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Sperm whale diet in New Zealand

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List of abbreviations

km kilometre

m metre

cm centimetre mm millimetre

°C degrees Celsius

° degree (e.g., of latitude, longitude)

' minute (e.g., of latitude, longitude)

kg kilogram

g gram

sp. species singular

spp. species plural

% percentage

EOS Earth and Oceanic Sciences Research Institute

AUT Auckland University of Technology

IWC International Whaling Commission

LRL lower rostral length

ML dorsal mantle length

BM body mass

EEZ Exclusive Economic Zone

NZMS New Zealand Marine Society

DoC Department of Conservation

MFish Ministry of Fisheries

FoO frequency of occurrence

pers. comm. personal communication

pers. obs. personal observation

t/T tonne

SE standard error

Abstract

Stomach contents of 19 mature sperm whales, 18 males and one female, that stranded on New Zealand beaches between the mid 1990s and 2004 were examined, identified and measured. Three of the stomachs were empty. All other samples consisted almost entirely of cephalopod beaks. A total of 23,223 cephalopod beaks (10,647 upper and 12,576 lower), representing at least 36 species in 17 families were found in the remaining 16 stomachs. Non-cephalopod remains in the stomachs of sperm whales stranded in New Zealand included limited quantities of fish, salps, crustacean exoskeletons, a copepod, some wood and sand.

The present investigation represents the most comprehensive study of the diet of sperm whales in New Zealand since the early 1960s. The results show that oceanic squid of the families Histioteuthidae, Cranchiidae, Onychoteuthidae and Octopoteuthidae are the most common remains found in the stomachs of sperm whales stranded on New Zealand beaches, with the families Onychoteuthidae, Histioteuthidae, Octopoteuthidae and Architeuthidae being the most important by estimated weight in whale diet, and the families Cranchiidae, Pholidoteuthidae and Ancistrocheiridae secondarily so.

The beaks of three cephalopod species thought to be restricted to Antarctic waters (*Kondakovia longimana, Mesonychoteuthis hamiltoni* and *Psychroteuthis glacialis*) were found in 12 of the stomachs, suggesting these whales had recently migrated into New Zealand from more southern feeding grounds. The amount of local cephalopod beaks in the stomachs suggests some of the stranded sperm whales did not feed much within New Zealand waters in the days prior to stranding.

The beaks of *Taningia danae*, *Octopoteuthis megaptera*, *Octopoteuthis* sp. 'Giant' and *Lepidoteuthis grimaldii* are illustrated and described. Oblique and

lateral illustrations of the lower beaks are given, as well as sections of the rostrum, jaw angle, shoulder and lateral wall, to show the major identifying features for each of the species.

Squid are an important component of food chains in the Southern Ocean and they act as both high-level predators and prey for apex predators. Therefore, seasonal fluctuations in their abundance must have cascading effects on the diets of apex predators. With increasing global fishing effort, and with cephalopods representing over 4% of the global annual catch, there are competing interests between the ocean's top teuthophagous predators and the fishing industry.

Uncertainty of the effects fisheries have on the marine ecosystem has stimulated numerous research studies in recent years. However, despite the economic and ecological importance of cephalopods, there are few ecological studies on them or their significance in the trophic systems of the deep-sea and their life cycles and distribution patterns are only now beginning to be understood. Additional dietary studies that investigate the cephalopod composition and size-class structure in the diet of predators are needed to assess their importance in deep-sea food webs, and the potential impact that deep-sea fisheries might have on associated and dependant species, namely apex oceanic predators.

The results of this study provide the first significant insight into the diet of the sperm whale, one of the most important apex predators in New Zealand waters.

Chapter 1

Introduction

Studies on the diet of the sperm whale, *Physeter macrocephalus*, have shown that they prey mainly on cephalopods, while fish have proven to be regionally important, off Iceland, New Zealand and Antarctica (Gaskin & Cawthorn 1967a, 1967b, Klumov 1971, Clarke 1980, Martin & Clarke 1986, Clarke *et al.* 1993, Clarke & Pascoe 1997, Evans & Hindell 2004). The cosmopolitan distribution, large biomass and voracious appetite of the sperm whale, make it one of the most important oceanic predators, and they have been estimated to consume more cephalopods annually than the biomass of fish removed from the ocean by humans every year (Lockyer 1981, Rice 1989, Clarke *et al.* 1993, Clarke 2003).

It is frequently stated that many cephalopods found in the diet of sperm whales are rarely caught in nets, and even those specifically designed by researchers for their capture, often sample cephalopods that are smaller in size than the ones consumed by the whales (Clarke et al. 1976, Clarke & Young 1998, Xavier et al. 2002, Clarke 2003). However, the same does not entirely apply to waters surrounding New Zealand, where large-bodied squid are regularly retained in deep-sea commercial fishing nets. Nevertheless, dietary studies on sperm whales and other predators, have revealed a large amount of new information about the distribution, size range, growth, reproduction, and other aspects of cephalopod and predator biology (Clarke 1996b, 1996c). Historically, teuthologists used this source of material to describe new or redescribe old species of squid, contributing to our scientific knowledge of the marine environment and the species that are an important part of deep-sea food webs.

In and around New Zealand waters the diet of sperm whales is poorly known, having been reported on three occasions only: from commercially caught whales

from the vicinity of Cook Strait; from whales caught in the Tasman Sea, off north-western New Zealand; and from a stranded individual on west coast, North Island. In each account, the diet was reconstructed by identification of stomach contents. Gaskin and Cawthorn (1967a, b), reported the diet from stomach samples of sperm whales caught in the 1960s in the Cook Strait region, extending from Wairarapa to Kaikoura, central New Zealand; Clarke & MacLeod (1982) reported the diet from stomach samples of sperm whales caught in 1970 in the Tasman Sea and north-western New Zealand; and Clarke and Roper (1998) reported the complete stomach contents of a single individual that stranded on a south-western North Island beach in 1996.

The stomach contents of an additional 19 sperm whales that stranded on New Zealand beaches are reported here: 18 whales that stranded between 2002 and 2004, and one for which no precise stranding data is available the stomachs of three of these whales were empty. This newly reported collection is the largest thus-far reported from New Zealand. These stomach contents provide an opportunity to evaluate current diet and contrast it with historical accounts for the sperm whale, and offer new means to investigate sperm whale migrations in the region.

1.1 Objectives and thesis structure

Prior to 2000, the diet of the sperm whale in or adjacent to New Zealand waters was known only from three investigations. A unique opportunity to learn more about the natural history of this protected marine mammal and its prey, mainly deep-sea cephalopods was presented when 18 individuals stranded on New Zealand beaches between 2002 and 2004. A further sample was sourced from the Museum of New Zealand, although collection details are not precise.

Comparative analyses of the diets of marine apex predators, like the sperm whale, can substantially improve our knowledge of the marine environment (Evans & Hindell 2004). In addition to the knowledge gained about the predator,

dietary studies can help to determine the prey species' ecology, distribution, relative abundance, seasonal variations, and growth (Santos *et al.* 2001a). Dietary studies can also indicate possible fluctuations in community structure, and are useful in the development of predator-prey models (Santos *et al.* 2001a). These studies are the first step in determining the trophic relationships of the ocean, and can provide some of the necessary information for the management of otherwise poorly known marine systems.

Accordingly, the objectives of the present study are:

- To determine the current diet of the sperm whale in New Zealand waters through the identification of remains found in the stomachs of recently stranded whales.
- To compare current and historical dietary accounts.

1.2 Thesis outline

In accordance with these thesis objectives, Chapter 2 describes different aspects of the biology and ecology of the sperm whale, and reviews the diet of this species in the Atlantic, Pacific and Southern Oceans.

- Chapter 3 explains the materials and methods used for the collection, processing and analysis of samples, as well as the techniques used for beak description.
- Chapter 4 the results are divided into three sections. Section 1 reports the cephalopod component of the diet by individual whale (by cephalopod species); section 2 reports the non-cephalopod component of the diet; and section 3 presents detailed descriptions for lower beaks of species in the family Octopoteuthidae and Lepidoteuthidae that have proven problematic to identify.

Chapter 5 the general discussion is divided into six sections. Section 1 discusses the current diet of sperm whales in New Zealand compared to that of historical accounts including the size of cephalopods consumed, secondarily ingested prey, the retention times for prey remains and possible causes for stranding; section 2 compares the diet between New Zealand stranded sperm whales, and the relevance of regurgitation and stomach fullness; section 3 discusses descriptions of migration as reconstructed from cephalopod diet; section 4 discusses the beaks described in section 4.3; section 5 makes recommendations, presents possibilities for future research and describes the limitations of this study; and finally, section 6 presents the conclusions of this study.

Chapter 2

Literature review

The sperm whale, *Physeter macrocephalus* Linnaeus,1758, is the only species in the monophyletic family Physeteridae and is the most sexually dimorphic member of the toothed whales of the suborder Odontoceti (Rice 1989). This whale is an ecologically important oceanic predator (mainly of mesopelagic cephalopods), that occurs in all of the world's oceans (Clarke *et al.* 1976, Rice 1989, Rendell *et al.* 2004).

2.1 Sperm whale biology

2.1.1 Anatomy of the sperm whale

The sperm whale is the largest species in the suborder Odontoceti, with males reaching maximum lengths of 18–21 m and weights of 60 t, and females lengths up to 12 m and weights of 30 t (Berzin 1971). Adult sperm whales have a mean weight of approximately 40 t. At birth both male and female calves average 4 m in length and weigh approximately 1 t (Gosho *et al.* 1984).

The genus name *Physeter*, means 'blower', and the species name *macrocephalus* means 'big head'. The distinctive head of the sperm whale, which can be up to one third of the body length and one fourth of the body mass, contains the spermaceti organ and the junk (Berzin 1971, Clarke 1978). The spermaceti organ produces the highly valued spermaceti oil for which this species was extensively hunted during the 18th to 20th Centuries. The junk, which lies under the spermaceti organ and is derived from the odontocete melon, is filled with denser, less-valued oil (Berzin 1971, Carrier *et al.* 2002). The specific roles of the structures that make up the nasal complex of the sperm whale are

still unclear but several theories have been advanced (Raven & Gregory 1933, Norris & Harvey 1972, Clarke 1978, Carrier *et al.* 2002).

The unique forehead of the sperm whale and its role in the sinking of the Essex in 1820, inspired Melville's novel "Moby Dick". However, the spermaceti organ and the anatomical dimorphism of male and female sperm whales have significant implications on the feeding biology and ecology of both genders. The spermaceti organ is thought to function as a powerful sonar that allows prey echolocation, and males are known to dive deeper and for longer periods of time than females, migrating to higher latitudes in their search for food (Gosho *et al.* 1984, Rice 1989). This will affect the prey species that males and females encounter and will be reflected in the composition of the diet of both genders.

The spermaceti organ

The spermaceti organ and nasal passages of the sperm whale have been extensively described and studied; several theories have been proposed about the possible functions and evolution of the system (Raven & Gregory 1933, Berzin 1971, Carrier *et al.* 2002). It has been suggested that these structures function as a biosonar to locate prey, for acoustic sexual selection, and for buoyancy control (Clarke 1978). The production of sound by sperm whales may serve in male-male agonistic competition, as evidenced by head-butting during aggressive behaviour (Carrier *et al.* 2002); it could indicate the size of males to females (Norris & Harvey 1972, Cranford 1999, Møhl 2001, Møhl *et al.* 2003); and it could be also used for acoustic debilitation of prey (Norris & Møhl 1983, Møhl *et al.* 2000, Miller *et al.* 2004).

Although the functions of the huge nasal complex have not been definitely proven, it is evident that the sperm whale uses it to produce and direct a wide variety of sounds (Madsen *et al.* 2002), including slow clicks, codas, 'creaks' and usual clicks (Whitehead & Weilgart 1991, Weilgart & Whitehead 1997, Zimmer *et al.* 2005). Usual clicks, because of their elevated source levels and high

directionality, are used for locating prey and can also provide orientation cues to the whale (Møhl *et al.* 2003, Zimmer *et al.* 2005). Creaks, which are clicks with high repetition rates, seem analogous to the buzzes produced by bats as they close in on prey (Gordon 1987b, Miller *et al.* 2004). Slow clicks, believed to provide conspecifics information about individual size, are used as acoustic displays during male-female and male-male interactions (Gordon 1987b, Weilgart & Whitehead 1988) and for echolocation (Goold 1999, Tyack & Clark 2000). Codas, stereotyped repetitive patterns of clicks produced when sperm whales are in groups socialising at the surface, appear to aid in social cohesion (Weilgart & Whitehead 1988, 1997).

Feeding and the alimentary canal

A full description of the digestive system of the sperm whale can be found in Berzin (1971). The sperm whale has 17–29 pairs of teeth in its lower jaw, which can attain lengths of up to 27 cm (Berzin 1971). The teeth in the upper jaw rarely erupt in juvenile whales and are deeply curved, and absent or atrophied in adults (Gibbs & Kirk 2001). The mouth, tongue, oesophagus and first stomach are covered with a tough cuticular lining that is thought to protect the whale from the hooks and beaks of struggling squids (Clarke 1980). In New Zealand, the teeth and lower jaw of the sperm whale have an important cultural value. Maori use the jawbone and teeth for carving highly priced pendants, *taonga* or *rei puta* as well as combs, clubs and cloak pins (Kitea Tipuna pers. comm.*). Scientists can also use teeth to determine an individual's age, its exposure to environmental pollutants, its general health, its reproductive history and growth rates (Evans & Robertson 2001, Evans *et al.* 2002).

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How sperm whales catch their prey can only be inferred from dietary examination (stomach content analysis), functional analyses of the sperm whale's anatomy, and examination of the distribution, abundance and nature of scars in their skin. It is thought that after capturing the prey, the sperm whale swallows it by moving forward with little or no aid of the tongue, as nearly undamaged flesh of cephalopods and fish was often found in the first stomach of commercially caught whales (Berzin 1971, Clarke 1976, 1980, Martin & Clarke 1986). Digestive juices are secreted in the second stomach, acting on the flesh and digesting it. The hard parts of the prey, such as fish bones and otoliths, and the chitinous beaks of cephalopods, all withstanding chemical digestion to a certain extent and tend to accumulate in the second stomach for several days or even weeks (Clarke 1980).

From bioacoustical and dietary studies it is known that sperm whales are slow animals that feed at great depths, where there is no light except for bioluminescence (Heezen 1957, Nemoto & Nasu 1963, Clarke 1976, Watkins 1980, Watkins *et al.* 1993). Bioluminescent cephalopods can comprise 0–97% of the diet of sperm whales in different areas and slow swimming, neutrally buoyant cephalopod species comprise 82% of the diet of sperm whales in the central Atlantic (Clarke 1980, Clarke *et al.* 1993). Light emitted by prey could be used by the sperm whale to locate it but the way that they capture fast swimming cephalopods is still debated (Miller *et al.* 2004).

Ambergris, a non-volatile alcohol of high molecular weight, forms in the large intestine and can be found in 1–5% of sperm whales (Rice 1989). It can be found in lumps of up to 10 kg, often with cephalopod beaks embedded in it. It is highly valued in the perfume industry and, since the protection of the sperm whale came into force in 1985, many attempts have been made to find synthetic substitutes; several of them have become commercially important products for the perfume industry (Giacomini *et al.* 2003).

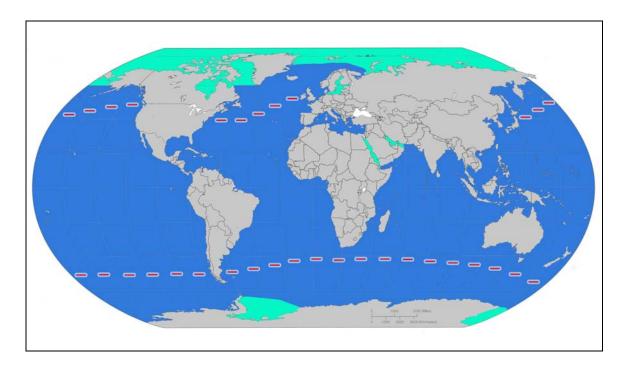
Ambergris was found in one of the samples recovered from a female sperm whale stranded near Napier. Officers from the Department of Conservation (DoC) reported this whale had peritonitis, which could have possibly caused or contributed to the stranding of this animal.

2.1.2 Distribution and migration

Sperm whales are found throughout the world's deep oceans, from the tropical waters of the equator to the polar regions (Berzin 1971, Best 1979). The distribution of this species is determined by gender and age group, and is closely related to prey availability and various oceanic factors like bathymetry, and primary and secondary productivity (Jaquet *et al.* 1996, Davis *et al.* 2002). Sperm whales appear to concentrate around highly productive areas, around the deep waters of steep continental shelves and oceanic islands. They also converge around areas with strong temperature gradients, which provide optimal conditions for the schooling of their main prey, cephalopods (Uda 1959, Clarke 1996b, Jarre-Teichmann 1998).

Mature males and females exhibit different distributional and diving behaviours, and spend most of their adult lives segregated (Berzin 1971, Best 1979, Clarke *et al.* 1993). Mature females, calves and juveniles form social groups that inhabit tropical and temperate waters year-round, and have ranges of approximately 1,000 km over time spans of ten years (Richard *et al.* 1996, Weilgart & Whitehead 1997, Whitehead & Weilgart 2000). Male sperm whales progressively move to higher latitudes with age (Best 1979). Adult males are mainly solitary, and have a broader distribution, reaching the drift ice in both polar oceans during the austral and boreal summers (Figure 1) (Berzin 1971, Best 1979, Rice 1989).

Figure 1. Distribution of sperm whales in the world's oceans*



Distribution of the sper

Distribution of the sperm whale (*Physeter macrocephalus*)

Range of female and immature males

During the austral and boreal summer months, sperm whales can be found in the highest latitudes of their distributional ranges (Rice 1989). In the Northern Hemisphere boreal groups of sperm whales of both sexes range between 0° and 25°N from October to March, travelling north to 25–40° N between April and September (Bolau 1895, Townsend 1931). In the Southern Hemisphere, groups of males and females move southward from the Equator during the austral winter, between April and September, then return north between October and March, during the austral summer (Berzin 1971).

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^{*}The dark shade of blue represents the range of the sperm whale and the red dotted line the range of immature males and females.

New Zealand distribution

Historical (1960s–1970s) research focussed on reporting the distribution and composition of groups of whales on the basis of sightings and catch records of Japanese and Russian pelagic whaling expeditions (Gaskin 1968, 1970, 1973). These studies determined that female sperm whales in the Tasman Sea (west of New Zealand), were restricted to waters north of 44°S, whereas those off the east coast, where warmer waters occur further south all year round, reached 48°S (Gaskin 1973). These studies also established that larger males migrated back to the warmer waters around Cook Strait to join the female groups during the mating season in November and December (Gaskin 1970). Between May and October the numbers of sperm whales in the Cook Strait region appear to decrease sharply (Gaskin 1968). Sperm whale movements from and to this area are thought to be determined by the start and end of the breeding season, and by the availability of prey that is influenced by the movement of isotherms (Gaskin 1968).

Concentrations of sperm whales have been also found east of New Zealand, around the Chatham Islands and neighbouring banks, as well as over the South Island's steep continental slope along the Subtropical Convergence (Gaskin 1973). Sperm whale catches were high around the Cook Strait region where the Southland Current met the East Cape Current, near the Subtropical Convergence. During this time prey may have been abundant in the area (Gaskin 1973). The number of sperm whales appeared to decrease eastward into the central South Pacific (Gaskin 1973). There also appeared to be fewer sperm whales between 60° and 70°S, where commercial catches amounted to less than 50% of those between 40° and 50°S (Ohsumi 1966, Gaskin 1973). This is partly due to the fact that only 40–60% of all mature males migrate to polar feeding grounds (Ohsumi 1966). In the Tasman Sea the population appeared to have concentrated in the austral summer around the Subtropical Convergence, near Lord Howe Rise and in the area halfway between the Tropical and Subtropical

Convergence (Gaskin 1973). This population appeared to migrate to the Kermadec Islands and Tonga during the austral winter (Gaskin 1973).

More recent research has focussed on studying the male sperm whale population residing off Kaikoura, east coast of South Island, particularly the impact of whalewatching on their behaviour, patterns in their seasonal abundance and distribution, and the function of clicks and sound production during dives (Childerhouse et al. 1995, Jaquet et al. 2000, Jaquet et al. 2001, Childerhouse 2002, 2004). These studies have shown solitary male sperm whales converge year-round over the deep-sea canyon at around 42°S off the Kaikoura Peninsula, South Island (Childerhouse et al. 1995, Jaquet et al. 2000). During the austral summer, they concentrate around the deep waters of the canyon over depths of up to 1,000 m, distributing more evenly during the winter (Jaquet et al. 2000). The onychoteuthid *Moroteuthis ingens* and arrow squid, *Nototodarus* spp., known to be of historical importance in the diet of the sperm whale in New Zealand, appear to be abundant in this area from late October to late February (Gaskin & Cawthorn 1967a, 1967b, Jaguet et al. 2000). Prey appears to be in ample supply in the underwater canyon year-round, with 66% of the sperm whales at Kaikoura being seasonally resident and only 33% transiting briefly through the area (Jaguet et al. 2000).

The migratory patterns and movements of sperm whales in New Zealand are not well known. However, studies that investigate the movements of sperm whales in the South Pacific should be encouraged as they can provide relevant information that could shed light on the feeding ecology of this species, aiding in their conservation.

2.1.3 Social structure

Mature females and immature whales of both sexes form long-term associations of approximately 13 individuals of mixed matrilines (Best 1979, Richard *et al.* 1996, Christal & Whitehead 2001, Coakes & Whitehead 2004). It has been

suggested that groups of females and juveniles may be restricted to lower latitudes because of: the energetic requirements imposed on females by deep diving, reproduction and lactation (Best *et al.* 1984); the thermoregulatory constraints of calves in colder waters (Lyrholm *et al.* 1999); and because prey at higher latitudes occurs too deep and outside the diving capabilities of females and juveniles (Best 1979).

Males disperse from these social groups at approximately six years of age and gradually move to the cold-water feeding grounds at higher latitudes, reaching 70°N in the Atlantic and 70°S in the Southern Ocean (Richard *et al.* 1996, Santos *et al.* 1999, Rendell & Whitehead 2003). Males exploit highly productive feeding grounds at higher latitudes, and in doing so may reduce competition for resources with females and juveniles, increasing males' growth rates to maturation (Lyrholm *et al.* 1999).

The evolution of highly structured social units that persist over long periods of time in schools of female sperm whales appears to be driven by benefits brought about by communal living (Whitehead 1996a, Christal & Whitehead 2001). Benefits include: shared knowledge about the presence of ephemeral food resources, over the sperm whale's vast spatial ranges; utilising the echolocation of other sperm whales nearby; increasing foraging efficiency while diving in groups (Whitehead 1989, 1996b); and communal suckling and care of calves, and cooperative protection against predators (Best *et al.* 1984, Arnbom *et al.* 1987, Whitehead 1996a).

Maturing and adult males are mainly solitary but can form small temporary associations called bachelor groups that become progressively smaller as males increase in size and age (Best 1979, Lettevall *et al.* 2002). The stability of these associations appears to depend on food availability, as they persist over shorter periods of time; they also seem to be more stable geographically than the aggregation of females and juveniles (Lettevall *et al.* 2002). When males reach sexual maturity in their late twenties, they leave their feeding grounds in colder

waters and return to lower latitudes, travelling between family groups during the breeding season (Whitehead 1993). It is during these migration periods that most of the strandings occur (Santos *et al.* 2002, DoC 2005).

2.1.4 Diving behaviour

Sperm whales spend most of their time underwater (Jaquet *et al.* 2000). Their diving behaviour has been studied using hydrophones (Madsen *et al.* 2002), sonar (Papastavrou *et al.* 1989, Watkins *et al.* 1993), acoustic recorders (Watkins 1980), time-depth recorders (Watkins *et al.* 2002), and video cameras (Marshall 1997).

The diving behaviour of sperm whales is influenced by body size, sex, oceanographic conditions, prey availability, and social conditions (Perry et al. 1999). Mature female and male sperm whales exhibit different diving behaviours and appear to reduce competition by vertically partitioning the habitat they feed in, with larger whales being able to exploit deeper resources (Gordon 1987b). Adult males can dive for more than 90 minutes at depths between 300 and 2,000 m (Clarke et al. 1993, Watkins et al. 1993). Females however, dive for shorter periods at depths between 200 and 1,200 m, normally staying in the top 500–800 m of the water column (Papastavrou et al. 1989, Gordon & Steiner 1992, Watkins et al. 1993). The social condition of sperm whale groups also affects the duration of dives (Gordon 1987a); groups of females with calves have average dive times of eight minutes, whereas groups of females without calves have average dive times of 25 minutes at shallower depths (Gordon & Steiner 1992). Although large male sperm whales are capable of prolonged dives of up to 138 minutes to depths exceeding 2,000 m, most dives by both sexes are shallower than 1,000 m and usually last about 30 to 45 minutes (Clarke 1976, Lockyer 1981, Watkins *et al.* 1985).

2.2 Sperm whaling

The exact number of sperm whales in New Zealand waters or the number killed commercially cannot be an exact science. However, estimates on the numbers of sperm whales in New Zealand, prior to their exploitation by sail whalers, go as high as 10,000 individuals and as low as 8,000 (Kaiser *et al.* 2000). American, British, Russian and colonial whalers are thought to have commercially killed around 5,829 sperm whales in New Zealand waters (Kaiser *et al.* 2000). Most of them were taken by offshore and pelagic whale ships between North Cape, the Kermadecs and Southern Tonga (Townsend 1931), leaving around 3,000 sperm whales alive today within the EEZ (Kaiser *et al.* 2000).

The first sperm whaling record dates back to 1712 when an American vessel that had been driven into the open ocean by a storm, caught a sperm whale specimen off the coast of America (Harmer 1928). The open-boat sperm whale fishery started in the early 18th century, rapidly expanding from the Atlantic after 1783 (Ohsumi 1980). Modern whaling started in the late 19th century when Sven Foyn invented the explosive harpoon and cannon mounted on a boat that allowed for intensive whaling operations with catches above 10,000 whales a year being taken by the 1950s (Berzin 1971). By the end of 1963 it was clear sperm whales required protection as fewer large males were being caught (Berzin 1971).

The first record of a sperm whale being taken in New Zealand dates back to 1791 and the industry was well established by 1805, with a small provisioning base at the Bay of Islands (Kaiser *et al.* 2000). The locally run sperm whaling industry was small, and only single specimens were taken by coastal sperm whalers in the early whaling years (Harmer 1928, Berzin 1971). However, British and American whale ships frequently visited New Zealand waters, and up to 13 vessels were operating by 1825 (Kaiser *et al.* 2000). From 1825, colonial whaling from Australian ports grew steadily, and after 1840 it declined as richer whaling

grounds were developed elsewhere (Kaiser *et al.* 2000). After 1840, the number of sperm whales taken was negligible until 1963 (Kaiser *et al.* 2000). However the development of crude explosive harpoons in 1911 at a small whaling station in Tory Channel, South Island, allowed whalers to concentrate on the catch of humpback whales with 3,747 caught between 1911 and 1962 (Kaiser *et al.* 2000). During this same time period only 15 sperm whales where caught and processed in the Tory Channel whaling station (Kaiser *et al.* 2000). During the 1963–1964 whaling seasons, 248 sperm whales were caught by a single vessel operating from Tory Channel (Gaskin & Cawthorn 1967a, Berzin 1971).

The Tory Channel whaling station was subsequently closed, ending all commercial whaling in New Zealand by December 1964 (Gaskin & Cawthorn 1967a). In 1982 the International Whaling Commission (IWC) decided that commercial catches for all whales should be set to zero. This decision came into force in 1985, after which only Japan and Iceland take whales under supposed scientific permits issued by their research agencies, while Norway has an objective to the IWC moratorium and is allowed to whale commercially.

2.3 Dietary studies

The diet of predators is usually reconstructed by identifying prey remains found in their digestive systems. In the case of protected marine mammals, stomach samples today are usually collected post-mortem. For sperm whales in particular, due to their large size and tendency to strand in relatively large numbers, it is logistically possible only to extract the contents of the first and second stomachs. The intestine and third stomachs may offer little material of diagnostic value, and sampling the entire alimentary canal is logistically impractical (Clarke 1980, 1986, Martin & Clarke 1986). Other dietary studies in cetacean species, have collected faecal samples and used stable isotope ratios of prey remains as tools to reconstruct diet and gain knowledge on cephalopod biology (Whitehead 1996b, Abend & Smith 1997, Cherel & Hobson 2005).

Cephalopods are rarely found in good enough condition to be identified inside the stomachs of caught or stranded predators. This has lead most researchers to study readily identifiable hard-part remains, primarily the beaks of cephalopods that accumulate in the stomachs and withstand digestion (Clarke *et al.* 1976, Santos *et al.* 2001a). Morphological differences between the lower beaks of cephalopods allow researchers to identify species but the upper beaks have not been studied as intensively, and are not normally used in the identification of cephalopods (Clarke 1962a, Clarke *et al.* 1976, Clarke 1980, 1986). This convention arose because lower beaks are more easily differentiated to species level than upper beaks, and because lower beaks alone should provide an accurate picture of the cephalopod composition in the diet of sperm whales (Clarke *et al.* 1976). However, the study of upper beaks should not be neglected since they can provide species diagnostic information and often accumulate in larger numbers in the stomachs of predators.

Estimations of the body mass (BM) and mantle length (ML) of individual cephalopods can be estimated from beak measurements, using allometric equations from the literature (Clarke 1986, Rodhouse *et al.* 1990, Lu & Ickeringill 2002). These equations are derived from the relations between beak morphometry and both BM and ML of complete specimens. The most common beak measurements used are the lower rostral length (LRL) for squid and the lower hood length (LHL) for octopods and *Vampyroteuthis infernalis*. However, morphometric analysis of rare species or species sizes in collections could have considerable effects in biomass calculations. In several cases, these allometric equations are not available for all species in a family and the equation for one species has to be applied to another. Precision is also required when measuring the beaks, since small errors in the measurement can significantly bias the estimates of cephalopod biomass (Santos *et al.* 2001).

2.3.1 Sources of error

Three main sources of error may arise when studying the diet of marine mammals. These are: heterogeneity in the sampled population, random error, and systematic error (Santos *et al.* 2001a). Heterogeneity in the sampled population may include ontogenetic changes in predator diet, and seasonal, interannual, geographic, and individual variation in prey (Santos *et al.* 2001a). Some of these sources of error may be addressed with a proper knowledge of sperm whale biology, including digestion rate, diving behavior, and ontogenetic shifts in diet, yet others, such as individual preference of prey cannot be quantified because individuals most likely can only be sampled once (Santos *et al.* 2001a).

The diet of cetaceans generally is based on opportunistic studies of stranded or commercially caught animals (Clarke & Young 1998, Pauly *et al.* 1998). Prior to the moratorium on sperm whaling declared by the International Whaling Commission in 1985, large samples, more representative of the whole population, could be collected from hunted animals. However, it should be noted that these samples were biased toward adult animals, especially males (Santos *et al.* 2001a). Recent studies have mostly relied on fewer stomach samples from stranding events. However, the cumulative information that has been collected and analysed, has given us a partial understanding of the ecological role of the sperm whale in the world's oceans.

Secondarily ingested prey, or the prey of sperm whale prey that may be found in the stomach contents of a predator but are not directly ingested by it, can also affect the results of dietary analyses. Secondarily ingested prey generally includes polychaetes, small crustaceans, and small cephalopods. However, small cephalopod species are thought to be underestimated in their predator's diet, since they pass through the intestine more easily than larger beaks (Santos *et al.* 1999).

Different prey remains have different digestion times, possibly affecting their chance of being detected and identified in the contents of a stomach (Santos *et al.* 2001a). For example, cephalopod beaks are less likely to be digested or evacuated than fish otoliths, and the importance of this prey group in the diet is therefore more likely to be overestimated (Clarke 1980, Santos *et al.* 2001a). Furthermore, problems with the identification of beaks arise due to the unresolved taxonomy of some cephalopod families and the high level of similarity or variability between and within the beaks of different species. However, carrying out unbiased dietary studies on protected marine mammals such as the sperm whale have proved to be very difficult, and although strandings may not accurately reflect the diet of a healthy population, they provide a unique opportunity to study the diet of protected species (Pauly *et al.* 1998, Santos *et al.* 2001a).

It is generally accepted that the size of cephalopods estimated from hard part remains is an accurate portrayal of the actual prey biomass consumed by a predator. Thus, it is implicitly assumed prey items are consumed whole, and the allometric equations used to estimate cephalopod weight are a precise tool for the estimation of cephalopod weight. However, prey items may not always be ingested whole, and the allometric equations that relate beak morphology and cephalopod weight could be greatly improved for most species (Santos *et al.* 2001a). Serious errors can arise from the use of allometric equations derived from small animals, to estimate the weight of larger animals from beak measurements (Santos *et al.* 2001a). However, set against some of the other sources of error present in dietary studies based on the identification of prey remains from stomach contents, errors in body mass calculation are arguably minor.

2.4 Review of sperm whale diet

Dietary studies have increased our knowledge of the sperm whale's foraging behaviour, diving prowess, and migration (Clarke 1962b, Santos *et al.* 1999, Santos *et al.* 2001a). They have shown that this species feeds both mid-water and near the seabed, between depths of 400 and 2,000 m (Martin & Clarke 1986), and that cephalopods dominate their diet in most of the world's oceans. However, in Iceland, New Zealand and Antarctica, fish are or have been an important source of food (Gaskin & Cawthorn 1967a, 1967b, Roe 1969, Klumov 1971, Martin & Clarke 1986, Clarke 1996a). Even though some cephalopod families, like Histioteuthidae, are of ubiquitous importance in the diet of sperm whales, their diet varies between sexes and age groups, as well as between regions, months, seasons, and years (Matthews 1938, Clarke 1980, Kawakami 1980, Rice 1989, Clarke 1996a, 1996b, Santos *et al.* 1999).

Male and female sperm whales appear to have somewhat different diets (Clarke et al. 1976, Clarke 1980, Clarke & MacLeod 1982, Santos et al. 2001a). Females stranded in Tasmania showed a higher proportion of tropical and subtropical cephalopod species in their diet, and males showed a higher proportion of Antarctic cephalopod species (Santos et al. 2001a). Females and small males also appeared to have eaten more of the smaller species than the large males in the Southern Hemisphere (Clarke 1980). These differences are probably a consequence of the different diving capabilities and foraging areas of the sexes and age groups (Rice 1989, Gordon & Steiner 1992, Santos et al. 1999). Furthermore, sperm whales associating in groups at the surface seem to separate three-dimensionally while foraging, probably feeding on different prey resources while diving (Watkins & Schevill 1977). Since cephalopod diversity changes with both latitude and depth, it has been suggested that this spatial segregation between sexes, both latitudinal and vertical, could reduce intraspecific competition for food, as evidenced in the differences in diet between sexes (Best 1979, Lyrholm et al. 1999, Evans & Hindell 2004).

More than 56 species of cephalopods from 24 families and more than 68 species of fish belonging to 49 families have been recorded from the stomachs of sperm whales worldwide (Kawakami 1980, Clarke 1996a). Apart from cephalopods and fish, other animals such as salps, crustaceans, gorgonians, colonial tunicates, jellyfish, sponges, starfish, elasmobranch eggs, echinoderms, seals and sea cucumbers have been reported from sperm whale stomachs (Klumov 1971, Kawakami 1980, Santos *et al.* 1999, Bor & Santos 2003). Man-made objects such as children's toys, plastic jugs, and discarded fishing and trawl nets also have been recorded from the stomachs of sperm whales in different regions (Martin & Clarke 1986, Clarke & Young 1998, Santos *et al.* 1999).

The following section reviews the findings of the diet of the sperm whale both in the Atlantic and the Pacific oceans. Samples and dates of collection are described, and the most important cephalopod families by number and by weight are named. Figures showing the relative numerical importance and the relative importance by weight of all the cephalopod families consumed by the sperm whales studied in each region are presented. Additional information on rare species occurrence is also noted.

2.4.1 Atlantic

Northeast Atlantic

Santos *et al.* (2002) studied the stomach contents of eight whales stranded in the Netherlands (5), Scotland (1), and Ireland (1) from 1996–1998. One of the whales stranded in the Netherlands in 1937 and allowed a historical comparison of the diet of the sperm whales for this region. Additionally, Santos *et al.* (1999) studied the stomach contents of 17 male sperm whales stranded in Scotland and Denmark from 1990–1996 between the months of November and March.

The diet of sperm whales in the northeast Atlantic consists mainly of oceanic cephalopods (Santos *et al.* 1999, Santos *et al.* 2002). A few fish bones belonging

to saithe, *Pollachius virens*, and monkfish, *Lophius* sp., were found in the stomachs of two whales stranded in the Netherlands (Santos *et al.* 2002).

The most important cephalopod prey families numerically were: Gonatidae, Histioteuthidae, Alloposidae and Cranchiidae. The most important families by weight were: Gonatidae, Architeuthidae and Alloposidae. *Gonatus* is a very important component of the diet of sperm whales in the North and Norwegian Seas, comprising more than 90% of the stomach contents by number of whales stranded in the Netherlands (Santos *et al.* 2002). The authors concluded that sperm whales are probably feeding on spawning aggregations of squid off Norway before they migrate South (Santos *et al.* 1999). Studies on the predators of *Gonatus fabricii* in the North Atlantic showed that predators of this species may be also attracted to the high concentrations of spawning females (Bjørke 2001).

Madeira

Clarke (1962a) studied the stomach contents of a single whale examined at the Madeira Islands, Portugal in 1959. He recovered more than 4,000 (2,136 lower) beaks from the stomach, belonging to 11 cephalopod species in nine families (Clarke 1962c, 1980). Clarke (1980) re-examined the beaks after 20 years, when a more detailed examination could be made of both calculated cephalopod weights and identifications. The most important families numerically were Histioteuthidae and Cranchiidae, and the most important families by weight were Architeuthidae, Histioteuthidae, Octopoteuthidae and Alloposidae (Clarke 1980).

Vigo

Clarke and MacLeod (1974) studied the stomach of a sperm whale caught in Vigo, Spain in 1966. The authors found 70 lower and 84 upper beaks comprising seven species in seven families. The most important families numerically were Histioteuthidae, Octopoteuthidae, Lepidoteuthidae and Cranchiidae, and the

most important families by weight were Octopoteuthidae, Architeuthidae, Histioteuthidae and Lepidoteuthidae.

The Azores

Clarke *et al.* (1993) investigated the diet of 15 male and two female sperm whales caught between 1981 and 1984 in the Azores Archipelago, 1,500 km west of Portugal. A total of 28,534 lower and 26,654 upper beaks, 233 additional buccal masses, several tunicates, and 16 fish were found in the stomachs of these whales. The lower beaks represented 40 species of cephalopods of which 12 could be identified from the flesh remains. The most important families numerically were Histioteuthidae, Octopoteuthidae, Cycloteuthidae and Cranchiidae, and the most important families by weight were Octopoteuthidae, Histioteuthidae, Architeuthidae, and Lepidoteuthidae. The authors concluded that sperm whales in this region appear to be targeting cephalopods of 400–500 g, but also consumed larger individuals.

Iceland and Greenland

Martin and Clarke (1986) studied the stomachs of 221 sperm whales taken from 200–400 m deep waters, between 62° and 67°N, in the 1977–1981 whaling seasons. All whales were male, between 11 and 17 m long. Of these, 26% of the stomachs examined were empty, attributed to stress-induced vomiting during capture.

The population of sperm whales in Icelandic waters is one of the few in the world to feed predominantly on fish instead of cephalopods. Fish comprised 76% and cephalopods only 24% of the diet of the sperm whales in these waters (Martin & Clarke 1986). A total of eight fish species were identified during the four years for which samples were reported, of which lumpfish, *Cyclopterus lumpus*, accounted for 50% of the biomass (Martin & Clarke 1986). A total of 22 species of cephalopods were identified from the stomachs of these whales, of which 94%

were mid-water oceanic squid, 84% of them ammoniacal, and 12% muscular (Gonatidae and Ommastrephidae). The most important families numerically were Cranchiidae, Histioteuthidae, Gonatidae, Ommastrephidae and Alloposidae, and the most important families by weight were Histioteuthidae, Cranchiidae, Ommastrephidae, Gonatidae and Lepidoteuthidae. The authors also found wood and other non-food items like rocks, plastic drinking cups, children's toys, newspaper, and a 63 kg fishing net. This last item was found stuck between the second and third stomach and would have most likely caused eventual death to the animal through starvation (Martin & Clarke 1986).

England

Clarke and Pascoe (1997) studied the diet of a single 13.5 m long male sperm whale stranded in Penzance, Cornwall; 125 lower beaks were recovered from the second stomach of the whale, representing four species of oceanic squid, one neritic squid and one neritic octopod. The most important cephalopod families consumed by this whale both by number and weight were Histioteuthidae, Architeuthidae and Ommastrephidae, of estimated ML's that varied between 126 and 1,056 mm.

North Sea

Santos *et al.* (1999) studied the stomach contents of 17 male sperm whales that stranded during their southward migrations in Scotland and Denmark between November and March, 1990–1996. From more than 12,000 beaks recovered, the importance of *Gonatus* spp. by weight always exceeded 90%. They also found skate eggs in two of the samples, a bone of a gadoid fish, and a piece of net of approximately 1,000 x 300 mm in one whale stomach.

2.4.2 Pacific

The study of the cephalopod component in the diet of predators in the Pacific has been hindered by the limited knowledge of cephalopods in this region (Clarke & MacLeod 1980). Studies on the diet of the sperm whale before the 1970s were mostly related to the western North Pacific, in Russian and Japanese waters, with little work being done on the eastern waters of this ocean (Berzin 1971, Klumov 1971, Clarke & MacLeod 1980). However, in recent years, very few authors have published studies on the diet of the sperm whales in the North Pacific (Clarke & Young 1998).

Hawaii

Clarke and Young (1998) studied the diet of six cetacean species that stranded on Hawaiian shores, which included two sperm whales. A fishing net was found in the stomach of the first whale, and it contained 14 lower and 25 upper beaks only: two cycloteuthids, six onychoteuthids, four histioteuthids, one ancistrocheirid, and one vampyroteuthid were identified from the lower beaks. The second whale had 278 lower and 287 upper beaks in its stomach from which 19 genera belonging to 14 families were identified. For the second whale, the most important families by number were: Histioteuthidae, Cranchiidae, Ommastrephidae and Mastigoteuthidae, whereas the most important families by weight were Architeuthidae, Ommastrephidae Octopoteuthidae and Histioteuthidae.

Western Canada

Clarke and MacLeod (1980) studied the stomachs of 20 sperm whales captured during the boreal summer, west of Vancouver Island (50°N), in 2,000 m deep waters. Most of the individuals studied were males. A total of 152 lower beaks were recovered from the stomachs, representing 11 cephalopod families. The most important families numerically were Gonatidae, Onychoteuthidae,

Cranchiidae and Histioteuthidae, and the most important families by weight were Onychoteuthidae, Gonatidae and some unidentified families.

Other Studies of the North Pacific

The diet of the sperm whale also has been studied in the Kurile region, and the Aleutian Islands (Beteshava & Akimushkin 1955, Okutani & Nemoto 1964). The squid *Gonatus magister* and *G. fabricii* (Gonatidae), and species of the Onychoteuthidae dominated the diet of sperm whales in the western North Pacific (Beteshava & Akimushkin 1955, Okutani & Nemoto 1964, Clarke & Young 1998).

Beteshava (1961) found 24 species of fish in the stomachs of sperm whales in the Kurile region. Benthic fish species such as rays, *Raja* spp., large gobies, *Myoxocephalus* spp., smooth lumpsuckers, *Aptocyclus ventricosus*, and anglerfish, *Oneirodes* sp., were some of the fish most commonly found in the stomachs. This study showed a decline in the proportion of sperm whale stomachs that had fish in them, from 30% in 1951, to 12% in 1955 (Beteshava 1961).

Peru and Chile

Clarke *et al.* (1976) studied random samples from the stomachs of four sperm whales caught between 1959 and 1961, off the coasts of Peru and Chile. The authors described the lower beaks for some species, and attributes 1,057 of them to 11 cephalopod families. The most important families numerically in these samples were Histioteuthidae, Chiroteuthidae, Octopoteuthidae and Ancistrocheiridae, and the most important families by weight were Histioteuthidae, Ommastrephidae, Vampyroteuthidae, and Ancistrocheiridae.

Australia

Evans and Hindell (2004) studied the stomachs of 36 sperm whales involved in two mass strandings during February 1998, on Tasmania's west coast. A total of 101,883 cephalopod beaks (52,109 upper and 49,774 lower beaks) were recovered from the stomachs, representing 48 species in 14 families of squid, two species of octopods and a single species of vampyroteuthid. The most important cephalopod families numerically were Histioteuthidae, Cranchiidae, Lepidoteuthidae, and Onychoteuthidae, and the most important families by weight were Onychoteuthidae, Histioteuthidae, Architeuthidae and Pholidoteuthidae.

Tasman Sea

Clarke and MacLeod (1982) reported the stomach contents of 66 sperm whales, comprising 43 males, 20 females, and three for which no sex data was available. These animals were caught in the Tasman Sea by Japanese whalers in 1970, *en route* to the Antarctic whaling grounds. Of the 3,335 upper and 3,299 lower beaks recovered from the stomachs of the whales, the authors identified more than 30 cephalopod species belonging to 14 families. This is a region of particular interest because the cephalopods of the area are very poorly known, and very few studies have analysed the diet of the sperm whale in the western South Pacific. The whales were captured in waters from 31°20' S to 46°56' S and from 174°28' E to 148°04' E, following a path from eastern Tasmania to northern North Island, New Zealand. The most important families numerically were Octopoteuthidae, Histioteuthidae, Cranchiidae and Onychoteuthidae, and the most important families by weight were Octopoteuthidae, Onychoteuthidae, Architeuthidae and Cranchiidae.

Cook Strait, New Zealand

Gaskin and Cawthorn (1967a, b) studied the stomach contents of 151 sperm whales, mostly males, caught between 1963 and 1964 throughout the Cook Strait region and processed at the Tory Channel whaling station, Cook Strait. At the time the identification of lower cephalopod beaks was in its infancy, and many of the beaks recovered could not be identified. Furthermore, regression equations for determining the fresh weight from the lower rostral length of the beaks were not yet available and hindered data analysis. The authors, however, grouped the beaks into classes, drew them and offered possible species or family names for the groups. Illustrations were subsequently reinterpreted, and tentative identifications are provided by Clarke & Roper (1998).

Quantitative analysis of the stomach contents of nine whales showed that in the early 1960s, the sperm whales were eating fish and squid at a 1:1.69 ratio by weight (Gaskin & Cawthorn 1967a, 1967b). The most common fish species encountered in the stomachs of the whales were: groper, *Polyprion oxygeneios*; ling, *Genypterus blacodes*; orange roughy, *Hoplostethus* sp.; an unidentified eel and southern kingfish, *Jordanindia solandri* (Gaskin and Cawthorn 1967a). Other fish species included: john dory, *Zeus faber*, spiney dogfish, *Koinga kirki*; lantern fish, *Myctophus humboldti*; *Echinorhinus cooki* and *Echinorhinus* sp. or *Dalatias* sp. (Gaskin & Cawthorn 1967a).

The authors noted that the fish species consumed varied from month to month (Gaskin & Cawthorn 1967a). The unidentified eels were only recorded between mid-January and mid-March, and the orange roughy (*Hoplostethus* sp.) was mostly recorded between the beginning of January and the end of March (Gaskin & Cawthorn 1967a). Southern kingfish and groper were mostly recorded from stomachs between the end of April and the end of June, and ling was found in the stomachs throughout the year (Gaskin & Cawthorn 1967a).

Samples from two whales totalling 2,118 lower beaks were grouped into 11 classes. From the redescription by Clarke and Roper (1998) the most important families by number proved to be Onychoteuthidae, Histioteuthidae, Ommastrephidae and Pholidoteuthidae. Since the authors had no weight-LRL regressions at the time, no weight estimates were calculated. The authors also found a coconut, box wood and fish lice, as well as coal, pumice and basalt in the stomachs of several of the hunted whales (Gaskin & Cawthorn 1967a).

Paekakariki, New Zealand

Clarke and Roper (1998) studied the stomach of a sperm whale that stranded on Paekakariki Beach, North Island. They recovered more than 3,000 beaks from the stomach (1,600 lower), which represented 24 cephalopod species from 13 families. The most important families numerically were Histioteuthidae, Onychoteuthidae, Cranchiidae and Octopoteuthidae, and most important families by weight were Histioteuthidae, Architeuthidae, Onychoteuthidae and Octopoteuthidae (Clarke & Roper 1998).

2.4.3 Southern Ocean

Clarke (1980) carried out the most comprehensive and complete study of the diet of the sperm whale, analysing 461 stomach samples collected between 1926 and 1969, from whaling operations in the Southern Ocean. A total of 194, 182, 46, and 35 complete and incomplete samples were collected for Durban and Donkergat in South Africa, Albany in west Australia, and the Antarctic respectively.

The most important families by number were, for Durban, Histioteuthidae, Octopoteuthidae, Chiroteuthidae, and Ancistrocheiridae; Donkergat, Histioteuthidae, Cranchiidae, Octopoteuthidae and Pholidoteuthidae; Albany, Histioteuthidae, Ommastrephidae, Pholidoteuthidae and Cranchiidae; and the Antarctic, Onychoteuthidae, Cranchiidae, Histioteuthidae and Gonatidae. The

most important families by weight were, for Durban, Histioteuthidae,
Octopoteuthidae, Chiroteuthidae and Ancistrocheiridae; for Donkergat,
Histioteuthidae, Cranchiidae, Octopoteuthidae and Pholidoteuthidae; for Albany,
Histioteuthidae, Ommastrephidae, Pholidoteuthidae and Cranchiidae and the
Antarctic, Onychoteuthidae, Cranchiidae, Histioteuthidae and Gonatidae.

Antarctic

Klumov (1971) studied the stomachs of sperm whales taken by Russian whaling fleets in the Antarctic between 1961 and 1968. Large cephalopods such as *Onychoteuthis banksii*, *Moroteuthis ingens* and *Mesonychoteuthis hamiltoni*, and large fishes such as *Dissostichus eleginoides* and *D. mawsoni* appeared to have similar importance in the diet of these whales (Klumov 1971). *D. eleginoides* however, has a lesser role in the diet of the sperm whale in the Antarctic because of its narrow and localized distribution (Klumov 1971). Blue whiting, *Micromesistius australis*, is third in importance in the fish diet of sperm whales in the Antarctic, which is often found in their stomachs, sometimes in large quantities (Klumov 1971).

2.5 Remarks

Even though the diet of the sperm whale has been better-documented for some areas, there is a lack of information regarding the diet of this species in the South Pacific, especially in New Zealand. Moreover, there is limited comparative information available to ascertain temporal trends in diet, although these have been reported on at least two instances elsewhere; in the Kurile region (Beteshava & Akimushkin 1955), and in the North-east Atlantic (Santos *et al.* 2002).

Strandings

Several theories have tried to explain strandings, and are divided into those focused on the physical factors and those focused on the biological and behavioural aspects of stranding events. Physical factors that have been proposed as responsible for strandings include, geomagnetic topography (Klinowska 1986), echo-distortion of gently sloping beaches (Dudok van Heel 1962), coastal configuration creating whale traps (Gilmore 1957), oceanic currents (Sergeant 1982), and weather conditions, especially electrical storms (Robson & van Bree 1971). Biological factors that could be responsible for strandings include, an instinctive land-seeking drive (Wood 1979), animals trying to follow an ancient migratory route that has since been closed (Genin *et al.* 1988), the social cohesion of some species could cause herd strandings when a whale beaches itself and sends out distress calls (Robson 1984), suicide (Geraci 1978), parasites and disease (Dailey & Walker 1978), lunatic effect (Robson 1984), harassment and predation (Geraci & Aubin 1979), and pollution (Geraci 1978).

In New Zealand sperm and pygmy sperm whales account for 22% of all strandings and 13% of all herd strandings (Brabyn 1991). Up to 1990, a total of 11 mass strandings had been recorded, five of them were either nursery or harem strandings, four of them at Kaipara Harbour, Northland, and one at Gisborne (Brabyn 1991). The other six mass strandings were bachelor strandings widely distributed along our coasts. Female strandings have been only recorded on North Island, and 78% of the strandings where sex has been recorded have been males (Brabyn 1991). Single strandings of sperm whales are concentrated around Wellington's coast and at Oputama Beach (Brabyn 1991).

New Zealand is recognised as one of the countries with highest stranding events for marine mammals in the world, providing a huge potential for investigating the diet of these protected species. Although dietary studies from strandings are susceptible to a range of errors, and determining the cause of stranding is not

always possible, every effort should be made to recover the stomach samples of stranded marine mammals.

Foraging

Sperm whales appear to be opportunistic predators that feed on the most abundant cephalopod or fish species present in their foraging area (Clarke 1980). All the information collected to date seems to indicate that sperm whales are voracious predators that feed mainly on medium-sized, oceanic cephalopods weighing less than 1,000 g. However, the larger species of cephalopods are an important source of energy, and constitute an important part of the diet of sperm whales where they are consumed.

It has been estimated that the sperm whale needs to consume between 2.0—3.5% of its own body mass per day (Lockyer 1981). For a sperm whale that weighs 40 t, this means it has to consume from 800—1,400 kg of food a day. In order to meet its high energetic demands, the sperm whale apparently targets aggregations of squid such as groups of spawning adults, preying on slow and sluggish ammoniacal squid, but also consumes some of the largest species of cephalopods (Santos *et al.* 1999, Bjørke 2001). Even though muscular species have a higher nutritional value, they are faster and possibly harder to capture than the slower ammoniacal squid (Clarke *et al.* 1985). By using all these strategies, the sperm whale may be able to acquire its energy from a relatively poor environment such as the deep-sea.

The size of cephalopods eaten by sperm whales varies from squid 30–40 mm long, weighing but a few grams, to squid over 13 m long and weighing more than 500 kg (Clarke 1996b). Mean estimated weights for individual cephalopods vary from under 600 g to over 500 kg (Clarke 1996a). Off Durban, male sperm whales eat squid weighing approximately 1 kg, while females and juveniles eat smaller squid of approximately 500 g (Clarke 1980). This could be a reflection of the

vertical migration of squid as they grow, as well as differential diving prowess for different sexes and ages (e.g. Clarke 1980).

Cephalopods in the diet of other predators in New Zealand

Cephalopods are an important part of the diet of sperm whales (Gaskin & Cawthorn 1967a, Martin & Clarke 1986, Clarke *et al.* 1993, Evans & Hindell 2004), porpoises (Morejohn *et al.* 1978, Fiscus 1993, Nesis 1998), seals (Klages 1996, Hjelset *et al.* 1999, dos Santos & Haimovici 2001), seabirds (Croxall & Prince 1996, Lorensen *et al.* 1998), sharks (Macnaughton *et al.* 1998, Nigmatullin & Arkhipkin 1998) and other fish (Roper & Sweeney 1975, Royer *et al.* 1998, Goldsworthy *et al.* 2002). In New Zealand, the diet of the pygmy sperm whale, *Kogia breviceps*, is known from 25 stranded animals on New Zealand between 1991 and 2003, and that of the pilot whale, *Globicephala melas*, is known from ten individuals stranded on Farewell spit, South Island on 2005 (Beatson in prep.).

Kogia breviceps

The diet of the pygmy sperm whale within New Zealand includes fish and crustaceans, but is comprised primarily of cephalopods. Between 0 and 512 lower beaks occurred within any one stomach (Beatson in prep.). The cephalopod prey comprised 31 species from 14 families, and is dominated by juvenile individuals of the families Histioteuthidae and Cranchiidae (Beatson in prep.). Adults of these families usually occur at depths exceeding 400 m, below the usual diving depth of the pygmy sperm whale.

Globicephala melas

The stomach contents of five male and five female whales were recovered from the stranding on Farewell Spit. The diet was found to be comprised exclusively of cephalopods, with 0–33 lower beaks within any one stomach sample. Prey is

attributed to only two species from two cephalopod orders; *Nototodarus* spp. (Teuthoidea: Ommastrephidae), and *Pinnoctopus cordiformis* (Octopoda: Octopodidae) (Beatson in prep.). This is the first time the diet of this whale has been reported in New Zealand waters.

Numerical importance of cephalopod families in the diet of the sperm whale

Figures 2–4 show the percentages by number of the different cephalopod families for the Atlantic, the Pacific and four regions of the Southern Hemisphere, respectively. Families like Histioteuthidae, Cranchiidae and Onychoteuthidae are numerically important in almost all regions (Figures 2–4). However, other families assume numerical importance in certain regions: the Gonatidae in the north Atlantic and north-eastern Pacific, the Cranchiidae in the Southern Ocean and the north Atlantic, and the Octopoteuthidae in the Tasman Sea (Figures 2–4). For the North Atlantic, the families Gonatidae, Onychoteuthidae and Cranchiidae assume a higher importance, while for the Antarctic, onychoteuthida are consumed in higher numbers (Figures 2, 4). The family Cranchiidae is also important in Scottish and Icelandic waters, and the family Architeuthidae appeared to be important in English waters.

Onychoteuthids appear to play an important role in temperate zones like New Zealand, Australia, the Tasman Sea and Western Canada (Figure 3). The octopoteuthids are also important in the Tasman Sea, and the chiroteuthids in Peru and Chile. However, it should be noted that some of the studies only analysed stomach samples from single individuals, and may not accurately represent the diet of the sperm whale population in a region.

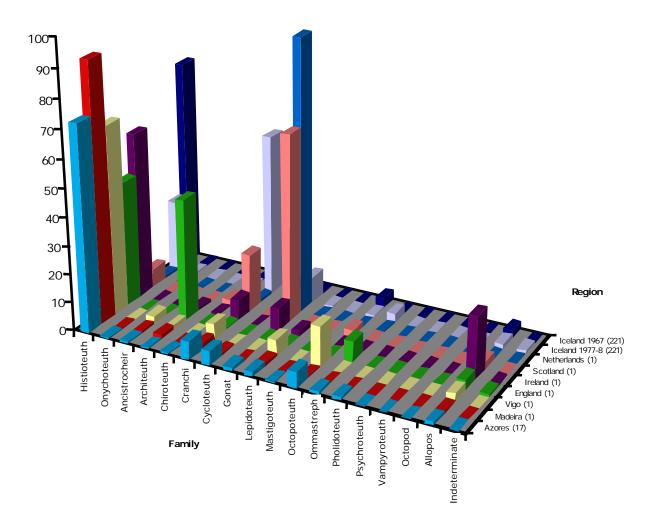


Figure 2. Cephalopod families by percentage frequency in the diet of sperm whales from the Azores (Clarke *et al.* 1993); Madeira (Clarke 1962c, 1980); Vigo (Clarke & MacLeod 1974); England, Ireland, Scotland and the Netherlands (Santos *et al.* 2002); and Iceland (Martin & Clarke 1986)*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

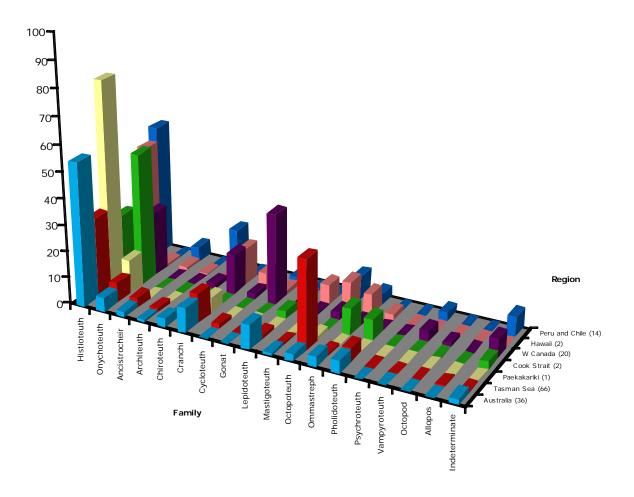


Figure 3. Cephalopod families by percentage frequency in the diet of sperm whales from Cook Strait, New Zealand (Gaskin & Cawthorn 1967a, 1967b); Paekakariki, New Zealand (Clarke & Roper 1998); the Tasman Sea (Clarke & MacLeod 1982); Australia (Evans & Hindell 2004); Peru and Chile (Clarke et al. 1976); Hawaii (Clarke & Young 1998); and Western Canada (Clarke & MacLeod 1980)*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

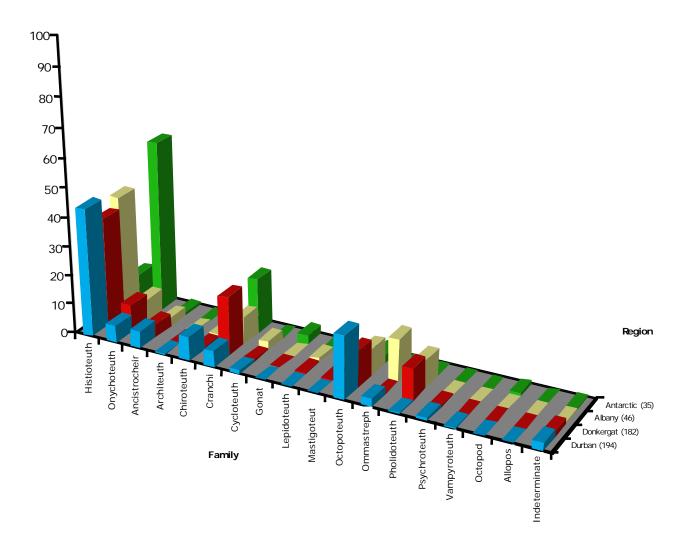


Figure 4. Cephalopod families by percentage frequency in the diet of sperm whales from the Antarctic, Albany, Donkergat and Durban (Clarke 1980)*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

Importance by weight of cephalopod families in the diet of the sperm whale

Figures 5–7 show the importance by weight for different families in the Atlantic, Pacific and four locations in the Southern Hemisphere. The family Histioteuthidae is numerically important in most regions, and even though most species in this family are small squid (with a BM ranging between 50 g and 1.4 kg), they are so abundant in the diet that they still represent a considerable amount of mass to the diet of sperm whales.

Large cephalopod species such as the subtropical *Architeuthis dux*, the Southern Ocean *Mesonychoteuthis hamiltoni*, and the cosmopolitan *Taningia danae* exaggerate their family's importance by weight in the diet of sperm whales wherever they occur. In the Pacific, more specifically off Peru and Chile and off Hawaii, oceanic ommastrephids have an ostensible importance by weight (Figure 6). However, the ommastrephid *Dosidiscus gigas*, provides the almost monospecific diet in the south-eastern Pacific.

For the north-eastern Pacific, (namely western Canada), and the south-western Pacific, (namely New Zealand, Australia and the Tasman Sea), onychoteuthids dominate the diet by weight. In the Arctic one gonatid species may provide almost all the food, and other members of this family also contribute an important amount of mass to the diet of sperm whales in the north Pacific. For the Antarctic, cranchiids and onychoteuthids are very important by weight; for Western Australia, ommastrephids, octopoteuthids and architeuthids, and for South Africa, pholidoteuthids, onychoteuthids, histioteuthids and octopoteuthids (Figure 7). Other families such as the Chiroteuthidae, Cycloteuthidae, Lepidoteuthidae, Ancistrocheiridae, Mastigoteuthidae, and Alloposidae, even though less known, are widespread in the diet of the sperm whale, contributing less than 10% of the weight.

It should also be noted in the figures that the relative importance of unidentified cephalopods varies from region to region. Dietary studies of sperm whales have been impacted by the few systematic studies on cephalopods in certain regions and more taxonomic studies should be conducted in areas where there are high numbers of unidentified cephalopod species.

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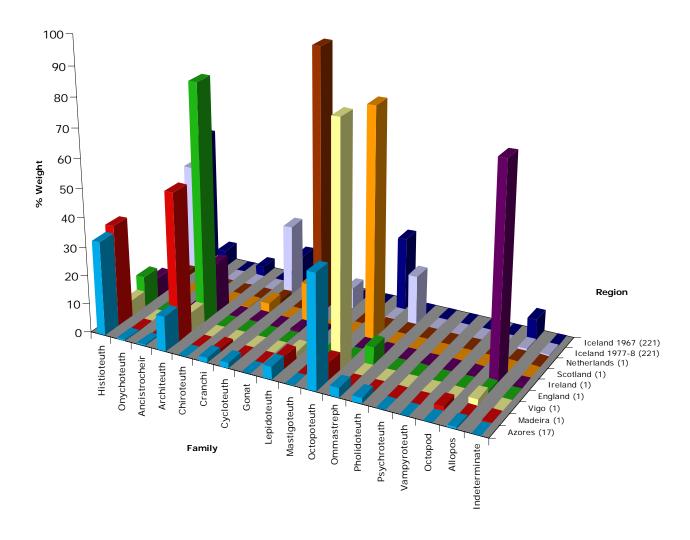


Figure 5. Cephalopod families by percentage weight in the diets of sperm whales from the Azores (Clarke *et al.* 1993); Madeira (Clarke 1962c, 1980); Vigo (Clarke & MacLeod 1974); England, Ireland, Scotland and the Netherlands (Santos *et al.* 2002); and Iceland (Martin & Clarke 1986)*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

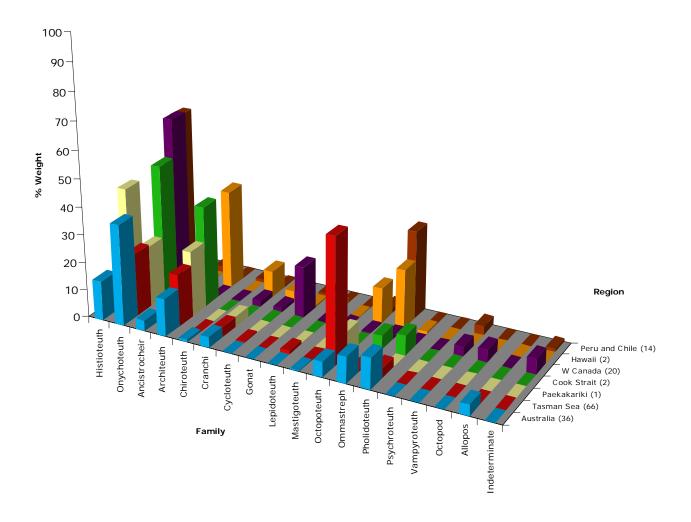


Figure 6. Cephalopod families by percentage weight in the diets of sperm whales from Cook Strait, New Zealand (Gaskin & Cawthorn 1967a, 1967b); Paekakariki, New Zealand (Clarke & Roper 1998); the Tasman Sea (Clarke & MacLeod 1982); Australia (Evans & Hindell 2004); Peru and Chile (Clarke et al. 1976); Hawaii (Clarke & Young 1998); and Western Canada (Clarke & MacLeod 1980)*

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^{*} The numbers in parentheses next to the region, represent the number of stomachs sampled, and the family names are abbreviated.

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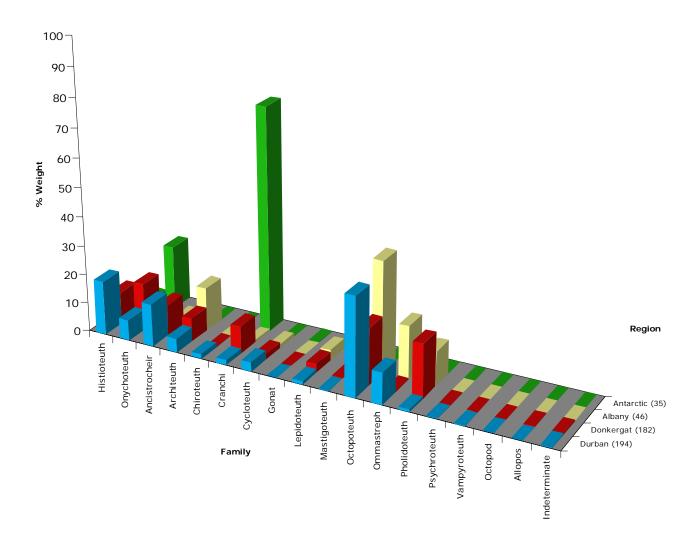


Figure 7. Cephalopod families by percentage weight in the diets of sperm whales from the Antarctic, Albany (Australia), Donkergat and Durban (South Africa) (Clarke 1980)*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled and the family names are abbreviated.

Chapter 3

Chapter 3 Materials and methods

Material and methods

3.1 Dietary analysis

3.1.1 Sample collection

Samples analysed comprise the stomach contents of 19 sperm whales stranded on New Zealand's coastlines. DoC officers and AUT-EOS staff collected 18 of the samples, and one other was sourced from the Museum of New Zealand, Te Papa Tongarewa, Wellington. Fifteen of the sperm whales stranded on Auckland's west coast, and one at each of Napier, Mahia Peninsula, Chatham Islands and the Cook Strait 'region' (Figure 9, Table 1). Three of these sperm whales had empty stomachs.

The stomach samples for this study were collected over an approximate 10-year period, and were recovered by a number of researchers. The 15 strandings on Auckland's west coast all involved AUT-EOS staff and entire stomach contents were collected. These were placed in 4% buffered formalin and later transferred to 70% ethanol. For the four other samples, collection and preservation techniques are unknown.

Notes on the material

Whales 1–12 stranded on Whatipu Beach, west Auckland on November 15th 2003. All of the whales were males ranging in length from 11.2 to 16.5 m, with a mean of 12.7 m. No prey remains were found in the stomachs of sperm whales 10, 11 and 12, and these whales are not considered as samples for the calculation of weight and frequency estimates.

Whale 13 stranded on Whatipu Beach, 4 km north of Nine Pin Rock, West Auckland, on November 30, 2004. This 15.8 m male was an old animal with many worn teeth, and was found dead within hours of stranding.

Whale 14 stranded on Whatipu Beach, 1 km from Nine Pin Rock, West Auckland, on October 11, 2004. This 14.7 m male was found alive, rolling in the surf and stranded as the tide went out. It presented no obvious injuries and died within three hours of stranding.

Whale 15 was a 13.0 m male that stranded on Oputama Beach, Hawkes Bay on November 28, 2002. It was first sighted in shallow water at 6:45 am, about 150 m offshore in shallow water. It was still swimming at the time and DoC officers went out in a boat from around 9:00 am to 11:30 am and tried to 'herd' it out to open water. Apparently the sperm whale made noises but did not move. At noon, while the tide was going out, the whale had beached and made no attempt to refloat itself; it had died by 5:00 pm. The next day, samples were collected from the liver, and stomach samples were collected. Five vertebrae and the jaw, which had approximately 50 teeth, were also removed from the carcass of this whale.

Whale 16 was a 15.1 m male that stranded on Muriwai Beach, West Auckland, on December 8, 2004, 1 km from the northern access to 26-mile Beach. Iwi removed the whale from the beach to bone it out.

Whale 17 was a 16.8 m male that stranded 1 km north of Hapupu on Hansey Bay Beach, Chatham Islands, on August 9, 2004. It had a large wound on its lower back, its intestines were coming out, and its skin was blistered. It had been on the beach for several days and could have washed up during a storm on August 6. The skull was fractured in many places, and it is possible that a large boat struck this animal.

The stomach samples of whale 18 were archived at Te Papa and lacked collection details, although this animal is thought to have stranded around Cook Strait in the early 1990s (Anton van Helden pers. comm.*)

Whale 19 was an 11.6 m female that stranded near Napier, Hawkes Bay on February 28th, 2004. It had a large obstruction of ambergris in the lower intestine and had signs of peritonitis, with a large fluid discharge and a large part of the lower intestine starting to rot. It is unknown whether the peritonitis contributed to stranding.

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^{*} Anton van Helden, Collection Manager, marine mammals, Museum of New Zealand, Wellington.

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Whale # AUT # TePapa #	1 G27	2 G28	3 G29			6 G32 S1 N4 ²	7 G36 1 01 36	8 G37	9 G69	10Š12 G39ŠG41	13 G34 -	14 G38 -	15 G35 -	16 G26 Q 10 175 192	17 G33 -	18 G68 -	19 TBD NZMS260 V21 483 720
Location		Whatipu Beach, West Auckland						Oputama Beach, east North Island			"Cook Strait"	Napier					
Date		15-Nov-2003 30-Nov-2004 11-Oct-2004						11-Oct-2004	28-Nov-2002	8-Dec-2004	9-Aug-2004	Early 1990s	28-Feb-2004				
Whale Length		11.2Ń16.5m 15.8m 14.7m						14.7m	13m	15.1m	16.8m	-	11.6m				
# Lower Beaks	509	299	163	186	32	128	1,485	1,949	254	0	879	422	426	70	13	618	5,143
# Upper Beaks	580	244	169	169	40	110	1,478	2,311	234	0	952	840	433	64	40	594	2,389
Total # Beaks	1,089	543	332	355	72	238	2,963	4,260	488	0	1,831	1,262	859	134	53	1,212	7,532

Table 1. Stranding information for the stomach samples and sperm whales from which they were collected*

* NZMS stands for New Zealand Marine Society and the AUT # (G...) refers to the number assigned to the samples in the AUT collections.

3.1.2 Diet analysis

All stomach samples were washed, sieved in a 0.5 mm sieve, and sorted into one of fish remains, cephalopod remains, nematodes and "other remains". Cephalopod beaks, eye lenses, fish scales and bones were separated from the soft remains (fish and cephalopod flesh including buccal bulbs), then identified to the lowest possible taxonomic level. The presence of ambergris in the sample suggests intestinal contents were collected.

Cephalopod beaks were sorted into upper and lower beaks, and counted. The lower beaks were then sorted into different types based on morphology, then identified to the lowest taxonomic level using methodologies described in Clarke (1980, 1986) and Smale (1993), with the aid of a cephalopod beak collection taken from whole specimens, and housed at AUT*. For the purposes of this investigation, only lower beaks have been identified because of the time frame of this investigation.

Histioteuthid beaks that could not be positively assigned as belonging to a species were separated into types A or B as described by Clarke (1986) and classified into putative species. Stomach contents sampled by EOS and DoC personnel are accessioned into the biological collections of EOS, whereas those from Te Papa have been returned.

Beak measurements and estimations of cephalopod body mass and mantle length

A total of 11,110 lower beaks representing 88.3% of the total number of lower beaks found in the stomach samples (12,576 lower beaks) were in sufficiently

^{*} Housed at the AUT Earth and Oceanic Sciences Research Institute (EOS), Auckland, New Zealand.

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good condition to be measured (where the rostrum was not broken or chipped). Standard measurements of the lower beaks were made to the nearest 0.01 mm using digital callipers. These were lower rostral lengths (LRL) measured for decapod squid, and lower hood lengths (LHL) measured for octopods and *Vampyroteuthis infernalis*.

Allometric equations that describe the relationship between LRL or LHL and both dorsal mantle length and fresh weight, are published in the literature (Clarke 1980, 1986, Rodhouse *et al.* 1990, Gröger *et al.* 2000, Lu & Ickeringill 2002), Bolstad in press), and were used to calculate dorsal mantle length (ML) and body mass (BM) for individual cephalopods taken by sperm whales (Table 2). However many of these equations are applicable to the family and not species specific.

The overall contribution of each taxon to the diet by weight of a single whale was calculated as the sum of all estimated BM for measured beaks. In cases where beaks could be attributed to a species but were too broken to be measured, overall consumption was calculated as the sum of (all estimated weights for measured beaks) + (the mean estimated weight for the cephalopod species in the diet of that particular whale) x (the number of unmeasured beaks).

3.2 Beak descriptions

Lower beaks of cephalopods present in the diet of sperm whales that are problematic to identify are illustrated; namely: *Taningia danae*, *Octopoteuthis megaptera*, *Octopoteuthis* sp. 'Giant' (Octopoteuthidae); and *Lepidoteuthis grimaldii* (Lepidoteuthidae). Lower beaks were removed from positively identified whole animals. Beaks were removed fresh from the buccal mass or dissected with the help of a diluted KOH solution. Illustrations of the lower beaks are drawn following the methodology described by Clarke (1986). Beak sections are illustrated according to Figure 8.

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Figure 8. Lower cephalopod beak showing rostral (D, E, F) and lateral wall sections (G, H, I) taken from voucher beak samples, and used for illustrating and describing the beaks

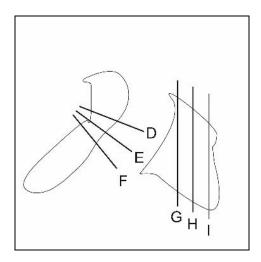


Figure 9. Sperm whale stranding locations from where stomach contents were collected

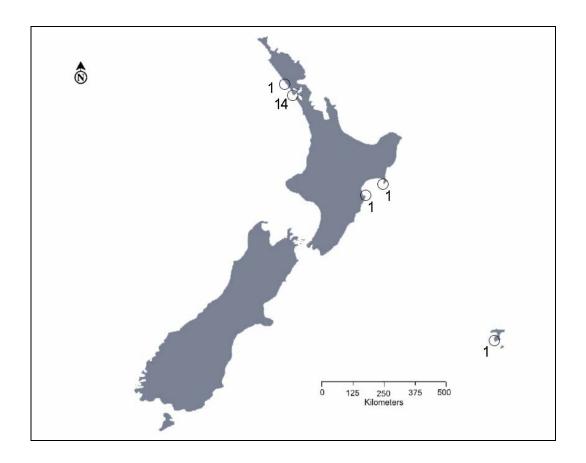


Table 2. Allometric equations for calculating mantle length (ML) and body mass (BM) from lower rostral length (LRL) $\,$

Species	ML	N	ВМ	N	Reference
Ancistrocheiridae					
Ancistrocheirus sp.	ML = -41.3 + 40.75(LRL)	23	ln(BM) = -0.194 + 3.56ln(LRL)	21	Clarke 1980
Architeuthidae					
Architeuthis dux	ML = -55.6 + 59.31(LRL)	11	ln(BM) = -1.773 + 4.57ln(LRL)	9	Clarke 1980
Chiroteuthidae					
Asperoteuthis sp.	ML = -1.8 + 29.08 (LRL)	47	ln(BM) = 0.184 + 2.88(LRL)	45	Clarke 1986
Chiroteuthis veranyi	ML = 11.4 + 24.46(LRL)	23	ln(BM) = -0.241 + 2.7ln(LRL)	14	Clarke 1980
Chiroteuthis sp. 2	ML = 11.4 + 24.46(LRL)	23	ln(BM) = -0.241 + 2.7ln(LRL)	14	Clarke 1980
Cranchiidae					
Galiteuthis sp. C (sensulmber)	ML = 12.2 + 40.78(LRL)	39	ln(BM) = 0.728 + 2.34ln(LRL)	38	Clarke 1980
Liocranchia sp.	-	-	ln(BM) = 1.58 + 1.85ln(LRL)	40	Clarke 1986
Megalocranchia sp. A (sensu Voss)	ML = -70.9 + 68.13(LRL)	20	ln(BM) = -0.108 + 2.73ln(LRL)	20	Clarke 1980
Taonius sp. A	-	-	ln(BM) = 0.786 + 2.19ln(LRL)	74	Clarke 1986
Taonius sp. B (sensuVoss)	-	_	ln(BM) = 0.786 + 2.19ln(LRL)		Clarke 1986
Mesonychoteuthis hamiltoni*	-	-	ln(BM) = 0.786 + 2.19ln(LRL)	74	Clarke 1986
Tewthowenia pellucida	-	-	ln(BM) = 0.786 + 2.19ln(LRL)	74	Clarke 1986
Cycloteuthidae					
Cycloteuthis akimushkini	ML= 31(LRL)	_	ln(BM) = 1.89 + 1.95ln(LRL)	-	Clarke 1980
Histioteuthidae	, ,		. ,		
Histioteuthis atlantica	ML = -13.6 + 22.21(LRL)	54	ln(BM) = 1.594 + 2.31ln(LRL)	53	Clarke 1980
Histioteuthis bonnellii	ML= 17.1 + 8.99(LRL)	19	In(BM) = 1.594 + 2.31In(LRL)		Clarke 1980
Histioteuthis macrohista	ML= -13.6 + 22.21(LRL)	54	In(BM) = 1.594 + 2.31In(LRL)		Clarke 1980
Histioteuthis miranda	ML= -7.0 + 25.82(LRL)	27	In(BM)= 1.783 + 2.44In(LRL)	14	Clarke 1980
Histioteuthis Type A5	ML= -13.6 + 22.21(LRL)	54	In(BM) = 1.594 + 2.31In(LRL)	53	Clarke 1980
Histioteuthis Type B4	ML= -13.6 + 22.21(LRL)	54	In(BM) = 1.594 + 2.31In(LRL)	53	Clarke 1980
Lepidoteuthidae			(=)		
Lepidoteuthis grimaldii	ML= -556.9 + 75.22(LRL)	15	ln(BM) = -0.874 + 3.42(LRL)	_	_
Mastigoteuthidae			(2)		
Idioteuthis cordiformis	ML= 1.8+29.08(LRL)	_	ln(BM) = -3.53 + 4.67ln(LRL)	5	Lu and Ickeringill 2002
Idioteuthis sp.1	ML= 1.8+29.08(LRL)	_	ln(BM) = -3.53 + 4.67ln(LRL)	5	Lu and Ickeringill 2002
Mastigoteuthis sp.	ML= 1.8+29.08(LRL)	_	-	-	
Octopoteuthidae	= (=)				
Octopoteuthis megaptera	ML = -0.4 + 17.33(LRL)	30	ln(BM) = 0.166 + 2.31ln(LRL)	_	Clarke 1980
Octopoteuthis sp. 'Giant'	ML= -0.4 + 17.33(LRL)	30	In(BM) = 0.166 + 2.31In(LRL)	_	Clarke 1980
Taningia danae	ML= -556.9 + 75.22(LRL)	15	ln(BM) = -0.874 + 3.42ln(LRL)	_	Clarke 1980
Ommastrephidae	WIE 330.7 1 73.22 (ERE)	13	III(BNI) = 0.074 + 0.42III(ERE)		
Ommastrephid (indeterminate)	ln(ML) = 4.11 + 0.793ln(LRL)	407	ln(BM) = 1.91 + 2.37ln(LRL)	403	Clarke 1986
Onychoteuthidae	m(mz)= 4.11 + 0.775m(ERE)	407	III(BM) = 1.71 + 2.37III(ERE)	400	
Kondakovia longimana*	ML = 65.5 + 44.24(LRL)	_	ln(BM) = 0.576 + 3.00ln(LRL)	_	Clarke 1986
Moroteuthis ingens (Female)	ML= -12.174 + 40.192(LRL)	_	BM= 1.9976(LRL) ^2.8899	36	Bolstad in prep
Moroteuthis ingens (Male)	ML= 8.31 + 32.023(LRL)	_	BM= 3.3332(LRL) ^2.4067	30	Bolstad in prep
Moroteuthis robsoni	ML= -652.91 + 151.03(LRL)	8	InBM= -9.15 + 8.07In(LRL)	6	Lu and Ickeringill 2002
Pholidoteuthidae	WE= -032.41 + 131.03(ERE)	0		O	La ana ickeringin 2002
Pholidoteuthis boschmai	ML = 11.3 + 41.09(LRL)	12	ln(BM) = 0.976 + 2.83ln(LRL)	15	Clarke 1980
Psychroteuthidae	WIL= 11.3 + 41.09(ERL)	12	III(BNI) = 0.470 + 2.83III(ERE)	15	Clarke 1700
rsychioteuthuae	ML= 50.6895(LRL) -				
Psycroteuthis glacialis	8.6008(LRL)^2 +	211	ln(BM) = 0.3422 + 2.1380ln(LRL)	211	Groger et al. 2000.
y u u no gradiano	1.0823(LRL) ^3 - 8.7019		+ 0.2214ln(LRL)^3		•
Argonautidae	, , , , ,				
Argonauta nodosa	ML = -57.67 + 9.02(LHL)	12	ln(BM) = -3.98 + 3.20ln(LHL)	12	Lu and Ickeringill 2002
Octopodidae	` ,		• • • • • • • • • • • • • • • • • • • •		
Octopodid (indeterminate)	ML = 3.38 + 26.57(LHL)	-	ln(BM) = 1.68 + 2.85ln(LHL)	-	Clarke 1986
Vampyroteuthidae					
Vampyroteuthis infernalis	ML = 5.86 + 4.70(LHL)	11	ln(BM) = -2.38 + 2.99ln(LHL)	11	Lu and Ickeringill 2002
			· · · · · · · · · · · · · · · · · · ·		

Chapter 4

Results

4.1 Cephalopod component of the diet

Beaks found in the stomach samples of New Zealand stranded sperm whales were attributed to three categories representing their distribution, locally (groups A and B) and non-locally consumed cephalopods. Those species referred here to as 'local' taxa include those abundantly represented in museum collections, and those that rarely (or very rarely) occur in New Zealand waters, (being at their northern or southern distributional ranges). The rationale for doing so is to determine the relative importance of locally consumed taxa to those consumed outside New Zealand waters. This distinction between these three prey categories is based largely on the probability any given taxon was consumed in the New Zealand EEZ, on the basis of the following criteria:

- The condition of the beaks within a stomach, as an indication of time of retention within it.
- The presence and relative abundance of cephalopod species in museum collections from the New Zealand EEZ.
- The incidence of cephalopod species (beaks) also present in the stomach contents of Kogia breviceps, recovered from New Zealand stranding events (a species considered to be resident in New Zealand waters).

As many species found locally also occur outside the New Zealand EEZ, it cannot be definitely stated that prey was consumed within New Zealand waters. Similarly, it cannot be definitely stated that non-local taxa do not occur

in waters of the New Zealand EEZ that have not been trawled (very remote areas) or at depths outside the current fisheries range (1,500 m).

These two prey categories, A and B respectively, are probably and possibly consumed within our EEZ, although for the latter it is considered unlikely. Those cephalopod species referred to as 'non-local' taxa almost certainly were not predated in New Zealand waters, although this possibility cannot be discounted.

4.1.1 Whale diet from stomachs

In the following section, I present the results for the dietary analysis for each of the 19 individual whales, followed by a summary of the diet of all sperm whales stranded on New Zealand's coasts that have been described. The number of beaks found in each whale stomach, the species composition and estimated ML and BM are presented. It should be kept in mind the cephalopod biomass presented is an estimate susceptible to a number of biases.

Sperm whale 1

A total 509 lower beaks representing 26 cephalopod species, belonging to 14 families were recorded from the stomach of this whale. Of these 26 species, 24 could have been consumed within New Zealand, and two are considered to be non-local taxa. Cephalopod species found locally contributed 97.8% of the beaks and 88.2% by weight to the diet of this sperm whale, while non-local species contributed 2.2% by number and 11.8% by weight. The total cephalopod biomass estimated from beaks was 558.1 kg, estimated at less than a day's worth of food for a 40 t sperm whale (Table 3). However, cephalopod species from group A (those most probably consumed within the EEZ in the days prior to stranding) contributed 336.4 kg (60.3%) to the diet, while cephalopods from group B and non-local species together contributed 221.7 kg (39.7%). The mean BM for the cephalopods represented by beaks in

the stomach contents of sperm whale 1 was 1,096.5 g (SE = 114.85,), and had a mean estimated ML of 261.9 mm (SE = 9.1).

The most important cephalopod families in the diet of sperm whale 1 by number were Histioteuthidae, Cranchiidae, Ancistrocheiridae, and Onychoteuthidae, and by weight Onychoteuthidae, Octopoteuthidae, Histioteuthidae, Ancistrocheiridae and Architeuthidae (Figure 10, Appendix 1, see CD attached). The most important species in the diet of this whale were Taningia danae, Kondakovia longimana, Ancistrocheirus sp., Architeuthis dux, Moroteuthis robsoni, Pholidoteuthis boschmai, Histioteuthis miranda and Histioteuthis atlantica, collectively contributing 81.0% of the cephalopod biomass as represented by beaks in the stomach sample of sperm whale 1 (Figure 11, Appendix 1).

Table 3. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 1, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
		Architeuthidae				
		Architeuthis dux	4	0.79	61,993	11.1
		Chiroteuthidae				
		Chiroteuthis sp. 2	2	0.39		0.03
		Chiroteuthis veranyi	2	0.39	265	0.0
		Cranchiidae				
		Galiteuthis sp. C	19	3.73		0.8
		Liocranchia sp.	1	0.20		0.0
		Taonius sp. B	5	0.98		0.30
		Teuthowenia pellucida	15	2.95	1,446	0.2
		Cycloteuthidae				
		Cycloteuthis akimushkini	6	1.18	6,840	1.2
		Histioteuthidae				
		Histioteuthis atlantica	140	27.50		5.2
	Α	Histioteuthis miranda	93	18.27	30,755	5.5
		Lepidoteuthidae				
		Lepidoteuthis grimaldii	1	0.20	9,543	1.7
		Mastigoteuthidae				
		Mastigoteuthis sp.	1	0.20		0.0
		Octopoteuthidae				
		Octopoteuthid (indeterminate)	4	0.79	15,122	2.7
Local		Octopoteuthis megaptera	6	1.18	2,582	0.4
Local		Octopoteuthis sp. 'Giant'	1	0.20	weight (g) 61,993 149 265 4,891 44 1,655 1,446 6,840 29,260 30,755 9,543	0.1
		Taningia danae	15	2.95	111,468	19.9
		Ommastrephidae				
		Ommastrephid (indeterminate)	1	0.20	3,190	0.5
		Onychoteuthidae				
		Moroteuthis ingens	11	2.16	21,807	3.9
		Pholidoteuthidae				
		Pholidoteuthis boschmai	18	3.54		6.1
		Total local species group A	345	67.78	336,393	60.2
-		Ancistrocheiridae				
		Ancistrocheirus sp.	44	8.64	62,079	11.1
		Chiroteuthidae				
		Asperoteuthis sp.	2	0.39	1,867	0.3
		Cranchiidae				
	В	Megalocranchia sp. A	45	8.84	17,942	3.2
	_	Histioteuthidae				
		Histioteuthis Type A5	39	7.66	17,080	3.0
		Onychoteuthidae				
		Moroteuthis robsoni	21	4.13	56,728	10.1
		Alloposidae				
		Haliphron atlanticus	2	0.39		0.0
		Total local species group B	153	30.06	155,827	27.9
		Total local species	498	97.84	492,221	88.1
		Onychoteuthidae				
Non-l	ocal	Kondakovia longimana	10	1.96	65,410	11.7
INOI1-I	ocai	Psychroteuthidae				
		Psychroteuthis glacialis	1	0.20	476	0.0
		Total non-local species	11	2.16	65,886	11.8
		Total all species	509	100.00	558 107	100.0

Sperm whale 2

Nineteen cephalopod species in 11 families were represented by a total of 299 beaks found in the stomach of this whale. 14 cephalopods from group A, four cephalopod species from group B, and one non-local species. Local cephalopod species represented 99.7% by number and 99.3% by weight of the diet of this whale, while *Kondakovia longimana*, the only non-local species contributed 0.3% and 0.8% by number and weight to the diet, respectively. These 19 species were estimated to weigh 400.8 kg, less than half a day's worth of food for a 40 t sperm whale (Table 4). Moreover, the cephalopods from group A contributed only 265.3 kg (66.2%) to the diet, while the cephalopod species from group B and non-local species collectively contributed 135.5 kg (33.8%) to the diet of this whale. The mean BM for the cephalopods represented by beaks in the stomach contents of sperm whale 2 was 1,340.4 g (SE = 333.5), and the mean ML was 313.0 mm (SE = 12.6).

The most important cephalopod families by number in the diet of sperm whale 2 were Histioteuthidae, Cranchiidae, Onychoteuthidae and Pholidoteuthidae, while the most important families by weight were Architeuthidae, Onychoteuthidae, Pholidoteuthidae and Octopoteuthidae (Figure 12, Appendix 1). The most important cephalopod species in the diet of this sperm whale were *Architeuthis dux*, *Moroteuthis robsoni*, *Pholidoteuthis boschmai*, *Taningia danae*, *Histioteuthis miranda* and *Ancistrocheirus* sp., collectively contributing 83.6% of the cephalopod biomass as represented by beaks in the stomach. Two *Architeuthis* specimens were estimated to weigh a total of 108.0 kg, contributing 26.9% to the diet (Figure 13, Appendix 1).

Table 4. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 2, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
		Architeuthidae			3 (3)	
		Architeuthis dux	2	0.67	107,956	26.9
		Chiroteuthidae				
		Chiroteuthis sp. 2	10	3.34	680	0.1
		Chiroteuthis veranyi	4	1.34	634	0.1
		Cranchiidae				
		Galiteuthis sp. C	8	2.68	1,973	0.4
		Teuthowenia pellucida	19	6.35	1,939	0.4
		Cycloteuthidae			,	
		Cycloteuthis akimushkini	14	4.68	14,702	3.6
		Histioteuthidae			,	
	_	Histioteuthis atlantica	55	18.39	10,380	2.5
	Α	Histioteuthis miranda	56	18.73	20,909	5.2
		Lepidoteuthidae			,	
		Lepidoteuthis grimaldii	1	0.33	3,086	0.7
		Octopoteuthidae	•	0.00	0,000	0.
		Octopoteuthid (indeterminate)	2	0.67	7,561	1.8
Local		Octopoteuthis megaptera	4	1.34	1.055	0.:
		Octopoteuthis sp. 'Giant'	3	1.00	1,167	0.
		Taningia danae	5	1.67	35,714	8.
		Ommastrephidae	· ·	1.07	00,7.1	0.
		Ommastrephid (indeterminate)	1	0.33	1,050	0.3
		Pholidoteuthidae		0.55	1,030	0.2
		Pholidoteuthis boschmai	28	9.36	56,509	14.1
		Total local species group A	212	70.90	265,315	66.2
-		Ancistrocheiridae				
		Ancistrocheirus sp.	14	4.68	20,859	5.3
		Cranchiidae			20,007	0
		Megalocranchia sp. A	37	12.37	18,160	4.5
	В	Histioteuthidae		.=	,	
		Histioteuthis Type A5	1	0.33	498	0.
		Onychoteuthidae	•	0.00	.,,	0.
		Moroteuthis robsoni	34	11.37	92,926	23.1
!		Total local species group B	86	28.76	132,444	33.0
		Total local species	298	99.67	397,759	99.:
Non-le	ocal	Onychoteuthidae				
14011-1		Kondakovia longimana	1	0.33	3,013	0.
		Total non-local species	1	0.33	3,013	0.
		Total all species	299	100.00	400,772	100.0

Sperm whale 3

Beaks found in the stomach of this whale comprised a total of 17 cephalopod species in ten families, 11 cephalopod species from group A, four cephalopod species from group B, and two non-local species (Table 5). Local taxa contributed 97.6% by number and 94.1% by weight to the diet of this whale, while non-local taxa contributed 2.4% by number and 6.0% by weight. The 163 beaks represented cephalopods estimated to weigh a total of 246.0 kg, approximately one quarter of a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed only 151.1 kg (61.4%) to the diet, and cephalopod species from group B and non-local species together contributed 94.9 kg (38.6%). The mean BM for the cephalopods represented by beaks in the stomach contents of sperm whale 3 was 1,509.1 g (SE = 201.9), and a mean ML of 322.5 mm (SE = 18.0).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Ancistrocheiridae and Onychoteuthidae, while by weight, the families Octopoteuthidae, Architeuthidae, Onychoteuthidae and Pholidoteuthidae were most important (Figure 14, Appendix 1). *Taningia danae, Architeuthis dux, Moroteuthis robsoni, Pholidoteuthis boschmai, Ancistrocheirus* sp., *Histioteuthis miranda* and *Kondakovia longimana*, collectively contributed 90.0% of the cephalopod biomass as represented by beaks in the stomach (Figure 15, Appendix 1).

Table 5. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 3, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Architeuthidae				
		Architeuthis dux	5	3.07	48,374	19.67
		Chiroteuthidae				
		Chiroteuthis veranyi	1	0.61	161	0.07
		Cranchiidae				
		Galiteuthis sp. C	2	1.23	564	0.23
		Taonius sp. B	7	4.29	2,256	0.92
		Teuthowenia pellucida	3	1.84	287	0.12
		Cycloteuthidae				
	Α	Cycloteuthis akimushkini	3	1.84	3,383	1.38
		Histioteuthidae				
		Histioteuthis atlantica	23	14.11	4,701	1.91
		Histioteuthis miranda	42	25.77	15,449	6.28
		Octopoteuthidae				
Local		Octopoteuthis megaptera	2	1.23	725	0.29
		Taningia danae	6	3.68	49,053	19.94
		Pholidoteuthidae			•	
		Pholidoteuthis boschmai	11	6.75	26,118	10.62
Ī		Total local species group A	105	64.42	151,072	61.42
-		Ancistrocheiridae				
		Ancistrocheirus sp.	19	11.66	24,614	10.01
		Cranchiidae				
	В	Megalocranchia sp. A	12	7.36	5,719	2.32
	ь	Histioteuthidae				
		Histioteuthis Type A5	9	5.52	4,904	1.99
		Onychoteuthidae				
		Moroteuthis robsoni	14	8.59	45,029	18.31
		Total local species group B	54	33.13	80,266	32.63
		Total local species	159	97.55	231,338	94.05
		Onychoteuthidae				
Non-le	ocal	Kondakovia longimana	1	0.61	12,848	5.22
14011-10	ocai	Psychroteuthidae				
		Psychroteuthis glacialis	3	1.84	1,793	0.73
		Total non-local species	4	2.45	14,641	5.95
		Total all species	163	100.00	245,979	100.00

Sperm whale 4

Beaks found in the stomach of sperm whale 4 comprised a total of 16 cephalopod species, in eight families; ten cephalopod species from group A, five from group B, and a non-local species, *Kondakovia longimana* (Table 6). Local taxa contributed 98.9% by number and 85.1% by weight to the diet of this whale, while non-local taxa contributed 1.1% by number and 14.9% by weight. The 186 beaks represented cephalopods estimated to weigh a total of 106.0 kg, considerably less than a day's worth of food for a 40 t sperm whale. Locally occurring cephalopod species from group A contributed only 44.4 kg (41.9%) to the diet, while cephalopod species from group B and non-local species together contributed 61.5 kg (58.1%). The mean BM for the cephalopods consumed by this whale was 569.7 g (SE = 72.9), and a mean ML of 194.4 mm (SE = 10.8).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Ancistrocheiridae and Onychoteuthidae, while by weight, the most important families were Histioteuthidae, Onychoteuthidae, Ancistrocheiridae and Cranchiidae (Figure 16, Appendix 1). The most important species by weight in this whale's diet were *Histioteuthis miranda*, *Moroteuthis robsoni*, *Kondakovia longimana*, *Histioteuthis* Type A5, *Ancistrocheirus* sp., *Histioteuthis atlantica* and *Pholidoteuthis boschmai*, collectively contributing 89.7% of the total estimated cephalopod biomass as represented by beaks (Figure 17, Appendix 1).

Table 6. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 4, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Chiroteuthidae				
		Chiroteuthis veranyi	1	0.54	173	0.16
		Cranchiidae				
		Galiteuthis sp. C	6	3.23	1,506	1.42
		Taonius sp. B	4	2.15	1,247	1.18
		Cycloteuthidae				
		Cycloteuthis akimushkini	1	0.54	985	0.93
		Histioteuthidae				
	Α	Histioteuthis atlantica	29	15.59	6.218	5.87
		Histioteuthis bonnellii	1	0.54	217	0.20
		Histioteuthis miranda	77	41.40	27,149	25.62
		Octopoteuthidae			•	
		Octopoteuthis megaptera	3	1.61	1,122	1.06
		Onychoteuthidae	_		.,	
Local		Moroteuthis ingens	1	0.54	765	0.72
		Pholidoteuthidae	•			
		Pholidoteuthis boschmai	3	1.61	5,038	4.75
		Total local species group A	126	67.74	44,420	41.92
-		Ancistrocheiridae				
		Ancistrocheirus sp.	14	7.53	10,679	10.08
		Chiroteuthidae				
		Asperoteuthis sp.	1	0.54	1,129	1.07
	В	Cranchiidae				
	В	Megalocranchia sp. A	10	5.38	3,767	3.56
		Histioteuthidae				
		Histioteuthis Type A5	25	13.44	13,011	12.28
		Onychoteuthidae				
		Moroteuthis robsoni	8	4.30	17,199	16.23
		Total local species group B	58	31.18	45,785	43.21
		Total local species	184	98.92	90,205	85.13
Non-Io	and .	Onychoteuthidae				
Non-IO	JCal	Kondakovia longimana	2	1.08	15,756	14.87
		Total non-local species	2	1.08	15,756	14.87
		Total all species	186	100.00	105,961	100.00

Sperm whale 5

Beaks found in the stomach of sperm whale 5 comprised a total of 11 species in eight families; seven cephalopod species in group A, three cephalopod species in group B, and *Psychroteuthis glacialis*, the only non-local species (Table 7). Local taxa contributed 96.9% by number and 98.4% by weight to the diet of this whale, while non-local taxa contributed 3.1% by number and 1.6% by weight. The 32 beaks represented cephalopods that were estimated to weigh a total of 24.3 kg, considerably less than a day's worth of food for a 40 t sperm whale, with cephalopod species from group A contributing only 19.2 kg (78.7%) to the diet, and cephalopod species from group B and non-local species 5.2 kg (21.3%). The mean estimated BM for the cephalopods represented by beaks in the stomach was 760.9 g (SE = 160.7), and the estimated mean ML was 251.0 mm (SE = 37.8).

The most important families by number in the diet of sperm whale 5 were Histioteuthidae, Cranchiidae, and Pholidoteuthidae, while the most important families by weight were Pholidoteuthidae, Histioteuthidae, Onychoteuthidae and Cranchiidae (Figure 18, Appendix 1). The most important species in the diet of this sperm whale were *Pholidoteuthis boschmai*, *Histioteuthis miranda*, *Moroteuthis robsoni* and *Histioteuthis atlantica*, together contributing 80.2% of the diet as represented by beaks (Figure 19, Appendix 1).

Table 7. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 5, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Cranchiidae				
		Galiteuthis sp. C	2	6.25	436	1.79
		Taonius sp. B	2	6.25	591	2.43
		Cycloteuthidae				
		Cycloteuthis akimushkini	1	3.13	1,090	4.48
	Α	Histioteuthidae				
	A	Histioteuthis atlantica	7	21.88	1,369	5.62
		Histioteuthis miranda	11	34.38	4,295	17.64
		Octopoteuthidae				
Local		Octopoteuthis megaptera	1	3.13	426	1.75
Local		Pholidoteuthidae				
		Pholidoteuthis boschmai	4	12.50	10,943	44.94
		Total local species group B	28	87.50	19,151	78.65
-		Chiroteuthidae				
		Asperoteuthis sp.	1	3.13	936	3.84
	В	Cranchiidae				
	ь	Megalocranchia sp. A	1	3.13	966	3.97
		Onychoteuthidae				
		Moroteuthis robsoni	1	3.13	2,912	11.96
		Total local species group B	3	9.38	4,814	19.77
		Total local species	31	96.88	23,965	98.42
Non-lo	2021	Psychroteuthidae			•	
NON-IO	Juai	Psychroteuthis glacialis	1	3.13	384	1.58
	•	Total non-local species	1	3.13	384	1.58
		Total all species	32	100.00	24,349	100.00

Sperm whale 6

A total of 14 cephalopod species, belonging to nine families were recorded from the 128 beaks found in the stomach of sperm whale 6. Nine were cephalopod species from group A, four were cephalopod species from group B, and one was the non-local species *Kondakovia longimana*. Local cephalopod species represented 99.2% by number and 97.4% by weight, while non-local cephalopod species contributed 0.8% and 2.6% by number and weight to the diet of this sperm whale, respectively (Table 8). This sperm whale had an estimated 135.7 kg of cephalopods in its stomach, considerably less than a day's worth of food for a 40 t sperm whale. Cephalopod species in group A contributed only 78.9 kg (58.2%) to the diet of this whale, while cephalopod species in group B and non-local species together contributed 56.7 kg (41.8%). The mean BM for the cephalopods represented by beaks in the stomach contents of sperm whale 6 was 1,060.0 g (SE = 195.3), and the mean ML was 265.9 mm (SE = 17.9).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae and Pholidoteuthidae, while the most important families by weight were Pholidoteuthidae, Histioteuthidae, Onychoteuthidae and Cranchiidae (Figure 20, Appendix 1). The most important species in the diet of this sperm whale were *Pholidoteuthis boschmai*, *Histioteuthis miranda* and *Moroteuthis robsoni*, together contributing 74.8% of the total estimated cephalopod biomass, as represented by beaks (Figure 21, Appendix 1).

Table 8. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 6, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Architeuthidae				
		Architeuthis dux	2	1.56	28,335	20.88
		Chiroteuthidae				
		Chiroteuthis veranyi	1	0.78	153	0.11
		Cranchiidae				
		Teuthowenia pellucida	11	8.59	1,087	0.80
		Cycloteuthidae				
	Α	Cycloteuthis akimushkini	8	6.25	8,025	5.92
	A	Histioteuthidae				
		Histioteuthis atlantica	30	23.44	5,522	4.07
		Histioteuthis miranda	22	17.19	7,991	5.89
		Octopoteuthidae				
Local		Octopoteuthis megaptera	6	4.69	2,027	1.49
Locai		Taningia danae	1	0.78	13,149	9.69
		Pholidoteuthidae				
		Pholidoteuthis boschmai	4	3.13	12,641	9.32
		Total local species group A	85	66.41	78,929	58.17
		Ancistrocheiridae				
		Ancistrocheirus sp.	10	7.81	13,211	9.74
		Cranchiidae				
	В	Megalocranchia sp. A	4	3.13	2,006	1.48
		Histioteuthidae				
		Histioteuthis Type A5	14	10.94	5,647	4.16
		Onychoteuthidae				
		Moroteuthis robsoni	14	10.94	32,325	23.82
		Total local species group B	42	32.81	53,190	39.20
		Total local species	127	99.22	132,119	97.38
Non-le	ocal	Onychoteuthidae				
NOTIFIC	ocai	Kondakovia longimana	1	0.78	3,558	2.62
		Total non-local species	1	0.78	3,558	2.62
		Total all species	128	100.00	135,677	100.00

Sperm whale 7

A total of 26 cephalopod species, belonging to 15 families, were recorded from 1,485 beaks found in the stomach of this whale. Of these 26 cephalopod species, 18 were from group A, including the vampyromorph *Vampyroteuthis infernalis*, six from group B, including the oceanic octopod *Haliphron atlanticus*, and two were non-local taxa. Local cephalopod species represented 98.9% by number and 88.7% by weight, while non-local cephalopod species contributed 1.1% and 11.3% by number and weight to the diet of this sperm whale, respectively (Table 9). This sperm whale had an estimated 1,631.8 kg of cephalopods in its stomach, representing about two day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 858.1 kg (52.6%), around a day's worth of food to the diet of this whale, and cephalopod species from group B and non-local species collectively contributed 773.7 kg (47.4%). The mean biomass for the cephalopods represented by beaks in the stomach was 1,098.9 g (SE = 57.1), at a mean estimated ML of 318.1 mm (SE = 5.7).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Onychoteuthidae and Pholidoteuthidae, while the most important families by weight were Onychoteuthidae, Octopoteuthidae, Pholidoteuthidae and Histioteuthidae (Figure 22, Appendix 1). The most important species in the diet of this sperm whale were *Moroteuthis robsoni, Taningia danae, Pholidoteuthis boschmai, Kondakovia longimana, Histioteuthis miranda, Ancistrocheirus* sp. and *Megalocranchia* sp. A, collectively contributing 83.8% of the estimated weight found in the stomach (Figure 23, Appendix 1).

Table 9. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 7, stranded on Whatipu Beach, West Auckland, November 15, 2003

Architeuthis dux	Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
Chiroteuthidae Chiroteuthidae Chiroteuthis sp. 2			Architeuthidae				
Chiroteuthis sp. 2			Architeuthis dux	2	0.13	25,673	1.57
Chiroteuthis veranyi			Chiroteuthidae				
Cranchildee Galifeuthis sp. C 54 3.64 12,484 0.7			Chiroteuthis sp. 2	6	0.40	697	0.04
Galiteuthis sp. C			Chiroteuthis veranyi	14	0.94	2,123	0.13
Liccranchia sp. 2 0.13 104 0.00			Cranchiidae				
Taonius sp. B			Galiteuthis sp. C	54	3.64	12,484	0.7
Teuthowenia pellucida			Liocranchia sp.	2	0.13	104	0.0
Cycloteuthidae			Taonius sp. B	47	3.16	15,498	0.9
Cycloteuthis akimushkini			Teuthowenia pellucida	40	2.69	4,227	0.2
Cycloteuthis akimushkini			Cycloteuthidae				
Histioteuthidae				28	1.89	25,941	1.59
Histoteuthis atlantica							
A Histioteuthis miranda 347 23.37 131,838 8.0				240	16.16	46.856	2.8
Lepidoteuthidae							8.0
Lepidoteuthis grinaldii		Α	I			,	
Cottopoteuthidae				4	0.27	60 144	3.69
Coctopoteuthis megaptera 25 1.68 8.876 0.55 0.50 0.				-	0.27	00,144	0.0
Cotopoteuthis sp. 'Giant' 3 0.20 1,322 0.00 Taningia danae				25	1 60	9 976	0.5
Local							
Commastrephide				_		·	
Dommastrephild (indeterminate) 3 0.20 7,793 0.4 Pholidoteuthidae Pholidoteuthidae Pholidoteuthidae Pholidoteuthib boschmai 95 6.40 225,261 13.8 Argonautia nodosa 2 0.13 34 0.0 Vampyroteuthidae Vampyroteuthidae Vampyroteuthis infernalis 1 0.07 11 0.00 1.00			1 9	47	3.10	204,914	17.40
Pholidoteuthidae	Local			2	0.20	7 702	0.4
Pholidoteuthis boschmai				3	0.20	1,173	0.40
Argonautidae Argonautidae Argonautidae Argonautidae Vampyroteuthidae Vampyroteuthis infernalis 1 0.07 11 0.0 0.2				O.F.	4 40	225 241	12.00
Argonauta nodosa 2 0.13 34 0.00				95	6.40	225,261	13.80
Vampyroteuthis infernalis							
Vampyroteuthis infernalis				2	0.13	34	0.00
Indeterminate							
Total local species group A 965 64.98 858,055 52.5			1 , 3				
Ancistrocheirus sp.	-						
Ancistrocheirus sp. 85 5.72 124,514 7.60			Total local species group A	965	64.98	858,055	52.58
Chiroteuthidae			1			101.511	=
Asperoteuthis sp. 4 0.27 3,738 0.2			•	85	5.72	124,514	7.6
Cranchiidae Megalocranchia sp. A 222 14.95 95,256 5.8 Histioteuthidae Histioteuthis Type A5 73 4.92 40,852 2.5 Onychoteuthidae Moroteuthis robsoni 116 7.81 324,306 19.8 Alloposidae Haliphron atlanticus 3 0.20 504 0.0 Total local species group B 503 33.87 589,170 36.1 Total local species 1,468 98.86 1,447,224 88.6 Onychoteuthidae Kondakovia longimana 10 0.67 181,128 11.1 Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2 Total non-local species 17 1.14 184,561 11.3							
B				4	0.27	3,738	0.23
Histioteuthidae							
Histioteuthidae		В		222	14.95	95,256	5.84
Onychoteuthidae Moroteuthis robsoni 116 7.81 324,306 19.8		_	1				
Moroteuthis robsoni				73	4.92	40,852	2.50
Alloposidae Haliphron atlanticus 3 0.20 504 0.0 Total local species group B 503 33.87 589,170 36.1 Total local species 1,468 98.86 1,447,224 88.6 Onychoteuthidae			Onychoteuthidae				
Haliphron atlanticus 3 0.20 504 0.0 Total local species group B 503 33.87 589,170 36.1 Total local species 1,468 98.86 1,447,224 88.6 Onychoteuthidae Kondakovia longimana 10 0.67 181,128 11.1 Psychroteuthidae Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2 Total non-local species 17 1.14 184,561 11.3			Moroteuthis robsoni	116	7.81	324,306	19.8
Total local species group B 503 33.87 589,170 36.1 Total local species 1,468 98.86 1,447,224 88.6 Onychoteuthidae Kondakovia longimana 10 0.67 181,128 11.1 Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2 Total non-local species 17 1.14 184,561 11.3			Alloposidae				
Total local species			Haliphron atlanticus				0.03
Non-local Convention Non-local Non			Total local species group B	503	33.87	589,170	36.1
Non-local Kondakovia longimana 10 0.67 181,128 11.1 Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2 Total non-local species 17 1.14 184,561 11.3			Total local species	1,468	98.86	1,447,224	88.69
Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2			Onychoteuthidae				<u> </u>
Psychroteuthidae Psychroteuthis glacialis 7 0.47 3,432 0.2				10	0.67	181,128	11.10
Psychroteuthis glacialis 7 0.47 3,432 0.2 Total non-local species 17 1.14 184,561 11.3	Non-le	ocai					
Total non-local species 17 1.14 184,561 11.3				7	0.47	3.432	0.2
Total all species 1 485 100 00 1 631 785 100 0							11.3
			Total all enocios	1 //25	100.00	1 631 795	100.00

Sperm whale 8

Beaks found in the stomach of this whale comprised a total of 27 cephalopod species in 13 families. Seventeen were cephalopod species from group A, seven were cephalopod species from group B, and three were non-local taxa (Table 10). Local taxa contributed 99.1% by number and 94.6% by weight to the diet of this whale, while non-local taxa contributed 0.9% by number and 5.5% by weight. The 1,949 beaks represented cephalopods estimated to weigh a total of 1,838.5 kg, approximately two day's food for a 40 t sperm whale. Cephalopod species from group A contributed 935.0 kg (50.9%), around a day of food to the diet of this whale, while cephalopod species from group B and non-local species together contributed 903.5 kg (49.9%). The mean BM for the cephalopods represented by beaks in the stomach contents of this whale was 943.3 g (SE = 57.5), at a mean ML of 262.3 mm (SE = 4.8).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Onychoteuthidae and Ancistrocheiridae, while the most important families by weight were Onychoteuthidae, Histioteuthidae, Architeuthidae and Pholidoteuthidae (Figure 24, Appendix 1). The most important species in the diet of this whale were *Moroteuthis robsoni*, Architeuthis dux, Histioteuthis miranda, Ancistrocheirus sp., Pholidoteuthis boschmai, Taningia danae, Histioteuthis atlantica and Kondakovia longimana, together contributing 78.2% of the total weight, as represented by beaks (Figure 25, Appendix 1).

Table 10. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 8, stranded on Whatipu Beach, West Auckland, November 15, 2003

istribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of to weig
		Architeuthidae			<u> </u>	•
		Architeuthis dux	8	0.41	183,285	9.
		Chiroteuthidae				
		Chiroteuthis sp. 2	9	0.46	1,024	0.
		Chiroteuthis veranyi	20	1.03	2,884	0.
		Cranchiidae			·	
		Cranchiid (indeterminate)	23	1.18	7,549	0.
		Galiteuthis sp. C	67	3.44	15,322	0
		Liocranchia sp.	2	0.10	221	0
		•	1	0.10	122	0
		Taonius sp. A				
		Taonius sp. B	46	2.36	14,297	0
		Teuthowenia pellucida	140	7.18	14,601	0
		Cycloteuthidae				
		Cycloteuthis akimushkini	38	1.95	39,463	2
	Α	Histioteuthidae				
	A	Histioteuthid (indeterminate)	15	0.77	3,782	0
		Histioteuthis atlantica	468	24.01	95,153	5
		Histioteuthis miranda	461	23.65	169,558	ç
		Octopoteuthidae		20.00	.07,000	•
		Octopoteuthid (indeterminate)	13	0.67	40,812	2
		Octopoteuthia (indeterminate)	28	1.44		
					12,097	(
		Octopoteuthis sp. 'Giant'	5	0.26	6,584	(
Local		Taningia danae	16	0.82	123,776	6
		Ommastrephidae				
		Ommastrephid (indeterminate)	1	0.05	1,769	C
		Onychoteuthidae				
		Moroteuthis ingens	21	1.08	36,306	1
		Pholidoteuthidae				
		Pholidoteuthis boschmai	62	3.18	148.743	8
		Indeterminate	25	1.28	21,299	1
		Total local species group A	1,469	75.37	938,647	51
-		Ancistrocheiridae				
		Ancistrocheirus sp.	92	4.72	151,077	8
		Chiroteuthidae			·	
		Asperoteuthis sp.	5	0.26	4,060	(
		Cranchiidae	· ·	0.20	1,000	·
		Megalocranchia sp. A	172	8.83	68,370	3
			172	0.03	00,370	
	В	Histioteuthidae		. = -	F	
		Histioteuthis Type A5	92	4.72	54,876	2
		Mastigoteuthidae				
		Idioteuthis cordiformis	1	0.05	44,116	2
		Onychoteuthidae				
		Moroteuthis robsoni	104	5.34	480,746	26
		Alloposidae				
		Haliphron atlanticus	2	0.10	173	(
		Total local species group B	468	24.01	803,419	43
		Total local species	1,937	99.38	1,742,066	94
		Cranchiidae				
		Mesonychoteuthis hamiltoni	1	0.05	8,530	(
	_	Onychoteuthidae	•		-,3	·
Non-Id	ocal	Kondakovia longimana	5	0.26	86,059	4
		Psychroteuthidae	5	0.20	30,037	_
			,	0.21	1.070	,
		Psychroteuthis glacialis	6	0.31	1,872	(
		Total non-local species	12	0.62	96,462	Ę

Sperm whale 9

Beaks found in the stomach of this whale comprised a total of 19 species in ten families. Twelve were cephalopod species from group A, six were species from group B, and one was the non-local species *Kondakovia longimana* (Table 11). Local taxa contributed 90.2% by number and 51.6% by weight to the diet of this whale, while non-local taxa contributed 9.8% by number and 48.4% by weight. The 254 beaks found in the stomach of this sperm whale represented cephalopods that were estimated to weigh a total of 509.6 kg, approximately half a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 174.3 kg (34.2%) to the diet, while cephalopod species from group B and non-local species together contributed 335.3 kg (65.8%). The mean BM for the cephalopods represented by beaks in the stomach contents of this whale was 2,006.4 g (SE = 193.9), at a mean estimated ML of 241.3 mm (SE = 13.2).

The most important families by number in the diet of this whale were Histioteuthidae, Onychoteuthidae, Octopoteuthidae and Cranchiidae, while the most important families by weight were Onychoteuthidae, Octopoteuthidae, Pholidoteuthidae and Histioteuthidae (Figure 26, Appendix 1). The most important species in the diet of this sperm whale were Kondakovia longimana, a group of indeterminate octopoteuthid beaks, Pholidoteuthis boschmai, Moroteuthis robsoni, Taningia danae and Histioteuthis Type A5, collectively contributing 87.3% of the total cephalopod biomass as represented by beaks (Figure 27, Appendix 1).

Sperm whale 10-12

No prey remains were found in the stomachs of whales 10, 11 and 12.

Table 11. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 9, stranded on Whatipu Beach, West Auckland, November 15, 2003

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
		Chiroteuthidae				
		Chiroteuthis sp. 2	1	0.39	58	0.01
		Cranchiidae				
		Galiteuthis sp. C	1	0.39	290	0.06
		Taonius sp. B	1	0.39	392	0.08
		Teuthowenia pellucida	2	0.79	204	0.04
		Cycloteuthidae				
		Cycloteuthis akimushkini	4	1.57	2,827	0.55
		Histioteuthidae				
		Histioteuthis atlantica	51	20.08	10,026	1.97
	Α	Histioteuthis miranda	32	12.60	10,977	2.15
		Octopoteuthidae				
		Octopoteuthid (indeterminate)	17	6.69	64,270	12.61
		Octopoteuthis megaptera	4	1.57	1,180	0.23
		Octopoteuthis sp. 'Giant'	4	1.57	2,547	0.50
		Taningia danae	4	1.57	30,004	5.89
		Ommastrephidae				
Local		Ommastrephid (indeterminate)	1	0.39	2,927	0.57
		Pholidoteuthidae				
		Pholidoteuthis boschmai	16	6.30	46,918	9.21
		Indeterminate	2	0.79	1,704	0.33
		Total local species group A	140	55.12	174,323	34.21
		Ancistrocheiridae				
		Ancistrocheirus sp.	11	4.33	20,136	3.95
		Chiroteuthidae				
		Asperoteuthis sp.	6	2.36	5,634	1.11
		Cranchiidae				
	В	Megalocranchia sp. A	12	4.72	5,251	1.03
	ь	Histioteuthidae				
		Histioteuthis Type A5	47	18.50	24,301	4.77
		Onychoteuthidae				
		Moroteuthis robsoni	8	3.15	32,720	6.42
		Alloposidae				
		Haliphron atlanticus	5	1.97	554	0.11
		Total local species group B	89	35.04	88,597	17.38
		Total local species	229	90.16	262,920	51.59
Non-le	ocal	Onychoteuthidae				
NON-10	ucai	Kondakovia longimana	25	9.84	246,706	48.41
		Total non-local species	25	9.84	246,706	48.41
		Total all species	254	100.00	509,626	100.00

Sperm whale 13

Beaks found in the stomach of this whale comprised 20 cephalopod species in 11 families. Twelve were cephalopod species from group A, six were species from group B, and two were non-local species (Table 12). Local taxa contributed 97.6% by number and 81.9% by weight to the diet of this whale, while non-local taxa contributed 2.4% by number and 18.1% by weight. The 879 beaks correspond to cephalopods estimated to weigh a total of 759.7 kg, representing almost a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 365.7 kg (48.1%) of food to this sperm whale, while cephalopod species from group B and non-local species collectively contributed 394.0 kg (51.9%). The mean BM of cephalopods represented by beaks in the stomach contents of this whale was 864.2 g (SE = 73.2), and the mean estimated ML was 184.3 mm (SE = 6.5).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Onychoteuthidae and Ancistrocheiridae, while the most important families by weight were Onychoteuthidae, Histioteuthidae, Octopoteuthidae and Ancistrocheiridae (Figure 28, Appendix 1). The most important species in the diet of this sperm whale were *Moroteuthis robsoni*, *Taningia danae*, *Kondakovia longimana*, *Histioteuthis atlantica*, *Ancistrocheirus* sp. and *Histioteuthis miranda*, together contributing 84.0% of the total cephalopod biomass as represented by beaks (Figure 29, Appendix 1).

Table 12. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 13, stranded on Whatipu Beach, West Auckland, November 30, 2004

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
		Architeuthidae				
		Architeuthis dux	7	0.80	36,196	4.76
		Cranchiidae				
		Galiteuthis sp. C	16	1.82	3,728	0.49
		Taonius sp. B	5	0.57	1,513	0.20
		Teuthowenia pellucida	1	0.11	77	0.0
		Cycloteuthidae				
		Cycloteuthis akimushkini	3	0.34	2,486	0.3
		Histioteuthidae				
		Histioteuthis atlantica	519	59.04	103,147	13.5
	Α	Histioteuthis miranda	115	13.08	44,537	5.8
		Lepidoteuthidae				
		Lepidoteuthis grimaldii	2	0.23	7,899	1.0
		Octopoteuthidae				
		Octopoteuthid (indeterminate)	1	0.11	3,781	0.5
		Octopoteuthis megaptera	7	0.80	3,548	0.4
		Octopoteuthis sp. 'Giant'	5	0.57	6,537	0.8
Local		Taningia danae	17	1.93	149,583	19.6
		Pholidoteuthidae				
		Pholidoteuthis boschmai	1	0.11	2,652	0.3
		Total local species group A	699	79.52	365,683	48.1
-		Ancistrocheiridae				
		Ancistrocheirus sp.	30	3.41	56,867	7.4
		Chiroteuthidae				
		Asperoteuthis sp.	5	0.57	3,323	0.4
		Cranchiidae				
	_	Megalocranchia sp. A	37	4.21	14,975	1.9
	В	Histioteuthidae				
		Histioteuthis Type A5	56	6.37	26,018	3.4
		Onychoteuthidae				
		Moroteuthis robsoni	27	3.07	154,692	20.3
		Alloposidae				
		Haliphron atlanticus	4	0.46	388	0.0
		Total local species group B	159	18.09	256,263	33.7
		Total local species	858	97.61	621,946	81.8
		Cranchiidae				
NI- 1	1	Mesonychoteuthis hamiltoni	2	0.23	8,494	1.1
Non-lo	ocai	Onychoteuthidae				
		Kondakovia longimana	19	2.16	129,229	17.0
		Total non-local species	21	2.39	137,723	18.1
		Total all species	879	100.00	759,669	100.0

Sperm whale 14

Beaks found in the stomach of this whale comprised a total of 12 species in seven families (Table 13). The 422 beaks correspond to cephalopods estimated to weigh a total of 95.1 kg, representing less than one quarter of a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 89.3 kg (93.9%) to the diet, and species from group B contributed 5.8 kg (6.1%). The mean BM for the cephalopods represented by beaks in the stomach contents of this whale was 225.3 g (SE = 12.8), and the mean estimated ML was 122.0 mm (SE = 3.8).

The most important cephalopod family by weight in the diet of this whale was Histioteuthidae followed by Cranchiidae (Figure 30, Appendix 1). The most important species were *Histioteuthis atlantica*, *Galiteuthis* sp. C and *Cycloteuthis akimushkini*, collectively contributing 84.7% of the total cephalopod biomass as represented by beaks from the stomach (Figure 31, Appendix 1).

Table 13. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 14, stranded on Whatipu Beach, West Auckland, October 11, 2004

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Cranchiidae				
		Galiteuthis sp. C	40	9.48	7,956	8.37
		Taonius sp. B	1	0.24	49	0.05
		Teuthowenia pellucida	1	0.24	70	0.07
		Cycloteuthidae				
		Cycloteuthis akimushkini	5	1.18	5,402	5.68
	Α	Histioteuthidae				
	^	Histioteuthis atlantica	358	84.83	67,165	70.64
		Histioteuthis macrohista	2	0.47	209	0.22
		Histioteuthis miranda	6	1.42	2,166	2.28
Local		Octopoteuthidae				
Local		Octopoteuthid (indeterminate)	1	0.24	3,781	3.98
		Ommastrephidae				
		Ommastrephid (indeterminate)	1	0.24	2,516	2.65
		Total local species group A	415	98.34	89,315	93.93
		Ancistrocheiridae				
		Ancistrocheirus sp.	2	0.47	3,354	3.53
	В	Cranchiidae				
	ь	Megalocranchia sp. A	4	0.95	783	0.82
		Onychoteuthidae				
		Moroteuthis robsoni	1	0.24	1,629	1.71
		Total local species group B	7	1.66	5,767	6.07
		Total local species	422	100.00	95,082	100.00

Sperm whale 15

Beaks found in the stomach of this whale comprised a total of 21 cephalopod species in 12 families. Fourteen were cephalopod species from group A, six were locally occurring species from group B, while the other two were non-local taxa (Table 14). Local taxa contributed 99.3% by number and 97.3% by weight to the diet of this whale, while non-local taxa contributed 0.7% by number and 2.7% by weight. The 426 beaks correspond to cephalopods estimated to weigh a total of 743.5 kg, representing little less than a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 430.2 kg (57.9%) to the diet, cephalopod species from group B and non-local species together contributed 313.3 kg (42.1%). The mean BM of cephalopods was 1,745.3 g (SE = 275.9), and the mean estimated ML was 280.8 mm (SE = 12.9).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, Onychoteuthidae and Octopoteuthidae, while the most important families by weight were Onychoteuthidae, Architeuthidae, Octopoteuthidae and Histioteuthidae (Figure 32, Appendix 1). The most important species in the diet of this whale were *Moroteuthis robsoni*, *Architeuthis dux*, *Taningia danae* and *Histioteuthis atlantica*, individually contributing 32.3%, 22.7%, 15.3% and 5.0% by weight, respectively, and collectively 75.2% (Figure 33, Appendix 1).

Table 14. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 15, stranded on Oputama Beach, east coast, Hawkes Bay, November 28, 2002

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Architeuthidae				
		Architeuthis sp.	5	1.17	163,447	21.98
		Chiroteuthidae				
		Chiroteuthis veranyi	4	0.94	606	0.08
		Cranchiidae				
		Galiteuthis sp. C	16	3.76	3,787	0.51
		Teuthowenia pellucida	2	0.47	214	0.03
		Cycloteuthidae				
		Cycloteuthis akimushkini	3	0.70	2,900	0.39
		Histioteuthidae			·	
		Histioteuthis atlantica	177	41.55	36,467	4.90
		Histioteuthis miranda	35	8.22	11,754	1.58
		Lepidoteuthidae	00	0.22	,,,,	
	Α	Lepidoteuthis grimaldii	4	0.94	32,400	4.36
		Mastigoteuthidae	7	0.74	32,400	4.50
		Mastigoteuthis sp.	4	0.94		0.00
		Indetreminate	15	3.52	12,779	1.72
		Octopoteuthidae	15	3.32	12,779	1.72
			7	1 / 4	24 272	2.07
		Octopoteuthid (indeterminate)	7 7	1.64	21,372	2.87
Local		Octopoteuthis megaptera		1.64	2,844	0.38
		Octopoteuthis sp. 'Giant'	1	0.23	965	0.13
		Taningia danae	12	2.82	110,612	14.88
		Onychoteuthidae				
		Moroteuthis ingens	2	0.47	3,736	0.50
		Pholidoteuthidae				
		Pholidoteuthis boschmai	8	1.88	26,349	3.54
		Total local species group A	302	70.89	430,233	57.86
Ī		Ancistrocheiridae				
		Ancistrocheirus sp.	16	3.76	27,958	3.76
		Chiroteuthidae				
		Asperoteuthis sp.	1	0.23	1,283	0.17
		Cranchiidae				
	В	Megalocranchia sp. A	36	8.45	19,227	2.59
	ь	Histioteuthidae				
		Histioteuthis Type A5	21	4.93	10,516	1.41
		Onychoteuthidae				
		Moroteuthis robsoni	43	10.09	233,995	31.47
		Alloposidae				
		Haliphron atlanticus	4	0.94	467	0.06
		Total local species group B	121	28.40	293,444	39.47
		Total local species	423	99.30	723,678	97.33
NI- 1	1	Onychoteuthidae				
Non-le	ocai	Kondakovia longimana	3	0.70	19,835	2.67
		Total non-local species	3	0.70	19,835	2.67
		Total all species	426	100.00	743,513	100.00

Sperm whale 16

Seventy beaks were found in the stomach of this whale, representing eight cephalopod species in six families. Five were cephalopod species from group A, one was a cephalopod species from group B, and two were non-local taxa (Table 15). Local taxa contributed 25.7% by number and 33.5% by weight to the diet of this whale, while non-local taxa contributed 74.3% by number and 66.5% by weight. The estimated cephalopod biomass was 1,079.3 kg, over a day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 309.5 kg (28.7%) to the diet, and cephalopod species from group B and non-local species together contributed 769.8 kg (71.3%). The mean weight for the cephalopods represented by beaks found in the stomach of this whale was 15.4 kg (SE = 1,398.4), and a mean estimated ML of 989.7 mm (SE = 74.7).

The most important families by weight in the diet of this whale were Onychoteuthidae, Architeuthidae, Cranchiidae, Octopoteuthidae and Histioteuthidae, collectively contributing 98.6% by number to the diet, and 94.6% of the total cephalopod biomass as represented by beaks (Figures 34, 35, Appendix 1).

Table 15. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 16, stranded on Muriwai Beach, West Auckland, December 8, 2004

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Architeuthidae				_
		Architeuthis dux	7	10.00	235,721	21.84
		Cranchiidae				
		Taonius sp. B	1	1.43	382	0.04
		Histioteuthidae				
	Α	Histioteuthis atlantica	1	1.43	130	0.01
		Octopoteuthidae				
Local		Octopoteuthid (indeterminate)	1	1.43	3,781	0.35
		Taningia danae	6	8.57	67,489	6.25
		Onychoteuthidae				
		Moroteuthis ingens	1	1.43	1,962	0.18
		Total local species group A	17	24.29	309,465	28.67
-	В	Mastigoteuthidae				
	ь	Idioteuthis sp. 1	1	1.43	52,407	4.86
		Total local species group B	1	1.43	52,407	4.86
		Total local species	18	25.71	361,872	33.53
		Cranchiidae				
Non-le	1	Mesonychoteuthis hamiltoni	16	22.86	115,473	10.70
Non-I	ocai	Onychoteuthidae				
		Kondakovia longimana	36	51.43	601,956	55.77
		Total non-local species	52	74.29	717,429	66.47
		Total all species	70	100.00	1,079,301	100.00

Sperm whale 17

Only 13 lower beaks comprise this collection, and they only represent a partial sample of the stomach contents of this whale. These 13 beaks were identified as belonging to *Histioteuthis atlantica*, and were estimated to belong to squid weighing 4.9 kg, of a mean BM of 378.0 g (SE = 16.2), and a mean estimated ML of 131.4 mm (SE = 2.7). It appears that within the collection there were some beaks of a 'giant squid', but attempts to get the samples for positive identification proved unsuccessful (Adam Bester DoC pers. comm.).

Sperm whale 18

The beaks of five locally occurring cephalopod species from group A, represented by 618 specimens were recovered from this sample (Table 16). Fish remains were also found in the stomach of this whale. The estimated weight of all the specimens represented by beaks in the stomach of this sperm whale was 867.0 kg, over a day's worth of food for a 40 t sperm whale. This whale appeared to have been feeding on a large aggregation of mature *Moroteuthis ingens*, comprising 86.7% of the diet by number and 97.8% by weight (Figure 36, Appendix 1). The squid consumed by this whale had a mean BM of 1,402.9 g (SE = 31.3), and a mean ML of 391.7 mm (SE = 3.5).

Table 16. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 18

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of total weight
		Cranchiidae				
		Teuthowenia pellucida	60	9.71	5,103	0.59
		Histioteuthidae				
		Histioteuthis atlantica	19	3.07	3,646	0.42
Local	Α	Octopoteuthidae				
Local	A	Taningia danae	1	0.16	7,501	0.87
		Ommastrephidae				
		Ommastrephid (indeterminate)	2	0.32	2,578	0.30
		Onychoteuthidae				
		Moroteuthis ingens	536	86.73	848,154	97.83
		Total local species	618	100.00	866,982	100.00

Sperm whale 19

Beaks found in the stomach of this whale comprised 23 cephalopod species in 14 families. Seventeen were cephalopod species from group A and six were cephalopod species from group B (Table 17). The 5,143 beaks found in the stomach of this female correspond to cephalopods estimated to weigh a total of 2,049.1 kg, representing over two and a half day's worth of food for a 40 t sperm whale. Cephalopod species from group A contributed 1,826.2 kg (89.1%), and species from group B and non-local species together contributed 222.9 kg (10.9%) of prey consumed. The mean BM for the cephalopods represented by beaks in the stomach contents of this whale was 410.5 g (SE = 9.5), and the mean estimated ML was 135.6 mm (SE = 1.5).

The most important families by number in the diet of this whale were Histioteuthidae, Cranchiidae, damaged beaks of indeterminate families, and Octopoteuthidae, while the most important families by weight were Histioteuthidae, Octopoteuthidae, beaks of indeterminate families, and Cranchiidae (Figure 37, Appendix 1). The most important species in the diet of this sperm whale were octopoteuthids of an indeterminate species, *Histioteuthis atlantica*, indeterminate squid, *Ancistrocheirus* sp., histioteuthids of indeterminate species, and *Histioteuthis* Type B4, collectively contributing 89.7% of the total cephalopod biomass in the stomach (Figure 38, Appendix 1).

Table 17. Distribution, abundance, numbers, and estimated weights for cephalopod species represented by beaks in the stomach of sperm whale number 19, stranded in Napier, Hawkes Bay, February 28, 2004

Distribution	Group	Taxon	Number	% of total #	Estimated weight (g)	% of tota weigh
		Architeuthidae				
		Architeuthis dux	5	0.10	8,947	0.4
		Chiroteuthidae				
		Chiroteuthis sp. 2	7	0.14	440	0.0
		Chiroteuthis veranyi	46	0.89	6,717	0.3
		Cranchiidae			-,	
		Galiteuthis sp. C	160	3.11	32,312	1.5
		Liocranchia sp.	4	0.08	182	0.0
		Taonius sp. B	14	0.27	4,791	0.2
		Teuthowenia pellucida	328	6.38	33,624	1.6
			320	0.30	33,024	1.0
		Cycloteuthidae	0	0.1/	/ 050	0.1
		Cycloteuthis akimushkini	8	0.16	6,858	0.3
		Histioteuthidae				
		Histioteuthid (indeterminate)	332	6.46	83,714	4.0
		Histioteuthis atlantica	3,159	61.42	631,915	30.8
	Α	Histioteuthis miranda	88	1.71	28,499	1.3
		Mastigoteuthidae				
		Mastigoteuthis sp.	20	0.39		0.0
		Indeterminate	375	7.29	319,478	15.5
		Octopoteuthidae				
		Octopoteuthid (indeterminate)	170	3.31	642,699	31.3
		Octopoteuthis megaptera	31	0.60	8,662	0.4
Local		Taningia danae	3	0.06	6,290	0.3
		Ommastrephidae	ū	0.00	0,2,0	0.0
		Ommastrephid (indeterminate)	2	0.04	4,277	0.2
		Pholidoteuthidae	2	0.04	4,277	0.2
			3	0.07	2.455	0.1
		Pholidoteuthis boschmai	3	0.06	3,155	0.1
		Octopodidae	_			
		Octopodid (indeterminate)	3	0.06		0.0
		Vampyroteuthidae				
<u> </u>		Vampyroteuthis infernalis	2	0.04	9	0.0
		Total local species group A	4,760	92.55	1,822,566	88.9
_		Ancistrocheiridae				
		Ancistrocheirus sp.	72	1.40	90,115	4.4
		Cranchiidae				
		Megalocranchia sp. A	56	1.09	21,968	1.0
		Histioteuthidae				
	В	Histioteuthis Type B4	215	4.18	70,349	3.4
		Histioteuthis Type A5	9	0.17	3,952	0.1
		Onychoteuthidae				
		Moroteuthis robsoni	24	0.47	36,395	1.7
		Alloposidae			•	
		Haliphron atlanticus	1	0.02	114	0.0
		Total local species group B	377	7.33	222,894	10.8
		Total local species	5,137	99.88	2,045,460	99.8
		Psychroteuthidae	-,		, ,	
Non-Io	ocal	Psychroteuthis glacialis	6	0.12	3,632	0.1
		i, sin ocoacino giudiano		0.12		
		Total non-local species	6	0.12	3,632	0.1

Cephalopod family importance in the diet of sperm whales in the South Pacific

Figures 39 and 40 show the percentage frequency, by number and by weight, of the cephalopod families found in the stomach contents of sperm whales stranded on New Zealand beaches.

The family Histioteuthidae was the most important family by number found in the stomachs of all whales stranded on our coast, followed by Onychoteuthidae, Cranchiidae and Octopoteuthidae. It appears all of the sperm whales consistently take large numbers of histioteuthids, onychoteuthids, cranchiids and octopoteuthids. The families Ancistrocheiridae, Cycloteuthidae and Pholidoteuthidae also contributed relatively significant numbers to the diets of whales stranded in New Zealand (Figure 39). On the other hand, the family Onychoteuthidae was the most important family by weight in the diet of recently stranded sperm whales, followed by Histioteuthidae, Octopoteuthidae and Architeuthidae. However, although the number of cephalopod families taken by sperm whales appears to be relatively consistent for individual whales, the weight these families contribute to the diet of individual whales varies considerably (Figure 40).

Figures 41 and 42 show the importance by number and weight of cephalopod families in the diet of sperm whales in the South Pacific. The most important families by weight in the region are Histioteuthidae, Onychoteuthidae, Architeuthidae and Pholidoteuthidae. The families Octopoteuthidae and Cranchiidae are important by weight off Australia and the Tasman Sea, and have gained importance in the diet of recently stranded sperm whales in New Zealand. The family Ommastrephidae was historically significant in the diet of whales from Cook Strait but its importance by weight in the diet of recently stranded sperm whales has decreased, at least locally. The most important families by number are Histioteuthidae, Onychoteuthidae and Cranchiidae. The family Lepidoteuthidae is important off Australia; the family Octopoteuthidae in the Tasman Sea; and historically, the families Ommastrephidae and Pholidoteuthidae in Cook Strait. The family

Histioteuthidae appears to be the most important in the diet of the whale stranded at Paekakariki and in some of New Zealand stranded whales, especially sperm whale 19. The family Onychoteuthidae is consistently important by weight throughout the region, as well as Architeuthidae.

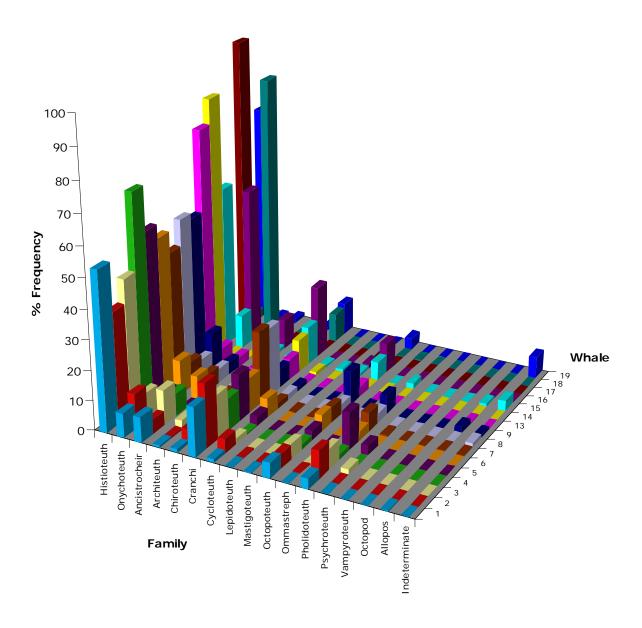


Figure 39. Cephalopod families by percentage frequency in the diet of sperm whales stranded on New Zealand beaches, *

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^{*} Family names are abbreviated. Whales 1 to 14 stranded on Whatipu Beach

of

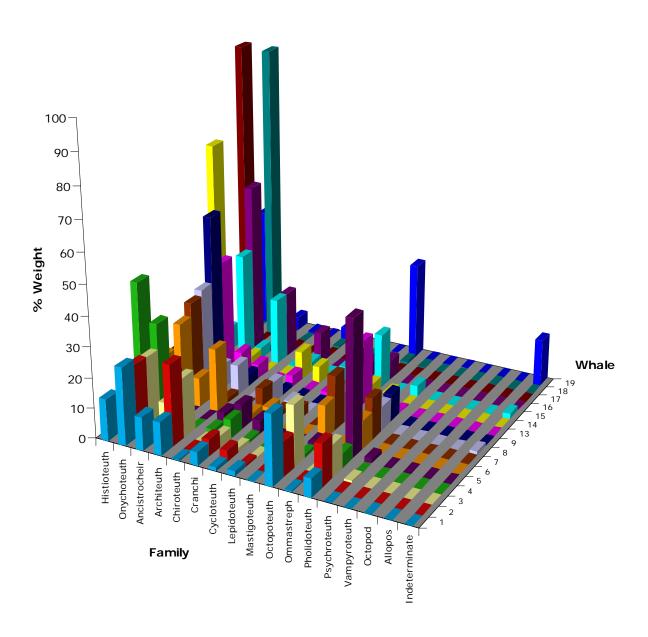


Figure 40. Cephalopod families by percentage frequency by weight in the diet of sperm whales stranded on New Zealand beaches*

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^{*} Family names are abbreviated. Whales 1 to 14 stranded on Whatipu Beach

Size of cephalopods in the diet

The size of cephalopods consumed by sperm whales globally will be influenced by the cephalopod composition in any given region. The size of cephalopod species consumed by New Zealand whales ranged from a specimen of *Argonauta nodosa* of ML 6.3 mm and weight 14.1 g, to a specimen of *Architeuthis dux* of estimated ML 1,023.3 mm and weight 97.1 kg (Figures 43, 44, 45, 46, 47). Figures 43 and 44 show marginal plots of ML and BM with histograms for both variables. Even though sperm whales consumed cephalopods with a wide range of both ML and BM (Figures 45, 48), cephalopods of ML less than 1 m and BM larger than 1 kg appear to prevail in their diet (Figures 43, 44, 45, 48, 49).

The results show that sperm whales in New Zealand consume cephalopods with an estimated mean ML of 220.0 mm (SE = 1.8) and mean BM of 880.6 g (SE = 23.2). This mean estimated BM is comparable to that consumed by mature male whales from other regions, where it ranges from 600 g to 7,200 g (Clarke 1996a). Although there is no clear correlation between mean cephalopod BM taken as prey by sperm whales and latitude, mean BM is greatest in the Antarctic (Clarke 1996a), and this is clearly noticeable for sperm whale 16, which had a large proportion of Antarctic species in its stomach, and had an estimated mean BM of 15.4 kg (SE = 1,398.4) and an estimated mean ML of 982.7 mm (SE = 74.7). The rest of the sperm whales had a mean estimated BM ranging between 225.3 and 2,006.4 g (Figures 49–51).

The 'longest' cephalopod consumed by any New Zealand stranded sperm whale was a specimen of *Mesonychoteuthis hamiltoni*, which had an estimated ML of 2,664 mm. Giant species with ML's exceeding 1,000 mm include *Architeuthis dux*, *Kondakovia longimana*, *Lepidoteuthis grimaldii*, *Mesonychoteuthis hamiltoni*, *Moroteuthis robsoni*, *Idioteuthis cordiformis* and *Taningia danae*. The heaviest species, with weights over 20 kg, include *Architeuthis dux*, *Idioteuthis* spp., *Moroteuthis robsoni*, *Kondakovia longimana*

and *Taningia danae*, but only 31 specimens, less than 1% of all squid represented by beaks in our collections, had weights over 20 kg.

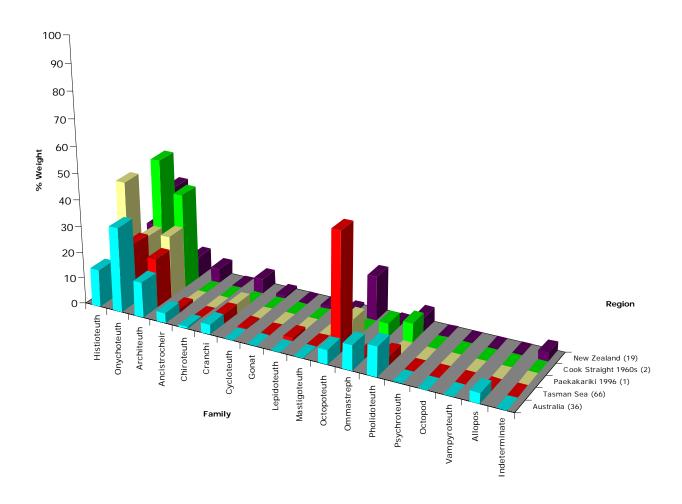


Figure 41. Cephalopod families by percentage frequency by weight in the diet of sperm whales from Cook Strait, New Zealand (Gaskin & Cawthorn 1967a, b); Paekakariki, New Zealand (Clarke & Roper 1998); the Tasman Sea (Clarke & MacLeod 1982); Australia (Evans & Hindell 2004), and in the diet of stranded sperm whales on New Zealand beaches*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

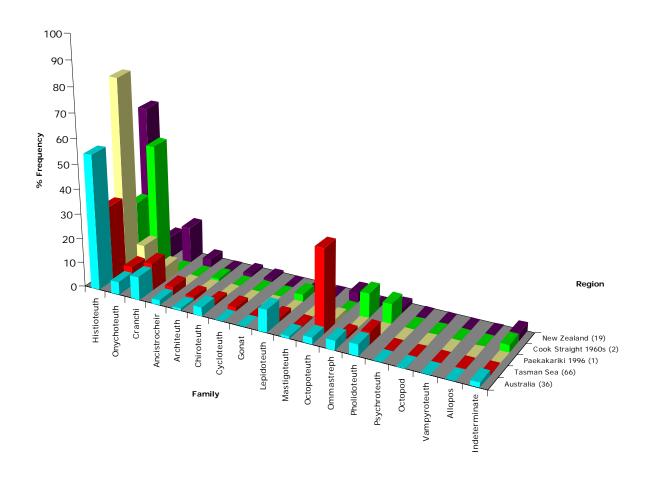


Figure 42. Cephalopod families by percentage frequency in the diet of sperm whales from Cook Strait, New Zealand (Gaskin & Cawthorn 1967a, b); Paekakariki, New Zealand (Clarke & Roper 1998); the Tasman Sea (Clarke & MacLeod 1982); Australia (Evans & Hindell, 2004), and in the diet of stranded sperm whales on New Zealand beaches*

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^{*} The numbers in parentheses next to the region represent the number of stomachs sampled, and the family names are abbreviated.

Figure 43. Marginal plot of estimated mantle length and body mass for all cephalopod species represented by beaks (n= 11,110) found in the stomach contents of sperm whales (n= 16) stranded on New Zealand beaches

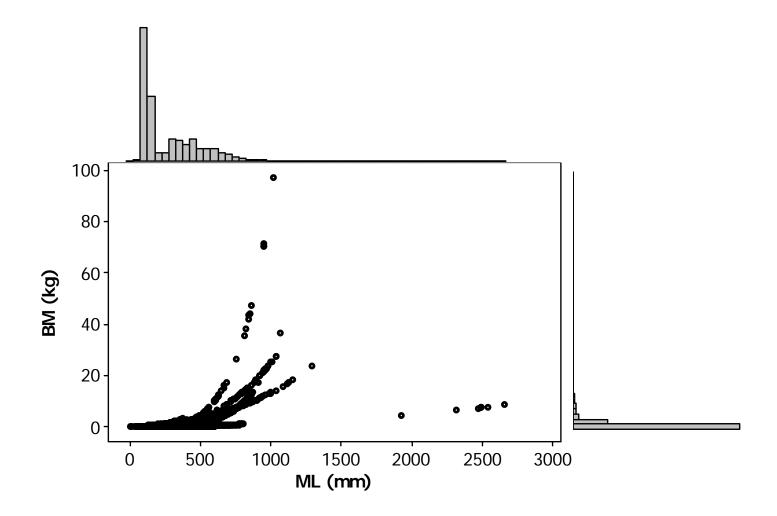


Figure 44. Detail of the marginal plot of estimated mantle length and body mass for all cephalopod species represented by beaks (n= 11,110) found in the stomach contents of sperm whales (n= 16) stranded on New Zealand beaches

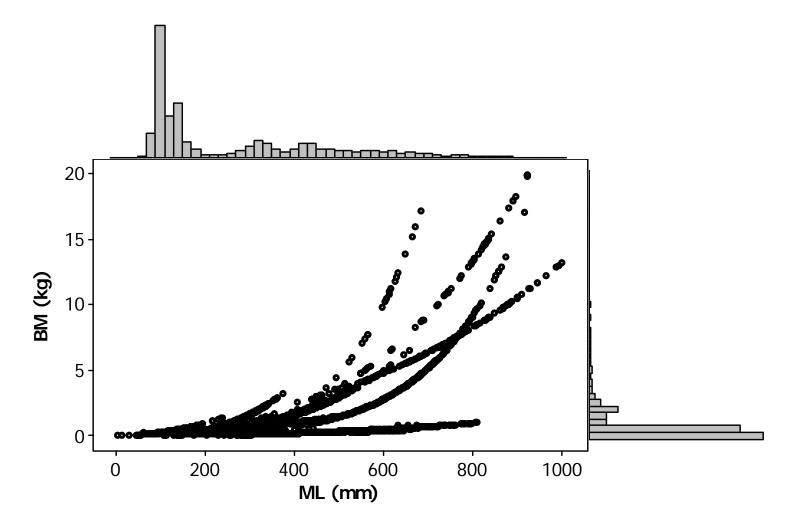
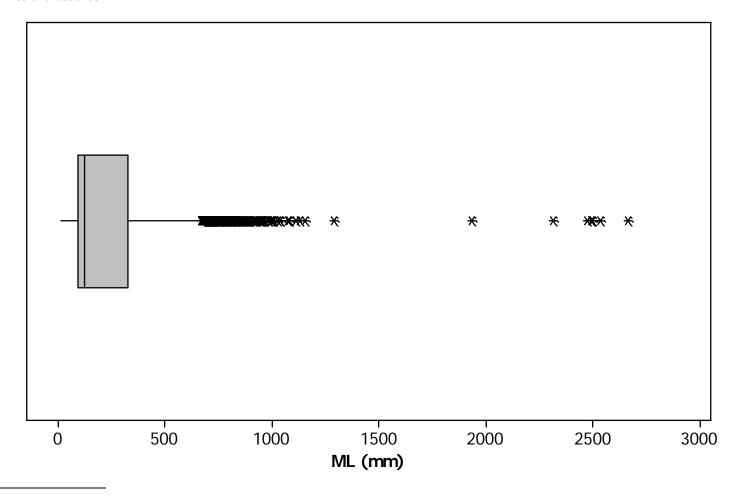
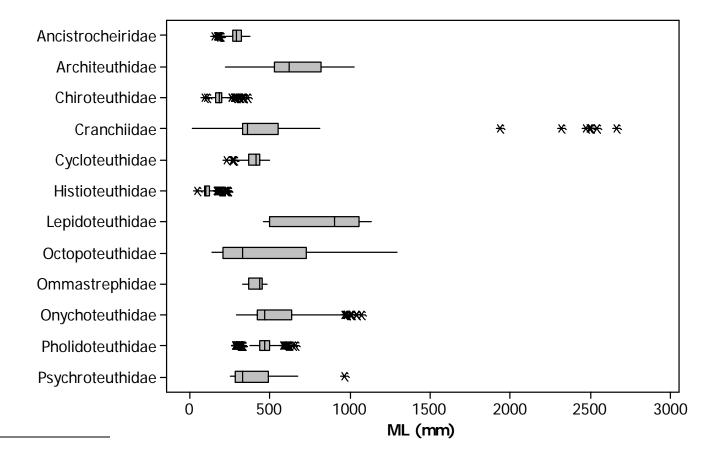


Figure 45. Boxplot for estimated mantle lengths of all cephalopods represented by measurable beaks (n= 11,110) in the stomach contents of 16 sperm whales stranded on New Zealand beaches*



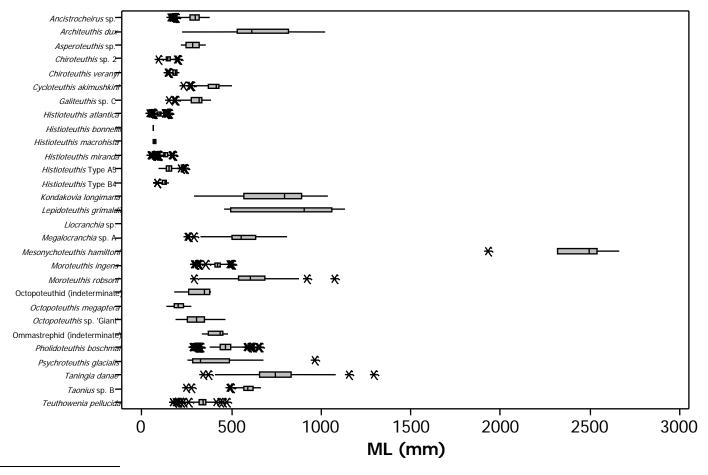
^{*}Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%).

Figure 46. Boxplots of estimated mantle lengths for all cephalopod families represented by measurable beaks (n= 11,110) found in the stomach samples of 16 sperm whales stranded on New Zealand beaches*



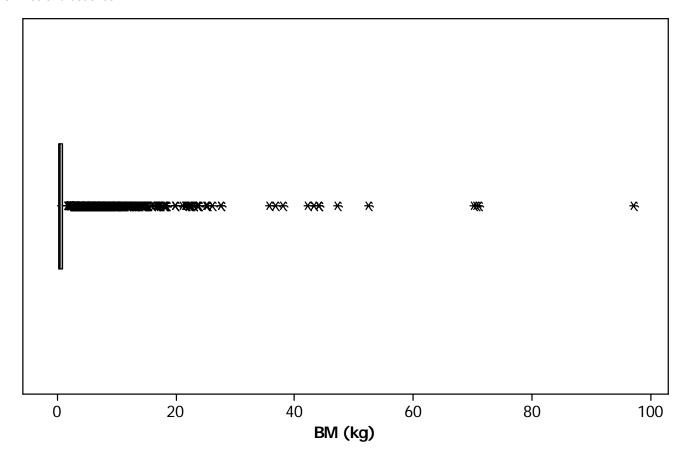
^{*} Shaded boxes indicate the interquartile range and crosses represent outliers (>95%). The outliers in the family Crachiidae represent (*Mesonychoteuthis hamiltoni*) The families Alloposidae, Argonautidae, Mastigoteuthidae, Octopodidae, and Vampyroteuthidae are not included because of the very small sample size for these families.

Figure 47. Boxplot of estimated mantle lengths for all cephalopod species represented by measurable beaks (n= 11,110) found in the stomach samples of 16 sperm whales stranded on New Zealand beaches*



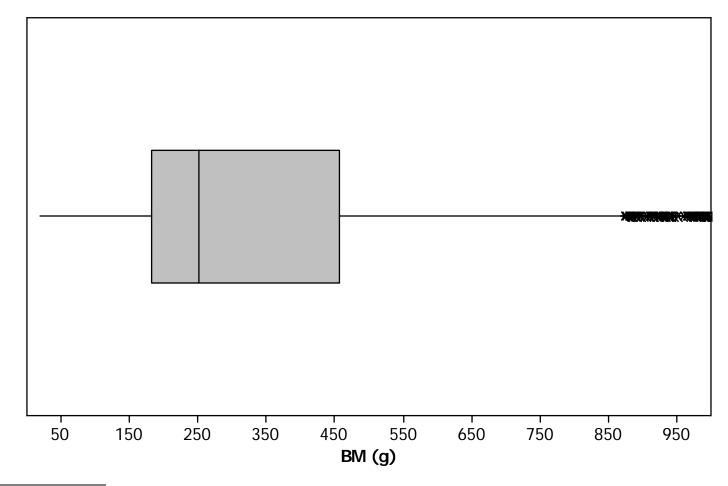
^{*} Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%). Species in the families Alloposidae, Argonautidae, Mastigoteuthidae, Octopodidae, and Vampyroteuthidae are not included because of the very small sample size for these families.

Figure 48. Boxplot of estimated body mass for all cephalopod species represented by measurable beaks (n= 11,110) found in the stomach contents of 16 sperm whales stranded on New Zealand beaches*



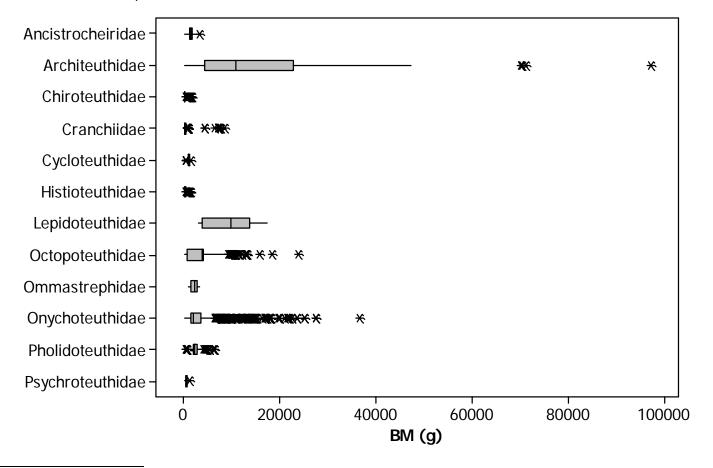
^{*} Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%).

Figure 49. Enlarged detail of the boxplot of estimated body mass for cephalopods weighing less than 1,000 g represented by measurable beaks (n= 11,110) found in the stomach samples of 16 sperm whales stranded on New Zealand beaches *



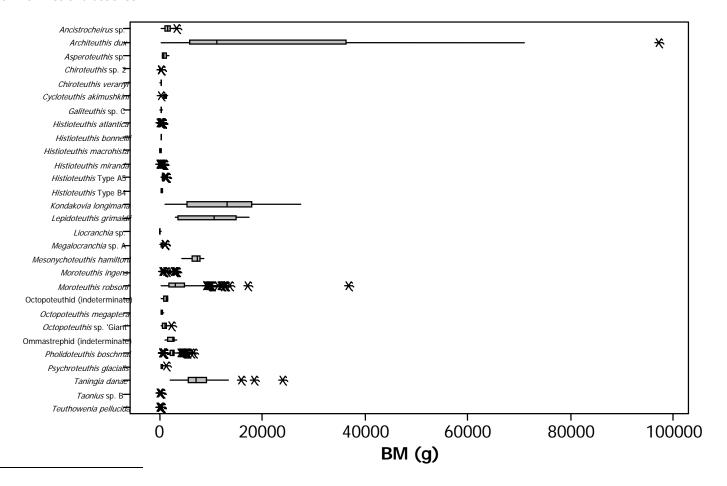
^{*} Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%).

Figure 50. Boxplots of estimated body mass for cephalopod families represented by measurable beaks (n= 11,110) found in the stomach samples of 16 sperm whales stranded on New Zealand beaches*



^{*} Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%). The families Alloposidae, Argonautidae, Mastigoteuthidae, Octopodidae, and Vampyroteuthidae are not included because of the very small sample size for these families.

Figure 51. Boxplots of estimated body mass for cephalopod species represented by measurable beaks (n= 11,110) found in the stomach samples of 16 sperm whales stranded on New Zealand beaches*



^{*} Shaded boxes indicate the interquartile range, and crosses represent outliers (>95%). Species in the families Alloposidae, Argonautidae, Mastigoteuthidae, Octopodidae, and Vampyroteuthidae are not included because of the very small sample size for these families.

Summary of diet results

Cephalopod remains identified from amongst stomach contents from New Zealand stranded whales include one arm crown, one tentacle, one mantle, some buccal bulbs, partial and complete gladii and eye lenses, and numerous hooks, sucker rings and upper and lower beaks. Cephalopod remains from three orders were found in 16 of 19 whale stomachs examined. The stomachs of three of the males involved in the Whatipu mass stranding of November 2003 were empty.

The most important families by number in the diet of these sperm whales were: Histioteuthidae, Cranchiidae, Onychoteuthidae and Octopoteuthidae, collectively accounting for 88.0% of the total number of beaks found in the stomach samples (Figure 52). Beaks of the family Histioteuthidae were the most abundant in our samples, comprising 60.6% of all beaks. The most important families by weight, as estimated from the beak morphometry, were: Onychoteuthidae, Histioteuthidae, Octopoteuthidae and Architeuthidae, followed by Cranchiidae, Ancistrocheiridae and Pholidoteuthidae, collectively contributing 93.0% of the total estimated cephalopod biomass consumed by all whales, as represented by the beaks found in these samples (Figure 53).

Oceanic cephalopods dominated the diet of these sperm whales, with seven families contributing over 90.0% of the total cephalopod biomass represented by beaks. Both octopodiforms and vampyromorphs contributed very little by number or weight to the diet.

In all, the collections analysed included 10,647 upper and 12,576 lower cephalopod beaks, representing at least 36 species in 17 families (Table 1). Of these 36 cephalopod species, 32 are squid in 13 teuthid families; one is a benthopelagic octopod (*Haliphron atlanticus*), one a pelagic octopod (*Argonauta nodosa*), at least one other unidentified octopod species, and the sole-recognised species of the order Vampyromorpha (*Vampyroteuthis infernalis*) (Table 18). The estimated cephalopod biomass represented by beaks was 11,049.3 kg, with a mean body mass (BM) of 878.6 g (SE = 23.2).

Of the 36 cephalopod species, 24 (66.7%) occur regionally. These were either represented by beaks in good condition that probably were not in the stomach for a long period of time, or are known from stomach contents of New Zealand stranded pygmy sperm whales, Kogia breviceps (a species that is believed to be a permanent resident in New Zealand waters) (Beatson, in prep.). Alternatively, beaks from these 24 species are well represented in museum collections from New Zealand waters. It is quite possible that these 24 species were consumed within the EEZ and are classed as local species group A although they do occur outside New Zealand waters. Nine (25%) other cephalopod species have also been reported in New Zealand, but are either rare in museum collections, or were represented by beaks in a bad condition. These beaks are likely to have been in the stomachs for a longer period of time than those of group A and could represent species that were consumed outside the EEZ. These nine species are classed under group B. The last three (8.3%) cephalopod species have never been reported in our waters, and are considered non-local taxa.

Species that are found locally represented 98.8% of the beaks, comprising 86.3% of the total cephalopod biomass. Local species in group A represented 81.9% of the beaks and 61.1% of the total cephalopod biomass. Rare species in group B represented 16.9% of the beaks and 25.2% of the cephalopod biomass. Non-local species contributed 1.2% of the total number of beaks, and contributed 13.7% by weight to the diet of sperm whales (Table 18).

Rare local cephalopod species include the oceanic squid *Ancistrocheirus* sp. (Ancistrocheiridae), *Asperoteuthis* sp. (Chiroteuthidae), *Megalocranchia* sp. A (Cranchiidae), *Histioteuthis* Type A5, *Histioteuthis* Type B4 (Histioteuthidae), *Idioteuthis* sp.1 (Mastigoteuthidae), *Moroteuthis robsoni* (Onychoteuthidae), and the benthopelagic octopod *Haliphron atlanticus* (Alloposidae).

Cephalopod species thought to have been consumed outside New Zealand's EEZ, south of the Subtropical Convergence are, *Mesonychoteuthis hamiltoni* (Cranchiidae), *Psychroteuthis glacialis* (Psychroteuthidae), and *Kondakovia longimana* (Onychoteuthidae).

There is some confusion in the identification of beaks attributed here to *Moroteuthis robsoni* with them being referred to as both *M. robsoni* and *M. knipovitchi*. All have been treated as *M. robsoni* in this study. In the event these are subsequently re-identified and shown to be a mixture of these two species, then the relative percentages of 'locally' (including those taxa probably and possibly, albeit unlikely) and non-locally predated taxa will require recalculation. As all beaks have been archived the opportunity for re-identification exists; unfortunately this could not be undertaken within the timeframe available.

Cephalopod species found in the diet of New Zealand Stranded sperm whales was divided into group A, those most probably consumed locally, group B, those known to occur in New Zealand waters, but not in sufficient numbers to account for sperm whale consumption, and non-local species. Table 19 shows a comparison between the relative contribution by weight of the different cephalopod groups to the diet of individual sperm whales. The non-shaded area shows a scenario where all cephalopods in group B were consumed outside the New Zealand EEZ and the shaded area shows a scenario where all cephalopods in Group B were consumed within the New Zealand EEZ. Four of the whales (whales 14, 17, 18 and 19) did not have non-local cephalopods in their stomachs.

Figure 52. Percentage frequency of cephalopod families in the stomach samples of 16 sperm whales stranded in New Zealand

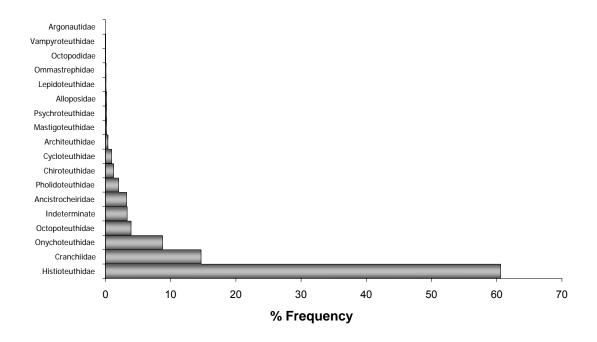


Figure 53. Percentage frequency by weight of cephalopod families in the stomach samples of 16 sperm whales stranded in New Zealand

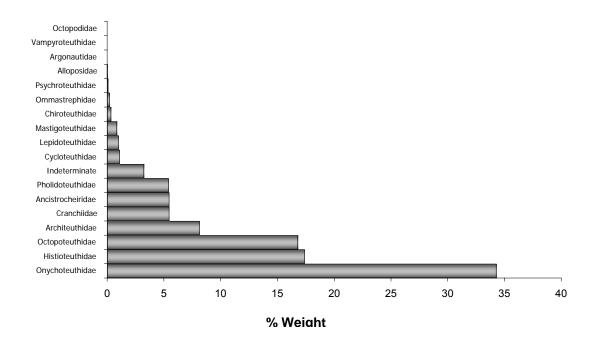


Table 18. Distribution, abundance, numbers, estimated weights, and frequency of occurrence (FoO) for cephalopod species represented by beaks in the stomach of sperm whales of 19 sperm whales stranded in New Zealand

Distribution	Group	Taxon	Number	%	Weight (g)	%	FoO	%
		Architeuthidae						
		Architeuthis dux	47	0.37	899,928	8.14	10	62.50
		Chiroteuthidae						
		Chiroteuthis veranyi	93	0.74	13,715	0.12	9	56.25
		Chiroteuthis sp. 2 Cranchiidae	35	0.28	3,049	0.03	6	37.50
		Cranchild indeterminate	23	0.18	7.549	0.07	1	6.25
		Galiteuthis sp. C (sensu Imber)	391	3.11	85,250	0.07	12	75.00
		Liocranchia sp.	9	0.07	550	0.00	4	25.00
		Taonius sp. A	1	0.01	122	0.00	1	6.2
		Taonius sp. B (sensu Voss)	133	1.06	42,673	0.39	11	68.7
		Teuthowenia pellucida	622	4.95	62,880	0.57	12	75.00
		Cycloteuthidae						
		Cycloteuthis akimushkini	122	0.97	120,904	1.09	13	81.2
		Histioteuthidae						
		Histioteuthid indeterminate	347	2.76	87,496	0.79	2	12.5
		Histioteuthis atlantica	5,289	42.06	1,056,867	9.56	16	100.0
		Histioteuthis bonnellii	1	0.01	217	0.00	1	6.2
		Histioteuthis macrohista	2	0.02	209	0.00	1	6.2
	Α	Histioteuthis miranda	1,385	11.01	505,876	4.58	13	81.2
		Lepidoteuthidae	12	0.10	113,072	1.02	5	31.2
		Lepidoteuthis grimaldii Mastigoteuthidae	12	0.10	113,072	1.02	5	31.2
		Mastigoteuthis sp.	25	0.20	_	0.00	3	18.7
		Octopoteuthidae	23	0.20		0.00	3	10.7
		Octopoteuthid indeterminate	216	1.72	803,177	7.27	9	56.2
		Octopoteuthis megaptera	124	0.99	45,142	0.41	12	75.0
		Octopoteuthis sp. 'Giant'	22	0.17	20,087	0.18	7	43.7
		Taningia danae	133	1.06	989,553	8.96	12	75.0
Local		Ommastrephidae						
LUCAI		Ommastrephid indeterminate	12	0.10	26,100	0.24	8	50.0
		Onychoteuthidae						
		Moroteuthis ingens	572	4.55	912,730	8.26	6	37.5
		Pholidoteuthidae						
		Pholidoteuthis boschmai	253	2.01	598,743	5.42	12	75.00
		Argonautidae		0.00		0.00		
		Argonauta nodosa	2	0.02	34	0.00	1	6.2
		Octopodidae Octopodid indeterminate	3	0.02		0.00	1	6.2
		Vampyroteuthidae	3	0.02		0.00		0.2
		Vampyroteuthis infernalis	3	0.02	20	0.00	2	12.50
		Indeterminate	422	3.36	359,519	3.25	5	31.2
		Total local species group A	10,299	81.89	6,755,462	61.14		
		Ta a series						
		Ancistrocheiridae	400	0.05	(05.4(0	F 40	40	75.0
		Ancistrocheirus sp.	409	3.25	605,463	5.48	12	75.0
		Chiroteuthidae	25	0.20	21,971	0.20	8	50.0
		Asperoteuthis sp. Cranchiidae	25	0.20	21,971	0.20	0	30.0
		Megalocranchia sp. A (sensu Voss)	648	5.15	274,391	2.48	13	81.2
		Histioteuthidae	040	5.15	2/4,371	2.40	13	01.2
	_	Histioteuthis Type A5	386	3.07	201,657	1.83	11	68.7
	В	Histioteuthis B4	215	1.71	70,349	0.64	1	6.2
		Mastigoteuthidae						
		Idioteuthis cordiformis	1	0.01	44,116	0.40	1	6.2
		Idioteuthis sp. 1	1	0.01	52,407	0.47	1	6.2
		Onychoteuthidae						
		Moroteuthis robsoni	415	3.30	1,511,603	13.68	13	81.2
		Alloposidae						
		Haliphron atlanticus	21	0.17	2,330	0.02	7	43.7
		Total local species group B	2,121	16.87	2,784,288	25.20		
		Total local species	12,420	98.76	9,539,749	86.34		
		Cranchiidae	12,420	70.70	7,337,147	00.54		
		Mesonychoteuthis hamiltoni	19	0.15	132,497	1.20	3	18.7
Non-local		Onychoteuthidae	17	5.15	132,777	20	3	
		Kondakovia longimana	113	0.90	1,365,499	12.36	11	68.7
		Psychroteuthidae		2.70	.,000,.,,	0 0		30.7
		Psychroteuthis glacialis	24	0.19	11,590	0.10	6	37.5
		Total non-local species	137	1.24	1,509,586	13.66		
		·						
		Total all species	12,576	100.00	11,049,335	100.00		

Table 19. Percentage weight of the different cephalopod groups to the diet of individual sperm whales stranded on New Zealand beaches

Whale #	% weight with B as non-local		% weight with B as local		
vviiale #	Group A	Group B + Non-local	Group A + B	Non-local	
1	60.3	39.7	88.2	11.8	
2	66.2	33.8	99.3	0.7	
3	61.4	38.6	94.1	5.9	
4	41.9	58.1	85.1	14.9	
5	78.7	21.3	98.4	1.6	
6	58.2	41.8	97.4	2.6	
7	52.6	47.4	88.7	11.3	
8	50.9	49.1	94.6	5.4	
9	34.2	65.8	51.6	48.4	
13	48.1	51.9	81.9	18.1	
14	93.9	6.1	100.0	0.0	
15	57.9	42.1	97.3	2.7	
16	28.7	71.3	33.5	66.5	
17	100.0	-	-	0.0	
18	100.0	-	-	0.0	
19	89.1	10.9	100.0	0.0	

4.1.2 Cephalopod species notes

Species composition

The species contributing most identifiable lower beaks in stomach samples were *Histioteuthis atlantica* (42.1%), *Histioteuthis miranda* (11.0%), *Megalocranchia* sp. A (5.2%), *Teuthowenia pellucida* (5.0%), *Moroteuthis ingens* (4.6%), *Moroteuthis robsoni* (3.3%), *Ancistrocheirus* sp. (3.3%), *Galiteuthis* sp. C (3.1%), *Histioteuthis* Type A5 (3.1%), unidentified histioteuthids (2.8%) and *Pholidoteuthis boschmai* (2.0%). These 10 species (and one unidentifiable group of histioteuthids) contributed 85% of all cephalopods by number consumed by sperm whales in New Zealand waters. The other cephalopod species recorded in sperm whale diet individually contributed less than 2.0% by number to the diet.

A total of 11.05 t of cephalopod biomass was consumed by all whales, as represented by beaks in the stomachs. The most important cephalopod families by weight in the diet of New Zealand stranded whales were:

Onychoteuthidae (34.3%), Histioteuthidae (17.4%), Octopoteuthidae (16.8%),

Architeuthidae (8.1%), Cranchiidae (5.5%), Ancistrocheiridae (5.5%) and Pholidoteuthidae (5.4%). These seven families contributed 10.3 t (93.0%) of the total estimated cephalopod biomass in all stomachs combined.

Twenty-six (68.4%) of the 38 cephalopod species found in our collections were bioluminescent, comparable with that for other regions in the Southern hemisphere. In South Africa, western Australia, and the Antarctic, bioluminescent species made up 77.5%, 80.0% and 60.0% of sperm whale diet respectively (Clarke 1980).

In the next section, I present a brief description of what was found in the stomach samples of sperm whales for individual cephalopod species. The contribution by weight of single cephalopod species to the diet of individual whales is presented in a bar graph. Histograms of lower rostral lengths and estimated mantle lengths and body mass for the cephalopod species are presented in graphs with smoothed frequency lines.

Oegopsida

Architeuthidae

Architeuthis dux

A total of 47 *Architeuthis* beaks occurred in ten samples (62.5%), with a maximum of eight beaks found in a single whale. Squid of this genus had estimated ML's ranging between 219.6 and 1,023.3 mm, and weights between 188.8 g and 97.1 kg. The allometric equations given by Clarke (1980) for this genus that were used to estimate the ML and BM for the beaks in this collection are low and the numbers presented here should be regarded as underestimates of the actual biomass consumed (Roeleveld & Lipinski 1991). This species proves to be important by weight in the diet of sperm whales on both the east and west coasts of New Zealand, contributing up to 26.9% of the total cephalopod biomass for a single whale (Figure 54). *Architeuthis* is the heaviest cephalopod in the sperm whale diet, with a mean

of 21.3 kg (SE = 3,228.1), and the sixth longest, with a mean ML of 643.8 mm (SE = 29.4). Even though the 47 *Architeuthis* beaks recovered made up <1% of the total number of beaks, they contributed 899.9 kg (8.2%) of the total cephalopod biomass consumed by all whales, making it the fourth family that conferred the most by weight to the diet. The LRL distribution for this genus ranged from 4.6-18.2 mm, with a peak around 12.0 mm and mean of 5.1 mm (SE = 0.5) (Figure 55).

Figure 54. Contribution by weight of Architeuthis dux to the diet of individual whales

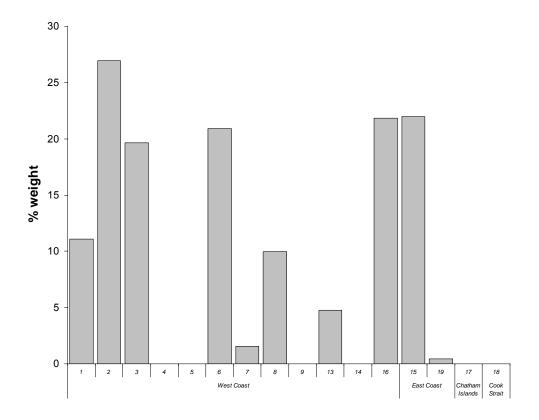
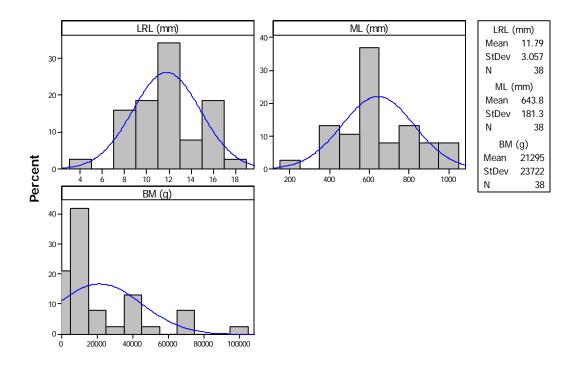


Figure 55. Histograms of LRL, estimated ML and BM for *Architeuthis dux* in the diet of sperm whales stranded on New Zealand beaches



Ancistrocheiridae

Ancistrocheirus sp.

A total of 409 beaks of *Ancistrocheirus* sp. were found in 12 (75.0%) of the whale stomachs, with a minimum of two and a maximum of 92 beaks found in any single whale. This species appears in both east and west coast samples, with a maximum contribution of 11.1% by weight to the diet of a single whale (Figure 56). The squid of this genus had estimated ML's of 153.9–373.5 mm and weights of 217.6–3,186.6 g. These squid had a mean estimated ML of 288.3 mm (SE = 1.9) and 1,483.8 g in weight (SE = 25.7). This genus contributed 3.3% of the total number of beaks and more than 605.5 kg (5.5%) to the total biomass of cephalopods represented by beaks. The LRL distribution for this species ranged from 4.8 to 10.2 mm, with a peak around 8.0 mm, and a mean of 8.1 mm (SE = 0.04) (Figure 57).

Figure 56. Contribution by weight of Ancistrocheirus sp. to the diet of individual whales

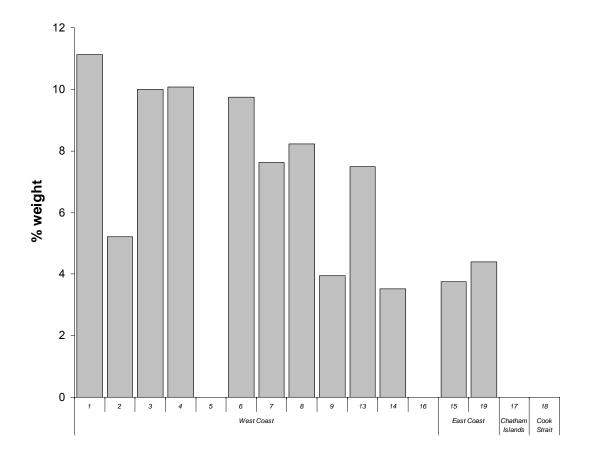
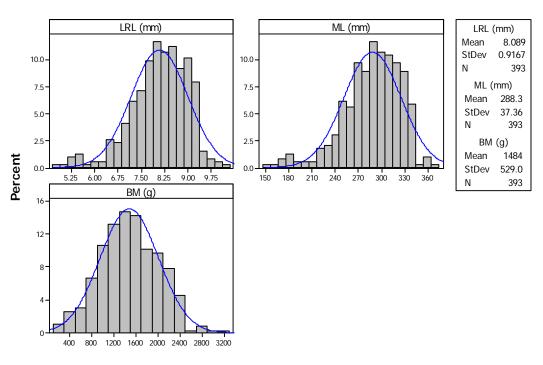


Figure 57. Histograms of LRL, estimated ML and BM for *Ancistrocheirus* sp. in the diet of sperm whales stranded on New Zealand beaches



Chiroteuthidae

Beaks belonging to this family occurred in 12 (75.0%) of the whales. Even though the taxonomy of the family is in need of revision and it is often difficult to identify species from whole specimens, morphological differences in the beaks suggest they belong to three species: *Chiroteuthis veranyi*, *Chiroteuthis* sp.2 and *Asperoteuthis* sp. The family Chiroteuthidae contributed 1.2% by number and <1% by weight to the diet of these whales.

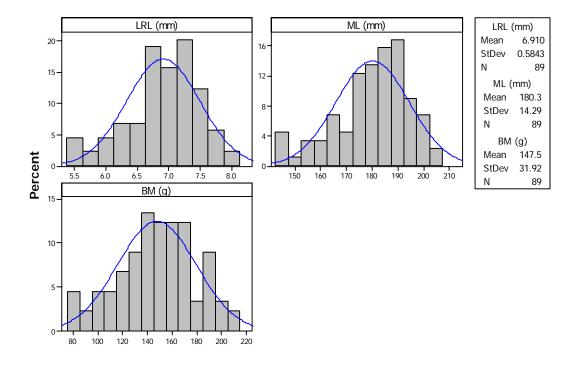
Asperoteuthis sp.

Between one and six *Asperoteuthis* beaks were present in eight (50.0%) of the samples, amounting to 25 beaks in total. The estimated ML's for this genus ranged between 212.5 and 357.1 mm, with a mean ML of 280.0 mm (SE = 8.2), and weighed between 378.6 and 1,670.7 g; the estimated mean BM was 878.8 g (SE = 72.4). This genus contributed <1% of the total number of beaks and <1% by weight to the diet of these sperm whales.

Chiroteuthis veranyi

A total of 93 beaks attributed to *Chiroteuthis veranyi* were present in nine (56.3%) of the samples; between one and 46 *C. veranyi* beaks occurred in any single whale. This species represented <1% of the total number of beaks and contributed 13.7 kg (0.1%) by mass to the diet of these sperm whales. These squid had estimated ML's that ranged between 143.8 and 206.2 mm, and weights ranging from 75.4–213.4 g, a mean estimated ML of 180.3 mm (SE = 1.5), and a mean estimated BM of 147.5 g (SE = 3.2). The LRL distribution for this species ranged between 5.4 and 8.0 mm, with a peak around 7.5 mm, and a mean of 6.9 mm (SE = 0.1) (Figure 58).

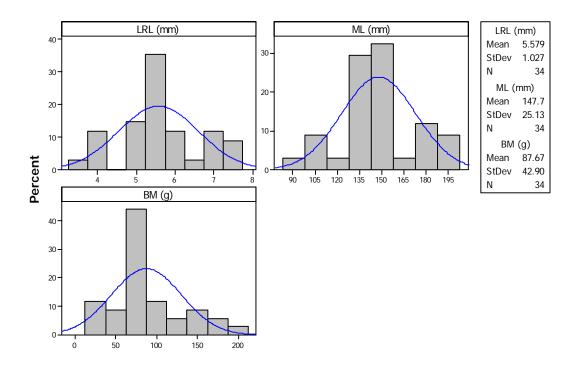
Figure 58. Histograms of LRL, estimated ML and BM for *Chiroteuthis veranyi* in the diet of sperm whales stranded on New Zealand beaches



Chiroteuthis sp. 2

A total of 35 beaks of *Chiroteuthis* sp. 2 were present in six (37.5%) whale stomachs, between one and ten beaks in any single whale. This species represented <1% of the total number of beaks and contributed <1% biomass to the diet, as represented by beaks. These squid had estimated ML's ranging from 92.2 to 198.6 mm, and BM ranging from 19.9 to 191.8 g, with a mean estimated ML of 147.7 mm (SE = 4.3) and mean estimated BM of 87.7 g (SE = 7.2). The LRL distribution had a peak around 6.0 mm and a mean of 5.6 mm (SE = 0.2) (Figure 59).

Figure 59. Histograms of LRL, estimated ML and BM for *Chiroteuthis* sp. 2 in the diet of sperm whales stranded on New Zealand beaches



Cycloteuthidae

Cycloteuthis akimushkini

A total of 122 beaks of *Cycloteuthis akimushkini* were found in 13 (81.3%) of the samples from both the east and west coast, contributing up to 5.9% by weight to the diet of any individual whale (Figure 60). These squid had estimated ML's that ranged between 226.9 and 498.5 mm, and an estimated BM from 321.1 to 1,489.6 g, with a mean ML of 400.2 mm (SE = 4.9), and mean BM of 985.0 g (SE = 19.3). They contributed 1.0% to the total number of beaks and 119.9 kg (1.1%) to the total cephalopod biomass represented by all beaks from all whales. The LRL distribution for this species ranged from 7.3 to 16.1 mm, and peaked around 14.0 mm, with a mean of 13.4 mm (SE = 0.2) (Figure 61).

Figure 60. Contribution by weight of Cycloteuthis akimushkini to the diet of individual whales

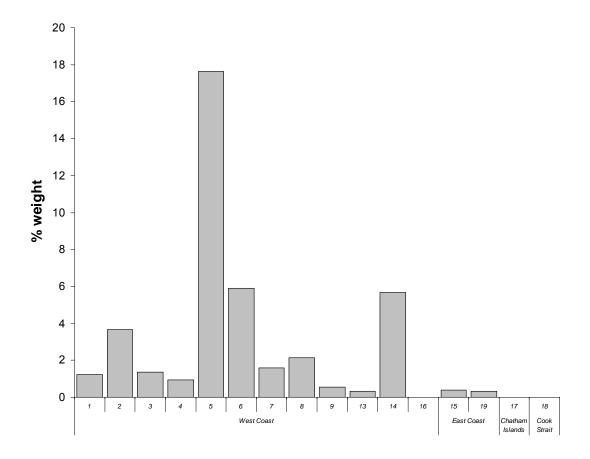
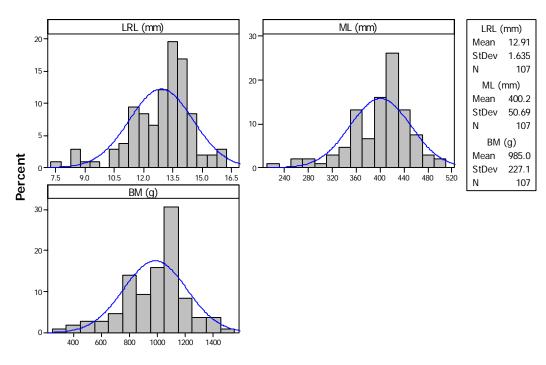


Figure 61. Histograms of LRL, estimated ML and BM for *Cycloteuthis akimushkini* in the diet of sperm whales stranded on New Zealand beaches



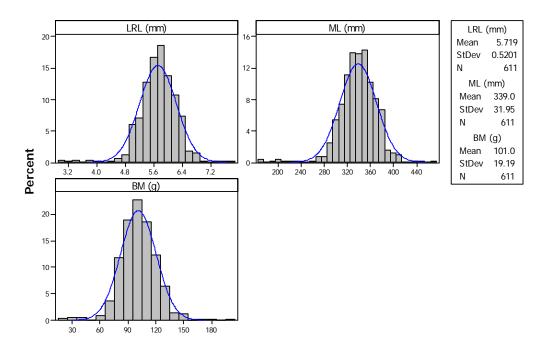
Cranchiidae

Six genera and seven species belonging to this family were present amongst stomach contents, collectively contributing 14.7% by number and 5.5% by weight to the diet of the whales. This family contributed 605.9 kg of cephalopods to the diet of the sperm whales in New Zealand, making it the fifth most important family with respect to biomass consumed by these sperm whales.

Teuthowenia pellucida

A total of 622 *Teuthowenia pellucida* beaks, representing 5.0% of the total number of beaks, occurred in 75.0% of the samples. Even though it contributed 5.0% of the beaks, the 622 specimens collected only contributed 62.9 kg (0.6%) of the total cephalopod biomass consumed by all whales. From one to 328 beaks of this species were found in any single whale. The LRL distribution ranged from 3.0–7.9 mm, with a strong peak around 6.0 mm, and a mean of 5.7 mm (SE = 0.02) (Figure 62). The estimated ML's for this species ranged between 132.9 and 332.3 mm, with a BM range of 26.2–257.1 g, and a mean ML of 238.9 mm (SE = 1.3) and mean BM of 115.2 g (SE = 0.8).

Figure 62. Histograms of LRL, estimated ML and BM for *Teuthowenia pellucida* in the diet of sperm whales stranded on New Zealand beaches



Megalocranchia sp. A

Megalocranchia sp. A sensu Voss et al. (1980, 1992) (=Phasmatopsis cymoctypus, nomen dubium Clarke 1980, Clarke et al. 1998) was the only species in the genus Megalocranchia found in the stomachs of New Zealand stranded whales. This species was found in 13 (81.3%) of the samples, contributing up to 5.8% by weight to the diet of any individual whale (Figure 63). A total of 648 beaks accounted for 5.2% of the total number of beaks and contributed an estimated 274.4 kg (2.5%) to the total cephalopod biomass consumed by all sperm whales. These squid are estimated to have ML's ranging from 479.6 to 1,626.9 mm, with a mean of 567.4 mm (SE = 4.2), and weights ranging from 64.6 to 966.1 g, with a mean of 426.5 g (SE = 6.6). The LRL distribution for this species ranged from 4.8 to 12.9 mm, with a peak from 9.0 to 11.0 mm, and a mean LRL of 9.4 mm (SE = 0.1) (Figure 64).

Figure 63. Contribution by weight of Megalocranchia sp. A to the diet of individual whales

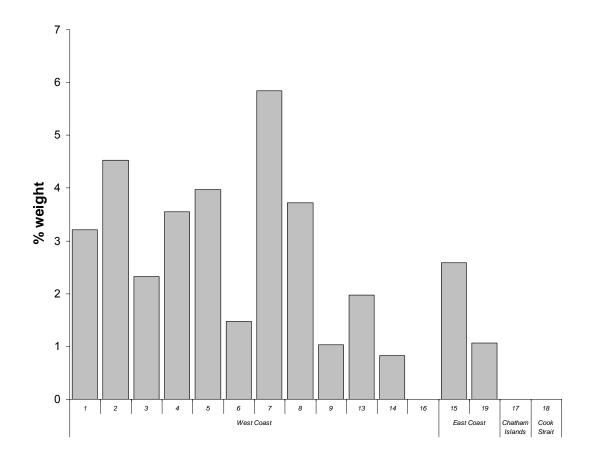
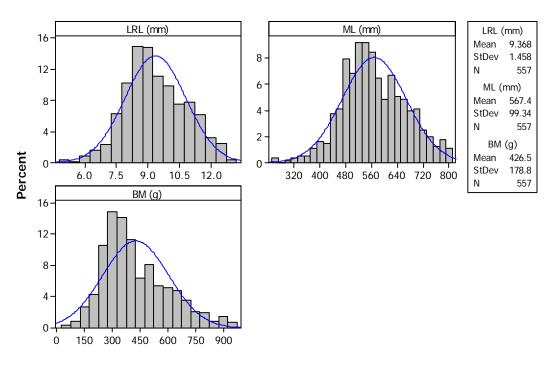


Figure 64. Histograms of LRL, estimated ML and BM for *Megalocranchia* sp. A in the diet of sperm whales stranded on New Zealand beaches



Mesonychoteuthis hamiltoni

A total of 19 *Mesonychoteuthis hamiltoni* beaks occurred in the stomach samples, representing <1% of the total number of beaks present amongst samples. *M. hamiltoni* was the longest cephalopod consumed by the sperm whales stranded in New Zealand, with a mean ML of 2,417.9 mm (SE = 89.3), ranging from 1,933.8–2,663.6 mm. These squid had estimated weights of 4.2–8.5 kg with a mean of 7.0 kg (SE = 238.0). The BM estimates for this species are thought to be gross underestimations of the true biomass consumed (see discussion). These squid contributed 132.5 kg (1.2%) of the total cephalopod biomass represented by beaks, and were only present in west coast-stranded whales, where they contributed up to 10.7% by weight to the diet of any individual whale (Figure 65). Only seven of the beaks could be measured and had LRL's that ranged between 31.7 and 43.6 mm, with a mean of 39.6 mm (SE = 1.5).

Taonius spp.

Two species of *Taonius* were found in the collections. One hundred and thirty-three (133) beaks of a large species of *Taonius* were found in nine (56.3%) whale stomachs. The LRL for *Taonius* sp. B (sensu Voss) had a mean of 9.7 mm (SE = 0.1) and ranged between 4.1 and 11.0 mm, with estimated ML's ranging from 241.4 to 661.6 mm, with a mean ML of 582.8 mm (SE = 4.7). BM estimates range from 49.0 to 416.3 g, with a mean of 320.3 g (SE = 4.4). These 133 specimens contributed 1.1% of the total number of beaks and 42.7 kg (0.4%) of the total cephalopod biomass consumed by all whales. The LRL distribution was fairly narrow, with a strong peak between 10.0 and 11.0 mm (Figure 66).

One beak of *Taonius* sp. A was found in one of the whale stomachs (sperm whale 8). It had a LRL of 6.3 mm, an estimated ML of 372.3 mm, and a BM of 121.9 g.

Figure 65. Contribution by weight of Mesonychoteuthis hamiltoni to the diet of individual whales

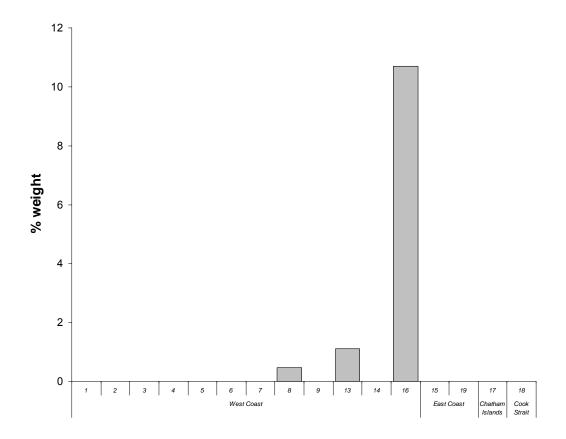
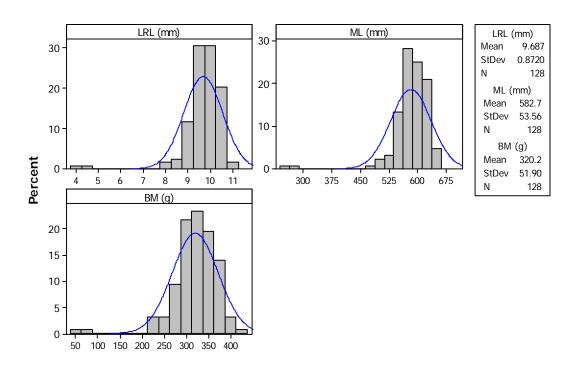


Figure 66. Histograms of LRL, estimated ML and BM for *Taonius* sp. B in the diet of sperm whales stranded on New Zealand beaches



Galiteuthis sp. C

One species of the genus *Galiteuthis* occurred in the stomach contents: *Galiteuthis* sp. C (=*Galiteuthis* stC sp. sensu Imber 1992). A total of 391 *Galiteuthis* sp. C beaks were present in 12 (75.0%) of the whale stomachs. They occurred in both east and west coast stomachs, where they contributed up to 8.4% by weight to the diet of any individual whale (Figure 67). This species contributed 3.1% by number and 0.8% by weight to the diet of all whales sampled. The LRL ranged from 4.3 to 6.5 mm, with a mean of 5.4 mm (SE = 0.1) (Figure 68).

Liocranchia sp.

Nine beaks are referred to a single species of *Liocranchia*. These nine *Liocranchia* sp. beaks had a mean LRL of 3.85 mm (SE = 0.3)., ranging from 3.0 to 5.4 mm.

Figure 67. Contribution by weight of Galiteuthis sp. C to the diet of individual whales

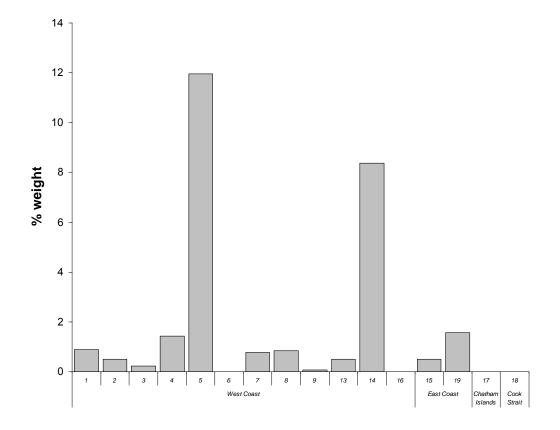
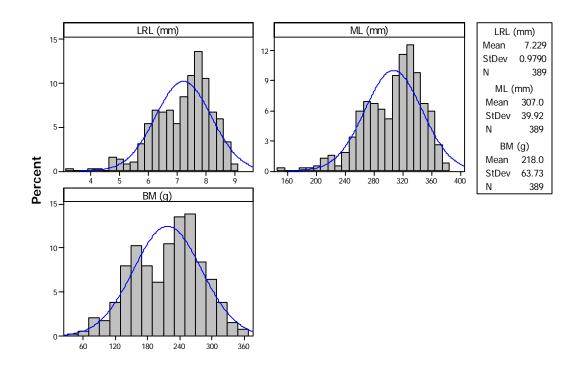


Figure 68. Histograms of LRL, estimated ML and BM for *Galiteuthis* sp. C in the diet of sperm whales stranded on New Zealand beaches



Cranchiidae (indeterminate)

Another 23 beaks found in the collections were identified only to indeterminate cranchiids, as they were too broken to be reliably measured or identified to genus or species. However, the estimated mean BM for all cranchiids was used to determine the weight that these specimens represented in whale diet. The mean BM for all cranchiids was 397.3 g (SE = 16.5), and these 23 specimens contributed 9.1 kg (<1%) the diet of all whales.

Histioteuthidae

Six species of the genus *Histioteuthis* were identified from the beaks reported here. The family Histioteuthidae was the most abundant by number and the second most important family by weight for these sperm whales.

Histioteuthis atlantica

From one to 3,165 *Histioteuthis atlantica* beaks were found in 16 (100.0%) of the samples, contributing up to 70.6% by weight to the diet of any individual whale, excluding whale 17, for which only beaks of *H. atlantica* were collected (Figure 69). A total of 5,289 beaks belonging to this species were present amongst all samples, representing 42.1% of the total number of beaks consumed. This species had estimated ML's ranging from 42.9 to 150.5 mm, with a mean of 95.2 mm (SE = 0.2), and an estimated weight range of 42.4–499.8 g, with a mean of 199.9 g (SE = 0.9). The LRL distribution ranged between 2.5 and 7.4 mm, was unimodal with a peak between 4.5–5.0 mm, and had a mean of 4.9 mm (SE = 0.01) (Figure 70). These 5,289 squid represented 1,057 kg (9.6%) of the diet of these sperm whales in New Zealand waters.

Figure 69. Contribution by weight of Histioteuthis atlantica to the diet of individual whales

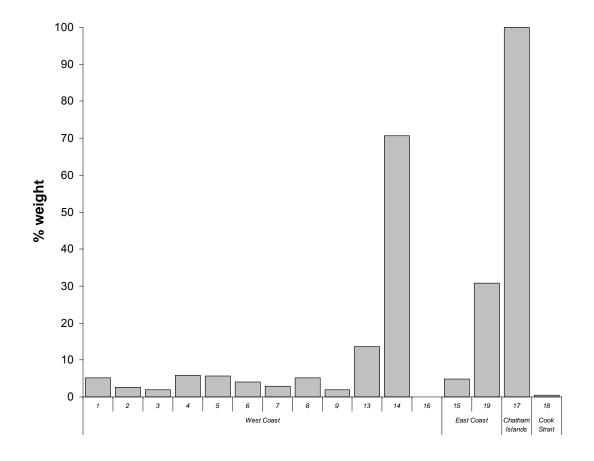
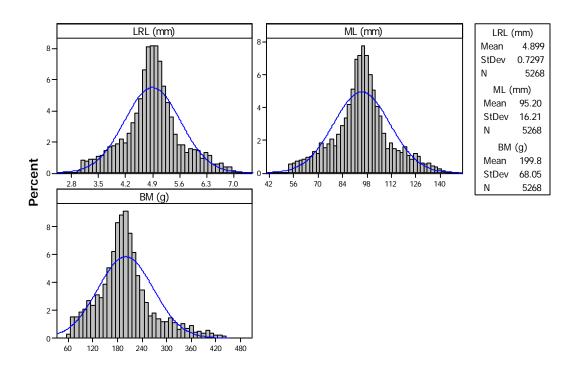


Figure 70. Histograms of LRL, estimated ML and BM for *Histioteuthis atlantica* in the diet of sperm whales stranded on New Zealand beaches



Histioteuthis miranda

A total of 1,385 *H. miranda* beaks were found in 13 (81.3%) of both east and west coast whales, contributing up to 25.6% by weight to the diet of any individual whale, with a maximum of 461 beaks in any one whale (Figure 71). Beaks of this species represented 11.0% of the total number of beaks in the collections. Estimated ML's for this species ranged from 47.3–169.4 mm, with a mean of 128.6 mm (SE = 0.4), and had an estimated BM range of 50.5–642.8 g, and a mean of 360.5 g (SE = 2.3). Lower rostral lengths ranged from 2.7 to 8.2 mm with a strong peak around 7.0 mm, and a mean of 6.4 mm (SE = 0.02) (Figure 72). *Histioteuthis miranda* was the second most important species in the diet of sperm whales by number, and at an estimated 505.9 kg, comprised 4.6% of the total cephalopod biomass consumed by all whales.

Figure 71. Contribution by weight of Histioteuthis miranda to the diet of individual whales

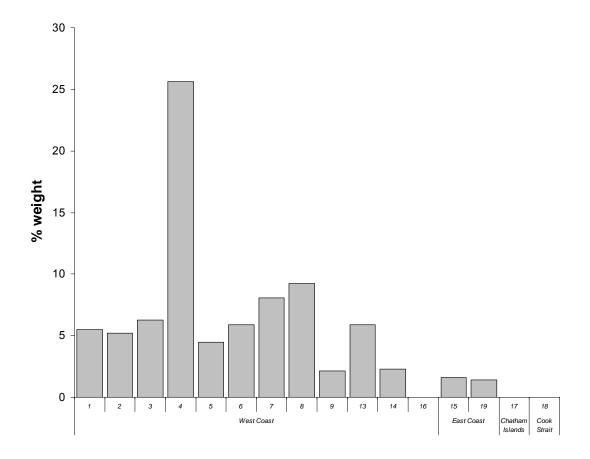
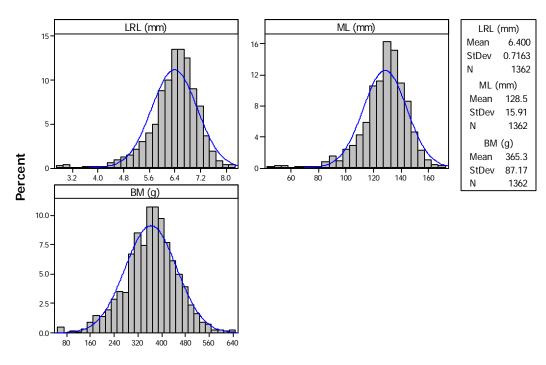


Figure 72. Histograms of LRL, estimated ML and BM for *Histioteuthis miranda* in the diet of sperm whales stranded on New Zealand beaches



Histioteuthis Type A5

A total of 386 *Histioteuthis* Type A5 beaks were found in 11 (68.8%) of the whale stomachs from both east and west coast samples, contributing up to 12.3% by weight to the diet of any single whale (Figure 73). Beaks of this species represented 3.1% of the total number of beaks, and had an LRL distribution ranging from 4.7 to 11.4 mm, with a broad peak between 7.0 and 9.0 mm, and a mean of 7.5 mm (SE = 0.1) (Figure 74). *Histioteuthis* Type A5 was the largest histioteuthid species found in the collections, with a mean ML of 151.8 mm (SE = 1.1), ranging from 90.1 to 238.7 mm. Estimated weights ranged from 173.1 to 1,349.6 g, with a mean BM of 522.1 g (SE = 8.2). All specimens of this species were estimated to weigh 201.7 kg, contributing 1.8% of the total cephalopod biomass to the diet of all whales.

Figure 73. Contribution by weight of Histioteuthis Type A5 to the diet of individual whales

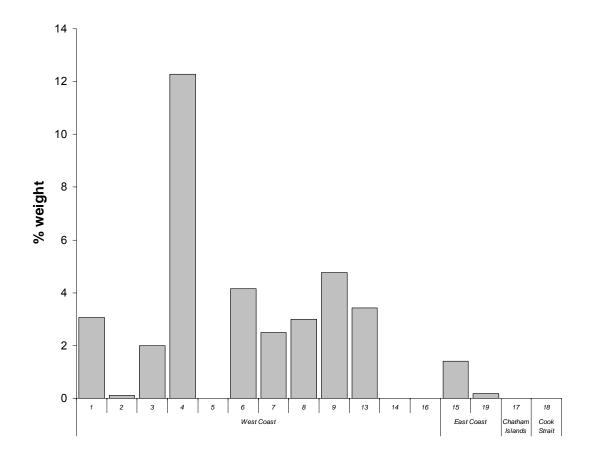
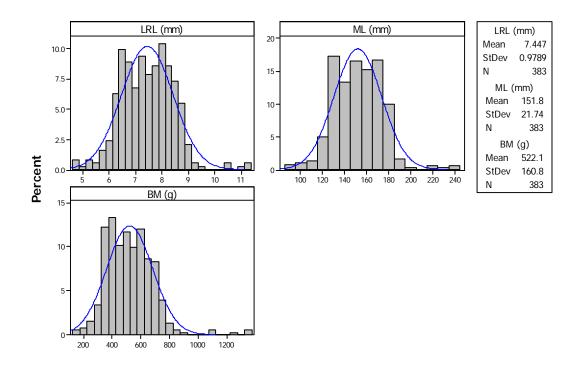


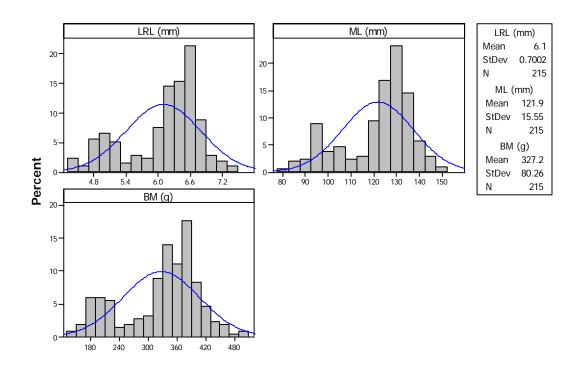
Figure 74. Histograms of LRL, estimated ML and BM for *Histioteuthis* Type A5 in the diet of sperm whales stranded on New Zealand beaches



Histioteuthis Type B4

A total of 215 *Histioteuthis* Type B4 beaks were found in one (6.3%) of the whale stomachs (sperm whale 19), representing 1.7% of the total number of beaks. This species had an estimated mean ML of 121.9 mm (SE = 1.1), ranging from 82.4 to 151.0 mm, and an estimated weight ranging from 144.6 to 502.5 g, with a mean of 157.6 g (SE= 5.5). The LRL distribution for this species ranged from 4.3 to 7.4 mm, with a peak between 6.5 and 7.0 mm, and a mean of 6.1 mm (SE = 0.1) (Figure 75). This species contributed 70.3 kg (0.7%) by weight to the total cephalopod biomass represented by the beaks in all stomach samples.

Figure 75. Histograms of LRL, estimated ML and BM for *Histioteuthis* Type B4 in the diet of sperm whales stranded on New Zealand beaches



Histioteuthis spp.

Two histioteuthid species, *H. bonnellii* and *H. macrohista* were also found in the stomach samples. A single *H. bonnellii* beak with a LRL of 5.2 mm, and two *H. macrohista* beaks of LRL 3.4 mm and 4.1 mm were found in whale 14. These two species contributed less than 500 g to the diet of this sperm whale.

Whales 8 and 19 had 15 and 332 beaks referable to the family Histioteuthidae, but they were too broken to be measured or identified to species. By averaging BM estimates for other histioteuthid species an estimate of the mass these cephalopods contributed to the diet of New Zealand stranded whales is reached. These beaks represented 87.5 kg (0.8%) of the diet of both whales.

H. atlantica was the most important species by number and the second by weight in the diet of all whales. The six histioteuthid species had a combined

estimated weight of 1,922.7 kg (17.4%) of the total cephalopod biomass consumed by all whales.

Onychoteuthidae

Three species of this family occurred in whale stomach samples, *Moroteuthis robsoni*, *M. ingens*, and *Kondakovia longimana*. This family contributed 8.8% by number and 34.3% by weight to the diet of New Zealand stranded whales.

Moroteuthis ingens

A total of 572 *M. ingens* beaks, representing 4.6% of the total number of beaks found in six (37.5%) of the whale stomachs, contributed up to 97.8% by weight to the diet of any single whale (Figure 76).

Morphological differences between male and female beaks for this species enable identification of sexes. A total of 169 male and 403 female beaks were found in six (37.5%) of the stomachs. Females have larger beaks and estimated ML and BM than males; female LRL's ranged from 9.1 to 12.9 mm, with a peak between 10.5 and 11.5 mm, and a mean of 10.8 mm (SE = 0.02) (Figure 77), and estimated ML's ranging from 354.8 to 504.3 mm, with a mean of 421.55 mm (SE = 1.3). Estimated weights ranged from 1,191.7 to 3,199.8 g, with a mean of 1,944.2 g (SE = 24.5).

Figure 76. Contribution by weight of Moroteuthis ingens (female) to the diet of individual whales

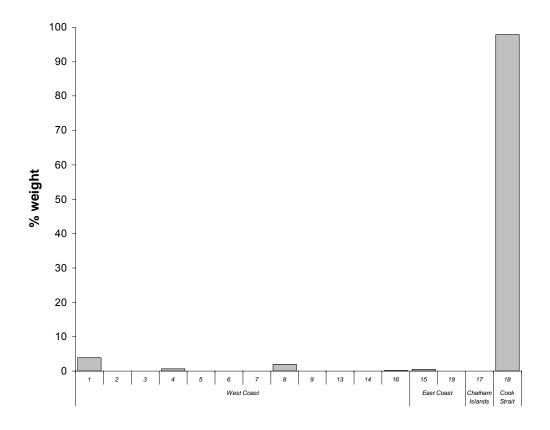
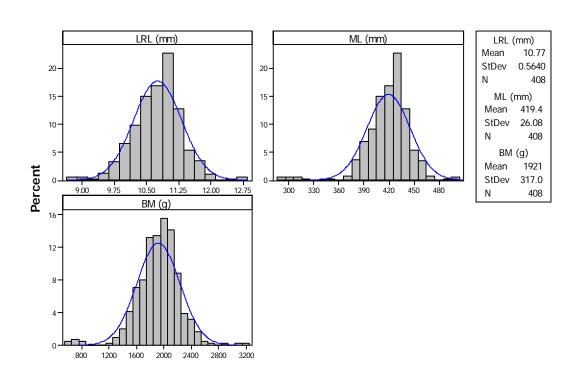


Figure 77. Histograms of LRL, estimated ML and BM for *Moroteuthis ingens* (Female) in the diet of sperm whales stranded on New Zealand beaches



The rostrum of most male beaks was broken, and only eight (4.7%) of them could be reliably measured. Their LRL's had a mean of 9.5 mm (SE = 0.01) and ranged from 8.7 to 11.9 mm; their ML's ranged between 286.3 and 389.1 mm, with a mean of 312.6 mm (SE = 0.9). Male BM ranged from 604.8 to 1,289.7 g, with a mean of 765.2 g (SE = 1.7). Both sexes contributed a total of 912.7 kg (8.3%) to the total cephalopod biomass consumed by all whales.

Moroteuthis robsoni

A total of 415 *M. robsoni* beaks were found in 13 (81.3%) of both east and west coast samples, representing 3.3% of the total number of beaks, and contributing up to 31.5% by weight to the diet of any individual whale (Figure 78). Mantle length ranged from 288.0 to 1,073.4 mm, with a mean of 610.4 mm (SE= 5.3), and an estimated weight ranging from 274.1 g to 36.7 kg, with a mean of 3.6 kg (SE = 145.9). These 415 squid contributed 1,511.6 kg (15.4%) to the diet of these sperm whales, and most by weight to all diet of the whales. The LRL distribution for *M. robsoni* ranged from 6.2 to 11.4 mm, with a peak between 8.0 and 9.0 mm, with a mean of 8.4 mm (SE = 0.04) (Figure 79).

Identification of these beaks proved problematic, and they could possibly include those of the otherwise morphologically similar *M. knipovitchi*. This is subject to ongoing research.

Figure 78. Contribution by weight of Moroteuthis robsoni to the diet of individual whales

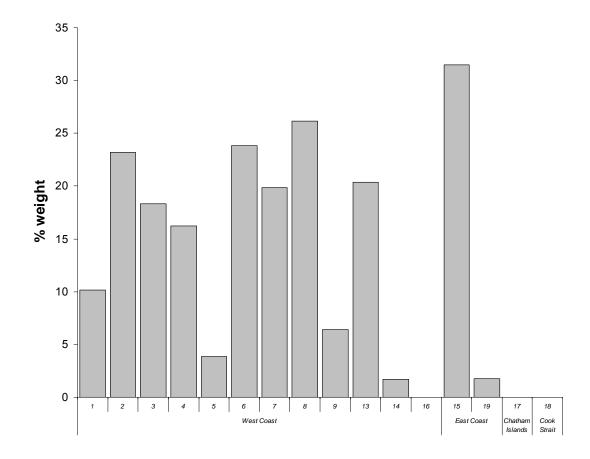
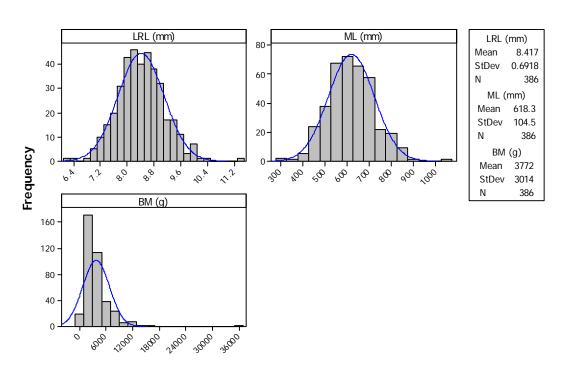


Figure 79. Histograms of LRL, estimated ML and BM for *Moroteuthis robsoni* in the diet of sperm whales stranded on New Zealand beaches



Kondakovia longimana

K. longimana was the largest species of this family found in the stomach samples analysed. It had estimated ML's ranging from 292.0 to 1,037.0 mm, with a mean of 734.0 mm (SE = 23.5). Beaks present in eight (50.0%) of the east coast samples contributed up to 55.8% by weight to the diet of any individual whale (Figure 80). Beaks for this species represented a total of 113 specimens estimated to weigh between 938.4 g and 27.5 kg, with a mean of 12.1 kg (SE = 602.8). LRL's ranged from 8.1 to 24.9 mm, with a mean of 18.1 mm (SE = 0.5), and a peak between 19.0 and 21.0 mm (Figure 81). These 113 squid contributed 1,365.5 kg (12.4%) of the total cephalopod biomass represented by beaks.

Figure 80. Contribution by weight of Kondakovia longimana to the diet of individual whales

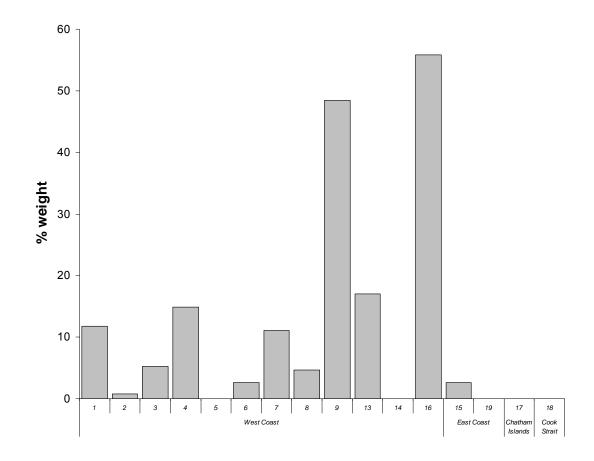
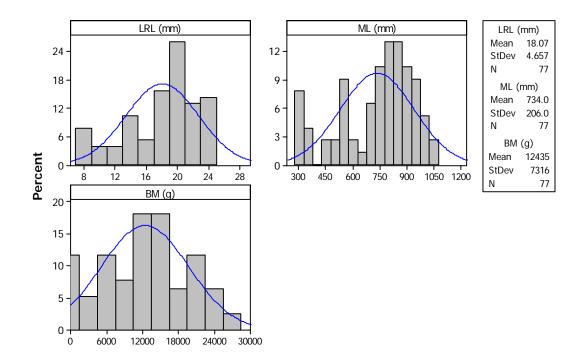


Figure 81. Histograms of LRL, estimated ML and BM for *Kondakovia longimana* in the diet of sperm whales stranded on New Zealand beaches



Pholidoteuthidae

Pholidoteuthis boschmai

A total of 253 beaks belonging to *Pholidoteuthis boschmai* were found in 12 (75.0%) of both east and west coast whale stomachs, contributing up to 44.9% by weight to the diet of any individual whale (Figure 82). Beaks of this species represented 2.0% of the total number of beaks, with an LRL distribution ranging from 6.5 to 15.7 mm, with a peak between 11.0 and 12.0 mm, and a mean of 10.8 mm (SE = 0.1) (Figure 83). Estimated ML's ranged between 279.6 and 658.1 mm with a mean of 455.5 mm (SE = 4.3), and estimated weights ranged between 537.1 g and 6.5 kg, and had a mean of 2.4 kg (SE = 57.6). The total estimated mass was 598.7 kg, representing 6.1% of the total cephalopod biomass consumed by all whales.

Figure 82. Contribution by weight of Pholidoteuthis boschmai to the diet of individual whales

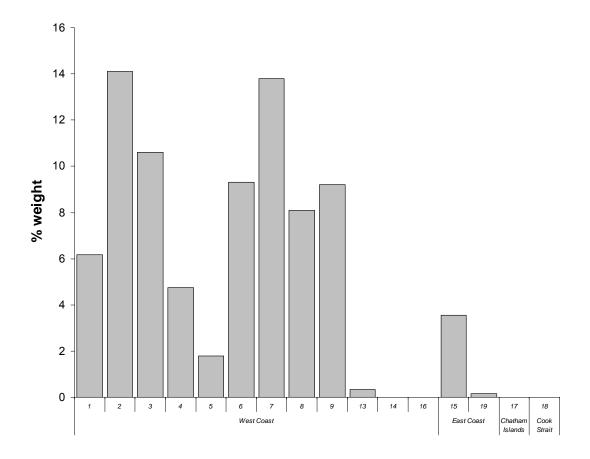
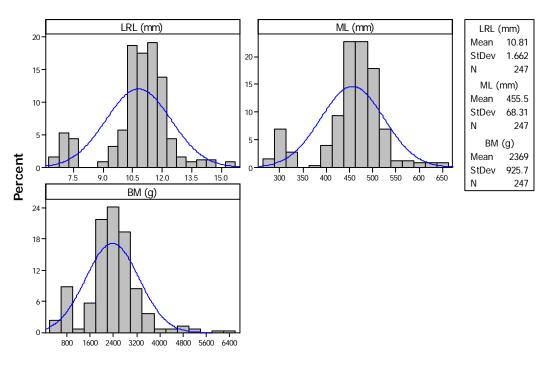


Figure 83. Histograms of LRL, estimated ML and BM for *Pholidoteuthis boschmai* in the diet of sperm whales stranded on New Zealand beaches



Octopoteuthidae

Beaks belonging to this family were found in 15 (93.8%) of the stomachs, and comprised two genera and three species: *Taningia danae*, *Octopoteuthis megaptera*, and *Octopoteuthis* sp. 'Giant'. This family represented 3.9% of the total number of beaks and 16.8% of the estimated cephalopod biomass consumed by all whales.

Taningia danae

A total of 133 *T. danae* beaks, representing 1.1% of the total number of beaks occurred in 12 (75.0%) of both east and west coast samples, contributing up to 20.0% by weight to the diet of any individual whale (Figure 84). Specimens of this species had estimated ML's from 337.5 to 1,292.0 mm with a mean of 746.8 mm (SE = 13.9); estimated weights ranged from 2.0 to 23.8 kg, with a mean of 7.5 kg (SE = 257.5), making it the third heaviest species consumed by sperm whales. The 133 *T. danae* contributed 989.6 kg (9.0%) of the cephalopod biomass to the diet of all sperm whales referred to here. LRL's ranged from 11.9 to 24.6 mm, peaked between 16.0 and 19.0 mm (Figure 85), with a mean of 17.3 mm (SE = 0.2).

Beaks of this species are described in section 4.3.

Figure 84. Contribution by weight of Taningia danae to the diet of individual whales

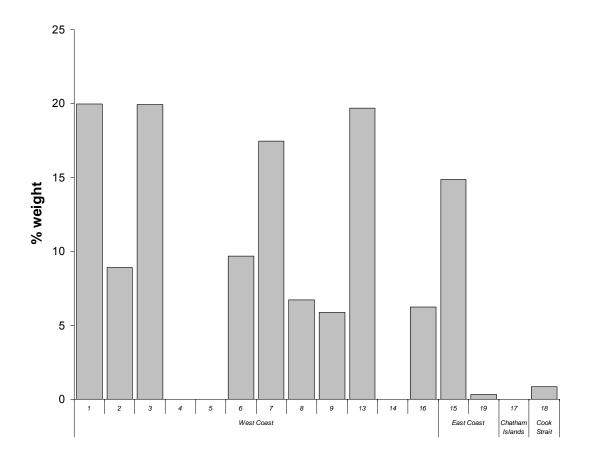
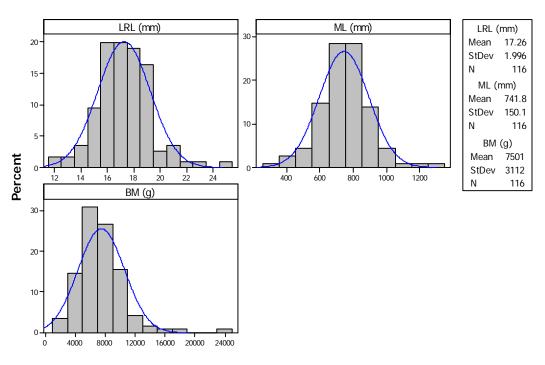


Figure 85. Histograms of LRL, estimated ML and BM for *Taningia danae* in the diet of sperm whales stranded on New Zealand beaches



Octopoteuthis sp. 'Giant'

Twenty-two very large octopoteuthid beaks, similar to those of *Taningia danae* were found in seven (43.8%) of stomach samples. They represented <1% of the total number of beaks, and their estimated weight contributed <1% of the total cephalopod biomass consumed by all whales. The estimated ML's of this species ranged between 187.5 and 463.4 mm, with a mean of 304.8 mm (SE = 17.4); their estimated weight ranges from 290.4 to 2,342.0 g, with a mean of 965.5 g (SE = 107.1). The LRL distribution for this species ranged from 10.8 to 26.8 mm, and had a mean of 17.6 mm (SE = 1.0).

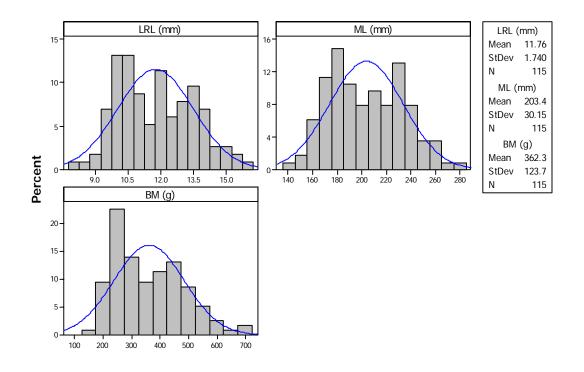
Beaks of this species are described in section 4.3.

Octopoteuthis megaptera

A total of 124 beaks attributed to *O. megaptera* occurred in eight (50.0%) of the stomach samples, representing 1.0% of the total number of beaks examined. These squid had an estimated ML's ranging from 135.1 to 275.5 mm, with a mean of 203.5 mm (SE = 2.8); estimated weight ranged from 136.6 to 705.6 g, with a mean of 362.3 g (SE = 10.8). *O. megaptera* contributed an estimated 45.1 kg (0.41%) to the diet of these sperm whales. The LRL distribution for this species ranged between 7.8 and 15.9 mm, with a mean of 11.8 mm (SE = 0.2), and two peaks at 10.5 and 13.5 mm (Figure 86).

Beaks of this species are described in section 4.3.

Figure 86. Histograms of LRL, estimated ML and BM for *Octopoteuthis megaptera* in the diet of sperm whales stranded on New Zealand beaches



Octopoteuthid (indeterminate)

Another 216 octopoteuthid beaks were too broken to measure or to be identified to species; these occurred in nine (56.3%) of the stomach samples, representing 1.7% of the total number of beaks. From the BM mean for the family this group of beaks contributed 803.2 kg (7.3%) to the diet of all sperm whales.

Lepidoteuthidae

Lepidoteuthis grimaldii

Twelve beaks belonging to *Lepidoteuthis grimaldii*, representing 0.10% of the total number of beaks were found in five (31.3%) of the stomach samples. The specimens of *L. grimaldii* found in our collections had estimated ML's ranging from 459.3 to 1,131.0 mm, with a mean of 802.3 mm (SE = 86.8), and estimated weights ranged from 3.1 to 17.4 kg, with a mean of 9.5 kg (SE =

1,489.3). The LRL distribution for this species ranged between 13.5 and 22.4 mm, and had a mean of 18.1 mm (SE = 1.2).

Beaks of this species are described in section 4.3.

Ommastrephidae

Ommastrephid (indeterminate)

A total of 12 beaks of this family, representing 0.1% of the total number of beaks, were found in eight (50.0%) of the stomach samples. Estimated ML's for species referred to this family taxon ranged from 329.9 to 478.4 mm, with a mean of 415.9 mm (SE = 14.0); estimated weight ranged from 1.1 to 3.2 kg, with a mean of 2.2 kg (SE = 200.2). This family contributed 26.1 kg (0.2%) by weight to the diet of all sperm whales.

Psychroteuthidae

Psychroteuthis glacialis

A total of 24 beaks referable to *Psychroteuthis glacialis*, representing 0.2% of the total number of beaks, occurred in five (31.3%) of the stomach samples. Specimens had estimated ML's between 251.6 and 961.5 mm, with a mean of 406.9 mm (SE = 39.8); estimated weight ranged from 262.5 to 1,181.2 g, with a mean of 477.0 g (SE = 48.2). The 24 *P. glacialis* specimens contributed 11.6 kg (0.1%) to the diet of these whales. LRL distributions ranged between 6.5 and 11.1 mm, with a mean of 7.81 mm (SE = 0.3).

Octopoda

Alloposidae

Haliphron atlanticus

A total of 21 beaks referable to *Haliphron atlanticus* occurred in seven (43.8%) of the stomach samples, representing 0.2% of the total number of beaks in the collections. This species had estimated weights from 37.7 to 185.9 g, a mean weight of 108.7 g (SE = 7.6), and contributed 2.3 kg (<1%) to the total cephalopod biomass consumed by all sperm whales. LRL's ranged from 2.2 to 6.2 mm with a mean of 4.5 mm (SE = 0.2).

Argonautidae

Argonauta nodosa

The beaks of two *Argonauta nodosa*, a muscular pelagic octopod, were found in one stomach sample. They had LRL's of 3.4 and 3.8 mm and contributed less than 0.01% to the diet of all sperm whales.

Vampyromorpha

Vampyroteuthidae

Vampyroteuthis infernalis

Three *Vampyroteuthis infernalis* beaks were found amongst stomach samples. Specimens reported herein had estimated ML's ranging from 15.4 to 28.9 mm, with a mean of 23.7 mm (SE = 4.2). The estimated weight ranged from 0.8 to 10.8 g, and had a mean of 6.5 g (SE = 3.0). Lower hood length ranged between 2.0 and 4.9 mm, with a mean of 3.8 mm (SE = 0.9).

4.1.3 Unidentified beaks

Three octopodid beaks found in the stomach of sperm whale 19 could not be identified to species.

Indeterminate

A total of 422 beaks were too broken to be identified to family. These represented 3.4% of the total number of beaks. No biomass estimates can be reliably provided so they were removed from the biomass calculations.

4.2 Non-cephalopod component of the diet

Non-cephalopod remains in the stomachs of sperm whales stranded in New Zealand included fish remains, salps, crustacean exoskeletons, a copepod, some wood and sand. A highly digested fish, fish bones and scales belonging to an unknown number of fish species occurred in the stomach of sperm whale 18. These remains were too digested to be of any taxonomic use.

4.2.1 Fish

Fish remains including bones, scales, vertebrae, and some flesh were found in one (6.3%) of the samples and were too digested to be identified further.

4.2.2 Other animals

The remains of other animals in the stomachs of these 19 whales are few, comprising a single parasitic copepod present in whale 18, and in more recently stranded whales, a minor number of salps and the exoskeletons of three crustacean decapods.

Final remarks

The mean number of cephalopod species present in stomach samples was 17, with a range of 0–26. Sperm whale number 18, for which there is limited

stranding data, contained a quantity of digested fish remains and 86.7% of the lower beaks found in its stomach belonged to adult *Moroteuthis ingens*.

Whale number 17 stranded in the Chatham Islands on August 9, 2004. 53 cephalopod beaks were found – 40 upper and 13 lower beaks belonging to *Histioteuthis atlantica*. This last sample represents only a partial sample of the stomach contents of the whale and attempts to retrieve the full stomach contents from the collector from DoC proved unproductive.

4.3 Beak descriptions

Because of the difficulties in accurately differentiating the lower beaks of *Taningia danae, Octopoteuthis megaptera, Octopoteuthis* sp. 'Giant' and *Lepidoteuthis grimaldii,* the following descriptive section is provided.

Octopoteuthidae

Beaks of different species of the family Octopoteuthidae are very similar to, and easily confused with those of *Lepidoteuthis grimaldii*. Beaks of two genera, *Octopoteuthis* and *Taningia*, and three species of this family are illustrated and described.

Taningia danae

Squid of this species reach ML's over 1,400 mm, with a LRL of 25.0 mm, and the wings in the lower beak appear to darken when LRL reach between 9.0 and 16.0 mm (Clarke 1986).

The lower beaks of mature specimens of this species are longer than deeper (Figure 87 A, B), characterised by a 'shelf' that protrudes from the anterior part of the lateral wall ridge that does not extend beyond the posterior edges of the hood (Figure 87 G), a cartilaginous shoulder (Figure 87 C, E, F), a sharp and thickened jaw edge (Figure 87 D), an obtuse or almost right angled jaw angle with a straight rostrum (Figure 87 C), and a thickened crest and

lateral wall fold (Figure 87 G). The lateral wall ridge becomes a fold as it progresses backwards and extends to a point below the midpoint between the crest and the free corner of the lateral wall (Figure 87 B). Some beaks present a small ridge in the posterior part of the lateral wall above the lateral wall fold, and another below the lateral wall fold that disappears anteriorly (Figure 87 G, H, I). The wings and hood are very broad and are easily damaged in the stomach contents of predators, where the shoulder cartilage is also often digested.

Octopoteuthis sp. 'Giant'

The lower beak described here was extracted from a specimen caught off South Island's west coast at 42° 36.0' S and 170° 20.9 'E (NZOI Stn Z1074).

The lower beaks of this species have a characteristic shape and may be confused with those of *Taningia* or *Lepidoteuthis*. The lower beaks of this species are longer than deeper (Figure 88 A, B), and characterised by a cartilaginous, sharp shoulder that, unlike *Taningia*, does not extend all the way to the jaw angle (Figure 88 C, E, F), a sharp jaw edge and straight rostrum (Figure 88 A, B, D), broad wings and hood, an anteriorly thickened crest that becomes thinner posteriorly (Figure 88 G, H, I), a thickened, well-defined lateral-wall ridge that extends posteriorly until a point below the midpoint between the crest and the free corner of the lateral wall (Figure 88 B, G, H, I), an obtuse jaw angle (Figure 88 C), a very low ridge that extends the rostrum past the jaw angle and into the anterior part of the lateral wall, and a darkening on the anterior part of this ridge (Figure 88 C). The jaw edge is thickened and sharp in the interior border, becoming broad outwards (Figure 88 D, E). The lateral wall is not noticeably thickened, except for the well-defined lateral wall ridge (Figure 88 G, H, I).

Octopoteuthis megaptera

The lower beak described here was extracted from a specimen of ML 170.0 mm and BM 320.2 g (TAN0317/078-Osq).

The lower beaks of this species do not attain the sizes of *Taningia danae*, Lepidoteuthis grimaldii or Octopoteuthis sp. 'Giant', but can be confused with the smaller size classes of these species. However, it should be noted that the smaller sizes of T. danae, L. grimaldii and Octopoteuthis sp. 'Giant' would not have darkened wings and could be readily differentiated. Lower beaks of O. megaptera are deeper than longer, giving them a typical elongate shape (Figure 89 A, B). They are characterised by a cartilaginous, sharp shoulder that, unlike Taningia and like Octopoteuthis sp. 'Giant', does not extend all the way to the jaw angle (Figure 89 C, E, F), a sharp jaw edge and slightly curved rostrum (Figure 89 A, B, D), slightly broad wings and hood, an anteriorly unthickened crest that becomes thicker posteriorly (Figure 89 G, H, I), a thickened, well-defined lateral wall ridge that lies on a lateral wall fold and extends posteriorly until a point below the midpoint between the crest and the free corner of the lateral wall (Figure 89 A, G, H, I), an obtuse jaw angle (Figure 89 C), a very low ridge that extends the rostrum past the jaw angle and into the anterior part of the lateral wall, and a darkening on the anterior part of this ridge (Figure 89 C). The jaw edge is thickened and sharp and the jaw angle is broad (Figure 89 D, E). The lateral wall is not noticeably thickened, except for the well-defined lateral wall ridge (Figure 89 G, H, I).

Lepidoteuthidae

Lepidoteuthis grimaldii

The lower beaks of this species can be easily confused with those of *Taningia danae* or *Octopoteuthis* spp. Lower beaks of *L. grimaldii* are deeper than longer (Figure 90 A, B), and are characterised by a cartilaginous shoulder that extends as a plug onto the wing rendering it thick, (Figure 90 A, B, C, F). A sharp jaw edge and almost straight rostrum (Figure 90 A, B, D); broad wings and hood; uniformly thickened crest along the antero-posterior axis (Figure 90 G, H, I); thickened, well-defined lateral wall ridge that becomes a broad lateral wall fold posteriorly, until a point well below the midpoint between the crest and the free corner of the lateral wall (Figure 90 A, G, H, I); almost right-angled jaw angle (Figure 90 C); and very low ridge that extends the rostrum

past the jaw angle and into the anterior part of the lateral wall with a particular darkening on the anterior part of the lateral wall that extends from the jaw edge downwards (Figure 90 C) further characterise this beak. Additionally the jaw edge is thickened and sharp, with a small ridge on the interior part of the rostrum (Figure 90 D); and the lateral wall has a particular thickening on its lower part, being more noticeable on the posterior end of the lateral wall (Figure 90 G, H, I).

Figure 87. Lower beak of *Taningia danae* in oblique profile (A), lateral profile (B), jaw detail (C), section of the rostrum (D), section of the jaw angle (E), section of the shoulder (F), and sections of the lateral wall from the posterior end to the anterior (G–I). LRL 22.1 mm.

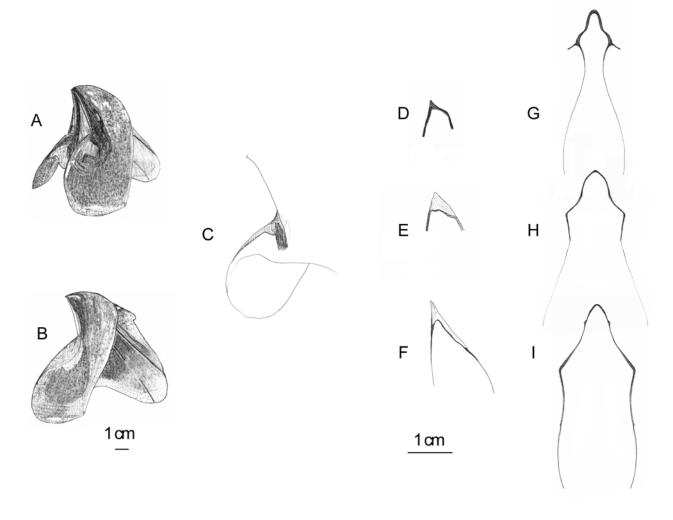


Figure 88. Lower beak of *Octopoteuthis* sp. 'Giant', in oblique profile (A), lateral profile (B), jaw detail (C), section of the rostrum (D), section of the jaw angle (E), section of the shoulder (F), and sections of the lateral wall from the posterior to the anterior end (G–I). LRL 23.2 mm

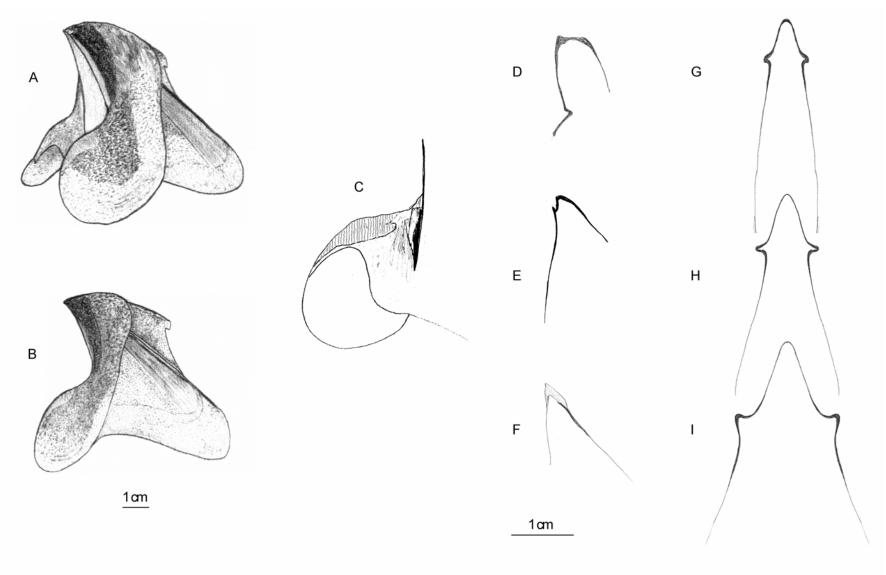


Figure 89. Lower beak of *Octopoteuthis megaptera*, in oblique profile (A), lateral profile (B), jaw detail (C), section of the rostrum (D), section of the jaw angle (E), section of the shoulder (F), and sections of the lateral wall from the posterior to the anterior end (G–I). LRL 9.5 mm

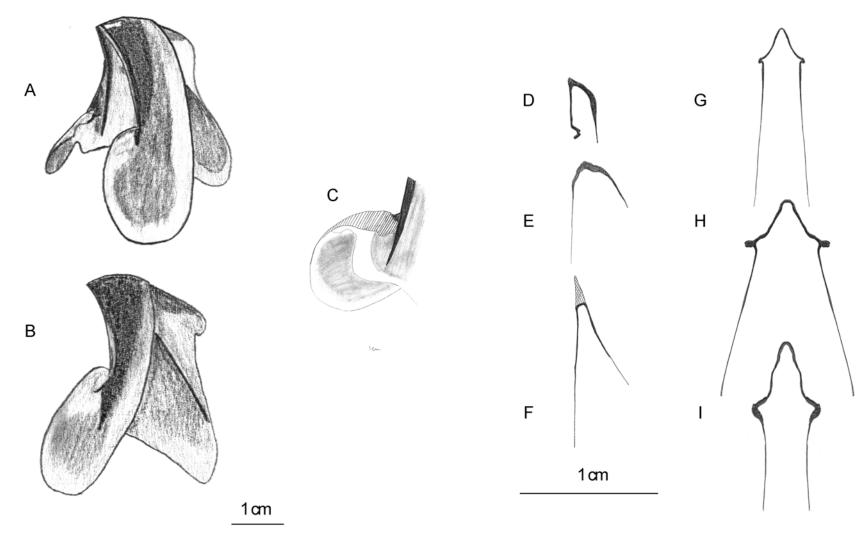
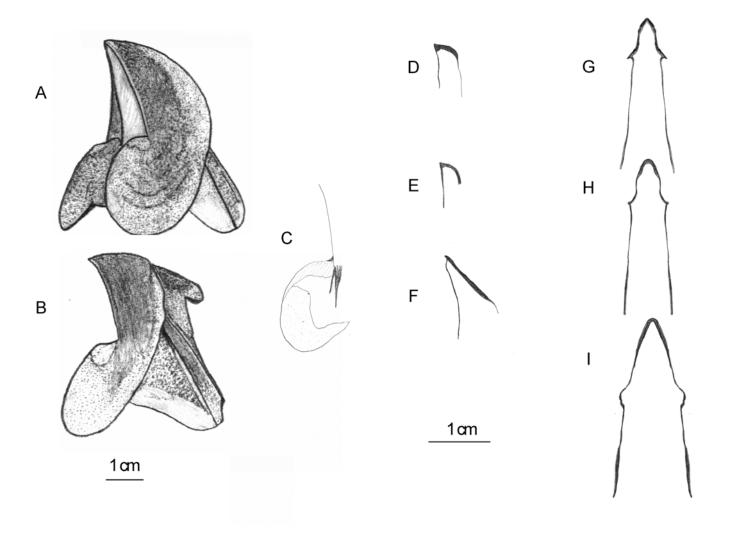


Figure 90. Lower beak of *Lepidoteuthis grimaldii* in oblique profile (A), lateral profile (B), jaw detail (C), section of the rostrum (D), section of the jaw angle (E), section of the shoulder (F), and sections of the lateral wall from the posterior end to the anterior (G–I). LRL 18.1 mm



Chapter 5

Discussion

This investigation represents the first large-scale study into the diet of sperm whales in New Zealand waters since the early 1960s. The results suggest that New Zealand stranded sperm whales predominantly prey on oceanic cephalopods of the families Histioteuthidae, Onychoteuthidae, Octopoteuthidae and Cranchiidae. Comparison of these results with earlier work in the area, reveal that small histioteuthid and larger onychoteuthid squid continue to be the major components of sperm whale diet in New Zealand waters, while fish appear to have a reduced importance in the diet of recently stranded whales. This raises two important questions:

- Have sperm whales changed their diet in the past 40 years?
- Do dietary studies from stranding events provide a true picture of the diet of this species in the region?

A better scientific knowledge of the foraging relationships in marine ecosystems is of paramount importance, given the increasing fishing pressure on the marine environment (Evans and Hindell 2004). Nevertheless, dietary studies on apex marine predators are subject to a wide range of errors and biases (Santos *et al.* 2001), including the differential digestion and retention of prey remains, the lack of representation of prey items due to temporal variability in consumption, and the inability to discern secondarily ingested prey from true prey. However, dietary studies can contribute to a better understanding of the energy flow and trophic links in marine systems, and samples from stranding events provide the only current-opportunity to investigate the role sperm whales, a protected species, play in the deep-sea trophic system, at least in New Zealand waters.

5.1 Limitations of this study

Dietary studies on marine mammals are based on opportunistic samples susceptible to sources of error including the heterogeneity of the sampled population that arises from spatial and temporal fluctuation in prey populations, as well as variation in individual diet; the differential digestion rates for prey items and secondarily ingested prey, the lack of standardisation in sample collection and processing, and the unresolved taxonomy of prey and the intraspecific variation of prey remains (e.g. Clarke 1980, Santos *et al.* 1999, Santos *et al.* 2001a). However, carrying out unbiased dietary studies on protected marine mammals such as the sperm whale has proven to be very difficult, and although strandings may not accurately reflect the diet of a healthy population they do provide an opportunity to study the diet of a protected species. Reconstructing diet based on stomach contents is by no means an exact science, and all available information on both the predator and prey natural history must be used in order to accurately reconstruct diet and feeding behaviour.

It is uncommon to find undigested prey in the stomachs of stranded sperm whales, and the morphometry of hard remains collected is often used to calculate the biomass of prey that was present in the stomach. The allometric equations used to calculate cephalopod BM are often based on very few collected individuals, and in some cases can only provide a broad reference to the general importance of relative biomass from the different cephalopod taxa to the diet (Clarke 1983, Lu & Ickeringill 2002). It should also be noted that the proportion of the stomach contents collected may also significantly influence the results of the cephalopod biomass calculation. However, the proportion of the stomach sampled did not seem to affect the species diversity in a dietary study from stranded sperm whales in Tasmania, Australia (Evans & Hindell 2004). However, prudence should be taken when analysing the estimated biomass represented by beaks in the stomach of individual whales, since partial samples or recent regurgitation may be confounded with lack of feeding.

Despite New Zealand being one of the countries with highest stranding numbers for sperm whales globally (Stephenson 1975, Brabyn 1991), and the large numbers of sperm whales caught in New Zealand waters between 1791 and 1964 (Kaiser *et al.* 2000), dietary information for this species is very limited. No samples were archived during this time period, and determining any temporal trends in the diet of the sperm whale in New Zealand waters is difficult, if not impossible.

Comprehensive, informative, well-maintained and accessible museum collections of prey species and stomach contents of predators, are essential to carry out accurate dietary studies, and to determine any temporal trends in the diet of predators. Even though a national stranding database for marine mammals exists for New Zealand, the protocol and techniques used in the stranding events are not standardised, nor do they maximise the information that samples from strandings could provide. Researchers would benefit from the implementation of standardised protocols for the collection of samples from marine mammal strandings that record all the appropriate information needed to carry out comprehensive well-designed studies on these protected animals.

Dietary studies on marine mammals are generally based on opportunistic studies of stranded or commercially caught animals (Clarke & Young 1998, Pauly *et al.* 1998). Prior to the moratorium on sperm whaling declared by the International Whaling Commission in 1985, large samples more representative of the whole population could be collected from hunted animals. However, it should be noted that these samples were biased toward adult animals, especially males (Santos *et al.* 2001a). Recent studies have relied on fewer stomach samples from stranding events. However, the cumulative information that has been collected and analysed has given us a partial understanding of the ecological role of the sperm whale in the world's oceans. Even though the biomass calculations are of great value, most of the equations are based on very few collected specimens,

and provide only a general guide to the general importance of the different cephalopod species to the diet.

5.2 The diet of the sperm whale in New Zealand

Historical reports of sperm whale diet in New Zealand are few, and can be divided into those from whales caught or stranded on the west coast and most probably inhabiting or migrating into or from the Tasman Sea, and those from whales caught in the Cook Strait region.

West coast

Two studies report stomach contents collected from west coast sperm whales. Clarke & Roper (1998) on the contents of a sperm whale that stranded on Paekakariki Beach, North Island in 1996, where a total of 24 cephalopod species from 13 families were identified. The most important families numerically in the stomach of this whale were Histioteuthidae, Onychoteuthidae, Cranchiidae and Octopoteuthidae, and the most important families by weight were Histioteuthidae, Architeuthidae, Onychoteuthidae and Octopoteuthidae (Clarke & Roper 1998). Clarke & MacLeod (1982) reported on the stomach contents of 66 commercially caught sperm whales in the Tasman Sea taken by Japanese whalers in 1970. However, this study appears to describe only partial stomach samples for these whales, since only 3,299 lower beaks were recorded from the stomachs of 66 sperm whales, and the authors do not describe in detail the collection methodology used to retrieve the stomach contents. A total of 30 cephalopod species belonging to 14 families were identified from the remains found in the stomachs of these whales. The most important families numerically in the region were Octopoteuthidae, Histioteuthidae, Cranchiidae and Onychoteuthidae, and the most important families by weight were Octopoteuthidae, Onychoteuthidae, Architeuthidae and Cranchiidae (Clarke & MacLeod 1982).

The contribution by weight of the different cephalopod families to the diet of sperm whales in the South Pacific changes by region, with some families being consistently important in almost all regions. Figure 42 shows the cephalopod families by percentage weight in the diet of sperm whales from Cook Strait region (Gaskin & Cawthorn 1967a, b), Paekakariki Beach (Clarke & Roper 1998), the Tasman Sea (Clarke & MacLeod 1982), Australia (Evans & Hindell 2004), and in the diet of stranded sperm whales on New Zealand beaches (this study). Based on this body of research the families Onychoteuthidae, Histioteuthidae and Architeuthidae are consistently the most important cephalopod families in the diet of sperm whales in both the Tasman Sea and the South Pacific Ocean. The family Ancistrocheiridae is relatively important by weight in Australia and New Zealand (this study). Cranchilds are not a major part of the diet by weight, but are consistently important in all areas except for the Cook Strait region. The family Octopoteuthidae is important in the Tasman Sea, and appears to be a significant component of the diet of whales stranded on both the east and west coasts of New Zealand. The family Ommastrephidae is important in southern Australia and in the Cook Strait region. The families Pholidoteuthidae and Alloposidae are important in southern Australian waters.

The relative contribution by numbers of the different cephalopod families to the diet of sperm whales in the South Pacific changes by region, with some families being consistently important in almost all regions. Figure 42 shows the cephalopod families by percentage frequency in the diet of sperm whales from the Cook Strait region (Gaskin & Cawthorn 1967a, b), Paekakariki Beach (Clarke & Roper 1998), the Tasman Sea (Clarke & MacLeod 1982), Australia (Evans & Hindell, 2004) and in the diet of stranded sperm whales on New Zealand beaches (this study). The families Histioteuthidae, Onychoteuthidae, Octopoteuthidae and Cranchiidae are consistently the most important families by number in the diet of sperm whales in both the Tasman Sea and the South Pacific Ocean. The family Lepidoteuthidae is important by numbers in southern

Australia, Octopoteuthidae in the Tasman Sea, Ommastrephidae in the Cook Strait region, whereas Pholidoteuthidae is consistently important in all areas.

In clear contrast to stomach samples collected during whaling activities in the Cook Strait region during the early 1960s (Gaskin & Cawthorn 1967a, b), no fish remains were reported from whaling activities in the Tasman Sea during the 1970s (Clarke & MacLeod 1982), or from the stranding on Paekakariki Beach (Clarke & Roper 1998), and very few fish remains are reported from recent stranding events in New Zealand waters (this study). Fish remains were found only in the stomach of whale 18, recently stranded in the Cook Strait region (early 1990s), and did not occur in the stomachs of any other whales. Thus, fish appear to be an important component of the diet of sperm whales only in this region of the country. This is consistent with a study off South America's west coast that showed sperm whale diet changed significantly between years, and in different areas where the study was conducted (Smith 1992). It also resembles the findings for waters of the Kuriles (south west of the Kamchatka peninsula), where the proportion of stomachs with fish in them, diminished over the years, from 30% in 1951, to 20% for 1953–1954, to 12% in 1955 (Beteshava 1961).

East coast

The only study on whales from the east coast of New Zealand is that of Gaskin & Cawthorn (1967 a, b), which reports on the stomach contents of two commercially caught sperm whales between 1963 and 1964. The authors also provide quantitative analysis information on the stomach contents of nine sperm whales and qualitative information on the stomach contents of a further 151 whales. Cephalopod remains from the stomach samples of two whales, totalling 2,118 lower beaks, were grouped into 11 classes. From the beak redescription of Clarke & Roper (1998), the most important families by number proved to be Onychoteuthidae, Histioteuthidae, Ommastrephidae and Pholidoteuthidae. Since the authors had no weight-LRL regressions at the time, no BM estimates were calculated (Gaskin & Cawthorn 1967 a, b).

5.2.1 Cephalopod component of the diet

The stomach samples analysed in this study comprised a total of 12,576 lower cephalopod beaks, 10,647 upper beaks, 11 buccal bulbs, a partially digested mantle, a severed tentacle, cephalopod eye lenses and gladii. The number of cephalopod species reported in the diet of the sperm whale in this study is comparable to that recorded elsewhere (Beteshava & Akimushkin 1955, Roe 1969, Martin & Clarke 1986, Clarke *et al.* 1993, Clarke & Pascoe 1997, Santos *et al.* 1999, Santos *et al.* 2002, Evans & Hindell 2004), and includes tropical to Antarctic; gelatinous to muscular, and pelagic to bathypelagic species.

In the following section, a review of the cephalopod taxa found in the stomachs of sperm whales stranded on New Zealand beaches is presented, followed by a comparison of our findings with those reported in historical accounts. An explanation as to why a given species was included in the local group A or B, or listed as a non-local species is also presented.

Oegopsida

Architeuthidae

Nineteen nominal species have been described in the mono-generic family Architeuthidae (Nesis 1987). However, all species in the genus *Architeuthis* are poorly defined, and until new evidence is discovered that helps clarify this taxonomic problem, all species should be treated as *A. dux* (Roeleveld & Lipinski 1991, Forch 1998). These non-bioluminescent squid reach ML's up to 2.3 m and weights of ~300 kg (Clarke 1966, O'Shea pers. comm.). They are widely distributed around the world, in association with islands and continental slopes, and even though their vertical distribution is unclear, it is thought the adults are found in depths between 300 and 1,000 m (Nesis 2003, Kubodera & Kyoichi 2005, O'Shea pers. comm., Okutani 2005). Buoyancy in this species is attained by a high concentration of ammonium ions that accumulate in the muscles of the

mantle and head, and to a lesser extent in the arms and tentacles (Clarke *et al.* 1979, O'Shea pers. comm.).

In New Zealand, submature and mature specimens of *A. dux* are often trawled off Banks Peninsula, on the South Island's east coast, during the austral summer, and off Hokitika Canyon, on the South Island's west coast during the austral winter (O'Shea 2003). It is unlikely that this species is a year-round New Zealand resident since no juveniles are known from New Zealand waters, and it is rarely trawled outside these two time periods, despite intensive year-round fishing effort at appropriate depths and locations (O'Shea 2003). For this reason *A. dux* was included in group A. However, this species is widely distributed and non-local consumption cannot be ruled out.

A. dux beaks contributed 1.6% by number and 18.7% by weight to the diet of sperm whales caught in the Tasman Sea, and <1% by number and 23.7% by weight to the sperm whale stranded on Paekakariki (Clarke & MacLeod 1982, Clarke & Roper 1998). For the sperm whales caught off the Cook Strait region in New Zealand, three Architeuthis beaks were found in one of the whales, representing <1% by number to the total number of beaks (Gaskin & Cawthorn 1967a). This species contributed 0.4% by number and 8.1% by weight to the stomachs of New Zealand stranded whales. Whale number 15 stranded on Oputama Beach, on the east coast of the North Island, had an A. dux beak in its stomach, with a LRL of 4.6 mm. This specimen was estimated to have a ML of 219.6 mm and a weight of 188.8 g, making it the first record of Architeuthis of this size in New Zealand waters, should this squid have been consumed within the New Zealand EEZ.

Results suggest that low numbers of *A. dux* are consumed by whales in this area of the Pacific. However, due to the squid's size, this species contributes significant biomass to the diet of whales wherever it is consumed. Recent studies have shown *A. dux* to be a much more active squid than previously thought

(Kubodera & Kyoichi 2005), and may not be such an easy prey as other more sluggish squid. The results also show that the overall contribution by weight of this species to the diet of all whales is not as large as that previously reported. However, in this study this species contributed as much as 26.9% by weight to the diet of any single whale, in accordance with the allometric equations used in this study.

Ancistrocheiridae

Members of the monotypic family Ancistrocheiridae reach ML's of over 400 mm, and are found in tropical and subtropical waters worldwide (Nesis 1987, Okutani 2005). This family was previously regarded as a subfamily of the Enoploteuthidae until it was elevated to family rank (Clarke 1988), and even though only one gelatinous, bioluminescent species is currently recognised in this family, differences between paralarvae in the Atlantic and Pacific Oceans suggest that more than one species exists: *Ancistrocheirus lesueurii* and *A. alessandrini* (Nesis 1978, Young *et al.* 1998). The species of this genus are thought to be associated with the ocean's benthos over the continental slope, around New Caledonia and off South Africa's west coast (Nesis 1987, Okutani 2005).

A. lesueurii beaks were found in the stomach samples of sperm whales caught in the Tasman Sea, where they contributed 3.5% by number and 1.4% by weight to the diet (Clarke & MacLeod 1982), and in that of the sperm whale stranded on Paekakariki, where they contributed <1% by number and <1% by weight to the diet (Clarke & Roper 1998). This species contributed 3.3% by number and 5.5% by weight to the diet of all whales, and contributed as much as 11.1% by weight to the diet of any single whale. The Ancistrocheirus sp. beaks found in this study were of a wider size range than those found in sperm whales caught in the Tasman Sea, where they had LRL's ranging from 8.4 to 8.8 mm (Clarke & MacLeod 1982).

At present a specific name cannot be assigned to the beaks referred to as Ancistrocheirus since they are identical to the beaks of A. lesueurii described by Clarke (1986), but do not coincide morphologically with beaks extracted from a locally sourced A. lesueurii. Further investigations on the taxonomy of this family are needed to elucidate the status of its species and the possible feeding areas for the whales. Furthermore, Ancistrocheirus specimens are not common in museum collections from New Zealand waters (O'Shea pers. comm.). For these reasons, Ancistrocheirus sp. was ascribed to group B, and it is plausible that sperm whales consumed these squid outside the New Zealand EEZ. However, the results show that this species contributed a relatively large amount of food to the diet of sperm whales stranded on New Zealand, and appears to have an enhanced importance in the diet of recently stranded sperm whales on both the east and west coasts, but not in the Cook Strait, occurring in 75% of the samples. Judging by the state of the beaks recovered, it is reasonable to assume that this species was consumed not long before stranding on New Zealand beaches, and it is possible that large aggregations of this species of Ancistrocheirus occur proximal to New Zealand waters.

Chiroteuthidae

Members of the family Chiroteuthidae are gelatinous, bioluminescent, and small to medium-sized squid, with ML's typically less than 400 mm. Over 12 nominal species have been described in three genera: *Asperoteuthis*, *Chiroteuthis* and *Planctoteuthis*, but the taxonomy of the family is in need of revision (Nesis 1987). Underwater footage revealed that these squid orient in an oblique position with their arms pointing up, due to the vesicles in their fourth arms that are filled with low-density ammonium chloride (Hunt 1996). *C. capensis* is found off South Africa and has been recorded from the regurgitations of the chicks of wandering albatross, *Diomedea exulans*, breeding in New Zealand (Imber 1992). Very little is known about the life history and biology of the species in the genus

Asperoteuthis, and A. lui is the only species of this genus that has been reported from New Zealand waters (Salcedo-Vargas 1999).

Two species of *Chiroteuthis* occurred in the stomach of the sperm whale that stranded on Paekakariki, contributing <1% by number and <1% by weight to the diet of this whale. These chiroteuthid species had an estimated mean weight of 176 g, similar to the mean weight of *Chiroteuthis veranyi* and almost twice as heavy as the BM estimated for *Chiroteuthis* sp. 2 (Clarke & Roper 1998). Clarke & MacLeod (1982) identified two chiroteuthid species from the collections of the sperm whales caught in the Tasman Sea, *Chiroteuthis joubini* and *Chiroteuthis* sp. C, that collectively contributed 1.4% to the total number of beaks found in the stomachs. *Chiroteuthis veranyi* and *Chiroteuthis* sp. 2 contributed 0.7% and 0.3% by number and 0.1% and 0.03% by weight respectively, to the diet of New Zealand stranded whales. *Asperoteuthis* sp. contributed 0.2% by number and 0.2% by weight to the diet of all whales.

Chiroteuthis veranyi is included in group A because it is known to occur in New Zealand waters (Nesis 1987, Young & Roper 1999, Okutani 2005). However, this species is widely distributed and local consumption cannot be definitely attributed based on stomach samples from New Zealand stranded sperm whales.

Even though the beaks *Chiroteuthis* sp. 2 could not be identified to species, it was included in group A because the state of the beaks suggests these squid were consumed shortly before stranding. However, non-local consumption of this species cannot be ruled out due to the wide distribution of the species in this genus.

Both ?Mastigoteuthis A and ?Mastigoteuthis B, reported by Clarke (1980) were collected from the stomachs of sperm whales caught off South Africa and Western Australia, and are now regarded as species of the genus Asperoteuthis. ?Mastigoteuthis A (Clarke 1980) has beaks identical to those of an undescribed species of Asperoteuthis named Asperoteuthis sp. A (Young et al. 1999). The

single species of *Asperoteuthis* reported here has beaks that are indistinguishable from those of *?Mastigoteuthis* B described by Clarke (1980), and from a beak extracted from an *Asperoteuthis* sp. specimen from the tropical Pacific. Specimens of *Asperoteuthis* sp. were present in 50% of the stomach samples of whales stranded on both the west and east coasts.

Both *Chiroteuthis* species and *Asperoteuthis* sp. contributed very little in terms of biomass to the diet of whales in the region, as in historical accounts. However, further sampling and taxonomic studies on the cephalopod fauna from the South Pacific will shed light on the distribution of the chiroteuthid fauna in the region.

Cycloteuthidae

This family is very poorly known, and contains two genera of mesopelagic squid with ML's less than 600 mm, namely *Cycloteuthis* and *Discoteuthis* (Nesis 1987, Okutani 2005). *Cycloteuthis akimushkini* is a bioluminescent and lightly muscled species distributed from the central to the western Indian Ocean, and has been recorded in the diet of sperm whales from South Africa, west Australia, and the north Atlantic (Clarke 1980, Clarke *et al.* 1993, Okutani 2005).

C. akimushkini beaks were found in the stomachs of sperm whales caught in the Tasman Sea, where they contributed <1% by number and <1% by weight to the diet of these whales. Flesh of this species was found in whales caught between 37 and 39° S, and 160 and 165° E, extending the distribution of this species to southwest Australia (Clarke & MacLeod 1982). This species contributed 1% by number and 1.1% by weight to the diet of New Zealand stranded whales. The beaks found in our collections have similar LRL peaks to those found in sperm whales caught off South Africa and western Australia (Clarke 1980).

Little is known about the biology or distribution of *Cycloteuthis akimushkini* and it is extremely rare from comprehensive cephalopod collections from New Zealand waters (O'Shea pers. comm.). Beaks of this species were present in 81.3% of the

stomach samples and contributed up to 5.9% by weight to the diet of any single whale, suggesting this species may be a fairly common resource exploited by sperm whales in the area. The relatively good state of the beaks and their frequency of occurrence in stomach samples (75%), suggest this species was consumed shortly before stranding. For this reason *C. akimushkini* is included in group A. However, non-local consumption of this species cannot be ruled out because of its rarity in local museum collections (O'Shea pers. comm.). The results show, as in historical accounts, that *C. akimushkini* is commonly consumed but contributes relatively little in both numbers and weight to the overall diet of sperm whales in the south Pacific. The results indicate that the accepted distribution for this species may include the Tasman Sea.

Cranchiidae

Cranchiids are gelatinous, bioluminescent squid that attain ML's of over 1 m, and have a circumglobal distribution, except for the Arctic Ocean (Nesis 1987, Okutani 2005). Galiteuthis glacialis has a strictly Antarctic distribution, where it is one of the most abundant species (Nesis 1987). Teuthowenia pellucida is a bioluminescent, moderate-sized, mid-water cranchiid, that reaches a ML of 200 mm. Species of the genus Megalocranchia are bioluminescent, gelatinous and ammoniacal squid that can attain ML's to 1,800 mm (Nesis 1987, Tsuchiya & Okutani 1993). The genus *Megalocranchia* is distributed in tropical and subtropical waters around the world (Voss et al. 1992). As adults, they inhabit mesopelagic waters during the day and migrate to the surface at night (Young 1978). Mesonychoteuthis hamiltoni is the only species in this genus, and is the largest known cranchiid, with adults attaining ML's over 2,500 mm (Nesis 1987). These squid are muscular and bioluminescent, and are the only cranchiids with hooks on the arms (Voss 1980). Juveniles of this species are found in subantarctic waters, while adults are restricted to Antarctic waters (Nesis 1987, Xavier et al. 1999, Nesis 2003, Okutani 2005). Five to seven species are recognised in the genus Galiteuthis (Voss et al. 1992). Species belonging to the

genus *Taonius* are large, gelatinous, and bioluminescent squid, reaching ML's of 660 mm (Nesis 1987). There are two recognised species in this genus, but up to five have been proposed (Voss *et al.* 1992). They inhabit mid-oceanic waters of the Atlantic, Mediterranean, northwest Pacific and the west Indian Ocean (Okutani 2005). Two moderate sized, gelatinous, bioluminescent species are recognised in the genus *Liocranchia* (Nesis 1987).

Seven cranchiid species were found in the stomach contents of the whale stranded on Paekakariki: Galiteuthis armata, Teuthowenia megalops, T. pellucida, Taonius pavo, Megalocranchia sp. A (= Phasmatopsis cymoctypus), Mesonychoteuthis hamiltoni and an unidentified cranchiid beak tip (Clarke & Roper 1998). Together, these seven cranchild species contributed 5.7% of the total number of beaks and 3.6% of the total estimated cephalopod biomass represented by beaks. As for the sperm whales caught in the Tasman Sea, five cranchild species were found in their stomachs: Mesonychoteuthis hamiltoni, Megalocranchia sp., Galiteuthis armata, Galiteuthis sp. B, and Taonius pavo (Clarke & MacLeod 1982). These five species contributed 11.0% of the total number of beaks and 3.6% by weight to the diet of these whales (Clarke & MacLeod 1982). No cranchiids were recorded in the diet of sperm whales caught off Cook Strait (Gaskin & Cawthorn 1967a). Also seven species were found amongst the cephalopod remains from the stomachs of New Zealand stranded whales. These were: Galiteuthis sp. C, Liocranchia sp., Taonius sp. A, Taonius sp. B, Teuthowenia pellucida, Megalocranchia sp. A and Mesonychoteuthis hamiltoni. These seven species contributed 14.7% by number and 5.5% by weight to the diet of New Zealand stranded sperm whales.

Teuthowenia pellucida is the most abundantly represented cranchiids squid in New Zealand collections. For this reason it is included in group A. However it is a very widely distributed species, and beaks found in the stomachs of sperm whales cannot be definitely accredited as being consumed locally.

Megalocranchia sp. A contributed <1% by number and <1% by mass to the diet of the sperm whale stranded on Paekakariki, and contributed 7.5% by number and <1% by weight to the diet of sperm whales caught in the Tasman Sea (Clarke & MacLeod 1982, Clarke & Roper 1998). In our samples, this species contributed 5.2% by number and 2.5% by weight to the diet of New Zealand stranded whales. Beaks of Megalocranchia sp. A reported amongst stomach contents from our samples have larger LRL's than those from the Azores, which had an 8.5 mm mean with a peak between 8.0 and 9.0 mm. However, 8.8% of beaks examined here are immeasurable because they were broken, due to the lower extent of darkening because of their small size. This would slightly overestimate the LRL mean, and estimated ML's and BM for this species.

Beaks of *Megalocranchia* sp. A found in our collections are identical to those previously referred to as *Phasmatopsis cymoctypus* by Clarke (1980) (*nomen dubium* Voss *et al.* 1992), and Imber (1998) considers the beaks of *Megalocranchia* sp. A to be undistinguishable from those he described as *Megalocranchia maxima*. Beaks of *Megalocranchia* sp. A were also found in the stomach contents of sperm whales caught off South Africa, western and eastern Australia, the Antarctic, Peru, Iceland and the Azores, and in the stomach of a sperm whale stranded on Paekakariki Beach (Clarke, 1986, Clarke *et al.* 1993, Clarke & Roper 1998). Beaks of this species with flesh attached to them, indicating recent consumption, were found only in the stomachs of sperm whales caught off South Africa and western Australia (Clarke 1986). Mature *Megalocranchia* are extremely rare in collections from New Zealand, and the species 'A' referred to here differs from that found locally (O'Shea pers. comm.). For this reason *Megalocranchia* sp. A is attributed to group B, and non-local consumption is probable.

Mesonychoteuthis hamiltoni was the longest cephalopod consumed by the sperm whales stranded in New Zealand, with a mean ML of 2,417.9 mm, ranging from 1,933.8 to 2,663.6 mm. These squid had estimated weights of 4.2–8.5 kg, with a

mean of 7.0 kg and contributed 132.5 kg (1.2%) of the total cephalopod biomass represented by beaks. Sperm whales in the Tasman Sea appear to be feeding on larger specimens of *M. hamiltoni*, which had a mean BM of 28.9 kg. This species is known to grow to weights of 300 kg (O'Shea pers. comm.), and the weights calculated here and in other publications appear to be too light for mature specimens with LRL's exceeding 30.0 mm. The estimated weights were obtained from regression equations for the family Cranchiidae which are gelatinous squid, and are thought to be inadequate for estimating the weight of *Mesonychoteuthis hamiltoni* which is a heavily muscular species. Therefore, the estimated biomass that this species contributed to the diet of New Zealand stranded whales would have been greatly underestimated.

Mesonychoteuthis hamiltoni is known mainly from the Antarctic, where it appears to be the main prey of sperm whales, which can feed almost exclusively on this species while foraging in these waters (Klumov 1971). The species composition in the diet of sperm whales was shown to change northward, where it becomes dominated by Taningia danae, Lepidoteuthis grimaldii and Todarodes sagitattus angolensis (Klumov 1971). Even though M. hamiltoni is known to occur in latitudes of up to 40° S off of South Africa (Xavier et al. 1999), it has never been recorded that far north around New Zealand. Beaks of this species have been found in the stomachs of sperm whales caught in the Tasman Sea (Clarke & MacLeod 1982), in the stomach of a stranded specimen on Paekakariki Beach (Clarke & Roper 1998), and in the stomach contents of whales reported here. They have also been reported from the regurgitations of the chicks of the wandering albatross, Diomedea exulans, from the Antipodes Islands and Macquarie Island (Simberloff 1998). However, none of these records confirms that *M* .hamiltoni occurs in New Zealand waters, since the wandering albatross can forage up to 1200 km from the nest site (Jouventin & Weimerskirch 1990), and sperm whales undertake extensive migrations (Berzin 1971). For these reasons M. hamiltoni is classed as a non-local species, and it seems highly unlikely this species was consumed locally.

Even though *Taonius* sp. A and B could not be positively identified to species, *Taonius* sp. B has been reported from the diet of Southern Buller's albatrosses (*Diomedea bulleri bulleri*) from the Snares, 140 km south of South Island (James & Stahl 2000). This albatross species is endemic to New Zealand and is known to forage off the east and west coasts of South Island (James & Stahl 2000). This species also has been recorded from the regurgitations of chicks of the royal albatross, *Diomedea epomophora*, nesting at Chatham Islands, Taiaroa Head, and Campbell Island (Simberloff 1998). For this reason, and due to the relatively good state of their beaks from stomach contents, both species were included in group A. However, *Taonius* sp. B has been recorded in the diet of Patagonian toothfish, *Dissostichus eleginoides*, off the subantarctic Crozet and Kerguelen Islands (Cherel *et al.* 2004), and non-local consumption cannot be ruled out.

Galiteuthis sp. C has been recorded from the regurgitations of chicks of the royal albatross, *Diomedea epomophora*, nesting at Chatham Islands, Taiaroa Head, and Campbell Island (Simberloff 1998). The royal albatross appears to feed over shallower waters closer to land than the wandering albatross within New Zealand, and avoids Antarctic waters (Simberloff 1998, Childerhouse 2003). For this reason and because of the good state of the beaks found in the stomach contents, this species was included in group A. However, this species is widely distributed, as it has been found in the diet of Patagonian toothfish, *Dissostichus eleginoides*, off the subantarctic Crozet Island (Cherel *et al.* 2004), and non-local consumption cannot be ruled out.

The beaks of *Liocranchia* found in the stomach samples from New Zealand stranded sperm whales were in a relatively good condition, suggesting they were consumed shortly before stranding. For this reason, *Liocranchia* sp. was included in group A. However, the species in this genus are widely distributed (Voss 1980), and non-local consumption cannot be ruled out.

Cranchiids appear to be a common prey for whales in this region of the Pacific, but because of their gelatinous nature, they only contribute a relatively small amount by weight to the diet of sperm whales. However, where sperm whales feed on *M. hamiltoni*, the importance of cranchiids in the diet is greatly increased.

Histioteuthidae

The genus *Histioteuthis* has 16 recognised species, which are bioluminescent and weakly muscular (Voss 1969). They are moderately sized squid, with ML's to 330 mm. This genus has a wide global distribution, and five of the species that occurred in our collections are found in New Zealand's EEZ and the Tasman Sea, namely *H. bonnellii*, *H. miranda*, *H. eltaninae*, *H. atlantica* and *H. macrohista* (Voss *et al.* 1998). *Histioteuthis* Type A5 and B4 have no clear distributions.

Three species of histioteuthids were identified amongst stomach contents of the sperm whale that stranded on Paekakariki Beach (Clarke & Roper 1998): H. meleagroteuthis, H. ?heteropsis and H. atlantica. These three species represented 78.7% of the total number of beaks and 41.2% of the total cephalopod biomass consumed by this whale. H. atlantica was the most abundant species in the diet of this whale, contributing more than 78.6% by number, and 41.0% by weight to the diet. Six histioteuthid species were found in the stomach contents of whales caught in the Tasman Sea: H. ?meleagroteuthis, H. bonnellii corpuscula, H. miranda, H. dofleini, H. atlantica and Histioteuthis sp. (Clarke 1980, Clarke & MacLeod 1982); together, these species contributed 30.4% of the total number of beaks, and 1.8% of the total cephalopod biomass consumed (Clarke & MacLeod 1982). Two species of Histioteuthis were recovered from the stomach samples of sperm whales caught in the Cook Strait region, Histioteuthis sp., and H. atlantica (= H. cookiana) (Gaskin & Cawthorn 1967a); these species represented 11.8% and 12.9% by number in the diet of these whales respectively. Six species of *Histioteuthis* are reported from all of our stomach samples, H. macrohista, H. bonnellii, H. atlantica, H. miranda,

Histioteuthis Type A5 and Histioteuthis Type B4; together these six species contributed 60.6% by number and 17.4% by weight to the diet of all whales.

Beaks of this cephalopod family were the most abundant amongst the stomach samples of sperm whales stranded on New Zealand beaches. Even though sperm whales appear to feed on very large numbers of these squid (up to 3,809 histioteuthid beaks found in the stomach of a single whale), due to their small size, they contribute a relatively small amount of biomass to the diet.

H. atlantica was the most abundant of all squid found in the stomach contents of sperm whales in this area. It should be noted that the majority of the beaks of H. atlantica had darkened wings, which is indicative of maturity. This coincides with observations in the Azores where mature male sperm whales fed mainly on sexually mature histioteuthids (Clarke et al. 1993). This species exhibits a circumglobal southern hemisphere distribution, including New Zealand, being regularly found over ocean basins, shelf and plateau areas (Voss et al. 1998). For this reason H. atlantica is included in group A. Even though this species appears to be common in New Zealand waters, non-local consumption cannot be discounted because of its wide distribution.

H. bonnellii is widely but unevenly distributed in the Atlantic; it is also found in a narrow band of subtropical waters that includes areas off Argentina, South Africa and the Tasman Sea between Australia and New Zealand (Voss *et al.*, 1998). For this reason *H. bonnellii* is included in group A. However, due to its occurrence in the Tasman Sea, non-local consumption of this species cannot be ruled out.

The type locality for *H. macrohista* is the Tasman Sea, 45°10' S, 160°10' E. This species mainly occupies the region near the Southern Subtropical Convergence between South America and Africa, off southern Australia and in the Tasman Sea between Australia and New Zealand (Voss *et al.* 1998). For this reason *H.*

macrohista is included in group A. However, due to its wide distribution, non-local consumption of this species cannot be ruled out.

H. miranda is found off southwest Africa, off south Australia and within New Zealand's EEZ. This species occurs near continental slopes, islands and submarine rises (Voss et al. 1998). Beaks attributed to H. miranda were found in 81.3% of the stomach samples from New Zealand stranded whales, and were in good condition, suggesting these squid were consumed shortly before stranding. For this reason H. miranda is included in group A. However, due to its wide distribution, non-local consumption of this species cannot be ruled out.

The beaks of *Histioteuthis* Type A5 were identified by Dr. Yves Cherel as belonging to *H. hoylei* (Cherel, Y. pers. comm.*), a histioteuthid species that has been reported throughout much of the tropical and subtropical Pacific and Indian Oceans (Voss *et al.* 1998). Unfortunately, we had no specimens of *H. hoylei* in our collections to confirm this identification. *H. hoylei* has been reported throughout much of the tropical Pacific and tropical Indian Oceans, off America's west coast, in the South Pacific, and in New Zealand (Voss, *et al.*, 1998). For this reason *Histioteuthis* Type A5 is included in group B, and these squid were likely to be consumed outside New Zealand.

The beaks of *Histioteuthis* Type B4 were found in whale 19, which stranded near Napier on February 2004. Beaks of this species were also reported from sperm whales caught off Albany and from the chick regurgitations of the shy albatross, *Thalassarche cauta*, in Tasmania (Hedd & Gales 2001). The adults of this albatross species are known to be relatively sedentary and forage year-round off south-east Australia (Brothers *et al.* 1997, Brothers *et al.* 1998). For this reason

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Histioteuthis Type B4 is included in group B, and these squid were likely to be consumed outside New Zealand.

Onychoteuthidae

Members of this family attain maturity at a small (70 mm) to very large (1,500 mm) size; they are oceanic squid with strong muscular mantles (Nesis 1987). There are around 14 recognised species but the taxonomy of the family is still unclear and is currently being revised (Bolstad in prep.). Three non-bioluminescent species of this family occurred in whale stomach samples, *Moroteuthis robsoni*, *M. ingens*, and *Kondakovia longimana*.

Historically, this family was important in the diet of sperm whales in New Zealand, contributing 7.5% by number and 22.7% by weight to the diet of sperm whales caught in the Tasman Sea, 12.7% by number and 21.9% by weight to the whale stranded on Paekakariki Beach, and 50.2% by number in the diet of whales caught off Cook Strait (Gaskin & Cawthorn 1967a, 1967b, Clarke & MacLeod 1982, Clarke & Roper 1998). The family Onychoteuthidae continues to be an important part of the diet of sperm whales in the region. In our samples, this family contributed 8.75% by number and 34.3% by weight to the diet of New Zealand stranded whales.

Moroteuthis ingens is a muscular squid widely distributed in waters between the Subtropical Convergence and the Antarctic Polar Front (Jackson 1995, 2001). Males of *M. ingens* reach ML's of up to 380 mm and weights over 1,200 g, while females are much larger, attaining ML's up to 550 mm and weights up to 5 kg (Nesis 1987, Jackson *et al.* 1997). Females of this species migrate to deeper waters to spawn, while males show no clear vertical distribution pattern (Jackson *et al.* 1997). They are believed to spawn in submarine canyon areas on the upper continental slope off California, and in New Zealand they form spawning aggregations over the Chatham Rise at depths exceeding 700 m (Gilly *et al.* 1986, Jackson 2001). In New Zealand's EEZ this species appears abundant over

the Chatham Rise, and off South Island over the Puysegur Bank, between 650 and 700 m depth, occurring down to 1,400 m (Jackson *et al.* 2000, Jaquet *et al.* 2000, Jackson 2001).

Sexual dimorphism in the beaks of *Moroteuthis ingens* is well known and maturity could be inferred by the extent of darkening of the beaks, the presence of complete wings and the conspicuous erosion on the rostrum of most of the male beaks and female beak hoods. This last character (differential beak erosion in both male and female beaks) is thought to be a consequence of head-to-head copulation for this species and suggest most individuals eaten by the sperm whale were part of a mating or spawning aggregation (Bolstad in press). This, the presence of buccal masses, and the large number of beaks of *M. ingens* found in sperm whale number 18 suggest it had been feeding on a spawning aggregation of *M. ingens* within New Zealand's EEZ immediately prior to stranding. As in whale 18, other whales that had *M. ingens* in their stomachs had far greater numbers of females than males, most with eroded beaks.

A total of 177 *Moroteuthis ingens* beaks were found in the whale stranded on Paekakariki, comprising 11.1% of the total number of beaks, with a mean BM of 595.0 g. This squid contributed 105.3 kg (15.3%) to the diet of this whale, with an LRL distribution ranging from 6.8–11.8 mm, peaking at 9.3–10.8 mm (Clarke & Roper 1998). *M. ingens* (= *Moroteuthis* A, *sensu* Clarke 1980) was not abundant in the stomachs of sperm whales caught in the Tasman Sea, where they represented 0.3% of the total number of beaks and 0.3% of the diet by weight (Clarke & MacLeod 1982). Gaskin and Cawthorn (1967a, b) identified female and male beaks for this species. Female beaks were grouped into type Aii and identified as *Moroteuthis* sp., while male beaks were grouped into type Aiii and identified as Onychoteuthidae sp. As in our collections, female *M. ingens* beaks were more abundant than male beaks in the stomach contents of sperm whales caught off Cook Straight, where 277 female (22.7%) and 65 male (6.8%) were found (Gaskin & Cawthorn 1967a, 1967b), possibly reflecting differential vertical

distributions for males and females of this squid (Jackson *et al.* 1997, Jackson *et al.* 1998, Jackson 2001). *M. ingens* contributed 4.6% by number and 8.3% by weight to the diet of all whales, and contributed up to 97.8% by weight to the diet of any single whale. The *M. ingens* specimens found in the stomach contents reported here had a larger mean estimated BM (1.6 kg), than those found in the sperm whale stranded on Paekakariki (0.6 kg) (Clarke & Roper 1998). These different results could be a product of the whales feeding on different cohorts of the same species, or to the fact different allometric regressions were used to calculate this species' BM in both studies.

Moroteuthis ingens is a common large-bodied squid found in New Zealand waters. It was found in the stomach contents of sperm whales caught in the Cook Strait region, and in this study, buccal bulbs were found in the stomach of sperm whale 18. The presence of flesh, the number of beaks and the good state they were found in suggest whale 18 consumed *M. ingens* locally shortly before stranding. For this reason *M. ingens* is included in group A, and it is likely these squid were consumed in local waters. However, for other whales non-local consumption cannot be ruled out due to the wide distribution of *M. ingens*.

There is strong evidence to suggest that *M. ingens* is preyed upon by sperm whales while it aggregates in large numbers, with female squid being more abundant in the stomach contents than males. This could reflect differential vertical distributions for the genders of this squid species, with females being most abundant between 750 and 800 m, while males exhibit no clear pattern in their vertical distribution (Jackson *et al.* 1997, Jackson *et al.* 1998, Jackson 2001).

Adults of *Moroteuthis robsoni* are distributed around the Subtropical Convergence, off south-western New Zealand and southern Africa (Kubodera *et al.* 1998). This study suggested *M. robsoni* reaches a maximum ML of 470 mm (Nesis 1987). However, it has been suggested two morphotypes exist, and

specimens with ML's of 775 mm have been studied in Tasmania (Sands 2000, Phillips *et al.* 2002). The specimens of *M. robsoni* represented by beaks found in stomach contents described here have estimated ML's that exceed the maximum reported ML for the large variant. However, onychoteuthid taxonomy is still unclear and the status of species as *M. robsoni* is in need of revision.

In the Tasman Sea, *M. robsoni* represented 4.1% of the number of beaks and 2.3% of the total estimated biomass consumed by whales. These squid were smaller than those reported in this study, with a mean estimated weight of 2,007.0 g (Clarke & MacLeod 1982). In the whale stranded on Paekakariki, beaks of *M. robsoni* represented 1.3% of the total number of beaks and 5.4% of the estimated weight. These specimens were also smaller than those found in our stomach samples, with a mean weight of 1,847.0 g (Clarke & Roper 1998). This species was not identified from the stomach samples of sperm whales caught off Cook Strait (Gaskin & Cawthorn 1967b, 1967a). In our stomach samples we found *M. robsoni* to be the species that contributed the most by weight to the diet of all whales, followed by *Kondakovia longimana*. This species contributed 3.3% by number and 13.7% by weight to the diet of all New Zealand stranded whales, and had a mean estimated BM of 3.8 kg.

It is interesting that *M. robsoni*, a rare species in local museum collections, appears to have a significant importance in the diet of sperm whales stranded on New Zealand beaches. The results suggest that large aggregations of this species could occur in the Tasman Sea and the Pacific Ocean, as they occurred in the stomachs of whales stranded on both the east and west coast. It is also possible that these beaks (or some of them) are referable to the Antarctic species *M. knipovitchi* (this is the subject of further research).

Kondakovia longimana is a large squid, with adults reaching ML's of 740–830 mm (Nesis 1987, Lu & Williams 1994). This species inhabits epi- and mesopelagic waters of the Southern Ocean, reaching northward to South

Georgia and off Argentina's east coast (Kubodera *et al.* 1998, Xavier *et al.* 1999, Okutani 2005). Like *Moroteuthis ingens* and *M. robsoni*, *K. longimana* has high concentrations of ammonium ions (relative to sodium ions) accumulated in its tissues, making it a positively buoyant species (Lu & Williams 1994). It is possible this species floats after death, as it is frequently scavenged upon by different species of albatross, *Diomedea* spp. (Xavier *et al.* 2003).

K. longimana was not recorded from the stomach samples of sperm whales caught off Cook Strait, but was important in the diet of those caught in the Tasman Sea (Gaskin & Cawthorn 1967b, 1967a, Clarke & MacLeod 1982). In the latter region, K. longimana represented 3.1% of the total number of beaks and 20.1% of the cephalopod biomass consumed by whales. However, the K. longimana specimens in the diet of sperm whales caught in the Tasman Sea were smaller than those in our collections, with a mean estimated BM of 2.4 kg (Clarke & MacLeod 1982). This was also the case for specimens of this species found in the stomach of the sperm whale stranded on Paekakariki, where the mean BM was 1.8 kg, and comprised 0.31% of the beaks, contributing 1.28% by weight to the diet. In our samples K. longimana contributed 0.9% by number and 12.4% by weight to the diet of all whales.

Even though *K. longimana* is not important numerically in the diet of locally stranded sperm whales, because of its large size, it contributes significant biomass to the diet of this predator.

Although *K. longimana* is a common prey of teuthophagous predators (Clarke 1983, Xavier *et al.* 2002, Xavier *et al.* 2003), very little is known of its biology or natural history. This species appears to be restricted to waters south of the Subtropical Convergence, and the relative importance in the diet of sperm whales in the Tasman Sea suggests these whales were migrating from southern feeding grounds into the Tasman Sea.

Pholidoteuthidae

The taxonomy of this family needs revision but is currently considered to be a monogeneric family with two recognised species, *Pholidoteuthis boschmai* (= *P. massyae* in review), and *P. adami. P. boschmai* is a large strongly muscular, non-bioluminescent squid, reaching ML's of up to 720 mm (Nesis 1987). It is found in south-western Australia, New Zealand, across the Indian Ocean and into the Atlantic (Okutani 2005). Furthermore this species was found in 75% of the samples and most of the beaks were in a good state, suggesting they were consumed not long prior to stranding. For this reason, *P. boschmai* is included in group A, and it is likely it was consumed locally. However, this species has also been found in the stomachs of sperm whales caught in South Africa, South Georgia and the Azores (Clarke 1983), and in the stomachs of whales stranded in Tasmania (Evans & Hindell 2004), non-local consumption cannot be ruled out.

In our samples *P. boschmai* contributed 2.0% by number and 5.4% by weight to the diet of all whales. *P. boschmai* has proved to be an important component of sperm whale diet in both numbers and weight, gaining importance by weight in southern Australian waters, where it contributed 4.6% numerically and 11.4% by weight to the diet of all whales stranded in Tasmania (Evans & Hindell 2004).

Octopoteuthidae

Specimens of the Octopoteuthidae are gelatinous, neutrally buoyant squid that can reach ML's of up to 1,700 mm (Roper & Vecchione 1993). *Taningia danae* is a large muscular species with a maximum reported ML of 1,700 mm, with large-lidded photophores on the tips of the second arms (Santos *et al.* 2001b). This species is cosmopolitan in distribution, being found predominantly in tropical and subtropical waters, but also in southern temperate and northern temperate waters (Roper & Vecchione 1993). *Octopoteuthis megaptera* is a widely distributed species, found throughout the Atlantic, off the coast of South Africa,

and throughout the Indian and western Pacific Oceans (Stephen 1985). The beaks attributed in this study as *Octopoteuthis* sp. 'Giant' resemble those of an undescribed species that was trawled in the North Atlantic and referred as *Octopoteuthis* sp. 'Giant' (Clarke 1986).

In the Tasman Sea, four octopoteuthid species were found in the stomach samples of caught sperm whales: *O. rugosa, Octopoteuthis* sp. A, *Octopoteuthis* sp. (Giant' (= *Octopoteuthis* sp. (giant) B, *sensu* Clarke & MacLeod 1982), and *T. danae* (Clarke & MacLeod 1982). These four species contributed 33.7% of the beaks and 45.3% by weight to the diet of these whales (Clarke & MacLeod 1982). The only octopoteuthid species found in the stomach of the sperm whale stranded on Paekakariki was *T. danae*, which represented 1.5% of the number of beaks and 8.6% of the total cephalopod biomass consumed by the whale (Clarke & Roper 1998). Seventy-four octopoteuthid beaks too broken to be reliably identified were found in the sperm whales caught off Cook Strait, representing 3.5% of the total number of beaks (Gaskin & Cawthorn 1967b, 1967a). Three octopoteuthis species were found in our stomach samples: *T. danae*, *Octopoteuthis* sp. 'Giant' and *O. megaptera*.

The species *Octopoteuthis rugosa* was described by Clarke (1980) from a partially digested specimen found in the stomach of a sperm whale. The characters separating this species included the lack of photophores on the mantle wall and ink sack, a rugose mantle in females, and lateral pigment bands on the ventral arms (Stephen 1985). However, a close examination of the holotype made by Stephen (1985) revealed photophores on the mantle and eyes of both sexes, the rugose mantle to be a secondary sex character found in all adult female *Octopoteuthis*, and the lateral pigment is also common to all *Octopoteuthis* species (Stephen 1985). Therefore, *O. rugosa* is considered a *nomen dubium,* and the beaks attributed to this species most probably belong to *O. megaptera*, which has a distribution extending east of Australia and into New Zealand (Stephen 1985, O'Shea pers. comm.).

Octopoteuthis megaptera is important in the diet of sperm whales worldwide and Clarke and MacLeod (1982) suggest at least three species in this genus are consumed. However, the species in the genus *Octopoteuthis* are poorly defined and their identification is therefore problematic. Nevertheless, LRL distribution alone should not be used to separate beaks into species, since the beaks could be sexually dimorphic, or the peaks could represent different cohorts of the same species. Our results show two peaks in the LRL distribution for this species at around 10.5 and 13.5 mm, similar to those found by Clarke (1986).

Specimens of *Octopoteuthis megaptera* are the most abundant octopoteuthid in New Zealand museum collections (O'Shea pers. comm.). For this reason, this species is included in group A, although their distribution extends considerably outside New Zealand waters, and beaks found in stomach samples could have been consumed anywhere throughout the South Pacific.

T. danae made up 1.5% of the beaks found in the stomach of the sperm whale that stranded on Paekakariki and contributed 8.6% by weight to its diet (Clarke & Roper 1998). The mean BM for these specimens was 2.5 kg, considerably smaller than those found in stomach samples reported here. T. danae beaks were not found in the stomachs of sperm whales caught off Cook Strait, but comprised 10.5% of the beaks found in the stomachs of sperm whales caught in the Tasman Sea, contributing 42.0% to their diet by weight (Gaskin & Cawthorn 1967a, 1967b, Clarke & MacLeod 1982). This species contributed 1.1% by number and 9.0% by weight to the diet of all New Zealand stranded whales. The LRL distribution for the beaks reported here is comparable to that of the Azores, which presented a 17.6 mm mean with similar distribution (Clarke et al. 1993). As with the other large squid species, T. danae contributes little numerically to the diet of whales, but its contribution by weight is relatively large due to its size.

Two 'morphologies' of *Taningia danae* have been trawled in New Zealand waters, being most easily differentiated on the basis of funnel morphology

(O'Shea pers. comm.). One of them with and one without lappet-like frills on the aperture; frilly funnelled vs. non-frilly funnelled from South Africa, *sensu* Clarke (1967). *T. danae* is not an uncommon large-bodied cephalopod to be caught regularly by trawls in New Zealand waters, and for this reason it is included in group A. However, local consumption cannot be undoubtedly determined from beaks recovered from the stomach contents of New Zealand stranded whales due to this squid's cosmopolitan distribution.

The beaks of *Octopoteuthis* sp. 'Giant' found in the stomachs of New Zealand stranded sperm whales have the same LRL mean as in the Azores (Clarke *et al.* 1993). This species was also consumed by sperm whales in the Tasman Sea, where it contributed 1.5% by number and <1% by weight to the diet of whales in this region (Clarke & MacLeod 1982). The specimens consumed in the Tasman Sea, however, had larger BM estimates than those from our collections, with a mean BM of 1.8 kg (Clarke & MacLeod 1982). This species was not found in the stomach contents of the sperm whale stranded on Paekakariki (Clarke & Roper 1998). In our stomach samples this species contributed 0.2% by number and 0.2% by weight to the diet of all whales, and *O. megaptera* contributed 1% by number and 0.4% by weight to the diet of all of New Zealand stranded whales.

The beaks attributed as *Octopoteuthis* sp. 'Giant' recovered from the stomachs of sperm whales stranded in New Zealand could belong to one of the two morphologies of *Taningia 'danae'* present in New Zealand waters, and are also indistinguishable from those of a 'Giant' *Octopoteuthis* trawled off the United Kingdom and in the North Atlantic (Clarke 1980, 1986), also known to occur in New Zealand waters (O'Shea pers. comm.). However, only one specimen of *Octopoteuthis* sp. 'Giant' is known from comprehensive museum collections from New Zealand waters (O'Shea pers. comm.), and beaks from specimens of both morphologies of *T. danae* were not available for comparison. Beaks of *Octopoteuthis* sp. 'Giant' were found in 92% of the stomachs from sperm whales caught in the Tasman Sea (Clarke & MacLeod 1982), and some of the beaks

found in the stomachs of New Zealand stranded whales were in very good condition suggesting recent consumption. For this reason, *Octopoteuthis* sp. 'Giant' was included in group A. However, non-local consumption of this species cannot be ruled out due to its rarity in local museum collections and wide distribution.

Because of its large size and cosmopolitan distribution, *Taningia danae* has proven to be one of the most important food sources for the sperm whale worldwide, and often increases the importance by weight of the family Octopoteuthidae in the diet of the sperm whale. *Octopoteuthis* sp. 'Giant' and *O. megaptera* contribute little by number and weight to the diet of the sperm whale in New Zealand waters.

Lepidoteuthidae

Lepidoteuthis grimaldii is a large, muscular species with males attaining ML's of 1,000 mm (Clarke 1960), and females of 2,000 mm (O'Shea pers. comm.). It has dermal cushions or 'scales', which are suggested to accumulate ammonium ions to aid buoyancy (Roper & Lu 1990). This species is very rare in collections, and little is known of its natural history.

L. grimaldii contributed 1.7% by number and 1.2% by weight to the diet of sperm whales caught in the Tasman Sea (Clarke & MacLeod 1982). These squid were estimated to have a BM mean of 2.5 kg, considerably smaller than those in our collections (Clarke & MacLeod 1982). L. grimaldii was also found in the stomach of the sperm whale stranded on Paekakariki, where it contributed 0.1% by number and 0.2% by weight (Clarke & Roper 1998). These two L. grimaldii specimens were also smaller than our specimens, with a mean BM of 1.3 kg (Clarke & Roper 1998). The BM estimates for L. grimaldii in the diet of sperm whales off South Africa, Western Australia and the Azores, were also smaller than those for our specimens. This species had a BM mean of 2.9 kg, 3.0 kg and 2.3 kg, off South Africa, western Australia and Azores, respectively (Clarke 1980,

Clarke *et al.* 1993). In the stomach samples of New Zealand stranded whales, this species contributed 0.1% by number and 1.0% by weight to the diet of all whales.

Lepidoteuthis grimaldii is a rare species in comprehensive museum collections from New Zealand waters (O'Shea pers. comm.), however given the good state of some of the beaks and its rarity in stomach samples, this species was included in group A. However, non-local consumption of *L. grimaldii* cannot be ruled out due to this species' wide distribution; tropical and subtropical waters of the Atlantic, Pacific and Indian Oceans (Nesis 1987). Historically the beaks of this species could have been confused with those of Octopoteuthis or Taningia. Beak morphology is described in section 4.3. *L. grimaldii* is not an important cephalopod species in the diet of sperm whales in New Zealand, probably due to its uncommonness in the area.

Ommastrephidae

Ommastrephids are small to large muscular squid, with ML's reaching 1,000 mm (Nesis 1987). There are 22 recognised species and some of them are fished commercially. Photophores are only present in the subfamily Ommastrephinae. Beaks identified as *Nototodarus* spp. contributed up to 18.6% of the total number of beaks recovered from sperm whales caught within the Cook Strait region (Gaskin & Cawthorn 1967a). In the Tasman Sea, *Todarodes* sp. beaks made up 0.9% of the total number of beaks and contributed 1.2% of the diet by weight (Clarke & MacLeod 1982); the estimated mean BM was 2.9 kg (Clarke & MacLeod 1982). One specimen of *Todarodes*, with an estimated BM of 1.5 kg, was found in the stomach of the sperm whale stranded on Paekakariki Beach, where it contributed 0.2% to the diet of this whale by weight (Clarke & Roper 1998). In our samples ommastrephid beaks contributed 0.1% by number and 0.2% by weight to the diet of all whales.

Specific identification for the beaks of this family proves difficult, and beaks identified in the past as *Nototodarus* spp. could belong to any of five locally occurring genera: *Nototodarus*, *Todarodes*, *Martialia*, *Eucleoteuthis* or *Ommastrephes*. *Martialia* is very rare in our waters and *Eucleoteuthis* has a more northern distribution; neither was likely consumed by whales in the Cook Strait region. The other three genera are the most plausible to have been eaten by whales in New Zealand waters, but until further sampling and dietary analysis takes place from predators in the region, the specific identification of cephalopods of this family from lower beaks will remain a mystery.

The results show ommastrephids are not usually found in the stomach contents of sperm whales in New Zealand. This is consistent with dietary results from the stomachs of sperm whales caught in the Tasman Sea and in the whale stranded on Paekakariki, but not with that found from whale stomachs from the Cook Strait (Clarke & MacLeod 1982). Limited samples from the east coast and Cook Strait made it impossible to gauge the importance of ommastrephids in the diet of whales off the east coast. However, it should be noted that in New Zealand there is a commercial trawl fishery for arrow squid, *Nototodarus* spp., around the subantarctic Auckland Islands (Sullivan et al. 2005). This fishery started in the 1970s and peaked in the early 1980s when over 200 jigging vessels were fishing within New Zealand's EEZ (Sullivan et al. 2005). In the early 1990s fishing effort moved to the southern Atlantic where new squid stocks had been discovered, leaving fewer than 20 commercial jiggers in New Zealand waters. Catches from trawlers between 1986 and 1998 fluctuated between 30,000 and 60,000 t, and declined in recent years due to a reduced abundance of squid in southern waters, and the fisheries management measures adopted to protect the Hooker's sea lion, *Phocarctos hookeri* (Sullivan et al. 2005).

It is not currently possible to estimate the consumption of ommastrephids by sperm whales in New Zealand waters, but in Australia sperm whales are a much more important predator on ommastrephids than the commercial squid fishery

operating in the region (Evans & Hindell 2004), and the potential competition and impacts the fishing industry has on sperm whale populations is far from understood.

Psychroteuthidae

Psychroteuthis glacialis is a muscular, bioluminescent squid species that reaches ML's of up to 440 mm, and is restricted to Antarctic waters (Nesis 1987). This species is very abundant in the Weddell Sea, along the continental shelf break, where it is captured in bentho-pelagic trawls from 200 to 900 m deep (Gröger et al. 2000). This species contributed 0.2% by number and 0.1% by weight to the diet of sperm whales reported here, and was only found in the stomachs of sperm whales stranded on the west coast.

Oceanic squid perform diel vertical migrations with juveniles and subadults occupying the surface layers and moving deeper in the water column as they mature (Daneri *et al.* 1999). Antarctic fur seals feed on *Psychroteuthis glacialis* with LRL's between 2.0 and 3.0 mm, representing subadult squid that occupy surface layers (Daneri *et al.* 1999), while New Zealand stranded whales fed on larger *Psychroteuthis glacialis* with LRL between 6.5 and 11.1 mm that were most likely consumed in deeper waters.

Psychroteuthis glacialis is recognised as an Antarctic species (Xavier et al. 1999, Gröger et al. 2000), and no specimens are known from comprehensive museum collections from New Zealand waters (O'Shea pers. comm.). For this reason, *P. glacialis* was included in the non-local cephalopod group, and local consumption seems very unlikely.

Octopoda

Alloposidae

Haliphron atlanticus (= Alloposus mollis) is a gelatinous octopod that attains ML's of 700 mm, and over 4,000 mm in total length (Nesis 1987, O'Shea 2004). It is widely distributed in tropical and subtropical waters, but only a single individual is known from New Zealand (O'Shea 2004). This species was consumed by sperm whales caught in the Tasman Sea, where it had a mean BM of 612.0 g (Clarke & MacLeod 1982). This species was not recorded in the diet of sperm whales caught off Cook Strait, or in the stomach of the sperm whale stranded on Paekakariki (Gaskin & Cawthorn 1967a, Clarke & Roper 1998). Specimens of Haliphron atlanticus appear to be significantly smaller than those consumed by sperm whales off the Azores, which had a mean LRL of 15.1 mm (Clarke et al. 1993).

Haliphron atlanticus appears to be abundant in the diet of sperm whales around southern Australia, but not within New Zealand (Evans & Hindell 2004). This species is also extremely rare in local museum collections (O'Shea pers. comm.). However, this species has been reported from a single specimen trawled off the eastern Chatham Rise (O'Shea 2004), and the beaks found in stomach samples from New Zealand stranded sperm whales had a much shorter LRL than those from Australia. For these reasons *H. atlanticus* has been included in group A.

Vampyromorpha

Vampyroteuthidae

The vampire squid is small, reaching ML's of 130 mm, is bioluminescent and very gelatinous. It occupies meso- to bathypelagic depths in tropical and temperate waters, and is the only currently recognised species in the family Vampyroteuthidae (Nesis 1987). Three specimens of *Vampyroteuthis infernalis*

found in our samples were significantly smaller than those consumed by sperm whales off the Azores, which presented LHL with a range of 4.5–25.8 mm (Clarke *et al.* 1993).

Indeterminate

The large number of beaks from indeterminate families in the diet of whale 19 was most probably due to the ambergris obstruction found in the intestines of this female (DoC 2005), which damaged a large proportion of the beaks collected.

5.2.2 Non-cephalopod component of the diet

Fish

New Zealand used to be one of few places in the world's oceans where fish were an important component in the diet of the sperm whales. In the 1960s fish contributed more than 37.0% of the diet by weight and were found in 93 (70%) of 133 stomachs of caught sperm whales (Gaskin & Cawthorn 1967a). Considering the historical importance of this group in the diet of the sperm whales it is surprising that so little fish were found in the stomach samples examined.

Summary of the diet of the sperm whale in New Zealand

The diet of the sperm whale in New Zealand waters is dominated by oceanic cephalopods, and is consistent with research elsewhere, showing high levels of variability in the number and diversity of specific prey items consumed (Clarke & MacLeod 1974, Clarke 1980, Clarke & MacLeod 1980, Kawakami 1980, Martin & Clarke 1986, Clarke et al. 1993, Clarke 1996b, Clarke & Pascoe 1997, Clarke & Roper 1998, Santos et al. 1999, Santos et al. 2002). The higher number of different cephalopod species reported from the diet of sperm whales in New Zealand is probably reflective of a more comprehensive study, including samples from 19 individuals. The results of this study, and those of stranded sperm whales in Tasmania, suggest that the sperm whale is an opportunistic predator

that exploits abundant or otherwise available prey resources in different foraging areas and at different times (Evans & Hindell 2004).

5.2.3 Size of cephalopod prey

In New Zealand, 31 (86.1%) of the 36 cephalopod species recorded from beaks in the stomachs of stranded sperm whales were estimated to have mean ML's shorter than 1,000 mm, and 20 (55.6%) of these 36 species had mean estimated weights of less than 1 kg. Cephalopod specimens shorter than 1,000 mm in the diet of sperm whales in New Zealand comprised 99.8% of the total number of measurable beaks.

Broken down further, cephalopods with an estimated weight of less than 1 kg represented 84.2% of the total number of beaks found in all whales, and comprised 28.2% of the total cephalopod biomass consumed. Cephalopods with an estimated weight of more than 1 kg represented 71.8% of the entire estimated cephalopod biomass. Cephalopods with estimated weights between 1 and 5 kg represented 13.0% of the beaks and 34.8% of the total cephalopod biomass; those with an estimated weight between 5 and 10 kg represented 1.8% of the beaks and 15.2% of the total cephalopod biomass, and cephalopods with estimated weights of more than 10 kg represented 1% of the beaks and 21.8 % of the total cephalopod biomass. These results suggest that sperm whales in this area of the Pacific consume mostly cephalopods with ML's of less than 1 m, and a wide range of cephalopod weight classes, with cephalopods weighing between 1 and 5 kg the most important weight class in the diet of these sperm whales.

For a 40 t sperm whale, a 5 kg cephalopod represents 0.01% of its body mass and it would need around 240 individuals of these squid per day in order to sustain its bulk, considering sperm whales need around 1,000 kg of food a day (Lockyer 1981). It seems unreasonable that a large species such as the sperm whale would feed on such small prey, unless large amounts of it can be reliably sourced. The large numbers of small cephalopod species found in the stomachs

of some of the whales suggest that they are feeding on large aggregations of sexually mature small-bodied squid, and individually capturing larger squid. However, whale 18 appears to have been feeding on a spawning aggregation of *Moroteuthis ingens*, a large cephalopod species, just prior to stranding.

The large number of beaks of *M. ingens* found in a the stomach of whale 18, the presence of *M. ingens* buccal masses in the stomach, and the state of darkening and consistent damage to most of the beaks of both sexes of *M. ingens*, suggests that this whale was feeding on a mating aggregation of *M. ingens* near the New Zealand's coast before it stranded. A total of 536 sexually mature M. ingens beaks (69.4% were female) were found in this stomach. Male and female beaks are morphologically different and can easily be identified; the male lower beak is weaker and has a cartilage plug in the rostrum that later becomes eroded while female lower beaks are usually found with damaged hoods and undamaged rostrums. This agrees with the state of beaks for sexually mature males and females of this species that have been caught in nets (Bolstad, in press). A pair of interlocked male and female buccal bulbs was also found in the stomach of whale 18. In this pair of buccal bulbs, the female beak was biting down on the male lower beak, in the place where the erosion usually occurs, while the upper male beak was also noted to be biting on the hood of the lower female beak. The erosion on the male beak is believed to be caused by the stronger female beak, and the damage to the female lower beak hood seems to be caused by the upper male beak, while mating in a head to head position. The damage observed in male and female beaks recovered from the stomach of whale 18 is consistent with that noted on sexually mature female and male M. ingens (Bolstad in press).

5.2.4 Secondarily ingested prey and prey remains retention times

Different prey remains have different digestion times, affecting their chance of being detected and identified in the contents of a stomach (Santos et al. 2001a). Cephalopod beaks are relatively indigestible and often accumulate in the second stomach of sperm whales until regurgitated or passed through the digestive system. Small cephalopod beaks may be underestimated in dietary analyses due to their small size, as they possibly pass through to the intestine, whereas larger beaks are more likely to accumulate in the stomach until regurgitated (Santos et al. 1999). Fish, on the other hand, have hard parts that are more readily digested and therefore are more likely to be retained for shorter periods of time in the stomach, making it easy to underestimate their importance in diet based on stomach content analysis. Thus, the importance of large cephalopods in the diet of predators would tend to be overestimated relative to that of fish or small cephalopods. However, fish otoliths and eye lenses are likely to remain in the stomach for relatively long periods of time, and cephalopod flesh is more readily digestible than fish flesh, making it also possible to underestimate cephalopod importance in the diet of predators (Martin & Clarke 1986). Even though stomach contents from strandings are normally incomplete and different prey types have different digestion rates, this in itself should not bias stomach content composition to an extent where an important prey class would go totally unnoticed.

Secondarily ingested prey is the food of prey that may be found in the stomach contents of a predator but not directly ingested by it. Secondarily ingested prey may bias the results of dietary analysis, and generally includes polychaetes, small crustaceans and small cephalopods. The absence of flesh in most of the stomachs, except for that of whale 18, which had an undetermined number of undigested fish, a cephalopod mantle, 11 buccal masses, and an arm crown, and whale 19 which had some flesh in one of the *Histioteuthis atlantica* beaks,

suggests most of these whales did not feed immediately prior to stranding. Smaller cephalopod beaks found in the stomach contents of predators could be the result of secondarily ingested prey from the stomachs of larger cephalopod species. However, the flesh of smaller cephalopod species has been found in the stomachs of sperm whales from other regions, suggesting direct ingestion by whales (Clarke *et al.* 1993 a). In the present study there is only evidence for the direct ingestion of *Moroteuthis ingens* through buccal masses, and for an unidentified species of fish present in the stomach of sperm whale 18. The presence of flesh around the beaks of smaller species, such as *H. atlantica*, their ubiquity in the samples, regardless of presence of larger cephalopod species, and the great number in which they were found also suggest these were directly consumed by the whales. In the other stomach samples there was no evidence for direct ingestion of either large or small cephalopod species, and it is reasonable to assume that all cephalopod species reported here were directly ingested by the whales.

5.3 Comparison between whales

Figures 39 and 40 show the percentage frequency by number and weight of the cephalopod families represented by beaks found in the stomachs of New Zealand stranded whales. Although there appears to be high variation in the percentage frequency by number in the diet of individual whales, families such as Histioteuthidae, Octopoteuthidae and Cranchiidae are consistently important in the diet of most whales. The families Ancistrocheiridae, Pholidoteuthidae, Cycloteuthidae and Onychoteuthidae are also important in the diet of most whales, but their contribution by numbers to the diet of individual whales appears to be more variable (Figure 39). The contribution by weight of cephalopod families to the diet of individual whales shows a larger variation (Figure 40), with families like the Onychoteuthidae and Architeuthidae gaining importance by weight, while families like the Histioteuthidae have a diminished importance by weight in the diet of individual whales, despite their large numbers.

Differences in the species composition and numbers found in the stomachs of individual whales could be a result of the social structure of sperm whales, differences between the cephalopod faunal composition of different foraging areas, or individual foraging behaviour. Since almost all stomach samples were from similar-sized males, the latter two appear more plausible. The high degree of individual variability and high numbers of specific prey species suggest sperm whales consume the most abundant species in their foraging area in an opportunistic manner.

On November 15, 2003, 11 sperm whales stranded on Whatipu Beach, on Auckland's west coast. It is not known whether these animals were travelling or foraging together before stranding. However, the differences in prey composition and stomach fullness suggest most of these animals were not feeding together. However, this does not rule out the possibility they were travelling together, since sperm whales associating at the surface may separate three dimensionally while diving (Watkins & Schevill 1977). It has been suggested that three-dimensional separation while foraging is advantageous because it prevents individuals from searching through areas that have recently been exploited by other whales (Evans & Hindell 2004). However, group hunting has been observed in other odontocete species (Hooker & Baird 2001, Gazda *et al.* 2005), and cannot be out ruled as a possible foraging strategy for the sperm whale. A comparison in diet between sexes was not possible, since only one female stomach was sampled.

5.3.1 Regurgitation and stomach fullness

Finding empty stomachs in stranded individuals is not uncommon. Three (11.3%) of the 19 sperm whale stomachs studied were empty, a similar proportion to the 15 (15.8%) empty stomachs reported by Gaskin & Cawthorn (1967a) in the early 1960s. No empty stomachs were recorded from sperm whales in the Tasman Sea, and the whale stranded at Paekakariki had more than 3,000 beaks in its stomach (Clarke & MacLeod 1982, Clarke & Roper, 1998).

There was a wide range in the number of beaks found in any single stomach, between 0 and 7,532, and analysing the significance of stomach fullness is bound to involve speculation. Relatively small stomach content samples could be due to the recent regurgitation of stomach contents, the partial collection of stomach contents, malnourishment, or because sperm whales may not feed as much during migrations. EOS staff were present for the mass stranding (whales 1–12), on November 2003, and for a single stranding (Whale 16) on December 2004 on west Auckland, and complete stomach contents were collected from these whales. However, the 53 beaks collected from whale 17 represent only the partial stomach contents from an individual stranded in the Chatham Islands, and the largest sample, that of whale 19 (7,532 beaks) may represent both stomach and intestinal samples, as evidenced by the presence of ambergris, which is only produced in the large intestine.

There are few studies on the retention times of prey remains in the stomachs of sperm whales. Ross (1999) showed captive bottlenose dolphins, *Tursiops truncatus*, to retain cephalopod beaks for up to three days. Clarke (1980) reported that female sperm whales would on average retain cephalopod remains for 2.1 to 2.5 days, and males of this species would retain beaks for 1.2 to 1.6 days. However, the presence of Antarctic and subtropical cephalopod species from the stomach samples of New Zealand stranded whales suggests that cephalopod remains may not be fully evacuated after regurgitating, and may be retained for longer periods of time than previously thought. Moreover, the occurrence of *Mesonychoteuthis hamiltoni* beaks (an Antarctic species) in the stomach contents of sperm whales captured off California (Fiscus 1993), demonstrate some beaks can be retained in the stomach for considerable periods of time.

It is apparent sperm whales in the Antarctic are less common to have a full stomach than baleen whales (Matthews 1938, Nemoto *et al.* 1988), suggesting that the prey of sperm whales may be widely distributed. Female sperm whales

off South America's west coast travel up to 500 km in five to six days in periods of food shortage (Whitehead 1996b). Widely distributed prey would force sperm whales to cover large foraging areas, or have to perform long distance migrations in order to secure sufficient prey. This could also be a response to fluctuations in the abundance of such an unpredictable resource as squid populations, for which population estimates can not be reliably calculated, as a result of their complex life cycles (Sullivan *et al.* 2005).

5.4 Migrations

The beaks of three non-local species occurred in 12 (75.0%) of the sperm whale stomachs. The presence of these beaks in the stomach samples from New Zealand stranded whales raises two questions:

- Were these cephalopod species consumed within the EEZ or were the whales migrating into New Zealand after visiting Antarctic foraging grounds?
- What was the most probable migration route?

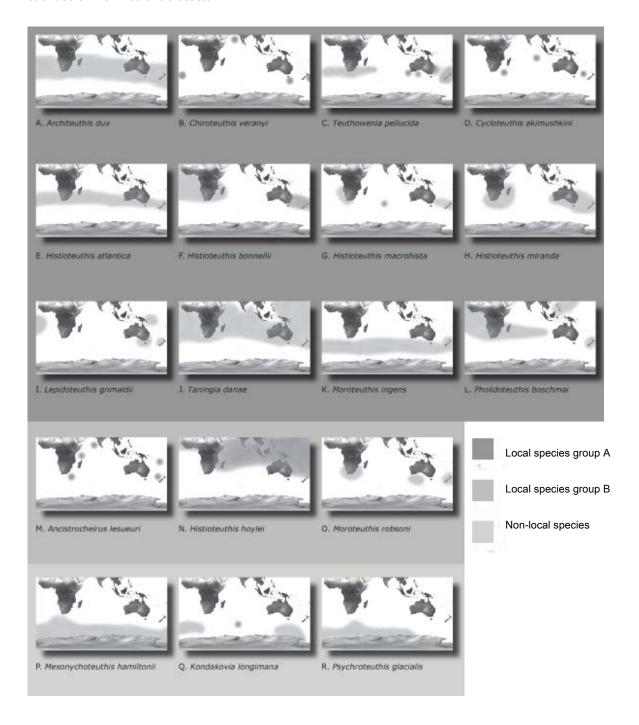
In regards to the first question, the three non-local cephalopod species were recorded from male whale stomachs only, and have never been previously reported from New Zealand waters. *Psychroteuthis glacialis* and *Mesonychoteuthis hamiltoni* only occurred in the stomachs of whales stranded on the west coast, while *Kondakovia longimana* occurred in the stomachs of both east and west coast stranded whales. These species are typically confined to waters south of the Subtropical Convergence, and it seems unlikely that adult specimens of these cephalopod species would occur within the EEZ. However, the Subtropical and Subantarctic Convergences act as boundaries for cephalopod species and are by no means static but dynamic systems (Klumov 1971, Clarke 1980, Voss 1985), and some subantarctic and Antarctic cephalopod species have been reported outside their usual range, in association with cold

water currents moving north (Nesis 1972). *K. longimana* was reported from the stomachs of female sperm whales caught in the Tasman Sea, and Clarke & MacLeod (1982) suggested that females could range farther south than previously thought, or that *K. longimana* could occur further north than earlier recognised. This dilemma will not be solved until more detailed investigations on the distribution and migrations of both cephalopods and the sperm whale in the South Pacific are undertaken. However, it appears reasonable to assume that both east and west coast male sperm whales that had non-local cephalopod beaks in their stomachs were migrating north after visiting foraging grounds south of the Subantarctic Convergence, prior to their stranding.

In regards to the second question, all of the whales that stranded on the west coast with cephalopod remains in their stomachs, had the beaks of cephalopods included in group B and of non-local species, and only whale 15 had three Kondakovia longimana beaks in its stomach. Figure 91 shows the distribution of 18 of the 36 cephalopod species found in the stomachs of New Zealand stranded whales (Nesis 1987, Xavier et al. 1999, 2002, Nesis 2003, Okutani 2005). Only taxa that were identified to species or for which accurate geographic information was available were included in the map. It should be noted that most locally occurring cephalopod species in group B have distributions west of New Zealand, and have rarely been recorded east into the Pacific. Considering the dietary and geographic information previously mentioned and the comparison of recent and historical accounts on the diet of the sperm whale, there is strong evidence to suggest that some of the whales stranded on both the east and west coasts of New Zealand had performed long-distance migrations from waters south of the Subantarctic Convergence, and appear to have fed little on locally occurring cephalopods in the days prior to stranding. Sperm whales stranded on the west coast appear to have undertaken migrations during the austral summer, and the most likely route appears to have been eastwards across the Tasman Sea in the days or weeks before stranding, and as implausible as it may seem, may have extended as far west as South Africa.

Sperm whale 16, stranded on Auckland's west coast, was the only whale that had a larger proportion of non-local cephalopods by biomass in its diet, than of local species. Sperm whale 16 had eaten squid of larger than the mean cephalopod weight for any other whale. The reason for encountering such a large proportion of non-local cephalopod beaks in the stomach of this whale is unknown but may include either recent regurgitation or a simple lack of feeding. However, the latter seems more likely, since there is no evidence that suggests regurgitation evacuates beaks preferentially. The reason whale 16 may have stopped feeding after visiting southern foraging grounds is unknown. However, this could be due to several factors, including foraging behaviour during migrations, individual foraging habits, sickness, or scarcity of food in and around New Zealand waters.

Figure 91. Distribution maps for selected cephalopod species found in the stomachs of sperm whales stranded on New Zealand's coasts.



5.5 Beak descriptions

Problems with the identification of beaks arise due to the unresolved taxonomy of some cephalopod families and the high level of similarity or variability between and within the beaks of different species. Beaks of the family Octopoteuthidae can be easily confused between species of the same family and with those of *Lepidoteuthis grimaldii* (Lepidoteuthidae). Here a description of otherwise very similar beaks of *Taningia danae*, *Octopoteuthis megaptera*, *Octopoteuthis* sp. 'Giant' and *Lepidoteuthis grimaldii* is presented, in order to facilitate their identification.

Three species of the family Octopoteuthidae are represented by lower beaks in our collections: *Taningia danae*, *Octopoteuthis megaptera* and *Octopoteuthis* sp. 'Giant'. *T. danae* has also reported by Clarke and MacLeod (1982) and Clarke and Roper (1998) in the diet of sperm whales in the Tasman Sea; *O. megaptera* has not been reported in the diet of sperm whales in this region before; and *Octopoteuthis* sp. 'Giant' reported only by Clarke and MacLeod (1982) as *Octopoteuthis* sp. B. *Octopoteuthis sicula* was reported by Rancurel (1970) in the diet of the long-nose lancet fish, *Alepisaurus ferox*, caught off New Caledonia, otherwise unknown from the South Pacific region. *Octopoteuthis rugosa* and *Octopoteuthis* sp. A, both effectively morphologically indistinguishable in terms of beak morphology were separated on the only basis of LRL length by Clarke and MacLeod (1982); the first with LRL up to 11.5 mm, and the second with LRL over 11.5 mm.

Taningia danae can be easily separated from other octopoteuthid beaks as it has a characteristic shape and a 'shelf' on the anterior part of the lateral wall ridge (Figure 85 C). Other octopoteuthid species beaks can be first separated on the basis of size; smaller beaks are likely to belong to *O. megaptera*, and should have a fully cartilaginous shoulder (Figure 89 F) like *T. danae*, but with no shelf protruding from the lateral wall ridge under the hood, a strongly thickened lateral

wall fold and ridge (Figure 89 H, I), and a sharp thickened rostrum (Figure 89 D); larger beaks could belong to *L. grimaldii* or *Octopoteuthis* sp. 'Giant', and can be differentiated by the general form and shape of the lateral wall ridge, being a strongly thickened fold in *Octopoteuthis* sp. 'Giant', and a thickened ridge in *L. grimaldii* (Figures 88 and 89 G–I). The beak of *Octopoteuthis* sp. 'Giant is also longer than that of *L. grimaldii*, and has a sharp rostrum ridge (Figure 88 E) that extends all through the rostrum's length (Figure 88 D).

5.6 Recommendations

Dietary studies on stranded marine mammals would benefit greatly from the development of a standard protocol for the collection of gut samples, implemented by a central authority like DoC. Samples should be archived and readily accessible to dietary researchers on a loan basis. Gut samples should also include intestinal contents when logistically possible, so reliable conclusions about the predator's feeding ecology can be drawn from estimates of biomass of prey consumed. Moreover, studies on the migration and feeding success of the sperm whale, and on the relationship of prey size (length and weight) with the morphometry of common hard remains are also needed to complement dietary studies and better understand the feeding ecology of this species. Finally, the identification of cephalopod hard remains from stomach contents can be advanced by the development of an accessible beak reference collection, comprising both local and non-local cephalopod species, and the publication of both lower and upper beak descriptions.

The following sections suggest possible research that could be undertaken to develop a better understanding of deep-sea food webs, especially the diet of teuthophagous cetaceans and pinnipeds, the effects changes in prey populations may have on top predators, and recommendations for future dietary analysis researchers.

5.6.1 Future research

Uncertainty of the effect fisheries have on the marine ecosystem has stimulated numerous research studies in recent years. However, despite the economical and ecological importance of cephalopods in the marine environment, there are strikingly few ecological studies on them, and their significance in the trophic systems of the deep-sea, their life cycles and distribution patterns are only beginning to be understood (Clarke 1996b, Piatkowski *et al.* 2001). Dietary studies that investigate the cephalopod composition and size-class structure in the diet of predators are needed to assess their importance in deep-sea food webs, and the potential impact that deep-sea fisheries might have on the diet and health of oceanic predators. Opportunistic dietary studies on top predators are insufficient to detect changes in community structure that affect the trophic assembly of the deep-sea. These studies should be complemented with other research that is able to detect changes in the structure of deep-sea communities by investigating the diet of more readily accessible predatory species.

Squid are an important component of food chains in the Southern Ocean and they act as both high-level predators and prey for apex predators (Jackson *et al.* 2000). However, very little is known about their distribution and abundance in the South Pacific (Rodhouse & White 1995, Jackson *et al.* 2000). Seasonal fluctuations in the abundance of primary prey items, particularly cephalopods and fish, must have an effect on the diet of the sperm whale. Fishing fleets have the ability to alter the size of fish populations, and it has proven very difficult to manage stocks and ensure the sustainable provision of this resource (Hall & Mainprize 2004). On the other hand, the overexploitation of finfish stocks has positively affected cephalopod populations (Piatkowski *et al.* 2001). Annual fluctuations in the abundance of fish and cephalopods are known to influence the diet of the long-finned pilot whale, *Globicephala melas* (Desportes 1985), and there is also evidence of partitioning of the cephalopod food resources within an area between different cetacean species that would reduce direct competition

between species (Clarke 1996a). With increasing global fishing effort, and with cephalopods representing over 4% of the global annual catch, there are competing interests between the ocean's top teuthophagous predators and the fishing industry that intuitively must also impact the diet of sperm whales and other top ocean predators (Hindell *et al.* 2003, FAO 2004). Moreover, cephalopod stocks are thought to be renewed every year, and their abundance may vary widely between years (Boyle & Boletzky 1996). Thus, both fisheries and teuthophagous predators must be able to turn to alternative resources in years of low abundance. Future research should try to understand the ways top predators respond to changes in the abundance of prey populations, and the underlying reasons for these fluctuations (Piatkowski *et al.* 2001).

Two species of cephalopod, *Opisthoteuthis mero* and *Idioteuthis cordiformis*, and one species of shark, *Dalatias* sp., recorded in the diet of sperm whales in New Zealand waters (O'Shea 1999, the present study, and Gaskin and Cawthorn 1967a, b, respectively), are recognised to be regionally threatened by trawling activity (Hitchmough 2002). Moreover, egg masses of one species of squid (and it is expected the egg masses of 77 other species of squid, of the 86 species in New Zealand waters) are likely to be impacted by trawling (O'Shea *et al.* 2004), of which at least 250,000 deep-sea commercial deployments have occurred between 1989 and 2003 (O'Driscoll and Clark 2005), all within the normal diving and feeding range of the sperm whale. Further research on the impact of bottom trawling on squid recruitment and top-predator diet are needed to devise conservation strategies that effectively protect squid and their predators.

5.7 Conclusions

Cephalopods are the most important component in the diet of sperm whales in New Zealand and other areas, and are one of the key trophic links in the Southern Ocean. Species like *Histioteuthis atlantica* and *Histioteuthis miranda* appear to be predominant local prey for whales that stranded on both the east

and west coasts. *Moroteuthis ingens* and at least one fish species were the major prey of a sperm whale from the Cook Strait region according to historical accounts of diet (Gaskin & Cawthorn 1967a, b), and could continue to be important in the diet of whales feeding in these waters. However, more dietary studies on sperm whales from stomach samples from the Cook Strait, together with biogeographical information on the distribution of fish and cephalopods in the area are needed to better understand why sperm whales in the Cook Strait region appear to feed on different species of cephalopods, and including fish in their diet. Local species that are not common in New Zealand waters, like *Moroteuthis robsoni* and *Ancistrocheirus* sp., also appear to predominate in the stomach samples but may have been consumed outside New Zealand's EEZ. Non-local cephalopod species comprised three cephalopod species, *Mesonychoteuthis hamiltoni*, restricted to the Antarctic, suggesting that whales stranded on New Zealand beaches could be migrating from colder waters south of the Subtropical Convergence.

Very low numbers of beaks were found in whales that had accidentally swallowed lost or discarded fishing nets in Hawaii, the North Sea and Iceland, indicating fisheries can have a direct, negative impact on sperm whales. Furthermore, some deep-sea cephalopods produce large, fragile, pelagic gelatinous egg masses that could be easily damaged or destroyed by trawl nets, killing the embryos (O'Shea *et al.* 2004), and consequently limiting recruitment of squid into the environment. Bottom trawling is the single most pervasive human activity in the high-seas (Clarke 1955, Kaiser 1998, Gianni 2004). Deep-sea fisheries have developed rapidly to depths of 2,000 m, regularly trawling to depths of 1,500 m (Drazen *et al.* 2003), but concrete scientific knowledge and evidence of the consequences these practices might have on the deep-water ecosystem is limited. It has been suggested that the more specialised diet of the northern bottlenose whale, *Hyperoodon ampullatus*, could be due to its deeper-diving habits, where there is a lower cephalopod diversity (Whitehead *et al.* 2003). Considering bottom trawling is a common practice within the diving range of the

sperm whale within the EEZ, and the effect it may have on squid population dynamics, every effort must be sought to minimize direct or indirect impacts commercial fisheries may have on protected marine mammals.

Seasonal changes in the relative numbers of cephalopod species, either natural or brought about by human influence, must influence the behaviour, distribution and survival of sperm whales. This study opens the door to multiple research opportunities and gives an insight to the diet of sperm whales in the South Pacific. However, the lack of knowledge on Southern Hemisphere cephalopods and their importance in the trophic system calls for more detailed, intensive research on their systematics; bathymetric, geographic and ontogenetic distributions; and the ways humans potentially impact them and their predators.

Differences in the prey composition found between dietary studies on stranded (Santos *et al.* 1999) and commercially caught whales (Martin & Clarke 1986) in the North Sea are difficult to interpret. One possibility is that the sperm whales in the Northern Sea have changed their diet over the past two decades, or that the results from stranded animals may not reflect the true diet of this species (Santos *et al.* 1999). Although these last authors address this issue, they provide no concrete conclusion, leaving an open question on the impact fisheries have had on the diets of top predators over past decades.

Based on local cephalopod distribution records, it is believed that from 61.1 to 86.3% of the total cephalopod biomass consumed by all whales was taken in New Zealand waters, and 13.7% may have been taken outside New Zealand's EEZ. The low percentage of food likely to have been consumed locally (61.1%), excluding local species in group B) is surprising, but until more accurate allometric equations are available, and investigations on the migration and feeding ecology (e.g. feeding success, prey retention times) of sperm whales in the South Pacific are undertaken, no reliable conclusions can be drawn from estimates of the relative local and non-local consumed prey.

The sperm whale's diet, large size, cosmopolitan distribution and postulated population numbers make it an important part of the global mesopelagic environment (Katona & Whitehead 1988, Whitehead *et al.* 2003). Recent reviews show that estimated numbers of sperm whales in the world's oceans need serious revision, and estimates have been down-scaled from two million to 360,000 (Whitehead 2002). Since the sperm whale is fully protected and its population numbers appear to be less than a fifth of previous estimates, any potential threat to the sperm whale or its prey should be carefully reviewed, and strategies proposed and enacted to minimise any further potential impact on this species, as considerable environmental variability over short time periods poses problems for individuals of this species (Whitehead 1996b).

The development and expansion of deep-water fisheries is much quicker than the rate at which scientific knowledge about the deep-sea ecosystem progresses, and ecological considerations on this environment have shown it to be much more vulnerable to disruption than shallower ecosystems (Haedrich *et al.* 2001). Moreover, the scientific information required to develop and implement management actions is difficult to obtain and usually peer-reviewed, while the management process that regulates fisheries rarely is. The application of a formal evaluation process on fisheries management could deliver beneficial and carry significant improvements (Hall & Mainprize 2004). Considering overexploitation of marine fisheries is a persistent problem (Lauk *et al.* 1998), even where intensive management has been applied, new forms of management that provide species with appropriate pristine environments, where they can recover from human impacts must be sought, investigated and implemented (Lauk *et al.* 1998, FAO 2004, Hall & Mainprize 2004).

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Appendix

Figure 10. Percentage frequency by weight of cephalopod families in the diet of sperm whale 1, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 558,107g)

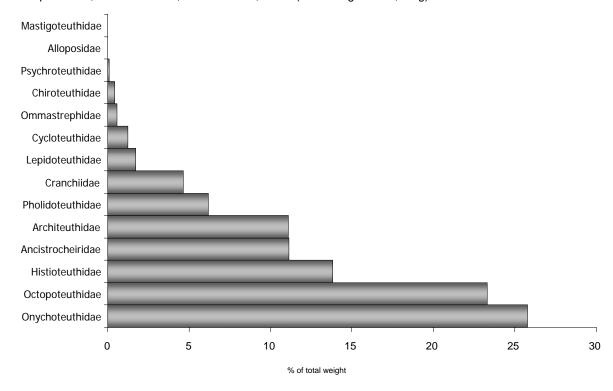


Figure 11. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 1, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 558,107g)

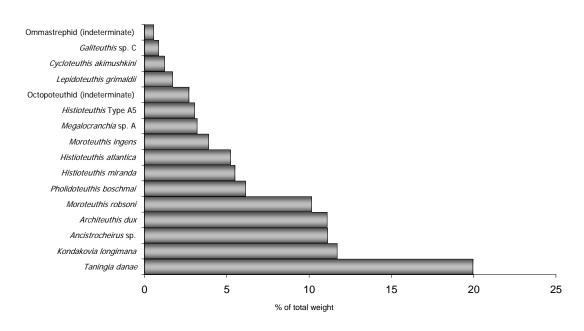


Figure 12. Percentage frequency by weight of cephalopod families in the diet of sperm whale 2, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 400,772g)

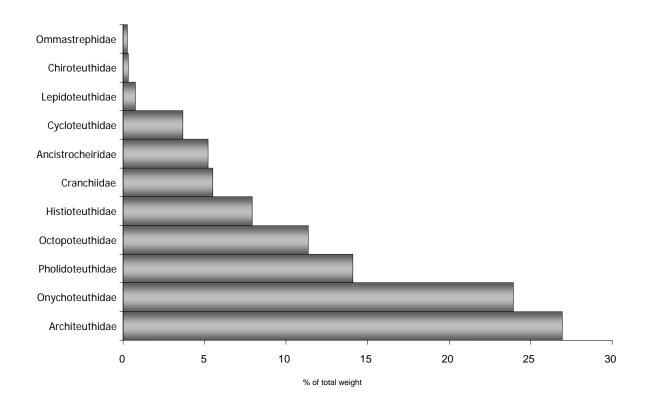


Figure 13. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 2, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 400,772g)

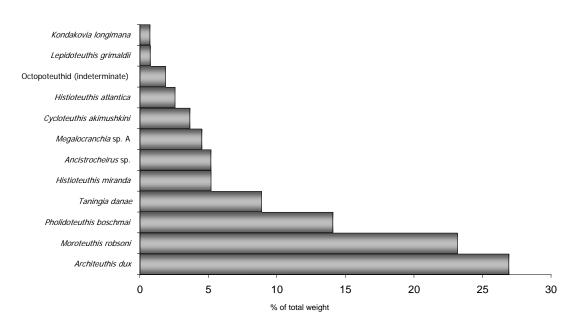


Figure 14. Percentage frequency by weight of cephalopod families in the diet of sperm whale 3, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 245,979g)

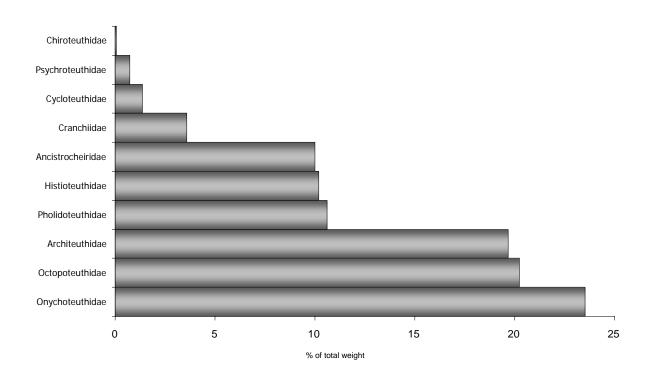


Figure 15. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 3, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 245,979g)

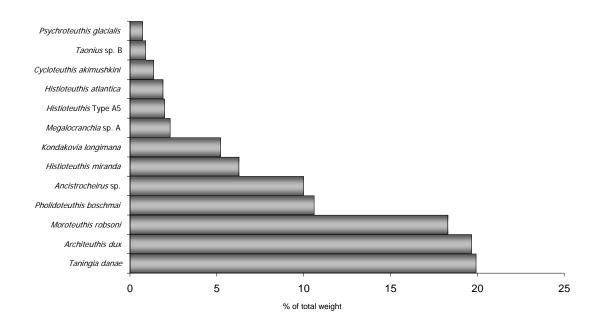


Figure 16. Percentage frequency by weight of cephalopod families in the diet of sperm whale 4, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 105,961g)

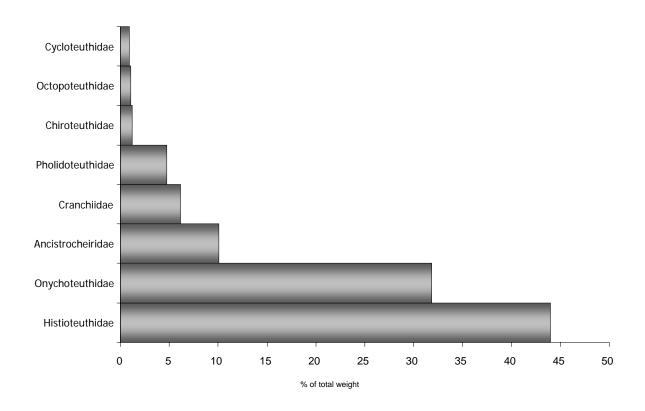


Figure 17. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 4, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 105,961g)

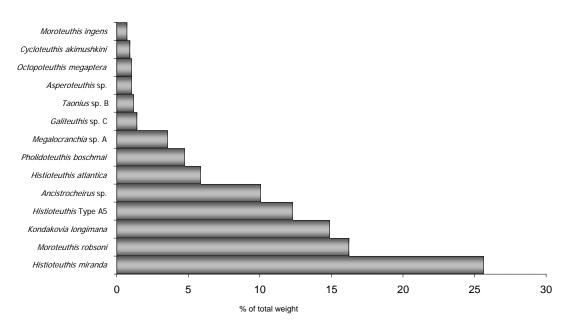


Figure 18. Percentage frequency by weight of cephalopod families in the diet of sperm whale 5, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 24,349g)

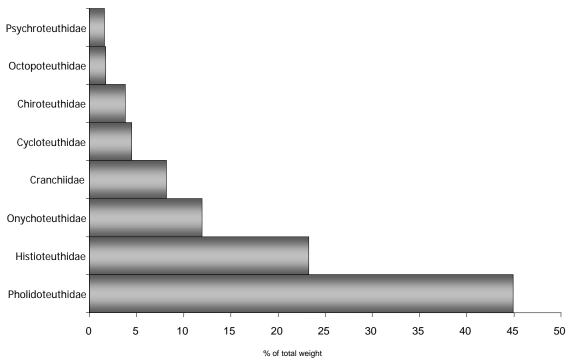


Figure 19. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 5, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 24,349g)

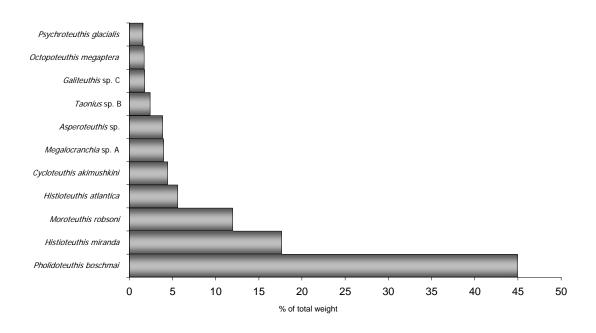


Figure 20. Percentage frequency by weight of cephalopod families in the diet of sperm whale 6, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 135,677g)

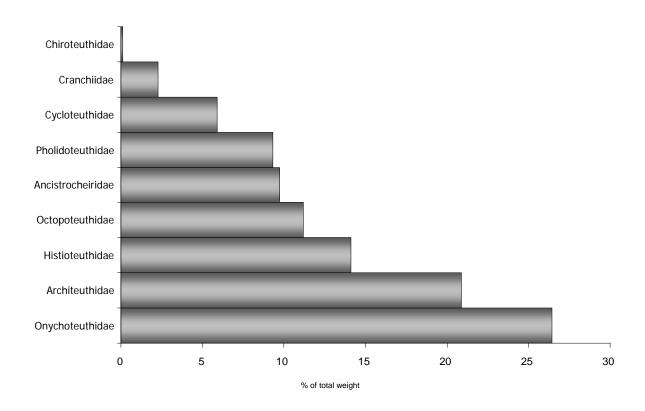


Figure 21. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 6, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 135,677g)

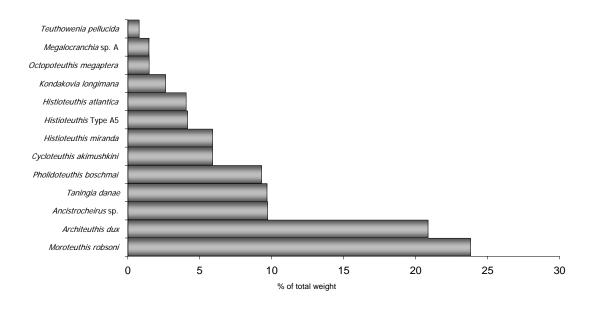


Figure 22. Percentage frequency by weight of cephalopod families in the diet of sperm whale 7, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 1,631,785g)

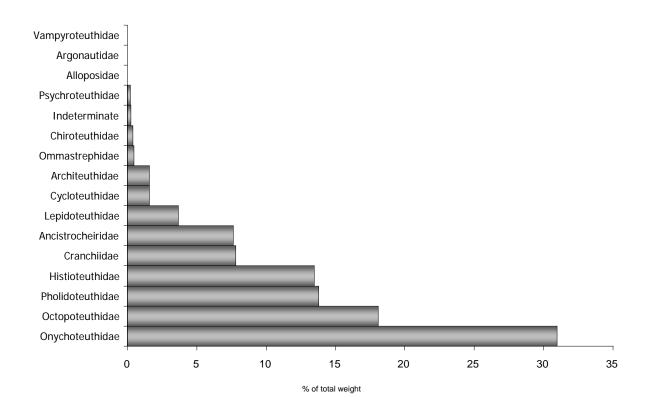


Figure 23. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 7, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 1,631,785g)

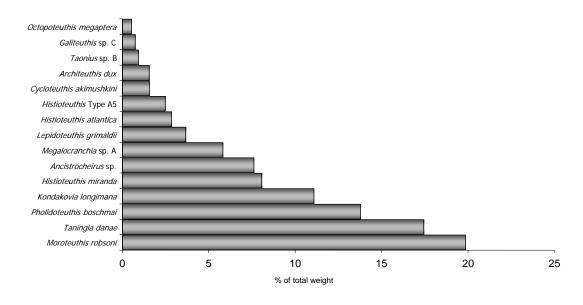
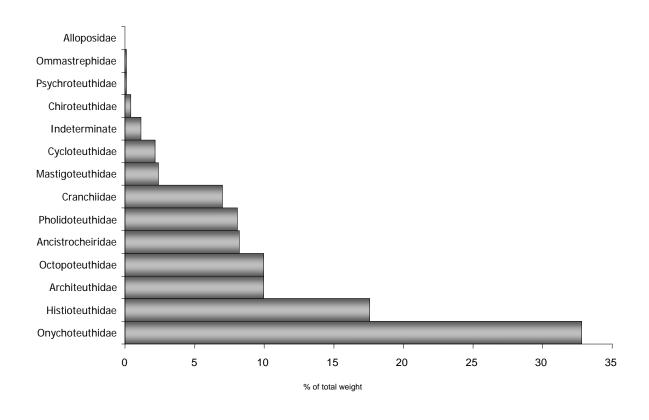


Figure 24. Percentage frequency by weight of cephalopod families in the diet of sperm whale 8, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 1,838,528g)



churchFigure 25. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 8, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 1,838,528g)

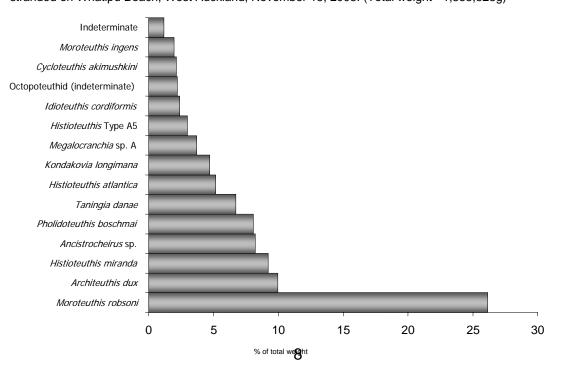


Figure 26. Percentage frequency by weight of cephalopod families in the diet of sperm whale 9, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 509,626g)

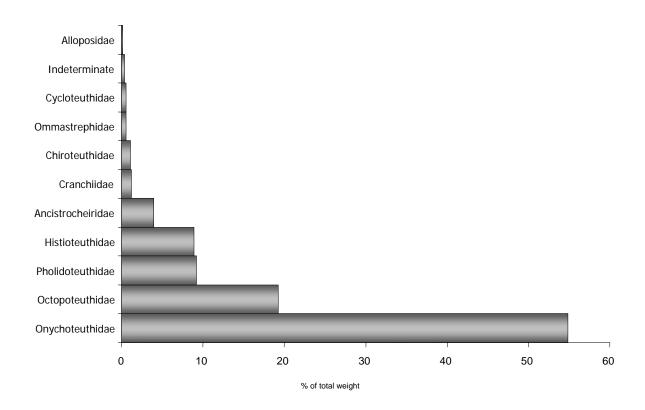


Figure 27. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 9, stranded on Whatipu Beach, West Auckland, November 15, 2003. (Total weight= 509,626g)

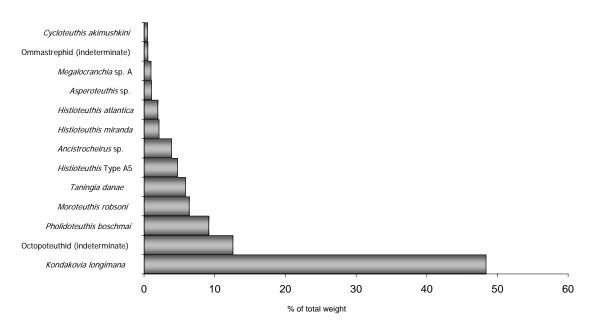


Figure 28. Percentage frequency by weight by cephalopod family in the diet of sperm whale 13, stranded on Whatipu Beach, West Auckland, November 30, 2004. (Total weight= 759,669g)

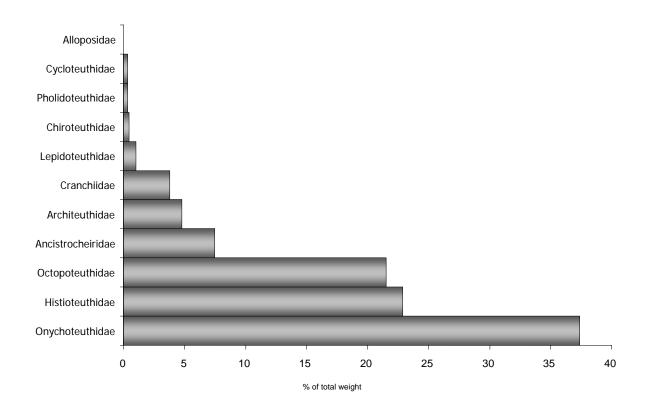


Figure 29. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 13, stranded on Whatipu Beach, West Auckland, November 30, 2004. (Total weight= 759,669g)

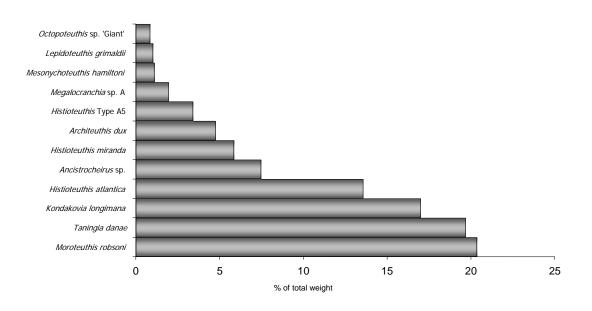


Figure 30. Percentage frequency by weight of cephalopod families in the diet of sperm whale 14, stranded on Whatipu Beach, West Auckland, October 11, 2004. (Total weight= 95,082g)

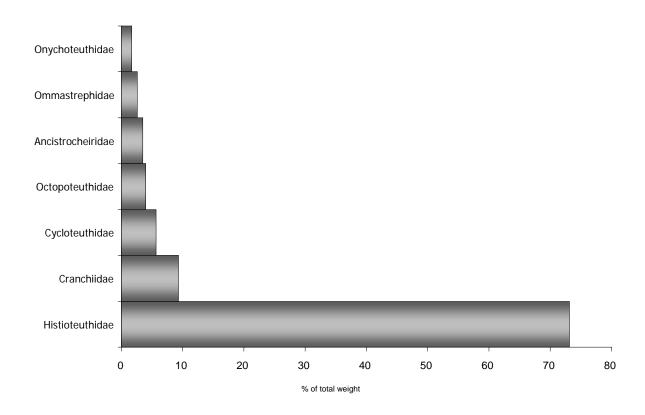


Figure 31. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 14, stranded on Whatipu Beach, West Auckland, October 11, 2004. (Total weight= 95,082g)

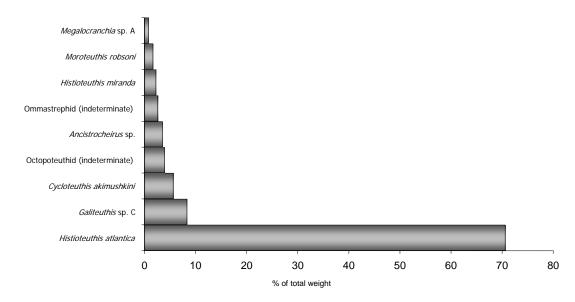


Figure 32. Percentage frequency by weight by cephalopod family in the diet of sperm whale 15, stranded on Oputama Beach, east coast, Hawkes Bay, November 28, 2002. (Total weight= 743,513g)

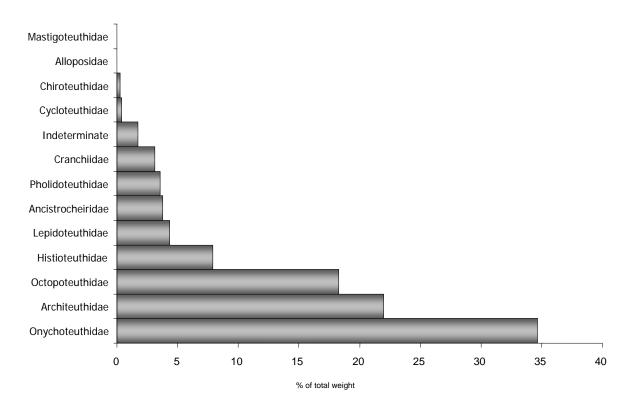


Figure 33. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 15, stranded on Oputama Beach, east coast, Hawkes Bay, November 28, 2002. (Total weight= 743,513g)

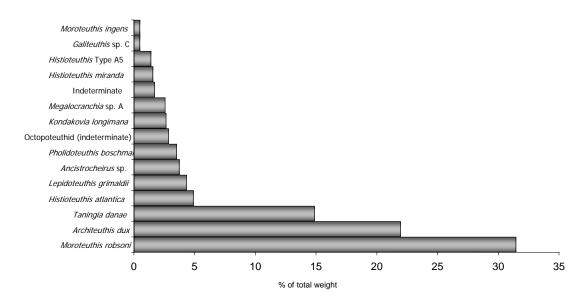


Figure 34. Percentage frequency by weight of cephalopod families in the diet of sperm whale 16, stranded on Muriwai Beach, West Auckland, December 8, 2004. (Total weight= 1,079,301g)

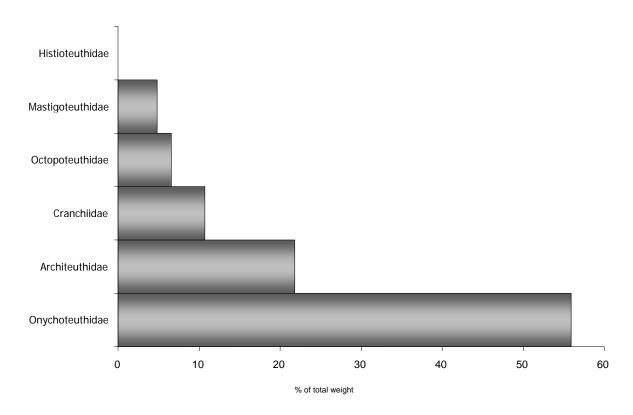


Figure 35. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 16, stranded on Muriwai Beach, West Auckland, December 8, 2004. (Total weight= 1,079,301g)

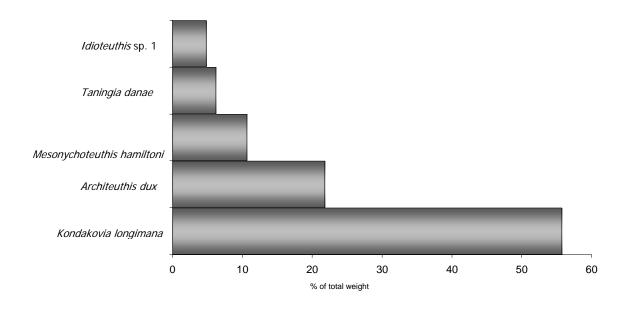


Figure 36. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 18. (Total weight= 866,982g)

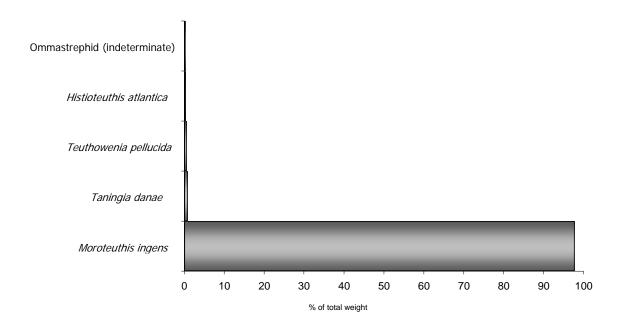


Figure 37. Percentage frequency by weight of cephalopod families in the diet of sperm whale 19, stranded in Napier, Hawkes Bay, February 28, 2004. (Total weight= 2,049,092g)

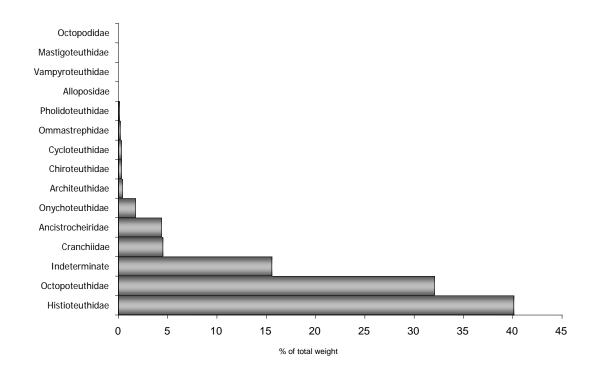


Figure 38. Percentage frequency by weight of cephalopod species in the diet of sperm whale number 19, stranded in Napier, Hawkes Bay, February 28, 2004. (Total weight= 2,049,092g)

