fatty acid analysis of polar bears *Ursus maritimus* which found reduced consumption of preferred prey also correlated with reduced body condition (indicated by lipid content; Florko et al. 2021). Furthermore, prey availability was the best predictor of body condition in killer whales (Stewart et al. 2021). The link between diet and body condition may, therefore, be worth investigating further in LFPWs in New Zealand waters.

As an exploratory study, both fatty acids and body condition were investigated for only a subset of individuals ($n = 15$). Consequently, it was not possible to conclude causality from this limited sample size. Notably, the role of blubber is multi-faceted (Lockyer 1993; Iverson 2009), so factors such as metabolism, growth, response to stimuli such as ocean temperature, or ontogeny could all contribute to changes noted to blubber (Guerrero and Rogers 2019; Tang et al. 2021), although they were not able to be explored here. Furthermore, other measurements of body condition have been used in marine mammals previously, including photogrammetry (Christiansen et al. 2020; Stewart et al. 2021), adipocyte number (Castrillon et al. 2017) and trunk mass (Gómez-Campos et al. 2011). Although this study was unable to examine all body condition measurements (Castrillon and Bengtson Nash 2020), these should be included in future studies for a more comprehensive study of body condition measurements for LFPWs.

6.4. Management and conservation implications

The LFPW is considered nationally "not threatened" within New Zealand waters, with qualifiers of "S?O" (an indication of uncertainty as to the security status of a species overseas) and "data poor" (Baker et al. 2019). Furthermore, an assessment of the risk to marine mammals from fishing vessels in the New Zealand exclusive economic zone showed a medium risk ratio for LFPWs from fishing vessels (Abraham et al. 2017). The risk assessment ranked 35 marine mammal species in terms of

their risk from fishing vessels; LFPWs were originally ranked 9th mainly due to data uncertainty (Abraham et al. 2017). This work was updated with both new data and methodology in 2022 to include a total of 54 species, with LFPWs ranked 15th most impacted based on estimated New Zealand population sizes (MacKenzie 2022). Whilst demographic parameters were available for LFPWs and others such as common dolphins, the recent assessment notes cautious interpretation is required given appropriate demographic parameters are unknown for many marine mammals species within New Zealand waters (MacKenzie 2022). This thesis contributed novel data on the foraging ecology of LFPWs to a nationally data poor species, which has implications for fisheries management, changing oceanic conditions and strandings.

6.4.1. Implications for fisheries

A total of 21 LFPWs have been incidentally captured by commercial fisheries in the 15 years between the 2002/03 to 2019/20 fishing years within New Zealand waters (Fisheries New Zealand Protected Species Bycatch Open Database), all occurring in areas of the continental shelf. Though LFPWs have the second highest recorded captures of any cetacean in New Zealand waters, the number is still relatively low in comparison to reported bycatch of common dolphins *Delphinus delphis* within the same time period (n = 220, Ministry for Primary Industries). Whilst the closely related short-finned pilot whale (*Globicephala macrorhynchus*) is regularly bycaught in long-line fisheries overseas (Stepanuk et al. 2018; Thorne et al. 2019), LFPWs are not as heavily captured. The largest of the LFPW incidental captures in New Zealand occurred in Taranaki (West Coast North Island), where six LFPWs were captured by trawl fisheries targeting jack mackerel in 2004/05 year (22.2% tows observed). A further two LFPWs were captured in the jack mackerel fishery in the 2008/09 year (37.5% tows observed) and five captures were recorded 2012/13 year (87.7% tows observed; Fisheries New Zealand Protected Species Bycatch Open Database; Abraham 2016). Trawl fisheries for hoki

(2017/18 fishing year; Childerhouse and Johnston 2019; 34.5% tows observed) and hake (2019/20 fishing year; 75.4% tows observed) accounted for two LFPW captures combined, whilst the further captures were recorded in a school shark setnet (n = 1; 2007/08 fishing year; 4% net observed) off west coast South Island and long-line fisheries for bluefin tuna (n =2; 2003/04 fishing year; 46.1% hooks observed), bigeye tuna (n = 1; 2017/18 fishing year; 9% hooks observed) and ling (n = 2; 2002/03 fishing year; 55.8% hooks observed; Fisheries New Zealand; Childerhouse and Johnston 2019).

New Zealand does also hold an active commercial fishery for arrow squid, the most important prey species in the diet of LFPWs according to this thesis. Fishing intensity for arrow squid is variable around New Zealand, with trawl vessels operating in the vicinity of the Stewart Snares shelf (near Stewart Island) accounting for most of the commercial catch in recent years (Fisheries New Zealand 2022). Observer effort of the squid trawl has increased from < 40% tows observed prior to 2012 to over 80% tows observed in more recent years; exceptions were the 2016/17 and 2019/20 fishing years where 74.2% and 79.4% tows were observed respectively (Fisheries New Zealand Protected Species Bycatch Open Database). Arrow squid are commercially sourced though trawling almost exclusively in New Zealand since jigging stopped on any large scale in the 2016/17 fishing year. Jigging is considered to produce less bycatch than other fishing techniques (Wakefield et al. 2016), though trawling is generally considered more dangerous for marine mammals (Slooten 2013; Allen et al. 2014). No direct interactions between LFPWs and the New Zealand arrow squid fishery have been reported between 2002 and 2020 (Finucci et al. 2019; Fisheries New Zealand Protected Species Bycatch Open Database; Fisheries New Zealand 2022). However, the reliance of LFPWs on arrow squid consumption appears to have persisted over at least a 12-year period 2005 – 2017 (Chapter 2, Beatson and O'Shea 2009), despite commercial arrow squid landings in New Zealand waters varying between 15,053 – 72,418 tonnes during the same time interval (Fisheries New Zealand 2022).

6.4.2. Implications of changing ocean conditions

Commercial vessels targeting arrow squid operate close to known LFPW stranding hotspots such as Stewart Island (Betty et al. 2020), and therefore, close to potential LFPW foraging locations. Accordingly, competition for resources in the changing marine climate are important management considerations. Negative anomalies of chlorophyll-a (CHL-a) were recoded off the West Coast of New Zealand's South Island during the study period of this thesis, indicating lower than usual productivity in the area (Pinkerton et al. 2019). One of two areas reporting the greatest decreasing trends in CHL-a was within Tasman Bay, Nelson, west coast of New Zealand (Pinkerton et al. 2019), where Farewell Spit is located. Increasingly, New Zealand is also experiencing ocean warming events such as that of 2017 (Salinger et al. 2019; Chiswell and Sutton 2020). The two LFPW prey species with the largest commercial catch, arrow squid and hoki, are both reported to decrease in size in response to warming waters (Lavin et al. 2022). The increased competition between these commercial fisheries and LFPWs as prey size reduces with a warming ocean is a management concern for LFPWs going forward. Any changes to density of prey species such as arrow squid should be viewed with caution as this could increase competition for marine resources (Corrales et al. 2018) which in turn could lead to an increase in interactions between LFPWs and commercial vessels. Indeed, potential effects of resource competition and foraging overlap between the commercial arrow squid fishery and the declining New Zealand sea lion population have been heavily discussed (Wilkinson et al. 2003; Robertson and Chilvers 2011; Bowen 2012; Chilvers 2012; Large et al. 2019).

Ocean warming is also projected to cause changes in squid distribution as current habitats become unsuitable (Rodhouse 2013; Alabia et al. 2015; Yu and Chen 2018). The consequences of this for LFPWs in New Zealand waters are unclear, but studies in the Northeast Atlantic have suggested

that range shifts caused by ocean warming could potentially cause LFPWs to become separated from their prey (Thorne and Nye 2021). Indeed, a recent report into the effects of climate on marine mammals suggested LFPWs may be displaced around New Zealand by the more typically tropical short-finned pilot whale (Roberts and Hendriks 2022). The discovery of several new species to the diet of LFPWs in New Zealand waters, including both fish and benthic species (Chapter 2), could point to some degree of climate related dietary diversification already occurring, although no links have been made to ocean warming thus far.

6.4.3. Implications for strandings

Stomach content analysis of LFPWs (Chapter 2) demonstrated evidence of short-term sexual segregation in target prey species, which was not fully evident from the longer-term methodologies of carbon and nitrogen stable isotope or fatty acid analyses (Chapters 3, 4). This could indicate that the more diverse diet observed in mature males (Chapter 2, Chapter 3) could be a function of stranding events, with males more able to forage for demersal octopus or carpet shark whilst in shallower waters. Alternatively, it is possible that this shallower coastal foraging could be a risk factor for single and/or mass stranding events, since LFPWs normally occupy more offshore waters. Indeed, the possible relationship between stranding and foraging in shallow environments was explored in bottlenose dolphins (McGovern et al. 2020), though no conclusive link was made. Cause and effect analysis between foraging and strandings lay outside the scope of this PhD but would be an interesting route to explore in the future.

Body condition measurements of stranded LFPWs indicated that girth measurements may correlate with both polyunsaturated and saturated fatty acids in LFPWs, and therefore may have a link to fatty acid deposition (see Chapter 5). Accurate body condition measurements could add value to health assessments of both free swimming and stranded cetaceans (Derous et al. 2020). Particularly,

any morphometric measurements that can be used to aid assessments of welfare and health could also potentially aid management decisions on re-flotation during live-stranding events.

6.5. Future research directions

6.5.1. Foraging ecology and distribution

A valuable next step for this research area would be to explore the diet of bycaught LFPWs, for comparison and validation of this dataset against wild swimming LFPWs. Furthermore, samples collected during the austral winter would elucidate whether arrow squid are seasonally important to LFPW diet, or if year-round dietary reliance on arrow squid is apparent. To further explore the role of arrow squid to LFPW diet, it is recommended that both stable isotope and fatty acid analyses be conducted on a wider range of potential LFPWs prey species, such as has been conducted on potential prey of other marine mammals (Kiszka et al. 2014b; Guerrero et al. 2016; Teixeira et al. 2021). DNA analysis of stomach contents could also help to reveal further prey species that may have been missed through hard parts identification, as was helpful in the case of both carpet shark and conger eel in this study. Combining these techniques may also help to discern which, if any, prey species were missed from the current analysis.

Furthermore, analysis of the macronutrient composition of prey, such as that performed on prey of the Franciscana dolphin *Pontoporia blainvillei* (Denuncio et al. 2017) and common dolphin (Stockin et al. 2022a) would assist the understanding of any potential consequences of prey shifts on the LFPW population, as well as drivers behind ontogenetic dietary variation presented in Chapter 2 and 3. The ontogenetic variation noted should also be validated by fatty acid analysis within a larger LFPW sample, to explore whether ontogenetic differences recorded in short-term diet and isotopic niche, are replicated over a longer temporal period. This would offer insights as to whether ontogenetic dietary differences occur longer term, or whether they are a function of stranding events themselves.

6.5.2. Body condition

The effects of ontogeny on blubber, body condition, and body composition have been noted in other cetacea (Dunkin et al. 2005; Mallette et al. 2016). Although no effects of reproductive group were observed on lipid content of blubber from LFPWs in the Faroe Islands and North-eastern Atlantic (Lockyer 1993), similar studies would be of use in New Zealand LFPWs, to detect physiological drivers and variation in LFPW body condition. Particularly, a larger sample size than was used in this thesis would be required to identify accurate relationships between body condition measurements, ontogeny, metabolism, diet, and health in LFPWs. Accurate body condition measurements would be particularly helpful when attempting to quantify the impacts of potential changes in LFPW diet and have been suggested as a possible monitoring tool for climate related effects on cetacea in New Zealand (Roberts and Hendriks 2022).

The assessment of morphometric body condition may hold promise in relation to LFPW stranding events. Accurate, non-lethal measurements of energy reserves may potentially serve as a useful predictor of health and survivorship after refloating stranded animals (Wiley et al. 2001). Particularly, research into aerial photogrammetry and morphometric measures including girth and BCI should be explored, alongside tagging of re-floated LFPWs at strandings (e.g., Gales et al. 2012; Wells et al. 2013), to help understand any links between LFPW body condition measurements and their post-stranding survival rate.

6.5.3. The New Zealand Pilot Whale Database and Tissues Archive

The continuation of the New Zealand Pilot Whale Database and Tissue Archive based at Massey University is invaluable to our understanding of the *G. m. edwardii* sub-species of LFPW in the Southern Hemisphere. Parameters such as sex, age, total body length, maturity status and reproductive status available for many of the LFPWs stranded have been central to this study and

allowed ontogenetic and spatiotemporal comparisons to occur. Future research involving this dataset is recommended to address knowledge gaps of *G. m. edwardii* in the Southern Hemisphere, including abundance and distribution data lacking in this sub-species (Kraft et al. 2020).

To better explain drivers behind the data presented in this thesis, three specific recommendations are made: 1) the sampling of LFPW stomachs should be continued to check for changes in target prey species, prioritising the sampling of LFPW stomachs from bycaught individuals, those stranded outside the austral summer and those stranded in areas not well represented in the literature (e.g., Chatham Islands, North Island New Zealand); 2) satellite tagging of LFPWs should be carried out (as also recommended by Betty 2019 and Stockin et al. 2022b) to understand foraging areas/depths and quantify level of overlap with commercial fisheries and 3) body condition measurements should be further explored, including the addition of adipocyte index (e.g., Castrillon et al. 2017) and aerial photogrammetry (Booth et al. 2020; Christiansen et al. 2020b; Aoki et al. 2021) to assess a) any changes in LFPW body condition in relation to potential prey species and b) links to stranding/re-floatation survivorship.

Finally, the addition of freeze-dried skin samples to the LFPW archive at Massey University has created the opportunity for investigations into the effects of long-term storage on LFPW skin. Samples from the same LFPWs are also stored in ethanol and/or frozen, to use for comparison of stable isotope values to assess effects of storage in stable isotope studies. Whilst the effects of storage have been investigated on some tissues from cetacea and their potential prey species over short time scales (e.g., Kelly et al. 2006; Burrows et al. 2014; Kiszka et al. 2014a; Olin et al. 2014; Javornik et al. 2019; Planas et al. 2020), data on the effects of longer-term sample storage on biochemical tracers (e.g., Newsome et al. 2018) are less common. Further research on species and tissue specific storage

implications is recommended (Carabel et al. 2009), which would benefit foraging ecology research more widely.

6.6. Conclusion

Prior to this study, the knowledge of the diet of LFPWs in New Zealand waters was limited to a snapshot of 37 LFPW stomachs from 2005, 2006 and 2008. This thesis provides novel data on dietary variation of the LFPW population from multiple locations across New Zealand, over an eight-year period. This research further explored, for the first time in New Zealand, insights into the relationship between diet and individual body condition. Thus, this thesis has provided comprehensive information on dietary composition and body condition measurements of LFPWs across both ontogenetic and spatiotemporal scales. The exploration of multiple dietary markers reduced biases from individual methodologies alone which allowed for greater insight to foraging ecology of LFPWs. It is hoped that research presented in this thesis will improve understanding of the interactions between LFPWs and the wider ecosystem, critical to ensuring effective ecosystem-based management actions. It is highly recommended that long-term datasets, such as the one used in this study receive continued support to identify change on individual species and wide-scale ecosystem health. Successful future management of LFPWs will require data on their distribution to be prioritised. It is hoped that the research presented here will assist in effective management of LFPW populations, through the use of largescale baseline foraging and body condition data to illuminate impacts of oceanic change.

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Appendices

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Name and title of main supervisor:	Professor Karen Stockin
In which chapter is the manuscript/published work?	Chapter 2
What percentage of the manuscript/published work was contributed by the student?	70%

Describe the contribution that the student has made to the manuscript/published work:
BH completed the prey identification work, statistical analysis, and graphical presentations for this study, and wrote the first draft of the paper. BH also contributed to the conception of the work, sample collection and final manuscript editing.

Please select one of the following three options:

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BH undertook all of the lab work and statistical analysis for this study, and wrote the first draft of the paper. BH also contributed to the conception of the work, sample collection and final manuscript editing.

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BH wrote the first draft of the paper. BH also contributed to the conception of the work, sample collection, lab work, statistical analysis, graphical representations and final manuscript editing.

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BH completed the lab work for this study, statistical analysis, graphical representations and wrote the first draft of the paper. BH also contributed to the conception of the work, sample collection, and final manuscript editing.

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Appendix 1.1. Use of samples from a strandings archive

Studies on stranded marine mammals in isolation have inherent biases that must be acknowledged. For example, animals that strand may be sick or injured (Praca et al. 2011) and therefore may not be displaying typical behaviours or chemical tracers in comparison to wild populations. Furthermore, it may be that some types of animals (e.g., immature, or pregnant females) may strand more frequently than others due to their relative ability to withstand stressors, therefore creating a biased sample. However, when pods strand en-masse (as long-finned pilot whales; LFPWs; *Globicephala melas edwardii*; do in New Zealand) they are less likely to be impacted by such biases (e.g., Chalcobsky et al. 2021), as a cross-section of the LFPW society is recorded stranded, often with no obvious signs of sickness or injury. In fact, the cause of cetacean strandings in New Zealand has not been established, but linkages to periods of low air pressure, moon cycles and local topography have all been suggested (Brabyn 1990; Brabyn 1991; Brabyn and McLean 1992; Lad and Brabyn 1993; Brabyn and Frew 1994). These unfortunate events can therefore present unprecedented access to a species not otherwise commonly encountered, and therefore may help further understanding of the species. Within New Zealand for example, LFPWs strand in greater numbers than any other marine mammal — a total of 8571 individuals were recorded stranded between January 1978 and December 2017 (Betty et al. 2020).

Archived, skin, blubber, and stomach contents of LFPWs collected from LFPW stranding events between 2009 and 2017 were accessed for this study. Tissue samples are accompanied by respective metadata including sex, total body length (TBL), girth, and blubber thickness (Betty 2019). Where possible, sex, sexual maturity status (immature, mature), reproductive status (pregnant, lactating,

resting) and age (assessed from growth layer groups in tooth dentine) were also included in assessments (Betty 2019; Betty et al. 2022).

Tissue samples used in this study, (skin and blubber) were taken on Day 1 of sampling an animal and immediately after measurements and photographs were taken. Decomposition state of tissues was therefore assumed to be the same as decomposition state as described from photographs.

Skin samples were taken using standard post-mortem procedure (e.g., Geraci and Lounsbury 2005) from as many individuals as possible, with no preference towards sex or size of the individual. This allows variability to be assessed within a pod or stranding group (e.g., Abend and Smith 1995; Evans and Hindell 2004). Samples of skin were taken for isotopic analysis as soon after death as possible and so are considered to have retained isotopic integrity. Skin is thought to be a homogenous (Borrell et al. 2018) so sampling location is not thought to effect isotope signatures in delphinids. Furthermore, no isotopic differences were found in skin samples of wild striped dolphins *Stenella coeruleoalba* and common dolphins from 11 locations on the carcass (Arregui et al. 2017) or between skin samples of tail fluke, dorsal fin, and other areas for captive bottlenose dolphins *Tursiops truncatus* and killer whales *Orcinus orca* (Williams et al. 2008). Using a scalpel blade, a sample of skin 3–5cm in length was taken preferentially from the tail flukes, or from the dorsal fin or pectoral flippers if tail fluke skin was not accessible. Care was taken to sample skin with all layers still intact, which were temporarily stored in plastic bags on ice before being frozen at -20 ℃. Although skin was initially stored frozen, samples were transferred to 70–95% ethanol for long-term storage. Whilst care was taken in sampling of skin, some samples were more difficult to obtain clean due to position of the LFPW carcass, weather etc. In this instance, all samples were removed of any excess tissue and washed in distilled water before processing.

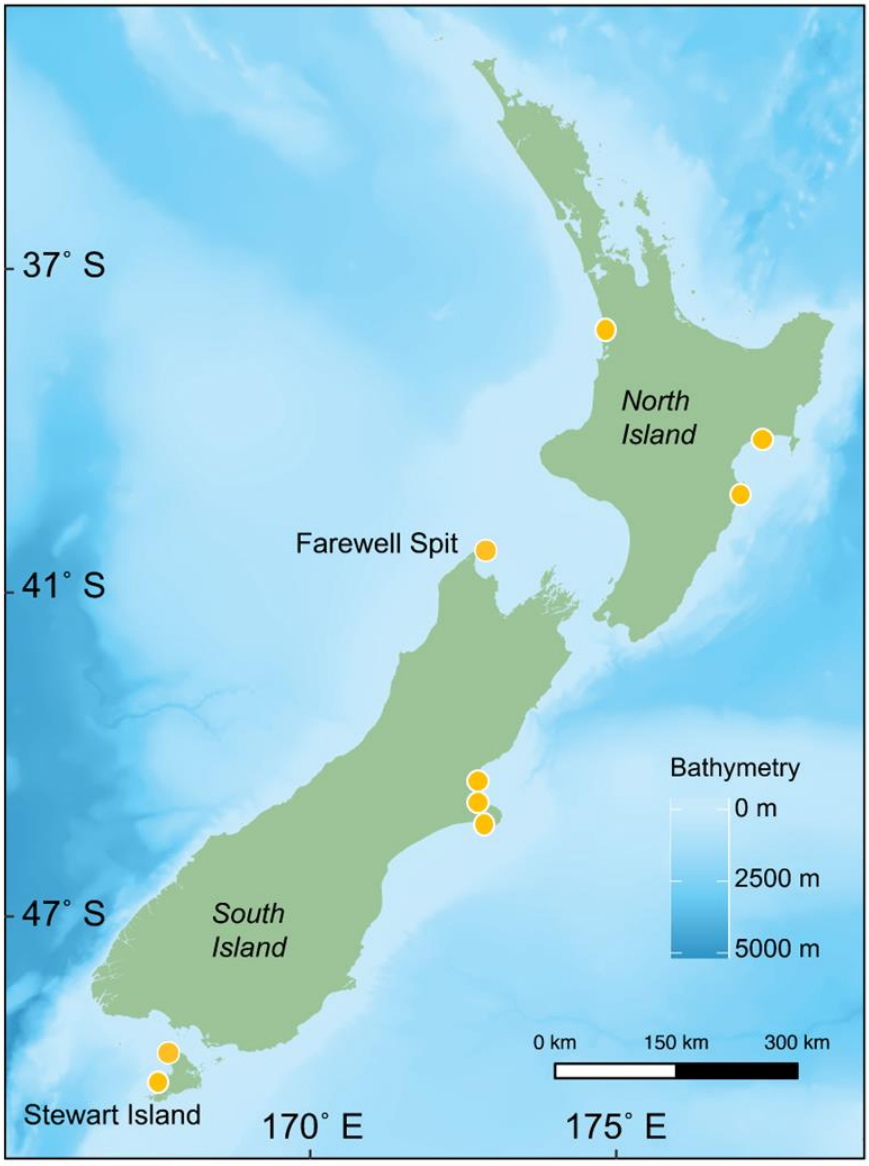
Blubber samples were collected from stranded individuals *in-situ* from directly under the dorsal fin, with care taken to ensure the full blubber layer from skin to muscle was sampled. Internal tissues such as blubber are thought to decompose quickly after death due to high internal temperatures of an individual (Burrows et al. 2014). Blubber was therefore taken as quickly as possible and put on ice whilst in the field. Blubber was then wrapped in foil and stored frozen at -20 ℃ prior to processing (e.g., Monteiro et al. 2015b). Blubber samples were considered viable after long-term storage as fatty acid profiles of blubber samples from Baltic grey seals *Halichorus gripus* were considered relatively unchanged after 4-6 years of storage at -25℃ (Lind et al. 2012).

Stomach contents were examined opportunistically at stranding events using standard procedures (e.g., Beasley et al. 2019). Stomachs (all three chambers) were sampled *in-situ* to extract contents, as is common practice with stranded individuals including false killer whales *Pseudorca crassidens* (Alonso et al. 1999) and sperm whales *Physeter macrocephalus* (Foskolos et al. 2020). Stomach contents were carefully removed from stomach chambers and placed into labelled bags. Stomach contents were stored frozen at -20 ℃ until ready for analysis.

Samples from strandings with as much metadata associated with them as possible were chosen for analysis. This allowed for assessment of ontogenetic variation of LFPWs as well as spatial and temporal variation. All stomach contents samples (n = 283) were analysed, regardless of year or location stranded. Skin samples (n = 125) were analysed from strandings in Farewell Spit 2009, 2011, 2014 and 2017 as well as Stewart Island in 2010 and 2011, allowing for assessment both temporal variation at the same stranding location and spatial variation between two stranding hotspots (Betty et al. 2020). Blubber samples (n = 15) were analysed from the Farewell Spit 2014 stranding event only.

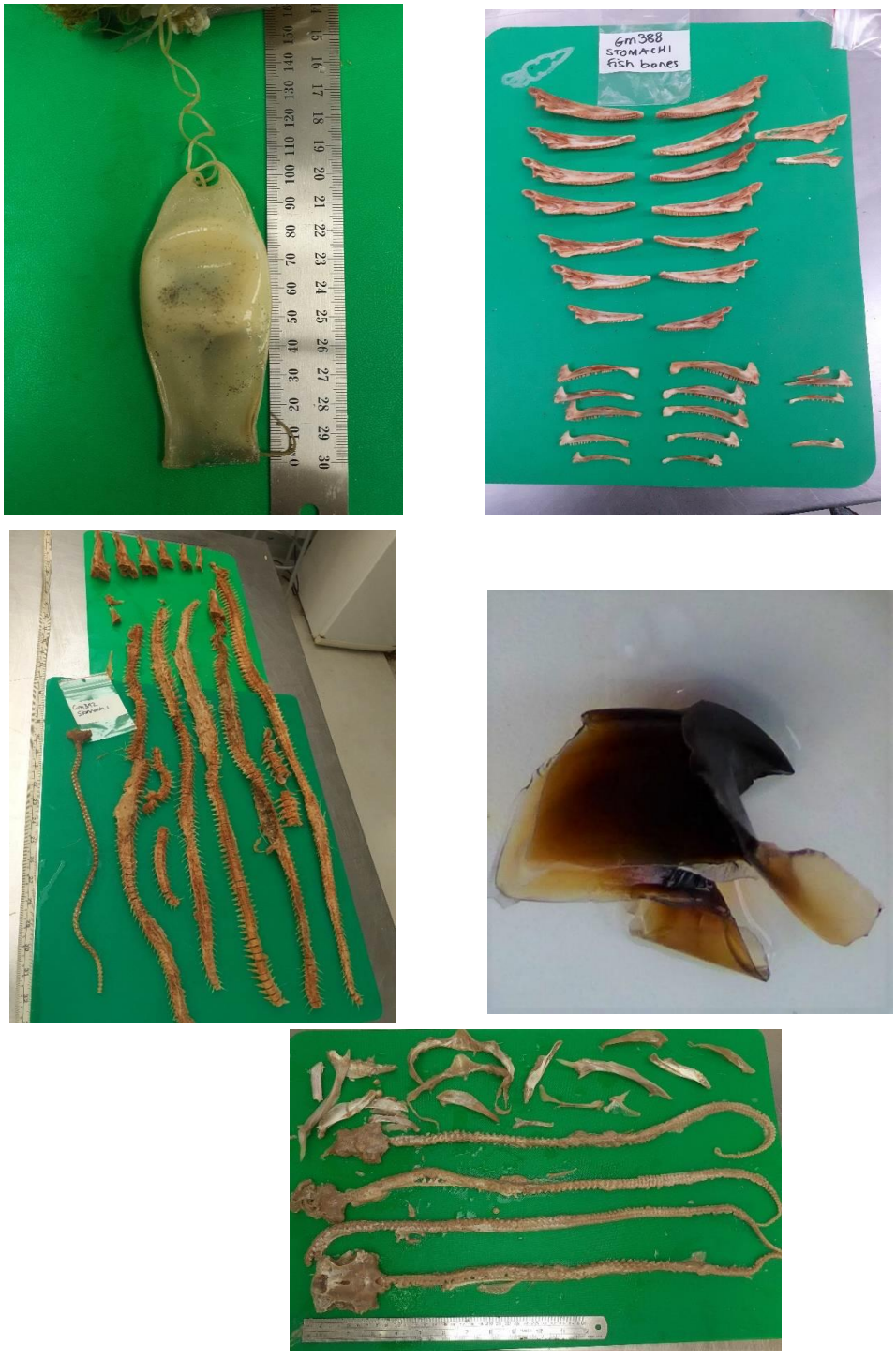
A focal stranding event for this PhD thesis was chosen to be Farewell Spit, Golden Bay 2014. This event was chosen as it had a wealth of associated metadata available, and individuals were deemed

to be in the best body condition. Choosing this focal stranding allowed for stomach content, stable isotope, and fatty acid analyses to be performed on the same individuals, allowing data from different dietary analyses to be compared with fewer confounding variables to consider during interpretation. All analyses were performed using the R programming language (R Core team 2021) software.



Locations of long-finned pilot whale (*Globicephala melas edwardii*) strandings on the New Zealand coast from which samples were collected for this study, 2009–2017. From North to South in the north island: Raglan, Wairoa, Waimārama. From North to South in the South Island: Farewell Spit, Spencer Park Beach, Port Levy, Te Oka. From North to South in Stewart Island: West Ruggedy, Mason Bay. Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted from National Institute of Water and Atmospheric research (NIWA) under a creativecommons by license (CANZ 2008), with permission from NIWA original copyright; Chapter 2).

Appendix 2.1 Example prey remains photographs.



Photographs of example prey remains found in the stomachs of long-finned pilot whales (LFPWS; *Globicephala melas edwardii*) stranded on the New Zealand Coast between 2009 and 2017.

Appendix 2.2. Summary statistics of correspondence analysis

Summary statistics of correspondence analysis from % frequency of occurrence (%FO) data of fish, cephalopods and empty stomachs investigated in long-finned pilot whales (*G. m. edwardii*) stranded on the New Zealand coast 2009 – 2017 presented by reproductive group, year, location, and stranding event. In (a) % = percentage variation explained, and cumulative = cumulative percentage variation explained of dimension 1 (Dim1) and dimension 2 (Dim 2). In (b), Iner*100 = relative inertia, ctr = contribution to data construction. In (b) and (c) Dim.1 = dimension 1, Dim.2 = dimension 2, cos2 = cosign^2 values.

Reproductive group

(a)

Eigenvalues	Dim1	Dim2	Dim 3
Variance	0.207	0.006	0.002
%	96.208	2.967	0.825
Cumulative	96.208	99.175	100.000

(b)

Rows	**Iner*1000**	**Dim.1**	**ctr**	**cos2**	**Dim.2**	**ctr**	**cos2**	**Dim. 3**	**ctr**	**cos2**
Lactating	38.889	-0.504	17.852	0.949	-0.116	30.852	0.051	0.000	0.000	0.000
Resting	16.335	-0.273	6.152	0.779	0.138	50.731	0.198	0.047	21.130	0.023
Pregnant	42.506	-0.505	20.097	0.978	0.32	2.690	0.004	-0.069	43.450	0.018
Immature	1.738	0.036	0.118	0.140	-0.072	15.576	0.572	0.051	28.226	0.28
Mature males	115.504	0.590	55.782	0.999	0.005	0.151	0.000	-0.020	7.195	0.001

(c)

	Iner*1000	Dim.1	ctr	Cos2	Dim.2	ctr	Cos2	Dim.3	ctr	Cos2
Arrow squid	48.475	-0.279	22.938	0.979	-0.041	16.214	0.021	-0.001	0.012	0.000
Octopus	29.827	0.543	13.722	0.952	0.035	1.885	0.004	0.117	74.764	0.044
Other squid	6.954	-0.110	0.913	0.271	0.179	77.830	0.714	-0.026	5.777	0.015
Fish	129.714	0.958	62.427	0.995	-0.043	4.072	0.002	-0.050	19.448	0.003

Year

(a)

Eigenvalues	Dim1	Dim2	Dim 3
Variance	0.139	0.091	0.005
%	59.017	38.932	2.011
Cumulative	59.017	97.989	100.000

(b)

	Iner*1000	Dim.1	ctr	Cos2	Dim.2	ctr	Cos2	Dim.3	ctr	Cos2
Arrow squid	35.591	-0.142	9.629	0.375	-0.184	24.316	0.625	-0.004	0.227	0.000
Octopus	52.735	-0.225	3.753	3.753	0.667	50.120	0.869	-0.128	35.822	0.032
Other squid	120.105	1.027	86.618	86.618	-0.015	0.029	0.000	-0.029	1.978	0.001
Fish	26.285	0.000	0.000	0.000	0.432	25.534	0.889	0.153	61.973	0.111

(c)

Rows	**Iner*1000**	**Dim.1**	**ctr**	**cos2**	**Dim.2**	**ctr**	**cos2**	**Dim. 3**	**ctr**	**cos2**
2009	48.083	-0.267	11.384	0.328	0.375	34.071	0.648	-0.072	24.322	0.024
2010	77.266	0.565	53.528	0.960	-0.116	3.410	0.040	0.000	0.001	0.000
2011	10.884	0.180	5.399	0.687	0.121	3.708	0.312	0.008	0.285	0.001
2014	23.028	-0.342	14.341	0.863	0.025	0.15	0.005	0.134	64.759	0.133
2017	75.453	-0.382	15.348	0.282	-0.608	58.696	0.712	-0.059	10.633	0.007

Location

(a)

Eigenvalues	Dim1	Dim2	Dim 3
Variance	0.377	0.082	0.006
%	81.055	17.719	1.225
Cumulative	81.055	98.775	100.000

(b)

Rows	**Iner*1000**	**Dim.1**	**ctr**	**cos2**	**Dim.2**	**ctr**	**cos2**	**Dim. 3**	**ctr**	**cos2**
Farewell Spit	90.636	0.581	13.047	0.543	0.533	50.294	0.457	-0.008	0.179	0.000
Stewart Island	24.660	0.344	4.419	0.675	-0.238	9.698	0.324	-0.009	0.195	0.000
Port Levy	45.707	0.377	4.292	0.354	-0.505	35.235	0.365	0.066	8.678	0.011
Ralgan	85.213	0.818	22.482	0.992	0.048	0.357	0.003	0.055	6.581	0.004
Te Oka	36.140	-0.336	8.528	0.890	-0.055	1.056	0.024	-0.105	54.773	0.086
Wairoa	182.697	-0.970	47.285	0.976	0.121	3.360	0.015	0.094	29.594	0.009

(c)

	Iner*1000	Dim.1	ctr	Cos2	Dim.2	ctr	Cos2	Dim.3	ctr	Cos2
Arrow squid	149.537	0.572	37.912	0.956	-0.117	7.276	0.040	-0.038	11.075	0.004
Octopus	99.715	1.038	13.344	0.504	1.014	58.330	0.482	0.170	23.654	0.014
Other squid	71.859	-0.448	15.343	0.805	-0.201	14.131	0.162	0.091	41.744	0.033
Fish	143.942	-0.743	33.401	0.875	0.271	20.263	0.116	-0.077	23.526	0.009

Stranding event

(a)

Eigenvalues	Dim1	Dim2	Dim 3
Variance	0.296	0.133	0.020
%	65.811	29.639	4.550
Cumulative	65.811	95.450	100.00

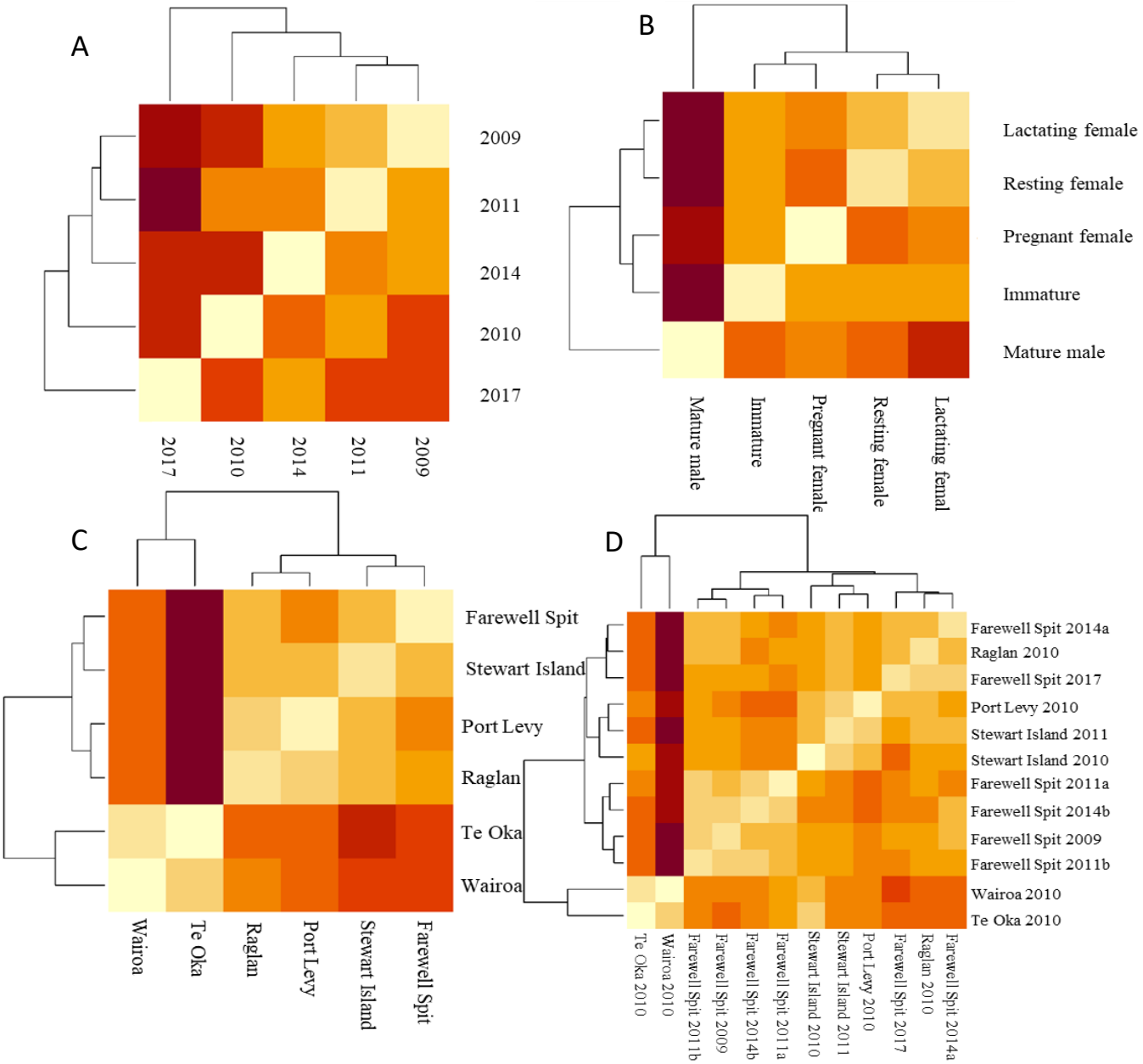
(b)

Rows	**Iner*1000**	**Dim.1**	**Ctr**	**cos2**	**Dim.2**	**ctr**	**cos2**	**Dim. 3**	**ctr**	**cos2**
Farewell Spit 2009	22.209	-0.452	5.296	0.706	0.276	4.384	0.263	0.094	3.276	0.030
Farewell Spit 2011	40.125	-0.256	2.506	0.185	0.527	23.544	0.783	0.107	6.287	0.032
Farewell Spit 2014	12.102	-0.238	1.636	0.400	0.286	5.265	0.580	0.052	1.126	0.019
Farewell Spit 2017	22.018	-0.560	5.845	0.786	-0.129	0.691	0.042	-0.262	18.460	0.172
Stewart Island 2010	28.762	-0.290	2.349	0.242	0.493	15.027	0.697	-0.146	8.567	0.061
Stewart Island 2011	49.098	-0.766	9.802	0.591	-0.553	11.355	0.309	-0.315	23.969	0.100
Port Levy 2010	14.691	0.215	1.489	0.300	-0.299	6.416	0.583	0.134	8.397	0.117
Raglan 2010	13.581	-0.130	0.388	0.085	-0.422	9.115	0.895	0.063	1.321	0.020
Te Oka	27.175	-0.037	0.028	0.003	-0.648	18.722	0.919	0.189	10.322	0.078
Wairoa	24.017	-0.057	6.195	0.764	-0.250	3.082	0.171	0.153	7.578	0.065

(c)

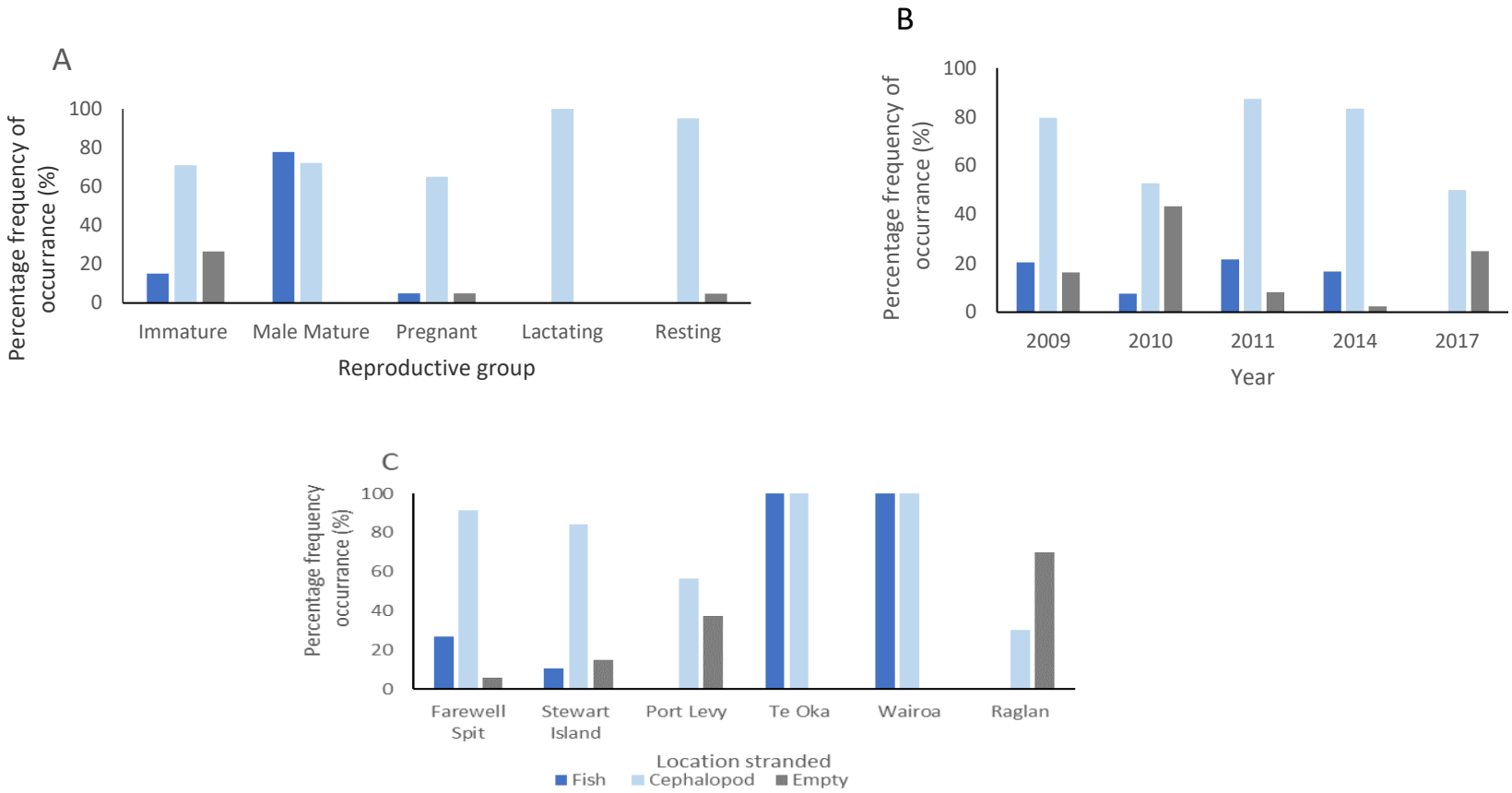
	Iner*1000	Dim.1	ctr	Cos2	Dim.2	ctr	Cos2	Dim.3	ctr	Cos2
Arrow squid	108.737	-0.417	29.443	0.802	-0.202	15.361	0.188	-0.045	4.977	0.009
Octopus	97.781	-0.568	10.432	0.316	0.789	44.708	0.610	0.275	35.281	0.074
Other squid	139.955	0.773	39.172	0.829	-0.306	13.660	0.130	0.171	27.750	0.041
Fish	103.676	0.546	20.953	0.599	0.411	26.271	0.338	-0.178	31.992	0.063

Appendix 2.3. Heatmaps and associated cluster dendrograms



Heatmaps and associated cluster dendrograms from Bray-Curtis similarity matrices for stomach contents of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast. Percentage frequency of occurrence data (%FO) was used comparing arrow squid (*Nototodarus* spp.), octopus (*Pinnoctopus cordiformis*), fish or "other squid" consumption. Graphs explore variation in %FO data by year stranded (A), reproductive group (B), location stranded (C) and stranding event (D). All graphs are coloured according to contribution to data construction, where red is highly different and yellow is very similar.

Appendix 2.4. Comparison of empty stomachs vs those with fish and squid remains.



The percentage frequency of occurrence (%FO) of long-finned pilot whales (*Globicephala melas edwardii*) stomachs that contained fish cephalopods, fish, or were empty by (A) reproductive group, (B) year, and (C) location.

Appendix 2.5. Types of prey remains recovered from stomachs of long-finned pilot whales *Globicephala melas edwardii*

Number of long-fined pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast between 2009 and 2017. Data are provided by stranding events. FWS = Farewell Spit. Strandings are only included in the table if some prey remains were found.

Stranding	Stomach contents recovered	Identifiable cephalopod beaks	Identifiable fish remains	Unidentifiable cephalopod remains	Unidentifiable fish remains	Other unidentifiable remains
FWS2009	42	38	3	3	7	6
Port Levy 2010	10	8	0	8	0	1
Stewart Island 2010	14	14	0	13	3	0
Te Oka 2010	1	1	0	1	1	0
Raglan 2010	6	6	0	5	0	0
Wairoa 2011	1	1	1	0	0	0
FWS2011a	7	7	2	6	3	2
Stewart Island 2011	66	60	4	62	5	1
FWS2011b	49	48	13	45	14	8
FWS2014a	35	31	4	32	4	0
FWS2014b	6	5	0	5	2	1
FWS2017	2	2	0	2	0	0

Appendix 2.6. DNA analysis of prey tissue

During identification of stomach contents from long-finned pilot whales (LFPWs), remains of two taxa were unable to be identified from visual means alone. Dental and premaxilla jaw bones of eel resembled the *Congridae* family (Leach 1997), though co-occurring cranial and vertebral column remains, as well as otoliths, were not able to confirm accurate identification. All remains were therefore only able to be classified to "order Anguilliformes, probable *Congridae*" based on visual remains, and were referred to as "eels".

Additionally, elasmobranch remains (cranium, vertebral column) were found in stomachs of 11 LFPWs across three years: 2009, 2011 and 2014. These stomachs also contained shark egg cases of carpet shark (*Cephoscyllium* sp.) but unfortunately, most of the recovered egg cases were too degraded to allow an assessment of the stage of embryonic development. However, all fully intact egg cases appeared to have been consumed prior to oviparity, as determined by the absence an embryo despite yolk. These observations suggest LFPWs most likely consumed gravid female sharks (Clinton Duffy, New Zealand Department of Conservation *pers. comms*). Furthermore, tooth plates believed to belong to the New Zealand eagle ray (*Myliobatis tenuicaudatus;* Leach 1997) were also noted in one stomach, alongside both carpet shark eggs and an elasmobranch skeleton. However, it is also possible that these tooth plates were ingested as secondary prey. As ray and shark skeletons are similar, this resulted in uncertainty as to which elasmobranch taxa were being consumed by New Zealand LFPWs. Therefore, all elasmobranch remains were initially classified to "Elasmobranchii, probable *Cephoscyllium* sp." based on visual identifications alone and referred to as "elasmobranch".

Tissue accompanied the remains of four shark and 11 eel species. Tissue attached to skeletal remains was limited in both quality and quantity due to decomposition effects. Still, subsamples were taken to investigate whether DNA metabarcoding was able to confirm taxa identification of prey remains recovered from LFPW stomachs. Methods described in Chapter 2 were followed for DNA metabarcoding analysis. Only three of the shark and 10 of the eel tissue samples were suitable for DNA identification. The BOLD method of DNA analysis was able to corroborate preliminary prey identification from visual means.

The eels were classified to family level as *Congridae* sp., though DNA was unable to specify whether samples were of the Southern conger eel *Conger verreauxi* or the Northern conger eel *C. wilsoni* species. Overall, eight samples were more likely to be the Southern conger eel *Conger verreauxi*, and three were more likely to be the Northern conger eel *Conger wilsoni*. Similarly, BOLD classified the elasmobranchs as *Cephaloscyllium* sp., with all three more likely to be the inshore carpet shark *C. isabella* than deepwater carpet shark *C. laticeps*.

Whilst *C. wilsoni* are thought to inhabit the North Island, *C. verrauxi* are more commonly thought to inhabit waters around New Zealand's South Island (Castle 1964). However, as neither species is commonly studied, their distribution may be inaccurate and therefore may not give much indication of probable LFPW feeding areas. Similarly, *Cephaloscyllium* spp. are not well studied. Whilst *C. isabella* are thought to occur throughout New Zealand waters, to depths of approximately 500 m (Horn et al., 2016), *C. laticeps* are also found in mainly coastal waters to about 60 m (Awruch et al. 2012). Unfortunately, however, analysis was inconclusive as to which species of *Cephaloscyllium* was recovered from LFPWs stomachs.

Still, both *Congridae* spp. and *Cephaloscyllium* spp. are considered benthic and/or reef associated, coastal inhabitants that exhibit a nocturnal lifestyle (Awruch et al. 2012; Hesse et al. 2016; Shoji et al.

Results of DNA barcoding of eel and elasmobranch samples found in stomachs of long-finned pilot whales *Globicephala melas edwardii* stranded on the New Zealand coast. The % similarity is given to indicate likelihood of a sample being a particular species.

Sample	BOLD match	Species	% Similarity
Eel	Conger	verreauxi	100.00
	Conger	wilsoni	99.83
Eel	Conger	wilsoni	100.00
	Conger	verreauxi	99.84
Eel	Conger	verreauxi	99.84
	Conger	wilsoni	99.67
Eel	Conger	verreauxi	100.00
	Conger	wilsoni	99.84
Eel	Conger	verreauxi	99.84
	Conger	wilsoni	99.67
Eel	Conger	verreauxi	99.84
	Conger	wilsoni	99.67
Eel	Conger	verreauxi	100.00
	Conger	wilsoni	99.84
Eel	Conger	verreauxi	100.00
	Conger	wilsoni	99.67
Eel	Conger	wilsoni	100.00
	Conger	verreauxi	99.83
Eel	Conger	verreauxi	100.00
	Conger	wilsoni	99.83
Shark	Cephaloscyllium	isabella	100.00
	Cephaloscyllium	laticeps	99.19
Shark	Cephaloscyllium	isabella	100.00
	Cephaloscyllium	laticeps	99.19
Shark	Cephaloscyllium	isabella	100.00
	Cephaloscyllium	laticeps	99.16

2017). It is therefore considered that the presence of these families in LFPW stomachs is an indicator of both benthic and nocturnal feeding. Whilst the tissue used for DNA barcoding was both limited in quantity and quality, analysis was still able to confirm visual identification of prey remains from

LFPW stomachs. The addition of DNA barcoding is therefore recommended for future studies to aid identification of remains from stomach contents.

Appendix 3.1. Summary of long-finned pilot whale skin samples used for stable isotope analysis.

Summary of long-finned pilot whale (*Globicephala melas edwardii*) skin samples used for carbon and nitrogen stable isotope analysis ($n = 125$), by year and location of stranding event on the New Zealand coast. The number of animals stranded at each event (No. stranded), and the total number included in isotope analysis (No. sampled) are reported. Sex and reproductive group are taken from the same *G. m. edwardii* population (Betty 2019; Betty et al. 2019). Table from Supplementary material of Hinton et al. (2022).

Date	Location	No. sampled/ No. stranded	Sex	Reproductive Group	*n*
December 2009	Farewell Spit	20/105	M	Immature	5
			M	Mature	5
			F	Immature	5
			F	Pregnant	2
			F	Lactating	0
			F	Resting	0
			F	Undetermined mature	3
November 2011	Farewell Spit	20/65	M	Immature	5
			M	Mature	5
			F	Immature	4
			F	Pregnant	2
			F	Lactating	2
			F	Resting	2
			F	Undetermined mature	0
January 2014	Farewell Spit	27/138	M	Immature	5
			M	Mature	5
			F	Immature	4
			F	Pregnant	5
			F	Lactating	5
			F	Resting	3
			F	Undetermined mature	0
January 2017	Farewell Spit	20/>400	M	Immature	5
			M	Mature	5
			F	Immature	5
			F	Pregnant	1
			F	Lactating	0
			F	Resting	1
			F	Undetermined mature	3
February 2010	Stewart Island	19/28	M	Immature	7

Appendix 3.1. continued

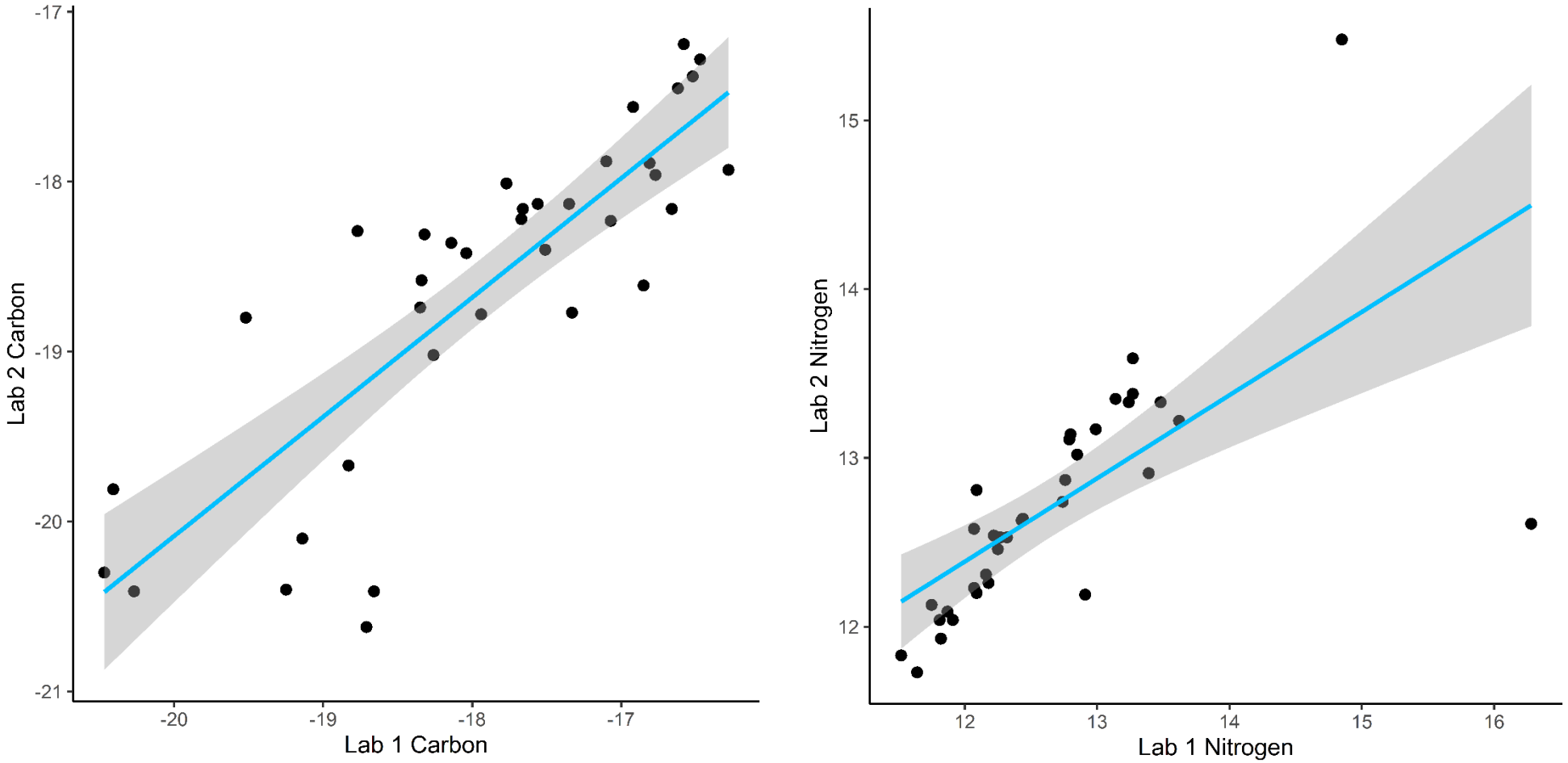
Date	Location	No. sampled/ No. stranded	Sex	Reproductive Group	*n*
			M	Mature	2
			F	Immature	2
			F	Pregnant	5
			F	Lactating	0
			F	Resting	0
			F	Undetermined mature	3
February 2011	Stewart Island	19/107	M	Immature	4
			M	Mature	5
			F	Immature	5
			F	Pregnant	2
			F	Lactating	2
			F	Resting	1
			F	Undetermined mature	0

Appendix 3.2. Tests of lipid correction equations

Testing lipid correction equations on $\delta^{13}C$ values of long-finned pilot whale (*Globicephala melas edwardii*) skin, including carbon stable isotope values and MSE (mean squared error) values. C_e = lipid extracted carbon value, C = carbon value, equations from Fry (2002), Post (2007), Logan (2008) and Peters (2022) are trailed alongside modified versions of Post et al. (2007; Post_this study) and Fry (2002; Fry_this study) using data from lipid extractions in this study.

C_e	C	Fry 2002	MSE	Post 2007	MSE	Logan 2008	MSE	Post_this study	MSE	Fry_this study	MSE	Peters 2022	MSE
-17.95	-18.04	-18.84	0.79	-18.13	0.03	-17.28	0.45	-18.80	0.72	-19.51	2.45	-16.89	1.13
-17.91	-19.82	-19.51	2.55	-19.28	1.87	-19.02	1.23	-19.50	2.51	-19.59	2.83	-17.83	0.01
-18.37	-19.78	-19.19	0.67	-19.04	0.45	-18.97	0.36	-19.12	0.56	-19.13	0.57	-17.81	0.32
-17.98	-20.41	-19.55	2.49	-19.46	2.19	-19.58	2.58	-19.39	1.99	-19.35	1.89	-18.14	0.03
-17.94	-19.57	-19.41	2.14	-19.13	1.40	-18.78	0.69	-19.41	2.16	-19.57	2.64	-17.70	0.06
-18.62	-18.66	-18.68	0.00	-18.33	0.09	-17.87	0.57	-18.70	0.01	-18.94	0.10	-17.21	1.98
-17.87	-18.83	-18.98	1.22	-18.57	0.49	-18.04	0.03	-19.00	1.27	-19.31	2.06	-17.30	0.32
-17.61	-18.55	-18.87	1.59	-18.40	0.61	-17.77	0.03	-18.89	1.63	-19.30	2.83	-17.16	0.21
-17.99	-20.00	-19.37	1.92	-19.23	1.54	-19.19	1.44	-19.29	1.68	-19.29	1.69	-17.93	0.00
-17.88	-20.27	-19.22	1.82	-19.15	1.63	-19.44	2.44	-18.96	1.19	-18.92	1.08	-18.07	0.04
Total		-19.16	1.52	-18.87	1.03	-18.59	0.98	-19.11	1.37	-19.29	1.81	-17.60	0.41

Appendix 3.3. Comparing carbon and nitrogen values from long-finned pilot whale *Globicephala melas edwardii* skin processed at two different facilities.



Comparison of normalised $\delta^{13}C$ and $\delta^{15}N$ values of long-finned pilot whales (*Globicephala melas edwardii*). Lab 1 (Environmental and Ecological Stable Isotope Analytical Facility, National Institute of Water and Atmosphere; Taihoro Nukurangi), Lab 2 (IsoTrace Limited). Figure from Supplementary material of Hinton et al. (2022).

Appendix 3.4. Summary of isotope values from long-finned pilot whale *Globicephala melas edwardii* skin

Range of carbon, nitrogen, and sulphur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), including lipid-corrected and Suess-corrected $\delta^{13}C$ values and C:N mass ratios of long-finned pilot whales *Globicephala melas edwardii*. Where duplicate samples were performed, the mean is given. Lab 1 = Environmental and Ecological Stable Isotope Analytical Facility, National Institute of Water and Atmosphere (Taihoro Nukurangi), Lab 2 = IsoTrace Limited. Table from Supplementary material of Hinton et al. (2022).

	n	**Normalised $\delta^{13}C$**	**Lipid corrected $\delta^{13}C$**	**Number lipid corrected**	**Suess corrected $\delta^{13}C$**	**Normalised $\delta^{15}N$**	**C:N ratio**	**$\delta^{34}S$**
Full dataset Lab 1	125	-20.47 to -15.72	-18.80 to -15.66	71	-18.80 to -15.53	11.52 to 16.28	3.06 to 4.48	-
Subset Lab 1	36	-20.47 to -16.28	-18.77 to -15.96	18	-18.57 to -15.82	11.52 to 16.28	3.08 to 4.48	-
Subset Lab 2	36	-20.62 to -17.19	-	-	-	11.73 to 15.48	3.05 to 4.48	18.61 to 22.91

Appendix 3.5. Summary of niche model outputs

Isotopic niche total area (TA), standard ellipse area (SEA) and standard ellipse area corrected (SEAc) of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) values for different reproductive status of long-finned pilot whales (*Globicephala melas edwardii*). Data are presented by location of stranding of *G. m. edwardii*. Table from Supplementary material of Hinton et al. (2022).

	Farewell Spit					Stewart Island			
		Male	Female				Male	Female	
	Immature	Mature	Pregnant	Lactating	Resting	Immature	Mature	Pregnant	Resting
TA	2.98	2.23	3.14	0.74	1.49	1.98	0.30	0.38	0.33
SEA	0.79	1.21	1.75	0.64	1.34	0.61	0.23	0.23	0.38
SEAc	0.82	1.33	1.96	0.77	1.67	0.65	0.27	0.27	0.57

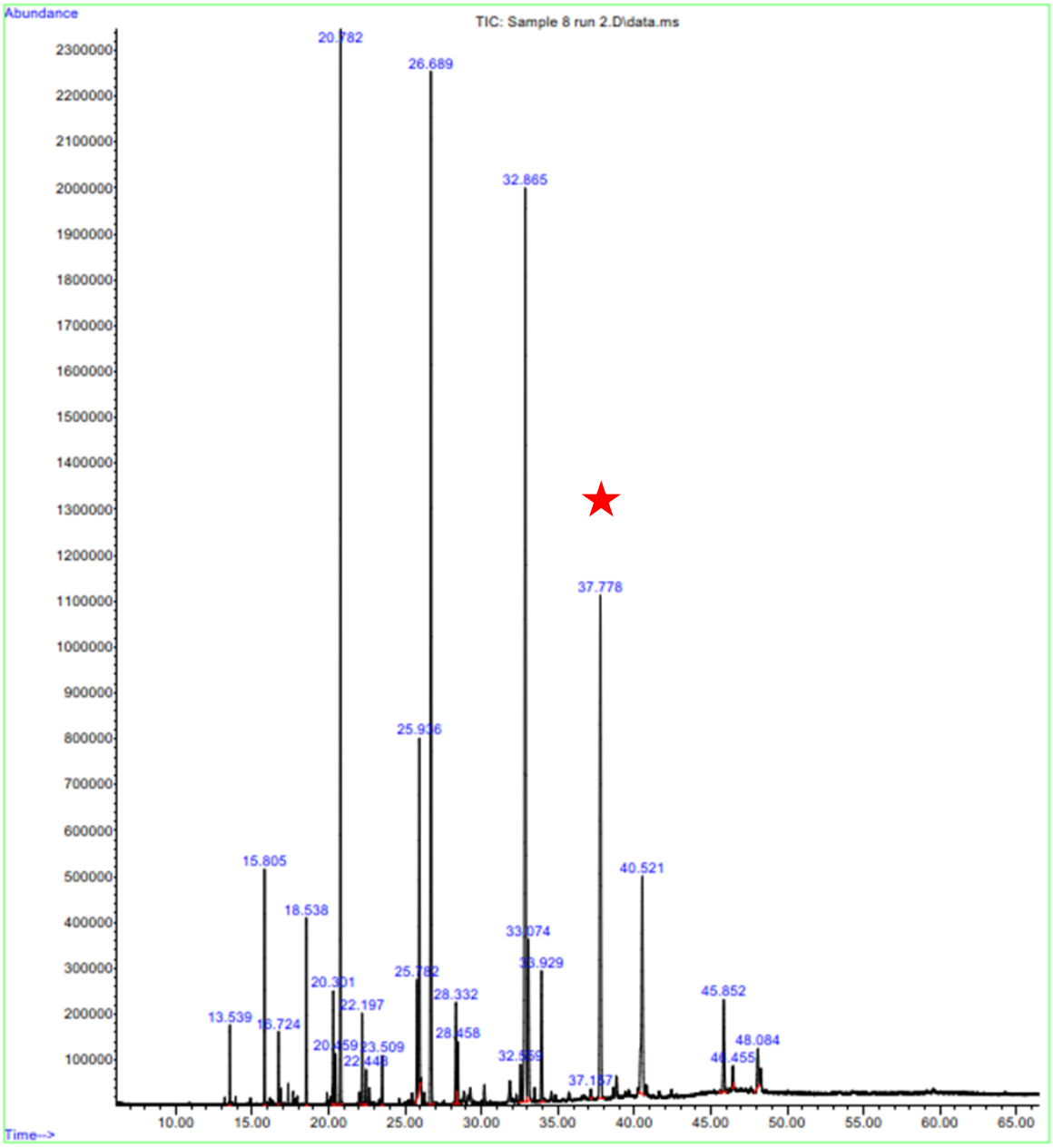
Appendix 4.1. Index of relative importance of prey found in stomachs of long-finned pilot whales Globicephala meals edwardii stranded at Farewell Spit

Index of relative importance of prey from long-finned pilot whales (*Globicephala melas edwardii*) stranded at Farewell Spit, New Zaeland between 2009 and 2017. Stomach contents are presented as counts of each item, which have been summed across forestomach, mainstomach and pyloric stomach. % FO = percentage frequency of occurrence, IRI = index of relative importance. The top five prey to diet (as estimated by %IRI) are labelled in bold.

Species	%FO	Number	Mass (kg)	% Number	% Mass	IRI	% IRI
***Congridae* sp.**	5.04	33.00	53973.70	1.09	5.41	0.33	**0.2369**
***Cephoscyllium* sp.**	0.39	7.00	12170.27	0.23	1.22	0.01	**0.0041**
Macruronus novaezelandiae	0.78	5.00	2790.81	0.16	0.28	0.00	**0.0025**
Lycoteuthis lorigera	0.39	2.00	143.47	0.07	0.01	0.00	0.0002
***Nototodarus* spp.**	79.46	2714.00	804432.05	89.34	80.64	135.05	**97.7202**
Pinnoctopus cordiformis	13.18	275.00	122660.94	9.05	12.30	2.81	**2.0355**
Teuthowenia pellucida	0.39	1.00	14.31	0.03	0.00	0.00	0.0001
Arripis trutta	0.39	1.00	1418.64	0.03	0.14	0.00	0.0005

Appendix 4.2. Example chromatogram

Example chromatogram used to identify fatty acids from blubber of long-finned pilot whales (*Globicephala melas edwardii*) stranded on the New Zealand coast, at Farewell Spit in January 2014. The red star shows the internal standard, C19.



Appendix 4.3. SIMPER model outputs

Similarity percentages (SIMPER) of fatty acids most contributing to dissimilarity between carpet shark (*Cephaloscyllium* sp.) and long-finned pilot whales (*Globicephala melas edwardii*) from New Zealand waters in 2010/2011 and 2014. The top seven fatty acids are presented as cumulative percentage dissimilarity.

Fatty acid	Cumulative contribution to dissimilarity
C22.1n11	0.07650689
C20.1n11	0.16654830
C18.2n6	0.26187170
C20.4n6	0.37208834
C20.1n9	0.48655210
C22.1n13	0.62695028
DHA	0.80380643

Appendix 4.4. Summary of stable isotope values of long-finned pilot whales *Globicephala melas edwardii* and their prey

Carbon, nitrogen and sulphur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) stable isotope values and C:N mass ratio values of skin from long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) involved in a mass stranding at Farewell Spit, New Zealand in 2014 and muscle from five of their key prey species. Carbon isotope values reported were lipid-corrected if mass C:N ratio >3.5 using equations from Peters et al. (2022) and Post et al. (2007). All $\delta^{13}C$ values were corrected for the Suess effect (Quay et al. 2003). Where multiple replicates were performed, the mean is given. *M. novaezelandiae = Macruronus novaezelandiae, P. cordiformis = Pinnoctopus cordiformis.*

ID	Class	Species	C:N ratio	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
AS1	Prey	*Nototodarus* spp.	3.41	-19.30	12.05	22.03
AS2	Prey	*Nototodarus* spp.	3.32	-19.65	9.85	22.10
AS3	Prey	*Nototodarus* spp.	3.46	-18.66	13.71	18.94
CE1	Prey	*Congridae* sp.	3.75	-17.32	17.28	23.19
CE2	Prey	*Congridae* sp.	4.06	-17.75	17.04	21.99
CE3	Prey	*Congridae* sp.	3.76	-17.68	17.62	21.09
S1	Prey	*Cephaloscyllium* sp.	3.75	-17.68	17.22	20.37
S2	Prey	*Cephaloscyllium* sp.	3.37	-17.28	14.82	NA
S3	Prey	*Cephaloscyllium* sp.	3.43	-17.40	14.53	NA
H1	Prey	*M. novaezelandiae*	3.06	-17.87	14.21	22.30
H2	Prey	*M. novaezelandiae*	3.06	-18.25	13.84	22.28
H3	Prey	*M. novaezelandiae*	3.11	-18.14	13.88	22.58
O1	Prey	*P. cordiformis*	3.35	-17.29	13.31	21.00
O2	Prey	*P. cordiformis*	3.34	-17.38	13.61	21.19
O3	Prey	*P. cordiformis*	3.34	-17.25	13.78	21.79
PW1	Consumer	LFPW	3.52	-17.07	12.34	NA
PW2	Consumer	LFPW	3.46	-18.21	12.07	NA
PW3	Consumer	LFPW	3.65	-17.26	12.07	NA
PW4	Consumer	LFPW	3.67	-17.31	12.63	NA
PW5	Consumer	LFPW	3.47	-18.50	12.14	NA
PW6	Consumer	LFPW	3.51	-17.01	12.16	NA
PW7	Consumer	LFPW	3.57	-17.15	12.28	NA
PW8	Consumer	LFPW	3.68	-17.29	12.49	NA
PW9	Consumer	LFPW	3.53	-17.11	11.83	NA
PW10	Consumer	LFPW	3.69	-17.40	11.85	NA
PW11	Consumer	LFPW	3.37	-18.23	11.92	NA
PW12	Consumer	LFPW	3.51	-17.32	11.52	21.75
PW13	Consumer	LFPW	3.64	-17.24	12.20	NA
PW14	Consumer	LFPW	3.42	-18.49	11.90	NA
PW15	Consumer	LFPW	3.44	-18.65	11.72	NA

Appendix 4.5. Prey polygon probabilities

Probabilities that long-finned pilot whale (*Globicephala melas edwardii*) carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) stable isotope values fell within the of 95% confidence interval of the prey polygon mixing region Model 1: uses trophic discrimination factors of LFPW collagen from R package SIDER, Model 2: uses trophic discrimination factors of $\delta^{13}C$ from LFPW collagen from R package SIDER ($\delta^{15}N$ 3.46 ± 1.60, $\delta^{13}C$ 1.57 ± 2.03; Healy et al. 2018) and $\delta^{15}N$ TDFs ($\delta^{15}N$ 1.7 ± 0.24; $\delta^{13}C$ 1.57 ± 2.03) from Abend and Smith (1997).

ID	Probability Model 1	Probability Model 2
PW1	0.015	0.066
PW2	0.013	0.036
PW3	0.010	0.045
PW4	0.020	0.080
PW5	0.011	0.036
PW6	0.010	0.055
PW7	0.011	0.063
PW8	0.015	0.073
PW9	0.007	0.039
PW10	0.007	0.039
PW11	0.010	0.028
PW12	0.005	0.030
PW13	0.011	0.055
PW14	0.008	0.027
PW15	0.007	0.021

Appendix 4.6. Prey remains found in long-finned pilot whales (*Globicephala melas edwardii)* assessed in Chapter 4

Stomach contents of long-finned pilot whales (*Globicephala melas edwardii*) stranded at Farewell Spit in January 2014. Stomach contents are presented as counts of each item, which have been summed across forestomach, mainstomach and pyloric stomach. Eel remains are all jaw, premaxilla, otolith and head to the right of the dotted line. * denotes that the tissue was unidentified due to small volume.

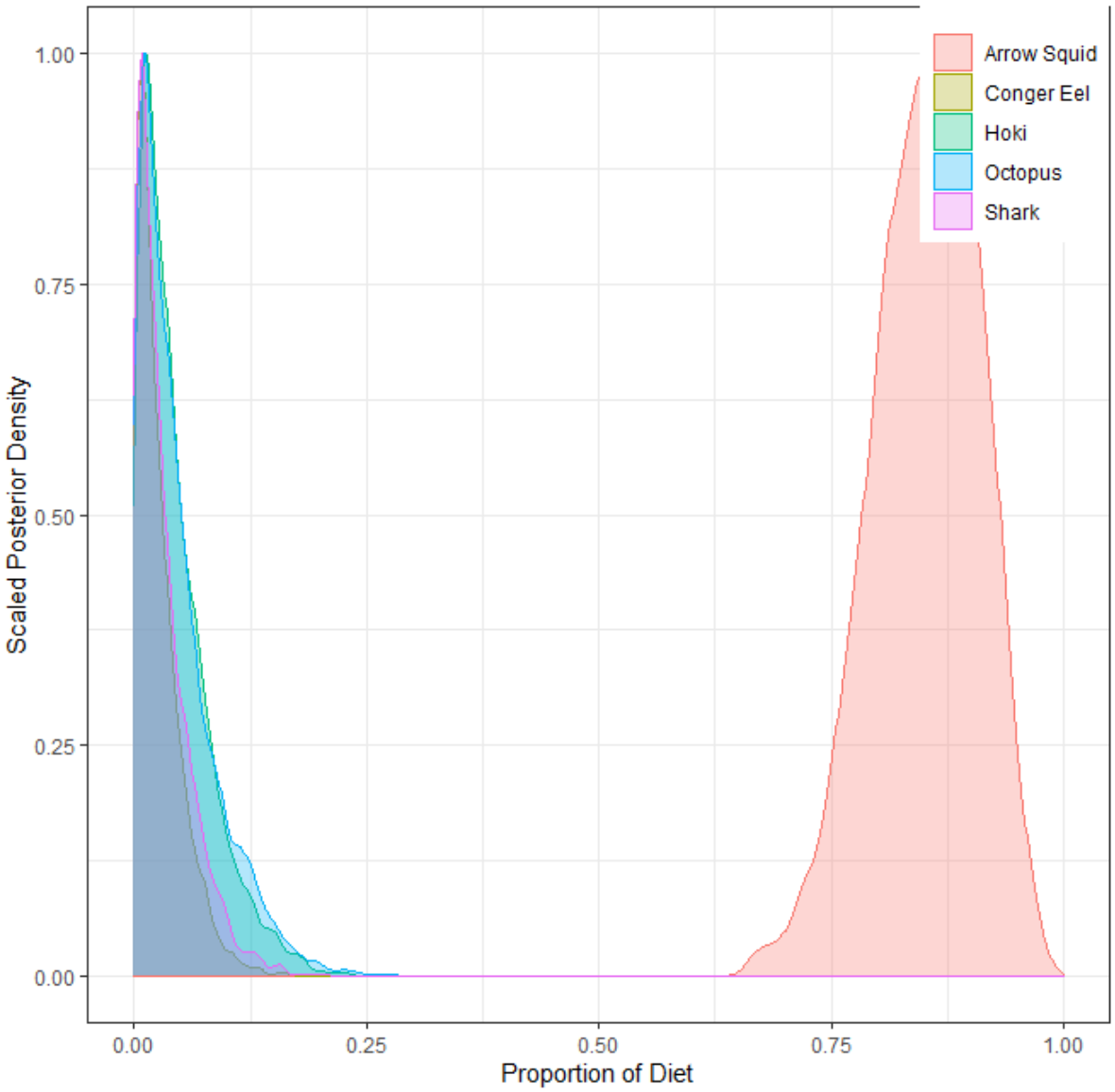
					Eel remains			
ID	Arrow Squid beaks	Upper beaks	Cephalopod eye lenses	Tissue*	Jaw	Premaxilla	Otolith	Head
PW1	13	12	16	0	0	0	0	0
PW2	40	21	112	0	0	0	0	0
PW3	4	4	11	0	0	0	0	0
PW4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
PW5	0	1	0	0	0	0	0	0
PW6	26	18	38	0	0	0	0	0
PW7	10	6	20	0	0	0	0	0
PW8	2	1	0	0	0	0	0	0
PW9	75	67	119	0	0	0	0	0
PW10	4	2	9	0	1	1	0	1
PW11	47	52	68	0	0	0	0	0
PW12	16	10	12	0	3	0	1	1
PW13	0	2	0	1	0	0	0	0
PW14	3	4	4	0	0	0	0	0
PW15	1	0	0	0	0	0	0	0

Appendix 4.7. Bayesian modelling

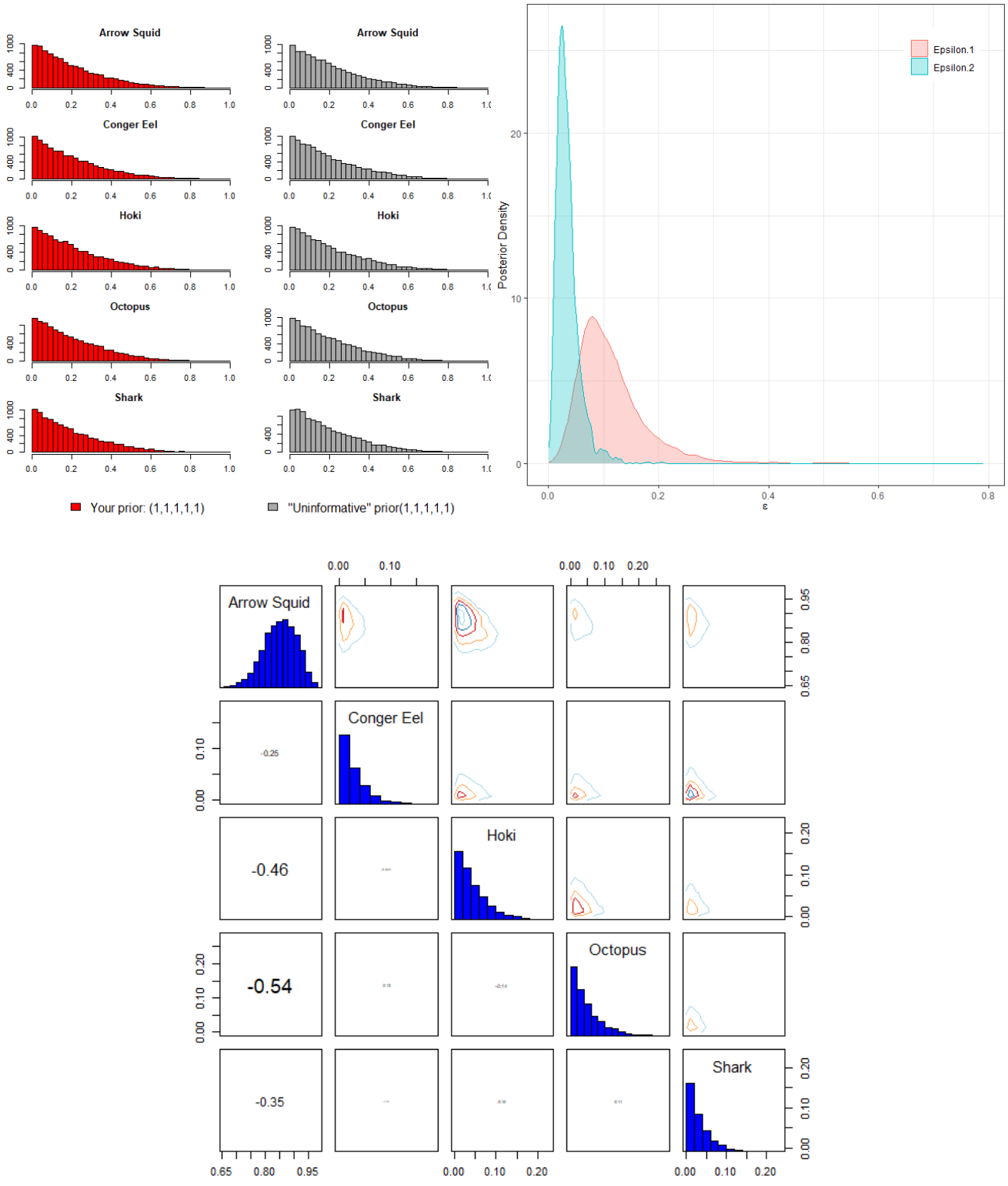
Prey polygons suggested that a proportion of diet was missing from analysis (Chapter 5), and therefore Bayesian analysis was not appropriate for this data (Smith et al. 2013). However, as long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) may rely heavily on one prey type (arrow squid *Nototodarus* spp., Chapter 2), this could partially explain why prey polygons revealed that data were not appropriate for Bayesian mixing model analysis. Bayesian mixing models were run on carbon and nitrogen stable isotope values of five key species to LFPW diet at Farewell Spit: arrow squid *Nototodarus* spp., conger eel *Congridae* sp, hoki *Macruronus novaezelandiae*, common octopus *Pinnoctopus cordiformis*, and carpet shark *Cephaloscyllium* sp. Uninformed priors only were used to see what results would have suggested if mixing models had been deemed appropriate. Results were largely consistent with stomach contents data presented in Chapter 2; whereby arrow squid were deemed the most important prey taxa to diet (74.1 – 94.8 % of diet) followed by common octopus *Pinnoctopus cordiformis* (0.1 – 13.5% of diet).

Proportional contribution of each prey species to LFPW diet calculated using uninformed priors. DIC = deviance information criterion, Proportions reported are the 2.5 – 97.5% confidence intervals.

Model	Priors	DIC	*Nototodarus* spp.	*Congridae* sp.	*Macruronus novaezelandiae*	*Pinnoctopus cordiformis*	*Cephaloscyllium* sp.
1	Uninformed	28.40	0.741 – 0.948	0.001 – 0.091	0.001 – 0.135	0.001 – 0.153	0.001 – 0.115



Estimated relative contribution to long-finned pilot whale (*Globicephala melas edwardii*) of five key prey spices involved in a mass stranding at Farewell Spit, New Zealand in 2014. The model that best fit the data used uniformed priors, so assuming each combination of prey was equally likely, ran using the MixSiar (Blake et al. 2018) in R, using 100,000 iterations, and had a burn-in of 50,000 thinning to 50. Shark referes to *Cephaloscyllium* sp.



Prior and epsilon distribution of the Bayesian isotope mixing model (uniformed priors) of contribution of prey species to long-finned pilot whale (*Globicephala melas edwardii*) diet. The model used uninformed priors, ran 100,000 iterations, and had a burn-in of 50,000 thinning to 50.

Appendix 5.1. Blubber lipid extraction method development

Two commonly used blubber lipid extraction methodologies (Folch et al. 1957; Bligh and Dyer 1959) were tested for appropriate methodology and sample mass prior to lipid extraction. A total of four blubber sub-samples were taken from a single long-finned pilot whale. Samples were weighed to 0.001 mg into a Kimax glass 15 mL test tube. Two mass categories over two different methodologies were tested, one of approximately 15 mg and the other of approximately 40 mg of sample.

For method one (Folch et al. 1957), all samples were transferred to 3 mL of chloroform:methanol:water (2:1:1.6, v:v:v) solution and left for approximately 20 hours. After 5 hours and 20 hours, samples were put on the vortex for 20 seconds each. After the second vortex, 1 mL of chloroform:water (1:1, v:v) solution was added to each sample for 4 hours. After 4 hours the lower chloroform phase was collected and put into a second pre-weighed tube. This phase was put under a stream of nitrogen gas whilst being heated to 45 °C for 1 hour. The second tube was weighed, with the mass of total lipid extracted from the mass of the starting sample to obtain a %lipid.

For method two, following (Bligh and Dyer 1959) 3.75 mL of chlorofrom:methanol (1:2, v:v) solution was added to samples, which were then vortexed for 4 minutes. A further 1.25 mL of chloroform was added to samples before a second vortex for 2 minutes. Following this, 1.25 mL of 8% NaCl in milliQ water was added to the sample followed by a final vortex for 1 minute. The sample and solution were put into the centrifuge at 2,000 rpm for 5 minutes. The bottom layer was extracted from the solution by first inserting a short plastic pipette, and a long glass pipette inside that in order to remove all lipids from the bottom layer. The bottom layer of sample was placed into a pre-weighed Kimax tube. The bottom layer was dried using a steady stream of nitrogen gas at room temperature for 1 hour. As this did not fully dry the solution, samples were heated to 40 °C whilst

under a stream of nitrogen gas for a further hour to remove the final residues of solvent. The Kimax tube containing lipid only was then weighed to 0.001 mg. The weight of the Kimax tube with sample was subtracted from the weight of tube without solvent in order to obtain the weight of the lipids only.

The smaller sample size had limited success with lipid extraction. Samples were kept under the nitrogen stream for three hours and were weighed every hour with no change in lipid weight. Of the samples that worked, the modified Bligh and Dyer (1959) method showed a higher lipid content than the modified Folch (1959) method, which had also been seen in Grahl Neilsen et al (2010). A sample of 40 mg was chosen using the Bligh and Dyer method for further analysis.

Methodology (Bligh and Dyer = Bligh and Dyer 1959; Folch = Folch 1957), sample mass, tube mass and lipid content (%) of lipid extracted from blubber of long-finned pilot whales *Globicephala melas edwardii*.

Method	Sample mass (mg)	Lipid weight (mg)	Lipid content (%)
Bligh and Dyer	38.272	26.503	69.249
Folch	36.993	17.794	48.101
Bligh and Dyer	14.345	14.537	101.338
Folch	18.543	88.945	479.669

Appendix 5.2. Effects of total body length of long-finned pilot whales (LFPWs; *Globicephala melas edwardii*) on body condition measurements

The total body length (TBL) of LFPWs was regressed against each body condition measurement to check for the effects of TBL, general linear models (e.g., Raverty et al. 2020) were used to assess significant correlation. Girth, lateral and ventral blubber thickness were significantly correlated with TBL, whereas dorsal blubber thickness, and lipid content were not.

General linear models with t value (t) and significance of correlation (*p*-value) of total body length (TBL) of long-finned pilot whales stranded in New Zealand 2014 against their body condition measurements. Girth = axillary girth, Dorsal = dorsal blubber thickness, Lateral = lateral blubber thickness, Ventral = Ventral blubber thickness, Lipid = % lipid content from inner blubber layer in dorsal region.

Measurement	Variable	t	*p*-value
TBL	Girth	4.383	**<0.05**
	Dorsal	1.235	0.239
	Lateral	3.001	**<0.05**
	Ventral	3.395	**<0.05**
	Lipid	-0.041	0.968

Appendix 5.3 Effects of total body length of long-finned pilot whales (LFPWs; *Globicephala melas edwardii;* LFPWs) on fatty acid measurements

Girth and ventral blubber thickness were correlated with total body length (TBL; Appendix 5.2) and were explanatory variables for fatty acid variation in Generalised Linear Mixed Effects Models in Chapter 5. However, TBL had been removed from GLMs due to high correlation with co-variables. To further explore these relationships, the correlation between TBL and each fatty acid group was assessed via general linear models. Whilst saturated fatty acids significantly varied with TBL, the other fatty acid groups did not. Optimal GLM models of monounsaturated fatty acids, polyunsaturated fatty acids, C20:1n9, C20:1n11 and DHA should be unaffected by TBL. A larger sample size would help to further explore these relationships.

General linear models with t value (t) and significance of correlation (*p*-value) of total body length (TBL) of long-finned pilot whales stranded in New Zealand 2014 against fatty acid groups. SFAs = saturated fatty acids, MUFAs = monounsaturated fatty acids, PUFAs = polyunsaturated fatty acids.

Measurement	Variable	t	*p*-value
TBL	SFAs	2.884	**0.013**
	MUFAs	-1.934	0.076
	PUFAs	-1.141	0.274
	C20:1n9	1.637	0.126
	C20:1n11	-1.307	0.214
	DHA	0.432	0.673