Diet and Foraging Behaviour of Juvenile Rig (*Mustelus lenticulatus*) from New Zealand Harbours and Estuaries

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Abstract

Smooth-hounds (Elasmobranchii, Triakidae) can form important commercial fisheries, and in New Zealand, rig (*Mustelus lenticulatus*) is marketed as "lemonfish". Despite this, little is known of their biology. Rig are small sharks known for making annual inshore migrations to harbours and estuaries to give birth and mate. These areas act as nursery grounds for newborn rig, providing an important food source, protection from predators, or both. A large-scale survey of the diet of juvenile (<1 year old) rig was undertaken throughout New Zealand in February-March 2011, sampling guts of 130 rig at eight sites from the northern North Island to the southern South Island. Rig fed mainly on benthic crustaceans, especially stalk-eyed mud crabs (*Hemiplax hirtipes*) and snapping shrimp (*Alpheus richardsoni*). Other prey groups found in their diet include mantis shrimps, hermit crabs, squat lobsters, various caridean shrimps and polychaetes, while molluscs were rarely taken and fish were not found at all. Two recently introduced species were found in rig diets from northern sites: the Japanese mantis shrimp (*Oratosquilla oratoria*) from Kaipara Harbour and the greentail prawn (*Metapenaeus bennettae*). While diets overlapped between all harbours and estuaries, significant differences were detected through pairwise Analyses of Similarity between sites. Differences in diet were associated with latitude and temperature, and related especially to the proportions of two mud crabs, *Hemiplax hirtipes* and *Hemigrapsus crenulatus*, the snapping shrimp *Alpheus richarsoni* and the prawn *Metapenaeus bennettae*. We suggest that newborn rig remain in harbours and estuaries primarily to feed. In addition to analysing juvenile rig diet, a behaviour study was performed to analyse the effects of sediment type on captive juvenile rig foraging effort and success. Six young of the year rig caught from Porirua Harbour were transferred to the NIWA, Greta Point, Wellington facility. No significant differences were observed in the time spent foraging or the number of strikes occurring on sand or mud. However, a significant increase in the time spent foraging and a significant decrease in the time spent resting was observed with the presence of crabs. Further research is required to determine the effects of sedimentation on juvenile rig behaviour.

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Chapter 1

Introduction: Biology, Ecology and Conservation of Rig

1.1 Introduction

Increased human population densities in coastal areas have threatened many marine ecosystems (Gray 1997) including many shark populations (Field et al. 2009). The life history traits of many shark species, such as slow growth, low fecundity, late age at maturity, long gestation periods and long life spans make them particularly vulnerable (Compagno 1990; Cortés 2000; Speed et al. 2010). For centuries it was believed that the ocean was too expansive for humans to ever deplete its resources, however this has been refuted, with the collapse of the Atlantic cod (*Gadus morhua*) being one of the most infamous examples of our ability to overexploit our oceans resources. The main threats to coastal sharks are overfishing and habitat destruction/degradation (White and Kyne 2010; Speed et al. 2010; Cortés 2000). These risks increase when sharks use specific habitats and have low dispersal rates (Speed et al. 2010; Walker 1998; Stevens et al. 2000).

1.2 Conservation and Management of Coastal Sharks

In 1998 the Food and Agriculture Organization of the United Nations (FAO) developed the International Plan of Action for Conservation and Management of Sharks (IPOA-Sharks). Its objective was to:

> "ensure the conservation and management of sharks and their long-term sustainable use"

Sharks were defined as all Chondrichthyans, including sharks, skates, rays and chimaeras. The FAO will aid states in the implementation of the IPOA-Sharks by providing technical support and funding (FAO c. 2010-2012). While the IPOA-Sharks is voluntary, the New Zealand Ministry of Fisheries approved the National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks) on 13 October 2008.

It is crucially important to conserve both chondrichthyan populations and biodiversity in order to maintain healthy marine ecosystems (White and Kyne 2010). Effective conservation and management of a species or ecosystem cannot exist without an understanding of the threats these species and ecosystems face. The following is a summary of the threats to coastal sharks and their habitats, and the management regulations in place to reduce these threats.

OVEREXPLOITATION

Intense exploitation during the market-colonial development period (prior to 1900) led to declines in many mammals, fish and invertebrates beginning with the most valuable, large species and moving onto smaller, less valuable ones (Lotze et al. 2006). Diadromous fish (salmon and sturgeon) were depleted first, followed by large pelagic fish (tuna and sharks), groundfish (cod and halibut) and then small pelagic fish (sardines and herring) (Lotze et al. 2006). Trawling led to overexploitation of habitat-forming filter-feeders, such as oysters, which led to loss of complex habitats and decreases in water quality (Lotze et al. 2006).

Fishing methods, such as bottom long line, trawl, gill-net, and recreational fishing are potentially more threatening to coastal sharks and sharks living within coastal nursery areas (Knip, Heupel, and Simpfendorfer 2010; Field et al. 2009). Myers and Worm (2005) suggested four strategies for reducing overfishing:

> “(i) reduce fishing mortality enough to avoid extinction of the most sensitive species; (ii) reduce bycatch mortality wherever possible; (iii) use spatial closures to initiate recovery; and (iv) establish permanently closed marine reserves in key areas, such as spawning grounds and diversity hot spots.“

Three out of four of these strategies are currently being used by MAF to help maintain shark populations, and the fourth strategy, while not currently being used, is certainly being investigated. Three types of management frameworks are used depending on the status of the fishery; these include non-Quota Management System (QMS), QMS or Prohibited Utilisation management frameworks (NPOA, 2008). In the QMS framework, Total Allowable Catch (TAC) is the primary management tool. TAC includes non-commercial take, other sources of mortality related to fishing and Total Allowable Commercial Catch (TACC) (MFISH 2008). Other sustainability measures for coastal sharks in New Zealand include limits on amateur daily catch (see Commercial and Recreational Fishing section), amateur and commercial set net mesh size, set net length, number of nets, and the proportion of a bay, channel, river, stream or sound that can be blocked by a net (Francis 1998; MFISH 2008). Several coastal areas around New Zealand are closed to trawling and Danish seining, including most harbours and semi-enclosed bays and many coastal areas (Francis 1998). There are also a number of set net restrictions for commercial and recreational fishermen, such as the ban of set nets at the entrances to Kaipara, Manukau, Raglan harbours and Waikato River. Set net bans and seasonal restrictions vary depending on the area; for details on these restrictions refer to the Ministry of Agriculture and Fisheries webpage (http://www.maf.govt.nz/).

Managing coastal shark fisheries in New Zealand is hampered by some factors: exceeding catch limits, mislabelling of sharks, uncertain biomass estimates and under-reporting of bycatch (Francis 1998; White and Kyne 2010). A lack of information on the life histories of many coastal sharks, especially surrounding inshore habitat use, will lead to increased uncertainty about stock sustainability and may limit our ability to maintain the population.

HABITAT DEGRADATION

Many coastal shark species use estuaries and harbours as nursery areas and these same areas may be important to adult sharks as breeding and foraging grounds. The loss or degradation of these coastal areas and estuaries could threaten coastal shark populations, which can have a cascade effect throughout the ecosystem. Habitat degradation and destruction can lead to changes in the dynamics, distribution and even behaviour of its inhabitants (Field et al. 2009). After overexploitation, habitat destruction is the second largest threat to species depletion (Lotze et al. 2006). The specific threats that lead to habitat degradation and destruction, which can either directly or indirectly alter coastal shark populations include overexploitation and destructive fishing methods, sedimentation, pollution, invasive species, tourism and recreation, and global climate change.

Overexploitation and Destructive Fishing Methods

Overexploitation was discussed in the previous section as a direct threat to the reduction of shark populations by removing them through fishing; however overexploitation can indirectly threaten sharks by aiding in habitat degradation. Overexploitation of a top predator can create a cascade effect down the food web, increasing the prey species of the overexploited predator, which then places greater pressure on other prey species, and this continues until a new equilibrium is reached. This phenomenon is known as trophic cascade and can occur in two directions, top-down or bottom-up. Ultimately loss of predators decreases species richness in many ecosystems, creating an imbalanced system that is more susceptible to collapse (Field et al. 2009; Worm et al. 2006).

Destructive fishing methods such as trawling, dynamite fishing and dredging can dramatically alter habitat structures (Field et al. 2009; Turner et al. 1999). All three of these fishing methods are capable of removing or destroying complex benthic habitats by directly removing biotic species (i.e. corals, sponges, hydroids, bryozoans, and sea grasses) and abiotic features such as sand depressions and boulders (Turner et al. 1999).

Sedimentation

High sediment load and very low sediment loads can cause serious threats to coastal environments (Thrush et al. 2004). However, high sediment loading or sedimentation is a much larger threat for New Zealand coastal areas. Sedimentation describes the process by which suspended particles settle out of a fluid. This settlement often occurs in coastal areas including harbours and estuaries. Deforestation, mining, farming and urbanisation, many kilometres inland, can lead to significant increases in terrestrial sediment deposits in estuaries and harbours (Gray 1997; Thrush et al. 2004; Thrush et al. 2003). Deforestation increases the amount of terrestrial sediment which is prone to runoff from land, rivers and landslides, especially during storm events (Gray 1997). The result is the smothering of estuarine and marine sediments and benthic communities (Gray 1997; Thrush et al. 2004; Thrush et al. 2003). In manipulative experiments of the Whitford embayment, New Zealand, only 3 mm of terrestrial sediment was enough to cause significant changes in macrobenthic community structure, additionally they found that small repetitive amounts of sedimentation can be more harmful than large events (Lohrer et al. 2004).

Increased turbidity from sediment loading can drastically alter estuarine ecosystems by blocking sunlight from plants and phytoplankton which rely on photosynthesis for survival (Thrush et al. 2004). In addition, inorganic silts and clays can have a negative effect on suspension-feeders, further reducing water quality (Gray 1997; Thrush et al. 2004). Increased turbidity from sedimentation can directly affect sharks by making it difficult for them to find prey, however increased turbidity may also decrease the risk of juvenile sharks from predation by larger fish while within estuaries. Sedimentation can also have an indirect effect on shark populations by altering the ecosystem in such a way to cause top-down and/or bottom up trophic cascades.

Pollution

There are several ways pollutants can affect the marine environment. Pollutants can cause changes in the physical properties of the environment, cause eutrophication, poison the environment or spread pathogens (Field et al. 2009). Often pollutants have multiple effects, such as excess nutrients or sewage disposal which contains harmful toxins that cause eutrophication resulting in oxygen depletion, which can range in effects from changing species compositions to mass mortalities depending on the severity (Field et al. 2009; Gray 1997).

Chondrichthyans are known to bio-accumulate heavy metals such as mercury, especially for coastal species living in shallow turbid estuaries (Field et al. 2009). Heavy metals and organic chemicals can adversely affect shark populations, often altering the endocrine system and decreasing reproductive output (Field et al. 2009; Gray 1997; Betka and Callard 1999; Gelsleichter et al. 2005). Sedimentation, while a pollutant in itself causing physical changes to the environment is also known to exacerbate heavy metal and organic chemical pollution when runoff from urban and farmland areas enters waterways.

Marine litter is becoming an increasing problem with plastics accounting for almost 75% (Gray 1997). Styrofoam, metal, glass and wood are the other major contributors to marine litter (Gray 1997). Discarded fishing gear, especially nets (sometimes referred to as ghost netting), can be harmful as they may continue fish the sea for many years (Matsuoka, Nakashima, and Nagasawa 2005; Stevens et al. 2005).

Oil spills and leaks can be harmful for marine species. Other environmental pollutants include thermal outflows and discharges and artificial electro-magnetic fields which can alter shark behaviour by disrupting their ability to search for prey (Field et al. 2009).

Invasive Species

New Zealand terrestrial species have been combating introduced predators for decades, yet a less visible problem is the introduction of marine species often carried over in ship ballasts. Invasive species can be seen as a form of pollutant as they can carry diseases and alter entire trophic webs (Field et al. 2009; Gray 1997; Stevens et al. 2005). This may not directly affect shark populations but invasive species can weaken ecosystems making them less resilient (Field et al. 2009; Stevens et al. 2005).

Tourism and Recreation

Tourism pressure exacerbates coastal habitat degradation and destruction. The construction of hotels and harbours for tourism is responsible for destroying many coastal habitats such as mangroves, wetlands and estuaries. The increase of humans in a tourist area can cause further degradation to habitats (i.e. trampling of coral reefs). Increased boat traffic in harbours and estuaries has been known to negatively affect marine species. Tourist operations targeting dolphin and whale populations have been known to alter the behaviour of these animals. In New Zealand tourist operators must follow specific protocols when approaching marine mammals (Tizard 1992); yet there are no regulations for tourism operations affecting shark populations. Cage diving operations targeting the endangered white shark (*Carcharodon carcharias*) in New Zealand occur largely unregulated. Recreational fishing in harbours and estuaries can also have negative effects on shark populations and the ecosystem.

Global Climate Change

Global climate change is likely to exacerbate habitat change by increasing species ranges and allowing invasive species to spread more easily. It also exacerbates sedimentation in coastal areas by increasing the number and severity of storms. Global climate change may not directly affect shark populations but it can indirectly influence important ecosystems

Mitigating Habitat Degradation and Destruction

One option for mitigating habitat degradation is to create Marine Protected Areas (MPA) (Kingsford et al. 2009). MPA's are most effective for coastal resident sharks (or certain age/size classes) that have small home range sizes, for example, creating MPA's to protect shark nursery habitats. MPA's are not as effective for managing pelagic species of sharks and when used to protect nursery habitats, other measures such as size and catch limits should be used in conjunction with MPA's to protect older juvenile and adult life stages (Heupel, Carlson, and Simpfendorfer 2007; Kinney and Simpfendorfer 2009). The New Zealand government has created over 30 marine reserves; including one of the oldest no-take marine reserves in the world (Cape Rodney-Okakari Point Marine Reserve, also known as Goat Island and Leigh Marine Reserve, established in 1975). These marine reserves make up 7% of New Zealand's territorial sea and only 0.3% of New Zealand's total marine environment, not including trawling closures (DOC 2012). In addition, the government has restricted set nets at the entrances of several harbours and has set up Benthic Protection Areas (BPA) where bottom trawling and dredging are prohibited. Future conservation efforts should concentrate on areas of important shark habitat, including nursery and foraging grounds. Focus is also needed on reducing anthropogenic threats such as fishing pressures, pollution, sedimentation, introduced species and the effects of tourism and recreation through better management and regulations.

1.3 Study Species: Rig (*Mustelus lenticulatus*)

Mustelus lenticulatus is a small coastal shark species from the Triakidae family. It is commonly referred to in New Zealand as rig, spotted smooth-hound or gummy shark (the last is the common name for the best known Australian relative *Mustelus antarcticus*). Rig is often marketed under the name lemon fish and is commonly sold as fish and chips (Ayling and Cox 1984). Depending on the area, Māori names referring to rig include kapetā, mangō, makoo and pioke, however they may also refer to other species such as school shark and spiny dogfish (Ministry of Fisheries 2011; Miru 2011).

TAXONOMY, MORPHOLOGY AND IDENTIFICATION

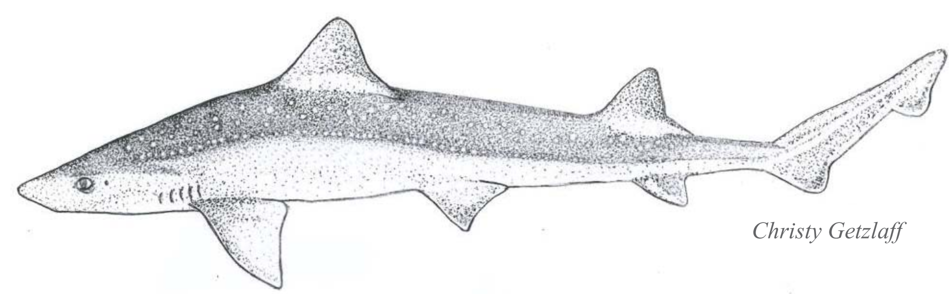


Figure 1.1: Author's illustration of Rig (*Mustelus lenticulatus*).

Kingdom:	Animalia
Phylum:	Chordata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Order:	Carcharhiniformes
Family:	Triakidae
Genus:	*Mustelus*
Species:	*M. lenticulatus*

Rig are small slender sharks, grey or bronze in colour gradually becoming lighter ventrally. They have numerous white spots on their dorsal surface and along their lateral lines. *Mustelus* spp. have a type two body form, described as having a ventrally flattened head and body surface, large pectoral fins, lower heterocercal tail angle, moderate pelvic, second dorsal and anal fins (Carrier, Musick, and Heithaus 2004, Chapter 5). According to Compagno (1990) smooth-hounds belong to the cancritrophic (having a diet consisting of Crustacea) littoral ecomorphotype. Sharks within this ecomorphotype are known for having strong jaws and small cutting or crushing teeth designed to feed on decapod crustaceans but may also feed on other benthic invertebrates or fish (Compagno 1990). Littoral sharks are active swimmers but can rest on the bottom (Compagno 1990). New Zealand rig were described as a species in 1932 by W. J. Phillipps, who named them *Mustelus lenticulatus*. The key morphological differences distinguishing *M. lenticulatus* from *M. antarcticus* include: gill slits that first increase in size and then decrease quite suddenly, third gill slit being the largest; an upper caudal lobe that is approximately equal in length to the head length (distance from snout to the last gill slit)(Phillipps 1932).

Rig are genetically distinct from the closely related Australian gummy shark (*M. antarcticus*). Allozyme, restriction enzyme analyses, mtDNA and morphology (number of pre-vertebral counts) fix for a haplotype that is very rare in *M. antarcticus*, confirming *M. lenticulatus* as a distinct species (Gardner and Ward 2002; Smith 1986).

DISTRIBUTION

Rig are endemic to New Zealand, closely related species occur in Norfolk Island and the Kermadec Islands (Francis pers. comm.). Movements of rig within New Zealand waters are known from tag and release studies of rig from the South Island and south-west North Island during the 1980's. Female rig travelled further than males (52% of females travelled more than 200 km 20 days after tagging, while only 15% of males travelled the same distance) and over half of the recaptured rig travelled more than 50 km from their tagging site (Francis 1988). The maximum average distance travelled per day was 21.1 km by a mature male, however most rig did not travel more than 7 km per day on average (Francis 1988). Rig tagged in 1978-1988 revealed that even after five years at liberty, most males were recaptured within one Quota Management Area (QMA, see Figure 1.2, Francis 2010). Females were more mobile and approximately 30% moved outside of the release QMA within 2-5 years of being tagged (Francis 2010).

Raglan and Kaipara harbours on the North Island's west coast had the highest numbers in a recent survey of juvenile rig (Francis et al. 2012). It is still not known where most of the South Island rig populations pup but this may be able to be determined through further tagging studies. Tagging studies of juveniles while within their nursery area would be useful to determine whether rig are philopatric (i.e. if they return to their natal estuary). Tagging would also be useful in determining which fish stocks the juveniles enter when they leave the estuaries.

Graham (1956) described finding rig throughout Otago Harbour, saying they were caught on rocky, sandy or muddy bottoms. A recent acoustic tagging study of juvenile rig from Porirua Harbour, Wellington discovered that rig moved into deeper water during the day and shallower areas at night, presumably to feed (Francis pers. comm.).

COMMERCIAL AND RECREATIONAL FISHING

Fisheries in New Zealand are managed under the Fisheries Act 1996 (MFISH 2008). The Ministry of Agriculture and Fisheries (MAF) is the government organisation responsible for providing fisheries management advice to the New Zealand Government as of 1 July 2011 (prior to this it was the Ministry of Fisheries; MFISH). Rig (*Mustelus lenticulatus*) is fished commercially throughout New Zealand (Blackwell and Francis 2010). Target set netting and bycatch from trawling are the two most common fishing methods for rig. Prior to 1986, 80% of rig were caught by set nets however in recent decades the number of rig caught by trawlers as bycatch has increased (Ministry of Fisheries 2011).

Prior to the 1940's, reported landings of rig were less than 200 t per year (Francis 1998). A steady increase of rig landings occurred during the 1950s and 1960s after which rig landings increased rapidly in the 1970s and early 1980s (Francis 1998). 1983 saw a peak landing of rig (3800 t) after which landings declined (Francis 1998). The

Quota Management System (QMS) was introduced in 1986 and a conservative Total Allowable Commercial Catch (TACC) was set low at 1420 t to allow for stock recruitment (Francis 1998; Francis and Ó'Maolagáin 2000; Ministry of Fisheries 2011). As of 2009/10 total TACC was set at 1919 t and the total landings for the year was 1262 t (Ministry of Fisheries 2011). Individual stock TACs were based on absolute biomass estimates from tag-recapture programs or on the proportion of recent landings (Francis 1998). For details about TACC and reported landings for fishing years between 1986-97 to 2009-10 refer to the Ministry of Fisheries Rig (SPO) assessment report (2011).

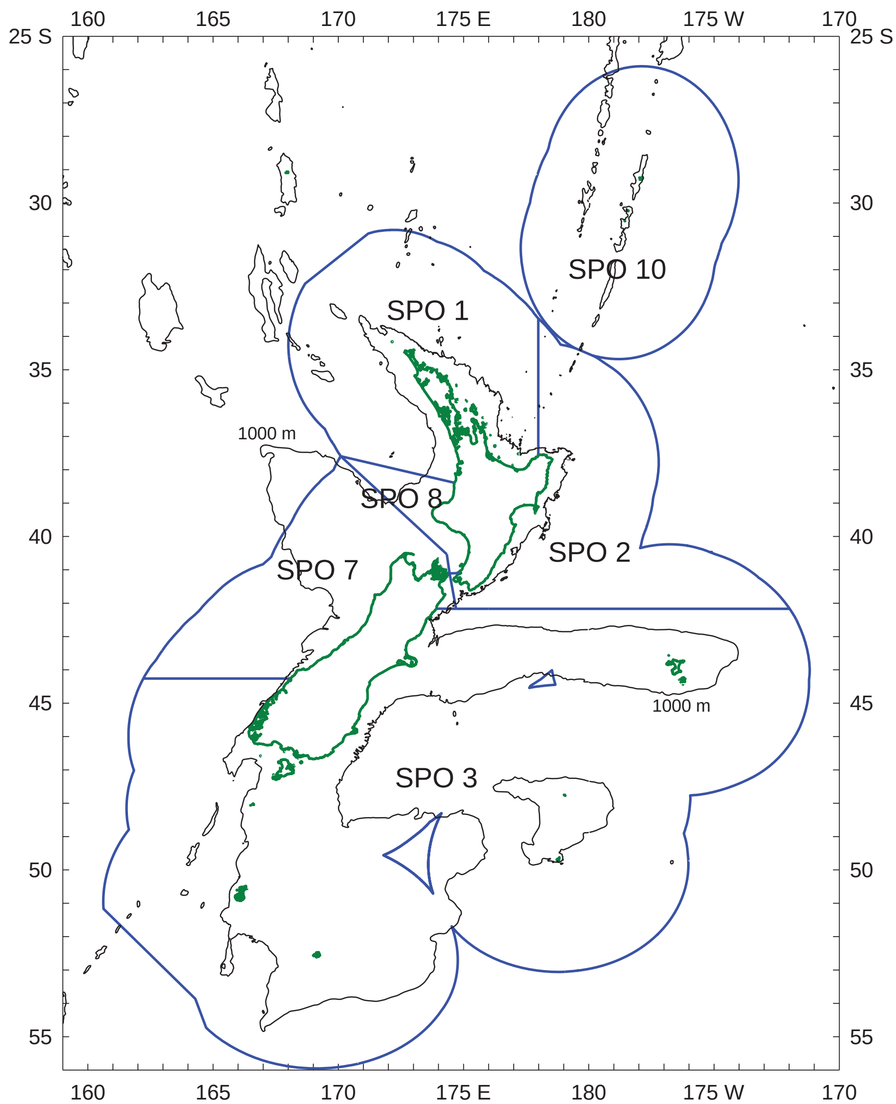


Figure 1.2: Rig (*Mustelus lenticulatus*) Quota Management Areas taken from Francis et al. in press. SPO is the three letter code for rig (spotted dogfish).

The recreational daily bag limit on rig ranges between 5 and 20 per person depending on the region. Rig caught by recreational fishers was reported as less than 15% of the total rig harvest between 1991 and 1994 (MFISH 2008). During the 1999-2000 fishing year, an estimated 86-190 t of rig were caught by recreational fishers (MFISH 2008). Historically, Māori fishers were known to catch large numbers of 'dogfish' (dogfish most likely included rig, school shark and spiny dogfish) but their major fishing expeditions died out early this century and the current Māori customary take of rig is not known (Francis 1998; MFISH 2008).

Peak rig landings in the early 1980s were caused by several factors. First, better fishing technology (i.e. the introduction of monofilament set nets) led to an increase in fishing effort. The switch to set nets was so swift that by the early 1980s more than 80% of rig were being caught in set nets compared to the 1950s and 1960s when more than 80% of rig were being caught as by-catch in trawl fisheries. Second, there was an increase in demand for rig in New Zealand and Australia. Australia's demand for rig was in response to a ban on school shark because of high mercury levels. Last, a reduction in other inshore fish species led to many fishers targeting rig (Francis 1998).

Due to rig's spring-summer inshore migrations (see below), important target set net fisheries exist at Ninety Mile Beach, Kaipara, Manukau and Raglan harbours, Hauraki Gulf, South Taranaki Bight, Tasman and Golden bays, Canterbury Bight, west coast South Island and Kaikoura (Blackwell and Francis 2010). During the 80's, most of the landings came from rig migrating to and from these breeding/pupping sites (Francis 1998; Ministry of Fisheries 2011). Target set net fisheries continue to concentrate their landings during spring-summer (Francis 1998) however there are areas where set nets are banned by MAF. The marine mammal sanctuary at Banks Peninsula covers 389 kilometres of coastline extending 12 nautical miles to sea and has a year round ban on amateur set netting and restrictions on commercial set netting and trawling. The West Coast North Island marine mammal sanctuary covers 2,164 kilometres of coastline to 12 nautical miles (DOC 2012). Although these areas were created for the protection of marine mammals such as the Hector and Maui dolphins (*Cephalorhynchus hectori*) and the southern right whale (*Eubalaena australis*), they also benefit coastal sharks such as rig. For information on the marine mammal sanctuaries refer to the Department of

Conservation website at http://www.doc.govt.nz/conservation/marine-and-coastal/marine-protected-areas/marine-mammal-sanctuaries/ or see the MAF website for fishing restrictions.

LIFE HISTORY OF RIG

Reproduction

Rig are aplacental viviparous and parturition occurs between late October and early December (Francis and Francis 1992), with a gestation period of 10-11 months (Francis and Mace 1980; Ministry of Fisheries 2011). The average number of eggs or embryos of rig from Kaikoura and Nelson was 10.7 (Francis and Mace 1980), while the maximum number of embryos found in a single rig was 37 embryos (Francis 1997; cited in Francis and Ó'Maolagáin 2000). Francis and Mace (1980) found that larger female rig had larger litters.

Female rig give birth to young in or near estuaries and large harbours and young are between 25-35 cm total length at birth (Francis and Mace 1980; Francis and Francis 1992). These new-born rig (also referred as young of the year, YOY, or 0+) spend their first 6-8 months living in estuaries and harbours until autumn or winter when they leave (Francis and Francis 1992). Mature male rig start entering harbours and estuaries in October-November. It is still unknown whether adult rig show breeding site fidelity.

Age, Growth and Maturity

Data on age, growth and maturity of rig are limited to only three fish stocks (SPO 1, 3 and 7, see Figure 1.2). SPO 7 covers most of the west coast South Island while SPO 3 covers the rest of the South Island coast including the Chatham Rise. The age and size at maturity of rig from the South Island were estimated at about 5-6 years and 85 cm total length for males and about 7-8 years and 100 cm total length for females (Francis and Francis 1992; Francis and Ó'Maolagáin 2000). Rig from SPO 1 East (Hauraki Gulf), seemed to mature at younger ages and smaller sizes (males at 4 years and about 72 cm, females at 5 years and about 82 cm total length) (Francis and Francis 1992). It is possible that different food sources, temperature, or population genetics could result in different growth rates and age at maturity.

Rig, as with other shark species, are difficult to age because they lack bony skeletons. Growth rates are also difficult to calculate because there are few data on the size at birth. Due to the lack of data, varying methods for calculating age and growth rate and bias in certain sampling methods, and studies estimating age and size at various life stages aren't always consistent. While one study analysing length-frequency and tag-recapture data found growth rates of female rig to be significantly higher than male rig from the South Island (Francis and Francis 1992), Francis and Ó'Maolagáin (2000) analysed the growth rings on rig vertebrae and found no significant differences between male and female growth rates from west coast South Island and no significant difference between growth rates between South Island's east and west coasts.

Average life expectancy for rig is still undetermined however Francis and Ó'Maolagáin (2000) stated that it is probably more than 15 years and may be longer than 20. A tagged male was at liberty for 13.8 years and was estimated to be 19.5 years old at recapture (Francis and Ó'Maolagáin 2000). The maximum lengths of rig recorded by Francis and Ó Maolagáin (2000) were 151 cm for females and 126 cm for males.

Natural Predators

Rig are a relatively small-sized shark, which increases their risk of predation by many larger fish species (Speed et al. 2010) and the predation risk increases even more for juveniles. Graham (1939, 1956) recorded rig in the stomachs of red cod (*Pseudophycis bachus*), bass (*Polyprion americanus*) and porbeagle sharks (*Lamna nasus*). King and Clark (1984) suggested that rig have few natural predators since their study found no rig in the stomachs of spiny dogfish (*Squalus acanthias*), northern spiny dogfish (*Squalus griffini*), thresher shark (*Alopias vulpinus*), bronze whaler (*Carcharhinus brachyurus*), carpet shark (*Cephalosycllium isabella*), school shark (*Galeorhinus galeus*), seven gill shark (*Heptranchias perlo*) and blue shark (*Prionace glauca*) caught in set nets alongside rig (King and Clark 1984).

While there are few records of rig predators in New Zealand, there are several records of smooth-hound predators in other parts of the world, some of which are found in New Zealand (Barnett et al. 2010; Lucifora et al. 2006; Barnett and Semmens 2011). Barnett et al. (2010) stated that the main prey item for broadnose sevengill sharks (*Notorynchus cepedianus*) are sharks from the genus *Mustelus*. Lucifora et al. (2006) examined school sharks (*Galeorhinus galeus*) from Anegada Bay, Argentina from October to April during 1998-2001 and found that both juveniles and adults consumed *M. schmitti* (0.11 % Index of Relative Importance and 0.02 %IRI respectively). Lucifora et al. (2005) studied the diet of the broadnose sevengill shark in the same bay in Argentina and found that sharks above 100 cm total length consumed *M. schmitti* (25.6 %IRI for sharks between 100-170 cm total length and 2.05 %IRI for sharks above 170 cm total length). The level of predation on rig in New Zealand is largely unknown, especially for juvenile rig living in harbours and estuaries. It is important to know the proportion of juvenile mortality that is attributed to natural predators in order to properly assess rig populations.

Diet

Diet of *Mustelus lenticulatus*

King and Clark (1984) published the most comprehensive description of diet of *Mustelus lenticulatus* from Golden Bay, New Zealand. They caught over 400 rig in commercial set nets between November 1979 and March 1981. They concluded that rig were opportunistic feeders, preying on slow moving benthic invertebrates. They also found that juveniles typically fed on smaller organisms such as pagurids (hermit crabs), *Nectocarcinus antarcticus* (paddle crab) and *Urechis novaezealandiae* (spoon worm).

Thomson and Anderton (1921), described rig from Otago Harbour as foraging near the bottom and 'groping' along banks, feeding primarily on crustaceans and polychaetes. They found the most common food for rig were crabs (*Cancer, Cyclograpsus, Nectocarcinus,* and *Ommatocarcinus*), crayfish (*Jasus*), shrimps (*Pontophilus*), mantis shrimp (*Squilla)*, whale-feed (*Munida)*, and isopods. Polychaetes were found less commonly and occasionally octopus were found in rig stomachs. According to Graham

(1939, 1956) rig's favourite (i.e. most abundant) food item from Blueskin Bay and Otago Harbour was the hairy-handed mud crab (*Hemigrapsus crenulatus*), however they also ate two species of fish (sprat and flathead), four species of molluscs (octopus, squid, *Maorimactra ordinaria*, *Zethalia zelandica*), ten species or groups of Brachyura (*Halicarcinus* spp., *Hombronia depressa*, *Cancer novaezealandiae*, *Nectocarcinus antarcticus*, *Ommatocarcinus macgillivrayi*, *Hemigrapsus sexdentatus*, *Hemigrapsus crenulatus*, *Cyclograpsus lavauxi*, *Helice crassa*, *Petrolisthes* spp.), seven species or groups of other crustaceans (*Squilla armata*, *Munida gregaria*, *Jasus lalandii*, *Philocheras australis*, *Alope spinifrons*, other Isopoda, *Exosphaeroma gigas*), six species of Annelida (*Glycera americana*, *Perinereis vallata*, *Lumbrineris sphaerocephala*, *Aphrodite talpa*, *Phycosoma annulata*, *Hemipodia simplex*), and one Echinoderm (*Cucumaria* sp.).

The only early account of contents of a juvenile rig stomach is from Webb (1972), who caught a juvenile male rig (32 cm total length) in Moncks Bay, near the mouth of Avon-Heathcote Estuary in 1965-66, which contained six crabs (*Hemigrapsus* sp.).

Diet of Young of the Year (YOY) Smooth-hounds

Most diet studies for smooth-hound (*Mustelus* spp.) and other sharks have separated sharks into different size classes rather than age classes (Smale and Compagno 1997; Morte, Redon, and SanzBrau 1997; Lipej et al. 2011; Saidi, Bradai, and Bouain 2009; Saidi et al. 2009; Kamura and Hashimoto 2004; Yamaguchi and Taniuchi 2000; Filiz 2009; Navia, Mejia-Falla, and Giraldo 2007; Talent 1982; Galván-Magaña, Nienhuis, and Klimley 1989). However, there are a few studies regarding smooth-hounds that describe the diets of YOY individuals (Chiaramonte and Pettovello 2000; Molina and Cazorla 2011; Van der Molen and Caille 2001; Rountree and Able 1996; Woodland, Secor, and Wedge 2011; Stevens and West 1997). Refer to Table 1.1 for a summary of juvenile smooth-hound diets.

Crustaceans were an important part of the diet for most YOY smooth-hounds, often present in more than half of the stomachs and representing more than half of the weight. Within the Crustacea, brachyurans were the group found most frequently in the diet of YOY *Mustelus* spp. The only exceptions were two studies of *M. schmitti*

Table 1.1: Summary of prey groups of juvenile *Mustelus* spp. measured as (A) percent frequency, (B) percent number, (C) percent weight, and (D) percent index of relative importance.

A

Species	Location	Citation	Age or Size	n	**Crustaceans**	Amphipods	Isopods	Stomatopod	Brachyura	Anomura	Shrimps	**Molluscs**	Cephalopods	Gastropoda	Bivalvia	**Fishes**	**Polychaetes**
M. antarcticus	Eastern Australia	Stevens & West 1997	YOY	9													
M. schmitti	Southern Patagonia, Argentina	Chiaromonte & Pettovello 2000	YOY	11	N/A			N/A		N/A		N/A		N/A	N/A		
M. schmitti	Anegada Bay, Argentina	Molina & Cazorla 2011	YOY	29													
M. schmitti	Bahia Engano, Argentina	Van der Molen & Caille 2001	YOY	65						N/A		N/A		N/A	N/A		
M. canis	Little Egg harbour-Great Bay, NJ, USA	Rountree & Able 1996	YOY	85		N/A		N/A				N/A	N/A	N/A			
M. mustelus	*Cape, South Africa (south coast)*	Smale & Campagno 1997	<60 cm	49		N/A	N/A	N/A				N/A		N/A	N/A		
M. palumbes	*Cape, South Africa (south coast)*	Smale & Campagno 1997	<60 cm	16										N/A	N/A		
M. palumbes	Cape, South Africa (west coast)	Smale & Campagno 1997	<60 cm	44		N/A	N/A		N/A			N/A	N/A	N/A	N/A		

50-100%
10-49%
<10%
0

B

Species	Location	Citation	Age or Size	n	**Crustaceans**	Amphipods	Isopods	Stomatopod	Brachyura	Anomura	Shrimps	**Molluscs**	Cephalopods	Gastropoda	Bivalvia	**Fishes**	**Polychaetes**
M. antarcticus	Eastern Australia	Stevens & West 1997	YOY	9													
M. schmitti	Anegada Bay, Argentina	Molina & Cazorla 2011	YOY	29													
M. mustelus	Gulf of Valencia, Western	Morte et al. 1997	≤50 cm	N/A		N/A	N/A			N/A			N/A	N/A	N/A		N/A
M. mustelus	Cape, South Africa (south coast)	Smale & Campagno 1997	<60 cm	49													
M. palumbes	Cape, South Africa (south coast)	Smale & Campagno 1997	<60 cm	16													
M. palumbes	Cape, South Africa (west coast)	Smale & Campagno 1997	<60 cm	44													

50-100%
10-49%
<10%
0

C

Species	Location	Citation	Age or Size	n	**Crustaceans**	Amphipods	Isopods	Stomatopod	Brachyura	Anomura	Shrimps	**Molluscs**	Cephalopods	Gastropoda	Bivalvia	**Fishes**	**Polychaetes**
M. antarcticus	Eastern Australia	Stevens & West 1997	YOY	9													
M. schmitti	Anegada Bay, Argentina	Molina & Cazorla 2011	YOY	29													
M. canis	Mid Atlantic Bight, Maryland, USA	Woodland et al. 2011	YOY	22			N/A	N/A									
M. griseus	Central Seto Inland Sea, Japan	Kamura & Hashimoto 2004	<50 cm	41		N/A	N/A					N/A		N/A	N/A		
M. manazo	Central Seto Inland Sea, Japan	Kamura & Hashimoto 2005	<50 cm	20		N/A	N/A					N/A		N/A	N/A		
M. manazo	Tokyo Bay, Japan	Yamaguichi & Taniuchi 2000	<40 cm	N/A		N/A	N/A						N/A	N/A	N/A		
M. manazo	Maziuru, Japan	Yamaguichi & Taniuchi 2000	<50 cm	N/A		N/A	N/A						N/A	N/A	N/A		
M. mustelus	Cape, South Africa (south coast)	Smale & Campagno 1997	<60 cm	49													
M. mustelus	*Cape, South Africa (Langebaan Lagoon)*	Smale & Campagno 1997	<60 cm	49		N/A	N/A	N/A	N/A	N/A	N/A	N/A		N/A	N/A		
M. palumbes	Cape, South Africa (south coast)	Smale & Campagno 1997	<60 cm	16													
M. palumbes	Cape, South Africa (west coast)	Smale & Campagno 1997	<60 cm	44													

50-100%
10-49%
<10%
0

D

Species	Location	Citation	Age or Size	n	**Crustaceans**	Amphipods	Isopods	Stomatopod	Brachyura	Anomura	Shrimps	**Molluscs**	Cephalopods	Gastropoda	Bivalvia	**Fishes**	**Polychaetes**
M. schmitti	Anegada Bay, Argentina	Molina & Cazorla 2011	YOY	29													
M. mustelus	Gulf of Gabes, Central	Saidi et al. 2009a	<50 cm	158		N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	*	N/A
M. punctulatus	Gulf of Gaves, Central	Saidi et al. 2009b	<50 cm	9		N/A	N/A	N/A	N/A	N/A	N/A		N/A	N/A	N/A	N/A	N/A
M. punctulatus	Gulf of Trieste, Southern Adriatic	Lipej et al. 2011	<60 cm	N/A		N/A	N/A	N/A	N/A	N/A	N/A	N/A		N/A			

** M. mustelus diet from Saidi et al. 2009a from Figure 3 shows Teleosts in the newborn diet however in the text, newborn diets are described as not having teleosts.*

	50-100%
	10-49%
	<10%
	0

from northern and southern Patagonia where shrimp were found more frequently in the diet than Brachyura (Chiaramonte and Pettovello 2000; Van der Molen and Caille 2001) and one study of *M. palumbes* under 60 cm from Cape West Coast, South Africa, where mantis shrimp *Pterygosquilla armata capensis* was the most frequent crustacean, followed by Anomura (Smale and Compagno 1997). While amphipods and isopods were present in the diet of young smooth-hounds, they rarely exceeded ten percent of the total weight or number of prey.

Molluscs occur in the diet of many juvenile smooth-hounds. Cephalopods were present in some juvenile *M. canis, M. schmitti, M. mustelus, M. palumbes,* and *M. punctulatus* diets. Young of the year *M. schmitti, M. canis*, and *M. punctulatus* diets contained a small proportion of bivalves and very few gastropods were found in the diet of YOY smooth-hounds.

Polychaetes were present in almost all diet studies of YOY smooth-hounds. Most diet studies found YOY smooth-hounds to contain a small proportion of fish, and the proportion of the diet comprising fish typically increased with shark total length. *Mustelus manazo*, *M. griseus, M. lenticulatus, M. antarcticus and M. palumbes* (from one location) were the only species that appeared not to eat fish at a young age (Kamura and Hashimoto 2004; Stevens and West 1997; Smale and Compagno 1997).

Foraging Ecology and Behaviour

Chondrichthyes is a diverse class with many alternative life-histories, including different foraging strategies. Juvenile rig tend to live in turbid muddy estuaries and are assumed to be night foragers, making it difficult to directly observe their foraging behaviour. For this reason, very little is known about their foraging ecology or behaviour in New Zealand harbours and estuaries. Previous diet studies have determined that smooth-hounds specialize in benthic prey, primarily crustaceans.

Sharks use a number of senses to locate prey items including visual, mechanical, chemical, and electrical stimuli (Kalmijn 1971). It is likely that sharks use a combination of these senses rather than relying on one. During a laboratory feeding experiment, chemical stimuli were observed to produce feeding frenzied behaviour of the small-spotted catshark (*Scyliorhinus canicula*) and thornback ray (*Raja clavata*), however, electric fields acted as a stronger, more accurate force than both visual or chemical stimuli (Kalmijn 1971). Electric fields are most likely used in close range prey location since voltage gradients emitted from animals rapidly decrease with increasing distance (Kalmijn 1971). Chemical odours spread gradually through the water column, attracting sharks from greater distances as time goes by. Vision did not appear to be an important sense for the small-spotted catshark or thornback ray (Kalmijn 1971), and this is probably due to the fact that these elasmobranchs are benthic foragers and their prey is often buried in the substrate. Mechanosenses, vibrations detected by the lateral line system, are used by sharks to detect tidal currents and locate prey, predators and conspecifics (Carrier, Musick, and Heithaus 2004, , Chapter 12).

Captive Behaviour Studies and Observations of Smooth-hounds

Smale and Compagno (1997) observed more than 30 *M. mustelus* and five *M. palumbes* in captivity during a five year period. They discovered that individuals often swam within 5 cm of the bottom of the tank, presumably in search of prey. They also noted that the sharks would occasionally swim higher in the water column, at a more rapid speed, usually around the edge of the tank. They observed aggregations of *M. palumbes* in captivity which suggests schooling behaviour.

Gerry and Scott (2010) studied competitive shark foraging behaviour and found that *M. canis* consumes more crabs when foraging in the presence of spiny dogfish (*Squalus acanthias*). Gerry et al. (2008) found that *M. canis* has a distinct biting behaviour in which “all adductor muscle pairs are activated repeatedly and synchronously prior to another activation of the *coracomandibularis*” and the sharks did not tend to change their biting behaviour when fed softer-bodied prey.

Smooth-hounds in Estuaries

Juvenile rig from Porirua Harbour exhibited diel patterns, moving into shallower waters at night (Francis pers. comm.). A study of adult *M. californicus* in the Full Tidal Basin of Bolsa Chica, California also revealed a distinct diel pattern of movement which was influenced by tide. Individuals were observed moving to the outer basin at night especially during outgoing and high tides, yet no diel pattern for depth was observed

(Espinoza, Farrugia, and Lowe 2011). Overall, individuals were most associated with the warmer habitats in the middle of the basin and with mud and eelgrass at night, presumably for foraging (Espinoza, Farrugia, and Lowe 2011).

Today, rig populations appear to be stable, which can be attributed to fishing regulations. During the 80's, rig catch rates declined significantly in many New Zealand fisheries. Many of these populations recovered once rig entered the QMS. However, pressure from habitat degradation (loss of prime nursery habitat and adult foraging and breeding grounds) could trigger another decline in the New Zealand rig population and post hoc monitoring of fisheries often detects declines when it is already too late.

1.4 Study Aims

The Ministry of Fisheries granted the National Institute of Water and Atmospheric Research (NIWA) the ENV2010/05 research contract titled "Habitats of particular significance for fisheries management: shark nursery areas." The overall objective was to "Identify and define important nursery areas for rig." The specific objectives were as follows:

1. Identify, from the literature, important nursery grounds for rig in estuaries around mainland New Zealand.

2. Design and carry out a survey of selected estuaries and harbours around New Zealand to quantify the relative importance of nursery ground areas.

3. Identify threats to these nursery ground areas and recommend mitigation measures.

While NIWA was surveying juvenile rig in estuaries and harbours around New Zealand to identify important nursery grounds and rate their level of importance, I was investigating the role of harbours and estuaries in the life history of rig, particularly focusing on the diet of YOY rig and the effects of sedimentation on their foraging behaviour. The specific aims for Chapters 2 and 3 are as follows:

Chapter 2

- Determine the diet of YOY rig living in New Zealand harbours and estuaries
- Determine differences in diet of YOY rig between sampling locations in relation to physical and environmental variables

Chapter 3:

- Determine the effects of sedimentation on captive YOY rig foraging effort and success
- Describe captive YOY rig foraging behaviour

Chapter 2

Diet of Young of the Year Rig (*Mustelus lenticulatus*) from New Zealand Harbours and Estuaries

2.1 Abstract

Smooth-hounds (*Mustelus* spp.) are known to forage on benthic invertebrates, particularly when young, but prior to this study, little was known about the diet of juvenile rig (*Mustelus lenticulatus*) from New Zealand. Juvenile rig less than one year old caught in New Zealand harbours and estuaries during February/March 2011 fed mainly on benthic crustaceans, especially stalk-eyed mud crabs (*Hemiplax hirtipes*; % Index of Relative Importance [%IRI]=60.90, % Frequency of Occurrence [%F]=86.15) and snapping shrimp (*Alpheus richardsoni*; %IRI=31.60, %F=63.08). The diet of young of the year (YOY) rig varied with location. Of the five major harbours and estuaries sampled, Porirua rig ate mostly crabs while rig from northern harbours and estuaries consumed high numbers of caridean shrimps. Raglan and Porirua Harbours were the only two where rig ate hermit crabs, and Otago Harbour was the only harbour where rig stomachs contained squat lobsters (*Munida gregaria*). Diets in two southern harbours (Porirua and Otago) were the only two to contain the mantis shrimp, *Heterosquilla tricarinata*. Two recently introduced species were found in diets; the Japanese mantis shrimp (*Oratosquilla oratoria*) from Kaipara Harbour and the greentail prawn (*Metapenaeus bennettae*) from Waitemata Harbour and Tamaki Estuary. While there was overlap among the diets of YOY rig from all harbours and estuaries, there appeared to be a slight north to south trend, as well as an east to west trend in the diets. This is most likely explained by the distribution and habitat specificity of prey species.

2.2 Introduction

In response to global concerns about declining shark populations, the Food and Agriculture Organisation (FAO) developed the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) which encourages 'states' to create national plans of action (FAO c. 2010-2012). In 2008, the Ministry of Fisheries (now the Ministry of Agriculture and Forestry) introduced the New Zealand National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks). One aspect within the "Action to improve information" is to identify important shark habitat such as spawning, pupping and nursery grounds (MFISH 2008). In 2010/11 the National Institute of Water and Atmospheric Research (NIWA) was commissioned by the Ministry of Fisheries (now MAF) to identify important nursery areas for rig (*Mustelus lenticulatus*).

Rig is a small coastal shark species from the Triakidae family. It is endemic to New Zealand and is commonly consumed in fish and chips (Ayling and Cox 1984). Adults can be found in many estuaries and harbours during spring and summer where they are known to pup and breed (Francis and Mace 1980). Rig are aplacental viviparous breeders and young are born in or near estuaries and large harbours at 25-35 cm total length (Francis and Francis 1992; Francis and Mace 1980). These new-born rig (also referred to as young of the year [YOY] or 0+ age class) spend the first 6-8 months living in these estuaries and harbours until autumn or winter when they leave (Francis and Francis 1992).

According to Heupel et al. (2007) a nursery area is identified on the basis of three criteria: (1) sharks are more abundant in the area than in other areas, (2) sharks tend to remain or return to the area for long periods, and (3) the area is repeatedly used by sharks year after year. It would appear that some New Zealand harbours and estuaries may act as nursery areas for young rig. There are two main theories as to why sharks and other fish use nursery grounds: (1) reduced risk of predation, and (2) availability of an important food source (Simpfendorfer and Milward 1993; Castro 1993; Heupel and Hueter 2002). It is thought that the risk of predation is the driving factor for young sharks to use shallow nursery habitats (Heupel and Hueter 2002).However, rig do not appear to have many natural predators in New Zealand (King and Clark 1984) and food may be the primary reason young rig remain in harbours and estuaries after birth.

Crustaceans have been well documented as an important part of the diet of smooth-hounds (species from the genus *Mustelus*) world-wide (Smale and Compagno 1997; Morte, Redon, and SanzBrau 1997; Lipej et al. 2011; Saidi, Bradai, and Bouain 2009; Saidi et al. 2009; Kamura and Hashimoto 2004; Yamaguchi and Taniuchi 2000; Filiz 2009; Navia, Mejia-Falla, and Giraldo 2007; Talent 1982; Galván-Magaña, Nienhuis, and Klimley 1989; Molina and Cazorla 2011; Rountree and Able 1996; Chiaramonte and Pettovello 2000; Van der Molen and Caille 2001). Crustaceans were found in more than half of the stomachs and represented more than half of the weight in most smooth-hound diet studies (see Ch1: Table 1.1). Within Crustacea, various crab and shrimp species were often the most important items in YOY smooth-hound diets (Molina and Cazorla 2011; Woodland, Secor, and Wedge 2011; Morte, Redon, and SanzBrau 1997; Van der Molen and Caille 2001; Rountree and Able 1996; Chiaramonte and Pettovello 2000), however mantis shrimps, hermit crabs and even isopods were considered important prey items in some young smooth-hound diets (Stevens and West 1997; Yamaguchi and Taniuchi 2000; Smale and Compagno 1997). Polychaetes were present in almost all diet studies of YOY smooth hounds (Molina and Cazorla 2011; Rountree and Able 1996; Van der Molen and Caille 2001; Compagno 1990; Kamura and Hashimoto 2004; Woodland, Secor, and Wedge 2011; Yamaguchi and Taniuchi 2000; Lipej et al. 2011) and a small proportion of molluscs and fish occur in diets of some YOY smooth-hounds (Lipej et al. 2011; Molina and Cazorla 2011; Woodland, Secor, and Wedge 2011; Yamaguchi and Taniuchi 2000; Rountree and Able 1996; Smale and Compagno 1997; Van der Molen and Caille 2001; Chiaramonte and Pettovello 2000). Table 1.1 from Chapter 1 gives an overview of diet studies of other juvenile *Mustelus* spp.

While it is important to identify areas which are commonly utilised by sharks, determining why an area is important and how it contributes to their success is crucial to the conservation and management of a species. Determining the diet of YOY rig will improve understanding of the biology and the role harbours and estuaries play in rig life history. In the current study, our specific aims were to (1) determine the diet of YOY rig in New Zealand harbours and estuaries, and (2) explain differences in diet of YOY rig between sampling locations in terms of certain physical and biotic factors.

2.3 Materials and Methods

Sampling Area and Fish Capture

Fourteen harbours were surveyed for YOY rig by NIWA in February and March 2011 (see Figure 2.1 and Table 2.1). Sharks were caught using monofilament nylon set nets, 60 x 1.85 m with a 76 mm (3”) stretched mesh size as described by Francis et al. (2012). Environmental variables including temperature, pH, salinity, turbidity, depth, latitude and longitude were collected at each station (Francis et al. 2012).

Once juvenile rig were extracted from nets, they were pithed if necessary, and stored in a cooler while aboard the vessel. On land, rig were transferred to a freezer and kept frozen until stomach analysis was undertaken.

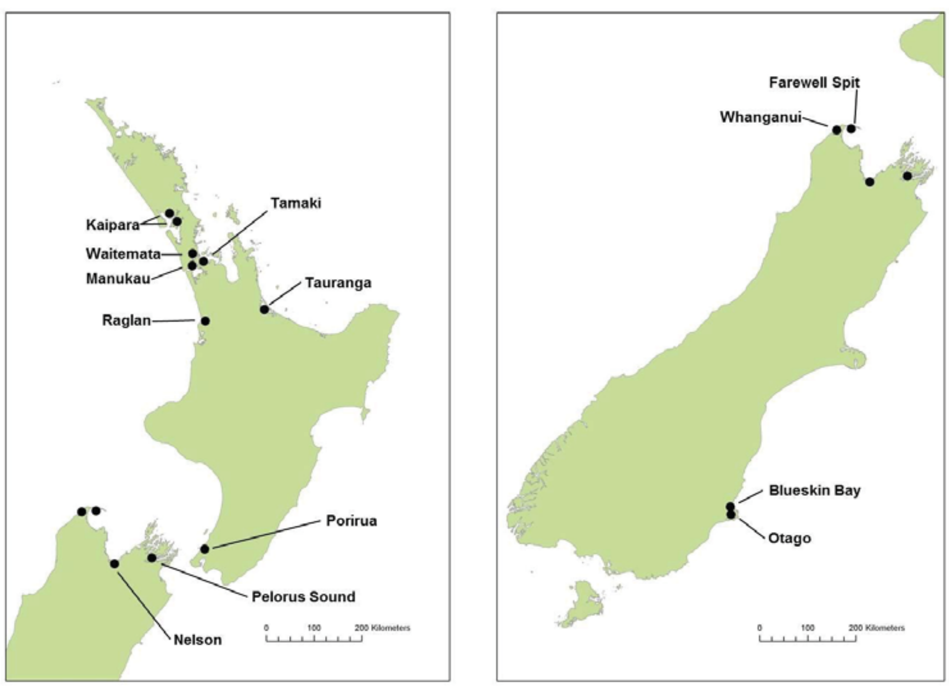


Figure 2.1: Sampling sites for juvenile rig (*Mustelus lenticulatus*). Map provided by NIWA.

Table 2.1: Sampling site details, including sampling dates and environmental characteristics from 14 New Zealand harbours and estuaries sampled during the 2011 Nationwide Rig Survey. See Francis et al. (2012) for further details of sampling methods.

Harbour/ Estuary	Dates Sampled	Latitude (°S)	Longitude (°E)	Depth (m)	Temp (°C)	Salinity (%)	pH	Turb.	Sed. Type*
Kaipara I (Arapaoa River)	9-10 Mar 2011	36.178	174.247	3.3	21.1	3.0	10.0	16.9	SM
Kaipara II (Oruawharo River)	10-14 Mar 2011	36.299	174.351	3.1	21.2	3.1	9.2	16.9	SM
Waitemata Harbour	24-26 Feb 2011	36.785	174.66	4.7	23.0	3.4	8.8	15.3	SM
Tamaki Estuary	2-4 Mar 2011	36.900	174.875	2.8	22.3	3.4	9.5	12.8	SM
Manukau Harbour	28 Feb - 2 Mar 2011	36.959	174.704	2.4	21.7	3.4	9.7	5.9	MS
Tauranga Harbour	18-20 Feb 2011	37.587	176.015	2.2	23.9	3.0	8.6	5.7	MS
Raglan Harbour	15-17 Feb 2011	37.787	174.909	2.3	22.6	3.0	8.3	20.3	SM
Porirua Harbour	8-10 Feb 2011	41.107	174.874	2.2	18.8	3.2	8.2	16.0	M
Farewell Spit & Golden Bay North	3-6 Mar 2011	40.577	172.837	4.0	17.7	3.3	8.2	3.3	S
Whanganui Inlet (Westhaven)	6-8 Mar 2011	40.577	172.59	3.5	16.6	3.3	8.3	6.9	S
Nelson	25-27 Feb 2011	41.277	173.188	3.4	21.5	3.3	8.3	5.2	S
Pelorus/ Kenepuru Sounds	23-25 Feb 2011	41.224	173.908	3.7	18.7	3.2	8.2	15.8	SM
Blueskin Bay	15-16 Feb 2011	45.734	170.594	2.0	15.6	3.2	8.2	3.6	SSH
Otago Harbour	17-19 Feb 2011	45.845	170.609	3.1	17.2	3.2	8.4	6.8	MS

**Sediment type was measured using a six-point scale: muddy (M), sandy mud (SM), muddy sand (MS), sand (S), sand and shell (SSH), and shell (SH).*

Stomach Contents and Analysis

Measurements of total length, first dorsal length, head length, pre-orbital length, pre-oral length, mouth width, mouth depth and total weight were taken from defrosted rig (Figure 2.2). Rig are known to shrink when frozen and thawed (Jones and Hadfield 1985). As time constraints prevented us from collecting external measurements on all juvenile rig at the time of capture, a sample of 13 YOY rig from Tamaki Estuary were measured before and after freezing to determine the amount of shrinkage that occurred. This shrinkage (2.29 ± 0.25%, Mean ± SEM) was used to estimate the total length at capture (ETL).

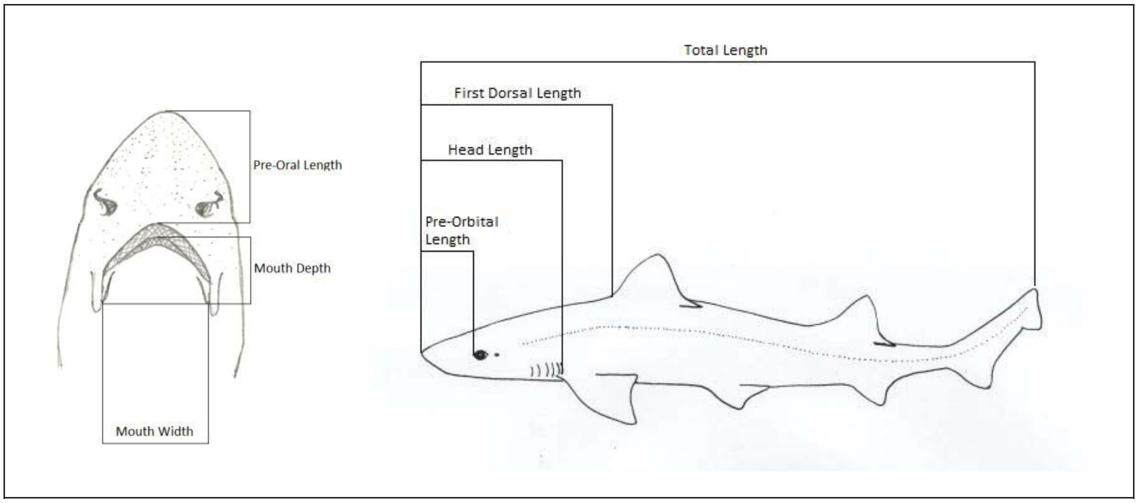


Figure 2.2: Physical measurements of rig sharks used within current study.

The abdominal cavity was cut open from anus to pectoral girdle and stomach fullness was estimated by eye using a four-point scale (1=0-25%, 2=26-50%, 3=51-75%, 4=76-100%). The liver was excised and weighed. The stomach was excised by cutting cranial to the oesophagus and caudal to the pyloric valve. The weight of the stomach contents was determined by weighing the stomach with contents intact and subtracting the weight of the empty stomach. Stomach contents were gently washed through a 500 µm sieve and prey items were identified to the lowest possible taxon, using a dissecting microscope when necessary. Most prey items were identified to species level, except polychaetes which were identified to Family level and isopods and amphipods which were identified to Order level.

Number (N) and mass (W) of prey items were recorded for individual rig stomachs. From these data, frequency of occurrence (F) of prey items was calculated, and these three measurements (N,W and F) were used to calculate the index of relative importance (IRI) using the following equation,

IRI = %F(%N + %W) (after Cortés 1997).

The result was converted to a percentage (%IRI). Parasites and particles were removed from IRI for YOY rig diets and analysed separately. In addition, items in the stomach were assigned a state of digestion according to the six-point scale from Filiz (2009), one meaning fresh prey items and six meaning a completely digested, empty stomach.

In order to determine whether sample sizes were large enough to adequately describe the diet of rig for each estuary, prey accumulation curves and prey diversity curves were constructed, randomizing the order of stomachs 100 times. The prey accumulation curve plots the cumulative number of prey species against sampling effort (in this study, each stomach represents one sampling effort). In contrast, the prey diversity curve plots a diversity index against sampling effort. In this study, we used the Brillouin Index of Diversity after Koen Alonso et al. (2002). Diversity indices take into account both occurrence and abundance of prey items. Prey accumulation curves tending towards an asymptote were considered to have a sufficiently large sample size to adequately describe the diet, while prey diversity curves which tend towards an asymptote indicate a sample size large enough to adequately describe the most important parts of the diet.

Community analysis (ordinations) of YOY rig diets was carried out using Primer-E version 6.1.13. Ordination is a type of multivariate analysis which maps samples in two or three dimensions, where the distance between samples reflects the values from a (dis)similarity matrix. For this study we used the Bray-Curtis dissimilarity matrix.

Only identifiable prey items were used for prey accumulation curves, prey diversity curves and ordination analysis. Vegetable matter and molluscs were excluded since the level of identification was low and these items are most likely incidentally ingested. Means are given with standard errors throughout.

2.4 Results

Sample Characteristics

Young of the year rig were caught in eight of the thirteen harbours surveyed (Table 2.2). From these eight harbours, 137 YOY rig were randomly selected for analysis with the goal of analysing at least 20 sharks from each harbour or estuary (physical measurements of rig and stomach contents can be found in the Appendix A, Table 2.1). Sixty-eight of the sub-sampled rig were female with ETL 34.4–47.2 cm (33.6 - 46.1 cm defrosted TL; Figure 2.3), and 68 were male, ranging in size from 28.1 to 49.6 cm ETL (27.5 – 48.5 cm defrosted TL; Figure 2.3) and one shark of undetermined sex measured 43.8 ETL (42.8 cm defrosted TL). The weight of these sharks ranged from 75–402 g with an average weight of 255.6 g ± 4.7. No significant differences were found between male and female estimated total lengths (Mann-Whitney Rank Sum Test: U=1311.5,

Table 2.2: Summary of rig captures by location. Numbers in parentheses represent empty or decomposed stomachs which were not included in the diet analysis.

HARBOUR/ ESTUARY	NO. OF YOY RIG CAUGHT	NO. OF STOMACHS EXAMINED
Kaipara I (Arapaoa River)	288	13 (2)
Kaipara II (Oruawharo River)	118	8
Waitemata Harbour	33	22 (3)
Tamaki Estuary	35	21
Manukau Harbour	3	3
Tauranga Harbour	0	0
Raglan Harbour	186	19 (1)
Porirua Harbour	51	32 (1)
Farewell Spit and Golden Bay North	0	0
Whanganui Inlet (Westhaven)	0	0
Nelson	0	0
Pelorus/ Kenepuru Sounds	2	2
Blueskin Bay	0	0
Otago Harbour	10	9
TOTALS	726	130 (7)

T=3299.5, P=0.110). It is possible that five individuals used for analysis were not young of the year since their estimated total lengths were greater than 46 cm (Figures 2.3 & 2.4), which was determined to be the maximum length of YOY individuals caught during the 2011 rig survey (Francis et al. 2012).

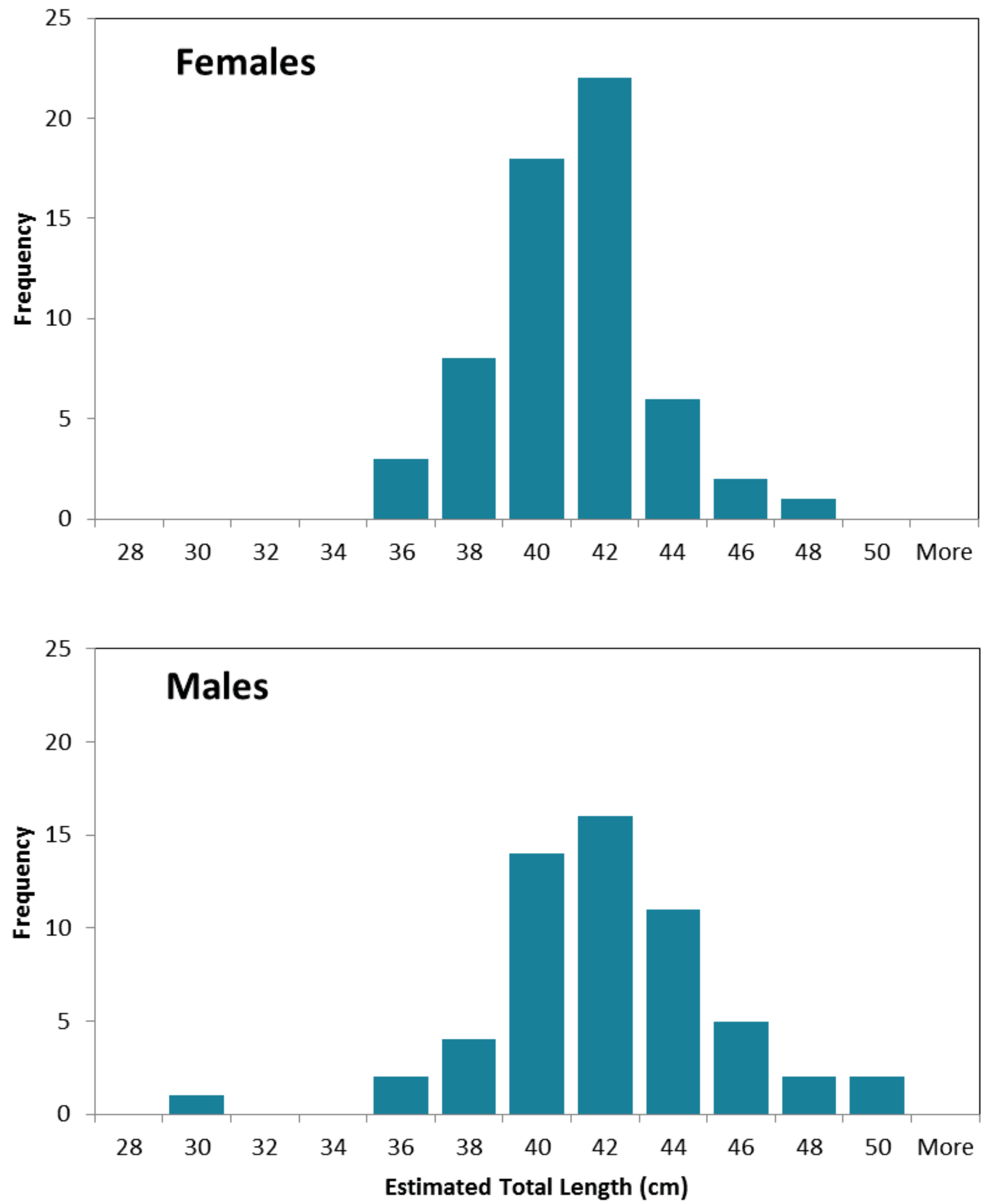


Figure 2.3: Estimated total length of YOY rig caught during the 2011 Nationwide Rig Survey (sharks with damaged tails were excluded; $n_{females}$=60 and n_{males}=53).

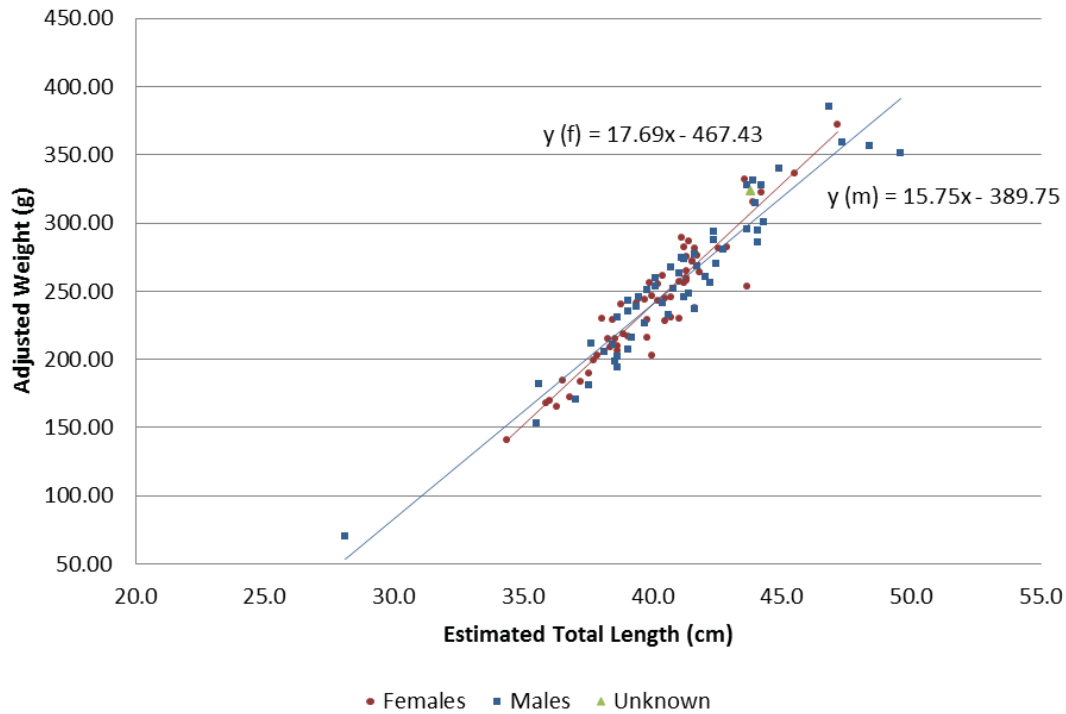


Figure 2.4: Relationship between estimated total length (cm) and adjusted weight (g) for male and female YOY rig from all harbours. Rig with damaged tails were excluded (n=114).

Adjusted weights of YOY rig (weights excluding stomach contents) increased similarly with body length for males and females (Figure 2.4). Stomach fullness, measured prior to removing the stomach from the shark, was on average more than 50% (mean = 2.74 ± 0.07; Figure 2.5). No significant differences were found between male and female stomach fullness (Mann-Whitney Rank Sum Test: U= 2063, T=4274, P=0.397).

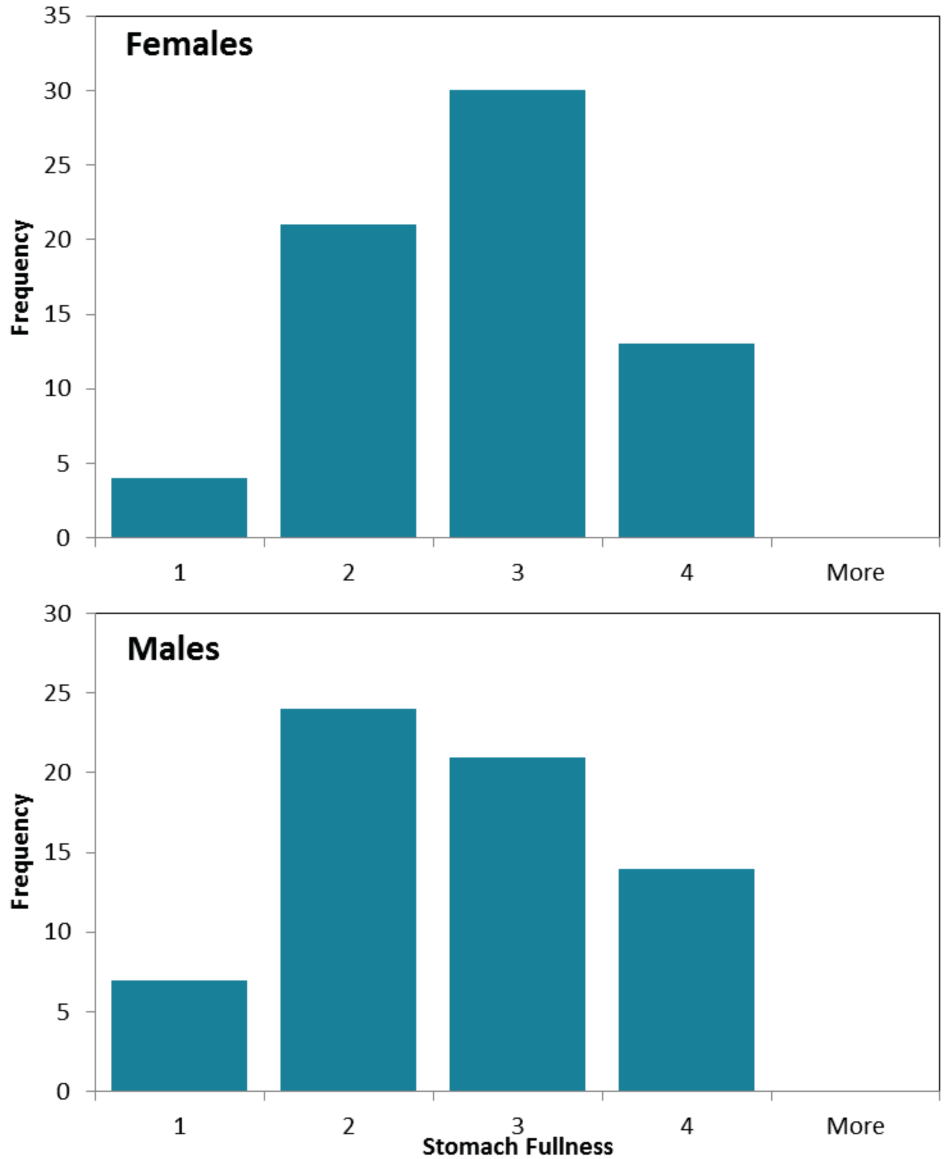


Figure 2.5: Stomach fullness of YOY rig collected during the 2011 survey. (1=0-25%, 2=26-50%, 3=51-75%, 4=76-100%; $n_{females}$=68, n_{males}=66)

Diet Composition

Of the 137 stomachs sampled, three showed signs of decomposition and four were empty (vacuity index [number of empty stomachs] = 2.99%). These were excluded from further analysis. Average mass of stomach contents was 10.96 g ± 0.46 (n=130) with an average 7.01 ± 0.45 (n=130) prey items per stomach. Average stomach content mass as a percentage of body mass was 4.29 % ± 0.16.

Table 2.3: Index of relative importance (IRI), frequency of occurrence (F), weight (W) and number (N) of prey items in young of the year rig (*Mustelus lenticulatus*) non-empty stomachs from six major harbours and estuaries (Kaipara I&II, Waitemata, Tamaki, Raglan, Porirua, Otago) and total non-empty stomachs (including Kenepuru and Manukau Harbours, n=5) with sample sizes in brackets. Bold values represent F, W, N, and IRI values for major prey groups.

Prey Items	Kaipara (21)				Waitemata (22)				Tamaki (21)				Raglan (19)				Porirua (33)				Otago (9)				Total (130)			
	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI	%F	%W	%N	%IRI
ARTHROPODA																												
CRUSTACEA																												
ISOPODA																					**11.11**	**0.42**	**2.44**	**0.24**	**0.77**	**0.04**	**0.10**	**<0.01**
AMPHIPODA																	**3.03**	**0.01**	**0.46**	**<0.01**					**0.77**	**<0.01**	**0.10**	**<0.01**
STOMATOPODA	**9.52**	**5.39**	**1.08**	**0.36**													**24.24**	**2.47**	**3.69**	**0.85**	**44.44**	**5.80**	**10.26**	**5.02**	**10.77**	**2.03**	**1.39**	**0.26**
Heterosquilla tricarinata																	21.21	2.46	3.21	0.84	33.33	5.66	7.32	3.26	7.69	1.09	0.99	0.14
Oratosquilla oratoria	9.52	5.39	1.08	0.40																					1.54	0.92	0.20	0.01
Stomatopoda unidentified																	3.03	0.01	0.46	<0.01	11.11	0.11	2.44	0.21	1.54	0.01	0.20	<0.01
DECAPODA																												
PLEOCYEMATA																												
ANOMURA													**10.53**	**0.41**	**1.49**	**0.11**	**12.12**	**0.91**	**2.30**	**0.22**	**33.33**	**18.53**	**15.38**	**7.96**	**6.92**	**1.90**	**1.39**	**0.16**
Paguroidea																												
Areopaguristes setosus													5.26	0.34	0.98	0.04	3.03	0.39	0.46	0.02					1.54	0.15	0.30	<0.01
Pagurus novizealandiae																	6.06	0.26	1.38	0.07					1.54	0.06	0.30	<0.01
Paguroidea unidentified													5.26	0.07	0.49	0.02	3.03	0.25	0.46	0.02					1.54	0.07	0.20	<0.01
Galatheoidea																												
Munida gregaria																					33.33	18.43	14.63	8.31	2.31	1.61	0.59	0.04
BRACHYURA	**95.24**	**66.55**	**51.61**	**65.80**	**72.73**	**10.13**	**11.88**	**9.49**	**71.43**	**45.96**	**41.46**	**41.39**	**100.00**	**54.87**	**50.75**	**58.46**	**100.00**	**94.52**	**75.12**	**96.41**	**100.00**	**62.73**	**48.72**	**78.44**	**89.23**	**58.82**	**47.06**	**65.67**
Hemiplax hirtipes	90.48	58.76	43.55	60.28	72.73	9.76	11.18	9.29	57.14	39.46	30.91	34.33	100.00	36.28	31.37	43.29	100.00	72.37	51.83	86.64	100.00	62.40	46.34	82.02	86.15	47.71	34.75	60.90
Hemigrapsus crenulatus	28.57	7.16	5.91	2.43					14.29	5.03	1.82	0.84	57.89	13.33	12.75	9.66	42.42	14.63	12.39	8.00					26.15	7.93	6.61	3.26
Notomithrax peronii																	3.03	1.87	0.46	0.05					0.77	0.45	0.10	<0.01
Notomithrax minor													5.26	1.76	1.47	0.11									0.77	0.30	0.30	<0.01
Notomithrax spp.													5.26	1.01	0.49	0.05									0.77	0.17	0.10	<0.01
Ovalipes catharus													5.26	0.57	0.49	0.04									0.77	0.10	0.10	<0.01
Halicarcinus whitei	4.76	0.34	1.61	0.06	4.55	0.32	0.62	0.03	4.76	0.33	4.24	0.19	21.05	1.81	3.43	0.71	18.18	1.53	4.59	0.78					10.00	0.83	2.76	0.31
Halicarcinus varius									14.29	1.06	3.64	0.57													2.31	0.18	0.59	0.02
Halicarcinus spp.									4.76	0.06	0.61	0.03													0.77	<0.01	0.10	<0.01
Brachyura unidentified																	9.09	4.11	5.50	0.61					3.08	1.05	1.28	0.06
CARIDEA	**85.71**	**24.44**	**40.32**	**32.46**	**100.00**	**74.18**	**61.25**	**80.32**	**95.24**	**40.97**	**40.24**	**51.26**	**94.74**	**35.64**	**37.81**	**38.51**	**15.15**	**0.85**	**3.23**	**0.35**	**33.33**	**6.79**	**7.69**	**3.40**	**70.00**	**29.25**	**34.33**	**30.93**
Alpheus richardsonii	85.71	24.42	39.78	35.84	100.00	72.80	58.39	80.04	85.71	39.21	30.91	51.31	94.74	35.25	35.78	43.06					11.11	0.04	2.44	0.21	63.08	27.84	30.60	31.60
Periclimenes batei									4.76	0.04	0.61	0.03													1.54	0.02	0.20	<0.01
Philocheras australis	4.76	0.02	0.54	0.02	13.64	0.88	1.86	0.23	38.10	1.71	8.48	3.31	10.53	0.32	1.47	0.12	15.15	0.85	3.21	0.43	11.11	2.29	2.44	0.40	16.15	0.94	3.06	0.55
THALASSINIDEA																									**1.54**	**1.02**	**0.50**	**0.02**
Upogebia hirtifrons																									1.54	1.02	0.49	0.02
DENDROBRANCHIATA					**45.45**	**14.02**	**15.63**	**7.99**	**38.10**	**10.56**	**10.37**	**5.28**													**13.85**	**3.23**	**4.18**	**0.71**
Metapenaeus bennettae					45.45	13.95	15.53	8.18	38.10	10.55	10.30	6.78													13.85	3.22	4.15	0.87
Shrimp** unidentified					9.09	0.62	1.24	0.10	4.76	0.04	0.61	0.03	5.26	0.09	0.98	0.04					22.22	4.85	4.88	1.63	4.62	0.51	0.69	0.05
Crustacea unidentified	4.76	0.29	0.54	0.03									5.26	0.09	0.49	0.02	3.03	0.01	0.46	<0.01	11.11	0.11	2.44	0.21	2.31	0.03	0.30	<0.01
ANNELIDA																												
POLYCHAETA	**28.57**	**2.97**	**4.84**	**1.30**	**18.18**	**0.44**	**2.50**	**0.32**	**9.52**	**0.44**	**1.22**	**0.10**	**36.84**	**1.16**	**4.48**	**1.15**	**12.12**	**0.44**	**2.30**	**0.19**	**33.33**	**4.92**	**7.69**	**2.96**	**22.31**	**1.42**	**3.78**	**0.81**
Nereididae	19.05	2.92	3.76	0.83	4.55	0.03	0.62	0.02					10.53	0.18	0.98	0.08									6.15	0.54	1.28	0.10
Glyceridae	4.76	0.04	0.54	0.02					4.76	0.42	0.61	0.04					6.06	0.28	1.38	0.07	11.11	4.50	2.44	0.58	3.85	0.54	0.59	0.04
Eunicidae																									0.77	<0.01	0.10	<0.01
Polychaeta unidentified	4.76	0.02	0.54	0.02	13.64	0.41	1.86	0.19	4.76	0.02	0.61	0.03	26.32	0.98	3.43	0.74	6.06	0.16	0.92	0.05	22.22	0.39	4.88	0.88	11.54	0.34	1.78	0.21
ECHIUROIDEA	4.76	0.50	0.54	0.03																					0.77	0.09	0.10	<0.01
MOLLUSCA	**4.76**	**0.09**	**1.08**	**0.03**									**5.26**	**<0.01**	**1.00**	**0.03**	**9.09**	**0.05**	**1.38**	**0.07**					**3.85**	**0.03**	**0.70**	**0.02**
GASTROPODA	4.76	0.05	0.54	0.02																					0.77	<0.01	0.10	<0.01
BIVALVIA*	4.76	0.04	0.54	0.02									5.26	<0.01	0.98	0.03	9.09	0.05	1.38	0.09					3.85	0.02	0.59	0.02
OTHERS																												
Vegetable matter*	4.76	0.05	0.54	0.02	31.82	1.23	8.70	1.93	38.10	1.56	6.06	2.48	26.32	7.80	3.92	1.97	27.27	0.74	11.47	2.32	33.33	0.81	7.32	2.04	25.38	2.00	6.02	1.74
Unidentified									4.76	0.51	0.61	0.05	5.26	0.11	0.49	0.02									2.31	0.18	0.30	<0.01

*items which may have been incidentally ingested

**Shrimp includes Caridea, Thalassinidea and Dendrobranchiata

A B C

Figure 2.6: Stomach contents of rig from Porirua Harbour: (A) adult male rig caught on 18/11/10, measuring 84 cm fresh TL, (B) female YOY caught on 16/12/10 and measuring 32.6 cm fresh TL, (C) female YOY rig caught during 2011 nationwide rig survey, measuring 41.3 cm ETL.

The diet of YOY rig was dominated by crustaceans, particularly the stalk-eyed mud crab (*Hemiplax hirtipes*; %IRI=60.90, %F=86.15; Table 2.3, Figure 2.7) and snapping shrimp (*Alpheus richardsonii*; %IRI=31.60, %F=63.08; Table 2.3). The hairy-handed crab (*Hemigrapsus crenulatus*) was the second-most-commonly identified brachyuran in rig diets (%IRI=3.26, %F=26.15). Stomachs from Waitemata Harbour and Tamaki Estuary both had a higher frequency of snapping shrimp than stalk-eyed mud crabs (Table 2.3), and were the only two to contain the recently introduced greentail prawn (*Metapenaeus bennettae*) in the YOY rig diets. The pillbox crab (*Halicarcinus varius*) seemed to occur in low numbers in the diet of YOY rig from most harbours except Otago where it was not found in the rig stomachs.

Figure 2.7: Stalk-eyed mud crab (*Hemiplax hirtipes*) 2010. Photo by Jess Costal.

Stomatopods were found in the rig diets from Kaipara, Porirua and Otago (Kaipara = 9.52 %F, Porirua = 24.24 %F, Otago = 44.44 %F), however the species in Kaipara was the introduced Japanese mantis shrimp (*Oratosquilla oratoria*), whereas the species in Porirua and Otago were smaller native species, mostly *Heterosquilla tricarinata*. Hermit crabs were found in rig stomachs from Raglan and Porirua, and squat lobsters (*Munida gregaria*) were found in stomachs from Otago. Vegetable matter (%F = 25.38, %W = 2.00) and molluscs (%F = 3.85, %W = 0.03) occurred in rig stomachs, although their percent weight was low.

Parasites

Parasites in the rig stomachs were also recorded. Porirua samples have a high incidence of *Profilicollis* spp. compared to the other harbours, and Kaipara, Raglan and Otago harbours had low incidences of nematodes (Table 2.4).

Table 2.4: Frequency of occurrence and total numbers of parasites and inorganic particles found in juvenile rig (*Mustelus lenticulatus*) stomachs from Kaipara, Waitemata, Tamaki, Raglan, Porirua, Otago Harbours, and Total (including Manukau and Kenepuru).

	Kaipara (21)		Waitemata (22)		Tamaki (21)		Raglan (19)		Porirua (33)		Otago (9)		Total (130)	
	F	**Total**	**F**	**Total**	**F**	**Total**	**F**	**Total**	**F**	**Total**	**F**	**Total**	**F**	**Total**
Parasites														
Profilicollis spp.	14.29	4	4.55	2	14.29	3	47.37	23	72.73	144	33.33	6	33.85	183
Nematode	4.76	1	31.82	22	38.10	33			30.30	19			20.00	75
Cestode			9.09	2			5.26	1	6.06	2			3.85	5
Parasite unidentified									3.03	3	11.11	2	1.54	5
Particle (inorganic)					4.76	1			3.03	1			1.54	2

Adult Diet from Porirua Harbour

Ten mature male rig between 81.5 and 95.0 cm TL were captured in Porirua Harbour on 18 November 2011 during NIWA's pilot study. The average stomach weight as percent body weight was 2.82 ± 0.27. All ten rig stomachs contained *H. hirtipes* (3-12 crabs per stomach), four of the stomachs contained *H. crenulatus,* and one contained parts of a crangonid shrimp, hermit crab and paddle crab (*Ovalipes catharus*).

Comparing Diets from Different Locations

Manukau (n=3) and Pelorus Sound (n=2) had few samples, so only the six major harbours (Kaipara, Waitemata, Tamaki, Raglan, Porirua and Otago) were used in statistical analysis. "Total" refers to rig from eight harbours, including Manukau and Kenepuru where possible. A one way analysis of similarity (ANOSIM) revealed no significant differences in diet of rig from the two arms of Kaipara Harbour ($R=-0.017$, $p=0.513$). Therefore, rig from Kaipara were treated as a single sample when compared with other harbours. The prey accumulation curves for the six major harbours and estuaries appear to continue increasing steadily, indicating that further sampling would result in more taxa being recorded in rig stomachs (Figure 2.8). However, the prey diversity curves clearly reached an asymptote (Figure 2.8). This indicates that the most important components of the diet have been adequately described, enabling valid comparisons to be made between harbours.

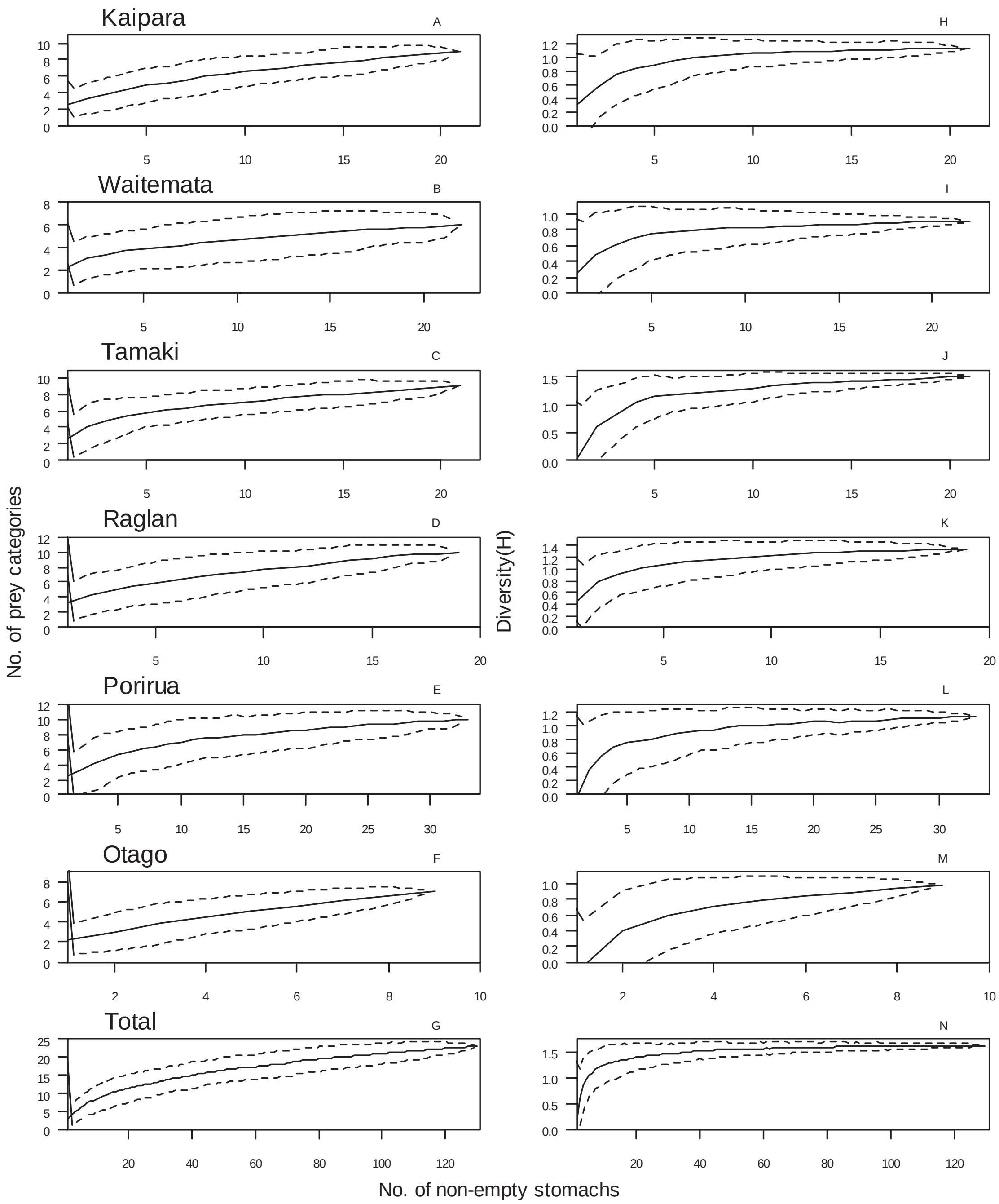


Figure 2.8: Randomized prey accumulation curves for six major harbours (A-F) and corresponding diversity curves (H-M), and total (including stomachs from Manukau and Kenepuru harbours) prey accumulation and prey diversity curves (G, N) for all non-empty YOY rig stomachs (mean and 95% CIs).

To test for differences between sites, we firstly confirmed that there were no sex differences in diet across all samples (R=-0.008, P=0.737; Figure 2.9). We therefore analysed males and females together in subsequent analyses.

Overall, there were significant differences in diet between most sampling sites (R=0.338, P=0.001). The only harbours where YOY rig diets were not significantly different from each other were Kaipara-Raglan, Kaipara-Tamaki, Tamaki-Waitemata and Porirua-Otago (Table 2.5). Basic differences in diet were evident in the coarse breakdown of diet into major prey groups (Figure 2.10), with YOY rig diets from Porirua Harbour containing the most Brachyura and those from Waitemata Harbour containing the most Caridea. Waitemata Harbour and Tamaki Estuary were the only harbours where YOY diets contained Dendrobranchiata. Kaipara, Porirua and Otago harbours were the only harbours where rig diets contained stomatopods, and Otago Harbour diets contained the most Anomura.

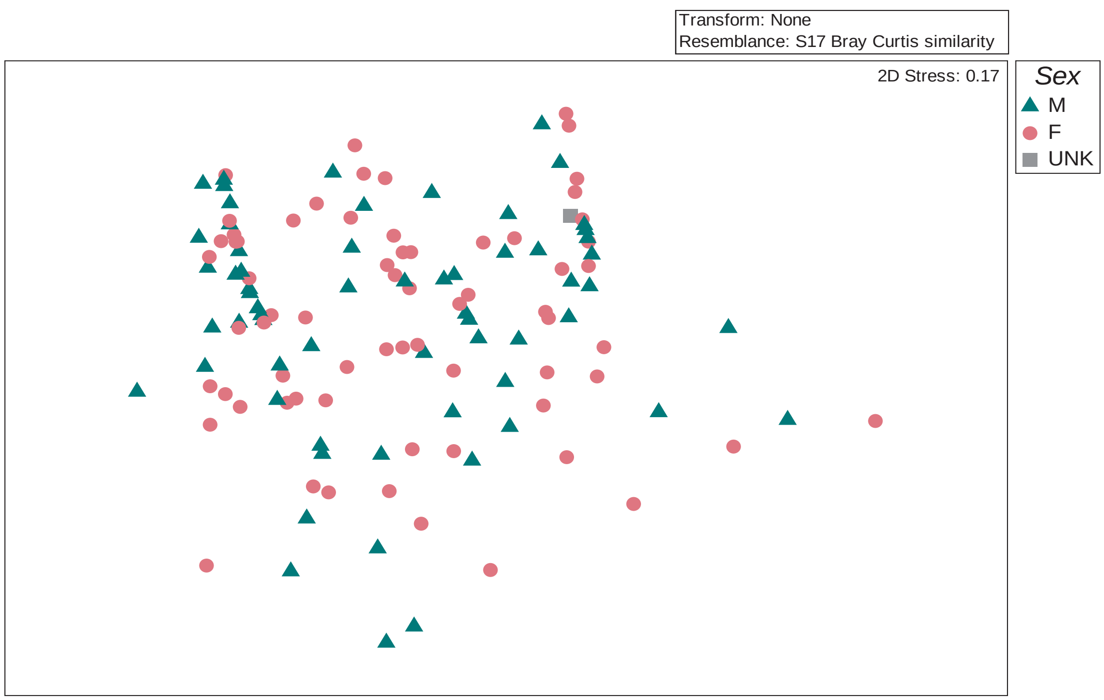


Figure 2.9: Ordination plot of YOY rig diets grouped by sex (n=130).

Table 2.5: One way ANOSIM pairwise tests comparing YOY rig diets between harbours, water depths and water temperatures (permutations = 999). Shaded pairs have significantly different diets.

Site or Variable	Pairwise Comparisons	R Statistic	P-value
Harbours	Kaipara, Otago	0.217	0.02
	Kaipara, Porirua	0.416	0.001
	Kaipara, Raglan	0.032	0.121
	Kaipara, Tamaki	0.042	0.075
	Kaipara, Waitemata	0.173	0.001
	Otago, Porirua	0.132	0.103
	Otago, Raglan	0.317	0.002
	Otago, Tamaki	0.404	0.001
	Otago, Waitemata	0.877	0.001
	Porirua, Raglan	0.25	0.001
	Porirua, Tamaki	0.594	0.001
	Porirua, Waitemata	0.862	0.001
	Raglan, Tamaki	0.095	0.011
	Raglan, Waitemata	0.333	0.001
	Tamaki, Waitemata	0.049	0.044
	Global	**0.347**	**0.001**
Depth	1-2, 2-3	0.000	0.496
	1-2, 3-4	0.501	0.001
	1-2, >4	0.889	0.001
	2-3, 3-4	0.172	0.001
	2-3, >4	0.202	0.032
	3-4, >4	-0.133	0.911
	Global	**0.175**	**0.001**
Temperature	16-18, 18-20	0.065	0.261
	16-18, 20-22	0.210	0.030
	16-18, 22-24	0.434	0.001
	18-20, 20-22	0.283	0.001
	18-20, 22-24	0.387	0.001
	20-22, 22-24	0.066	0.130
	Global	**0.261**	**0.001**
Sediment	MS, SM	0.062	0.012
	MS, M	-0.018	0.717
	SM, M	0.01	0.272
	Global	**0.012**	**0.242**

Ordination analysis, based on the diet composition of individual YOY rig from the eight main sites, revealed no discrete geographical clusters of individuals. Despite the fact there is considerable overlap among sites, substantial structure to the data is apparent (Figure 2.11). Geographic and environmental variables were correlated with the variation across the x-axis (latitude decreasing, temperature and depth increasing across the x-axis; Figures 2.11A and 2.12). A one-way ANOSIM for temperature and depth revealed significant differences in the diet of YOY rig, however sediment type was not significant (Temperature: R=0.261, P=0.001; Depth: R=0.175, P=0.001; Sediment: R=0.012, P=0.242; see Table 2.5 for pairwise comparisons).

Groupings of individuals in the ordination were driven in part by the frequency of the four main prey items in the diet: *Hemiplax hirtipes*, *Alpheus richardsoni*, *Hemigrapsus crenulatus and Metapenaeus bennettae* (Figure 2.11B).

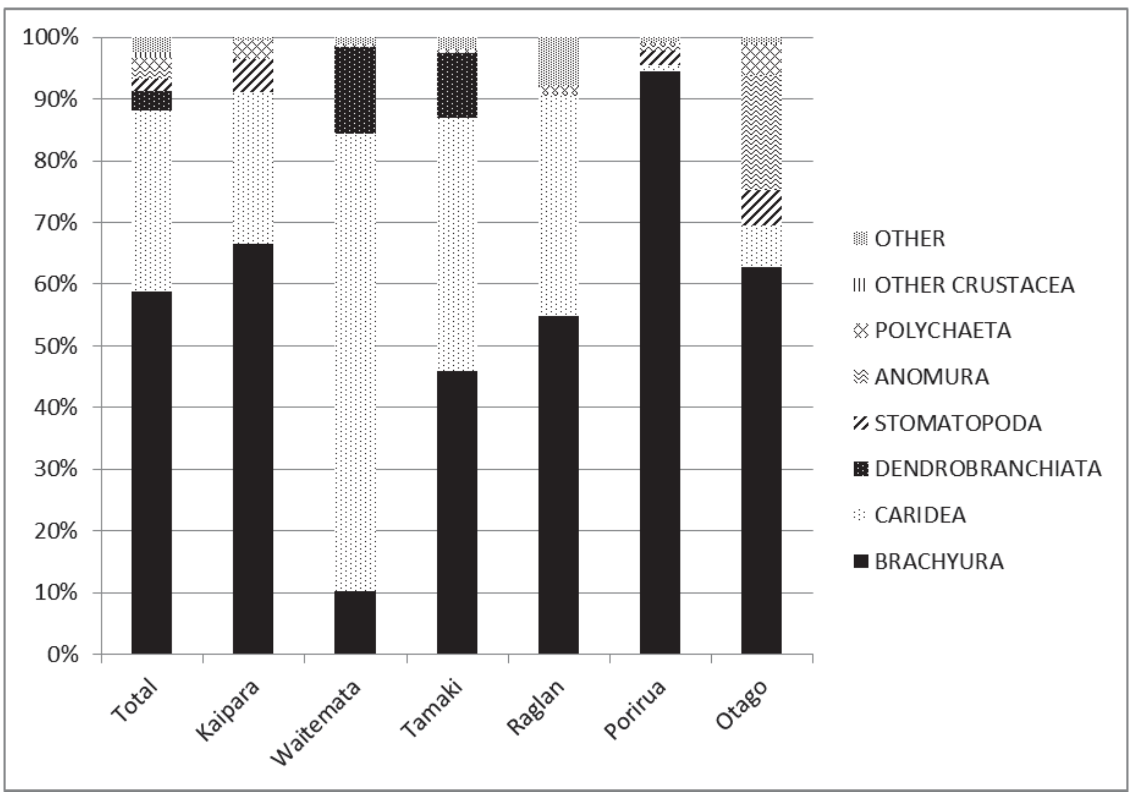
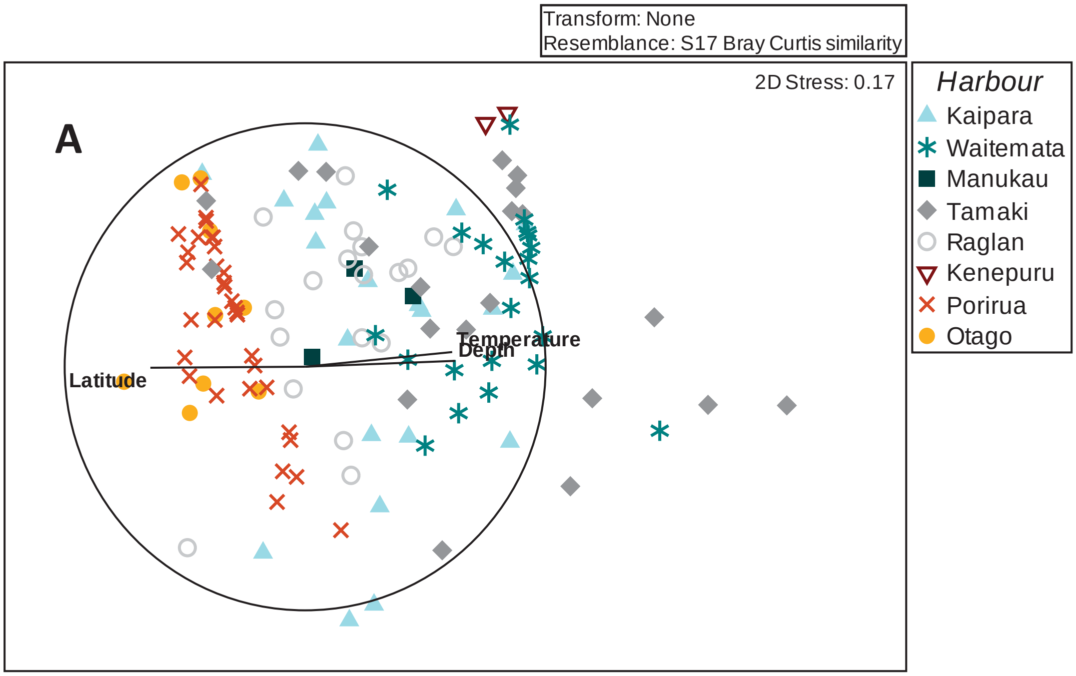


Figure 2.10: Diet of YOY rig (*Mustelus lenticulatus*) from six major harbours. Diet expressed as percent weight of major prey groups.



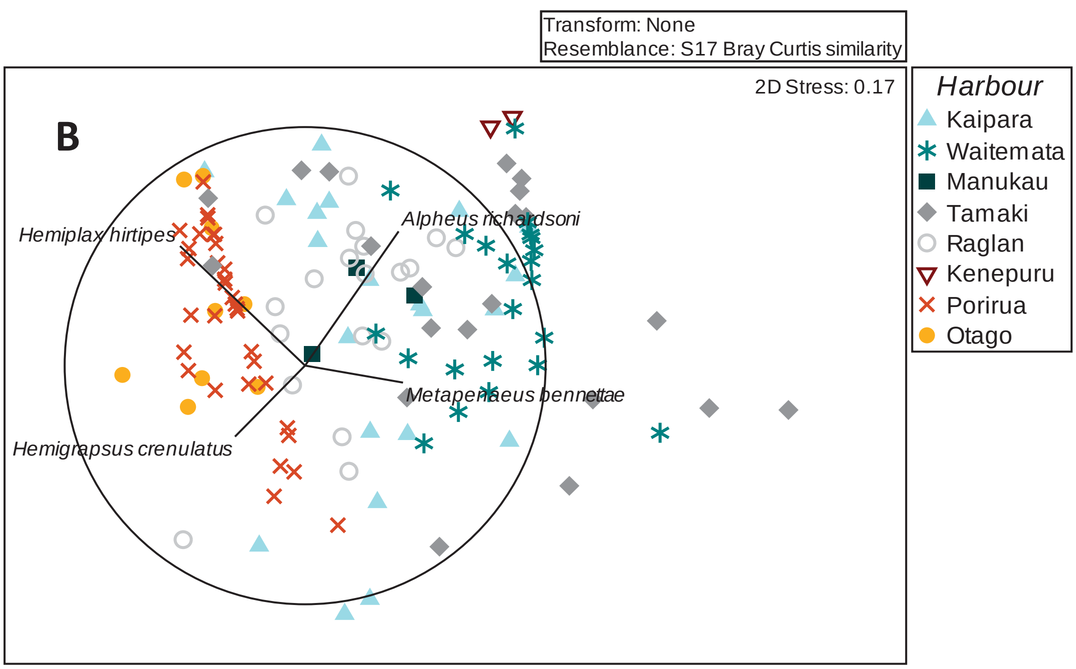


Figure 2.11: Ordination plots of YOY rig diets grouped by harbour. Circle overlay represents Pearson's correlation of (A) environmental variables (*r*=0.5) and (B) prey species (*r*=0.4). Lines reaching the circle are 100% correlated.

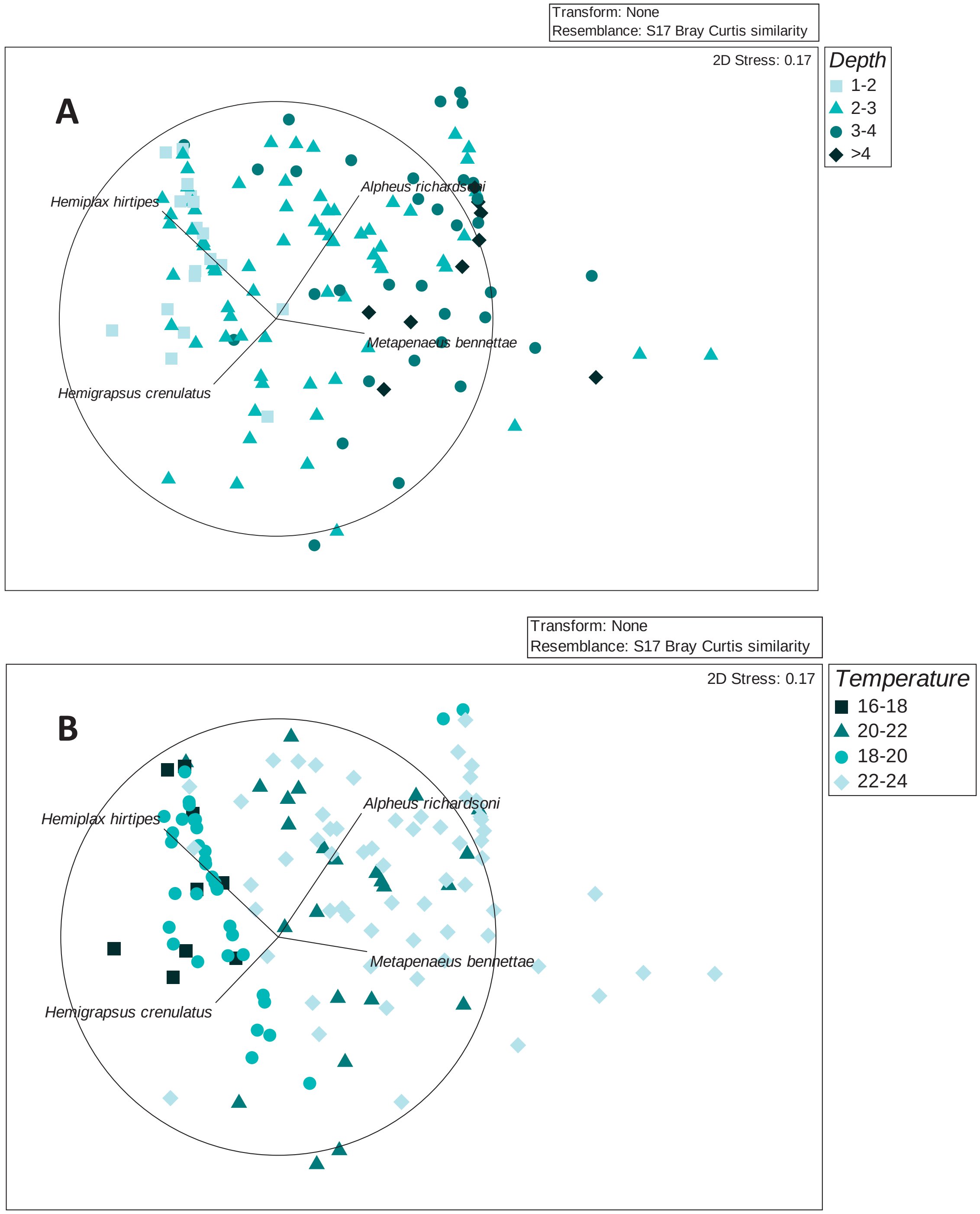


Figure 2.12: Ordinations of YOY rig diets grouped by (A) Depth and (B) Temperature with overlay of prey species (*r*=0.4).

There were significant differences in diet between sites from the west coast and the east coast of the upper North Island (one-way ANOSIM, R=0.129, P=0.001; west coast = Kaipara, Manukau and Raglan, east coast = Waitemata and Tamaki; Figure 2.13).

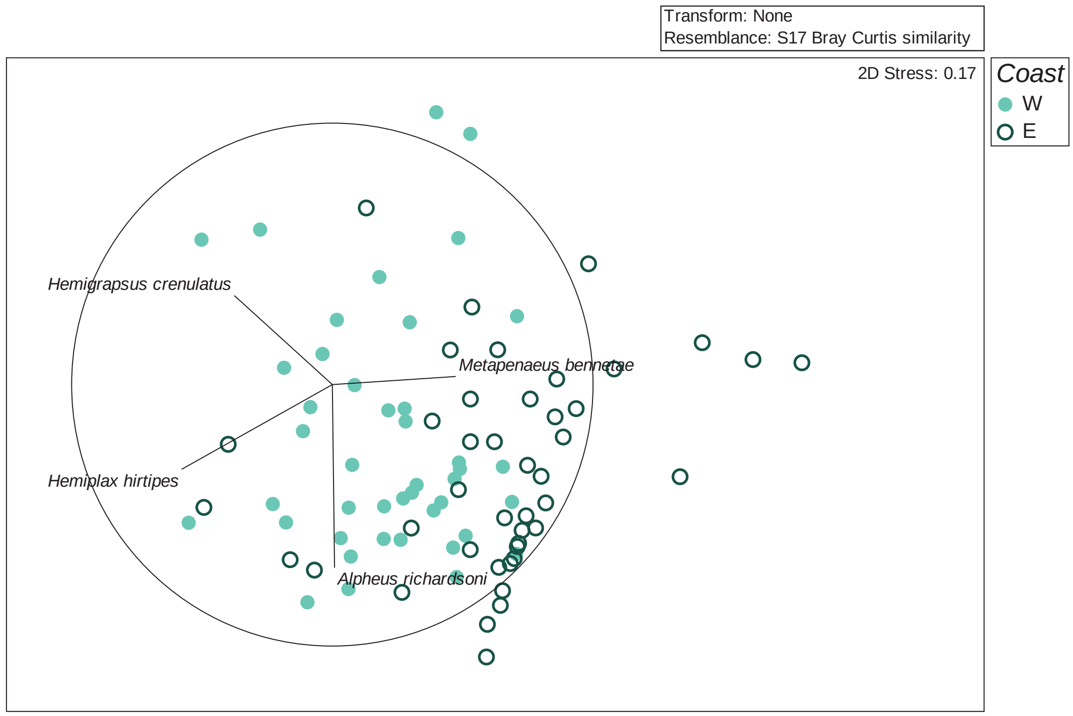


Figure 2.13: Ordination plot of young of the year rig diets from upper North Island harbours and estuaries grouped by East and West coast. Overlay of prey species (*r*=0.4).

2.5 Discussion and Conclusions

Diet studies of smooth-hounds (*Mustelus* spp.) have revealed that young of the year individuals primarily feed on benthic crustaceans (Van der Molen and Caille 2001; Chiaramonte and Pettovello 2000; Molina and Cazorla 2011; Saidi, Bradai, and Bouain 2009). We found crustaceans were an important part of the diet of YOY rig from all eight harbours and estuaries, however the dominant crustacean varied depending on location (see Table 2.3 and Figure 2.10). In Kaipara, Porirua and Otago Harbours the stalk-eyed mud crab (*Hemiplax hirtipes*) was the most important prey item of YOY rig, while in Tamaki Estuary and Waitemata Harbour the snapping shrimp (*Alpheus richardsoni*) was the most important prey item. However in Raglan Harbour, the two species were approximately equal in importance in YOY rig diets. The hairy-handed crab (*Hemigrapsus crenulatus*) was the third most important prey item overall, found in YOY rig stomachs from Kaipara, Tamaki, Raglan and Porirua Harbours and estuaries. The recently introduced greentail prawn (*Metapenaeus bennettae*) was found only in rig stomachs from Tamaki Estuary and Waitemata Harbour, yet it was the third most important prey item from these areas. Hermit crabs were only discovered in YOY rig diets from Raglan and Porirua Harbours, and *Munida gregaria* was only found in stomachs from Otago Harbour. Mantis shrimp were discovered in the diets of YOY rig from Kaipara, Porirua and Otago Harbours, however the species found in Kaipara Harbour was the recently introduced Japanese Mantis Shrimp (*Oratosquilla oratoria*), while the mantis shrimp species most commonly found in rig diets from Porirua and Otago Harbours was *Heterosquilla tricarinata*.

Polychaetes were consumed frequently by YOY rig, with the highest frequency of occurrence from Raglan Harbour and the highest %IRI from Otago Harbour. Polychaetes were typically identified by their jaws and setae, however they were most likely underestimated in the diets of YOY rig because they are much harder to detect than most crustaceans, as they lack exoskeletons and are readily digested. Despite being difficult to detect, polychaetes were present in most YOY diets of smooth-hounds throughout the world and were considered the most important prey group for newborn *M. schmitti* from the south-western Atlantic (Belleggia et al. 2011).

Molluscs did not appear to be an important prey group for YOY rig, and fish were absent from all YOY rig stomachs. A few small bivalves and one small gastropod were found in YOY rig stomachs but these are most likely incidental ingestions due to their small size and low frequency. *M. manazo* (<50 cm TL), *M. griseus* (<50 cm TL) and YOY *M. antarcticus* diets were similar to YOY rig diets in that they lacked cephalopods and fish, however some YOY smooth-hounds eat molluscs and fish (Saidi, Bradai, and Bouain 2009; Lipej et al. 2011; Morte, Redon, and SanzBrau 1997; Rountree and Able 1996; Saidi et al. 2009; Woodland, Secor, and Wedge 2011; Chiaramonte and Pettovello 2000; Molina and Cazorla 2011; Van der Molen and Caille 2001).

The few studies that compared the diet of young smooth-hounds from several different sites found the diet to vary with location (Smale and Compagno 1997;

Yamaguchi and Taniuchi 2000). Prey availability and opportunistic feeding strategies are thought to explain the variation in diet of smooth-hounds species collected from different locations (Saidi et al. 2009; Smale and Compagno 1997; Yamaguchi and Taniuchi 2000). It seems sharks would forage on the most abundant species in the area, and differences in diet among areas would reflect the different faunas from each area. However, despite being one of the most abundant crustaceans from Tokyo Bay, the rough shrimp (*Trachysalambria curvirostris*) was only found in a few stomachs of *M. manazo* (Yamaguchi and Taniuchi 2000). It is unknown why few *M. manazo* stomachs from Tokyo Bay contained rough shrimp. One explanation may be that rough shrimp are harder to catch than other crustaceans. The presence of recently introduced species in YOY rig diets suggests that rig are adaptive foragers, however the degree of YOY rig diet selectivity remains unknown. Examining the diet of sharks while simultaneously sampling the benthic community would aid our understanding of smooth-hound foraging strategies.

Influence of Environmental Variables on Diet

Environmental variables including location (latitude/longitude), depth, temperature, salinity, pH, turbidity and bottom sediment were collected during the rig survey as measures of habitat parameters of YOY rig. Through ordinations, we examined these variables in relation to YOY rig diets. Latitude, depth and temperature had the greatest influence on stomach samples of YOY rig analysed in this study, however, high turbidity, muddy substrates and lower salinity were the factors which best explained YOY rig abundance in harbours and estuaries (Francis et al. 2012, Table 2.2). Smale et al. (1993) found that depth, temperature, oxygen levels and bottom type had the most influence on habitat choice of demersal sharks. When only upper North Island harbours (Kaipara, Waitemata, Tamaki, Manukau and Raglan) were analysed in this study, an east-west trend in YOY rig diets was obvious (Figure 2.12) primarily driven by the presence of *Metapenaeus bennettae* in the diet of YOY rig from Waitemata Harbour and Tamaki Estuary. While it is useful to compare environmental variables with the differences in diet of YOY rig, only a limited number of environmental variables were available in this study. Other potentially influential variables (e.g. dissolved oxygen) were not measured and relationships between variables (e.g.

temperature and dissolved oxygen) can confound the results. Further investigation is needed to determine the relative importance of different environmental variables on YOY rig diets.

Comparing Young of the Year and Adult Diets

Many smooth-hound diet studies describe ontogenetic changes that occur in different size classes (Lipej et al. 2011; Yamaguchi and Taniuchi 2000; Morte, Redon, and SanzBrau 1997; Chiaramonte and Pettovello 2000; Belleggia et al. 2011; Smale and Compagno 1997; Saidi et al. 2009; Saidi, Bradai, and Bouain 2009). Overall, most studies on smooth-hound diets found an increase in the diversity of the diet as sharks increased in size.

While our study did not focus on ontogenetic changes of diet in rig, ten adult male rig from Porirua were sampled during the pilot study in November 2011. Weight and IRI were not calculated for adult rig diets but nevertheless a similar pattern in the diet of adult and YOY rig was observed. All adult rig sampled contained stalk-eyed mud crabs, which were the dominant prey for YOY rig from this harbour; the second-most-frequent prey of both adult and YOY rig from Porirua Harbour was *Hemigrapsus crenulatus*. Figure 2.6C illustrates prey items found in the stomach of an adult rig from Porirua Harbour. In fact, the only prey found in adult rig stomachs that was not present in YOY stomachs from this harbour was the paddle crab (*Ovalipes catharus*). Since paddle crabs do not usually occur within the Porirua Harbour, and NIWA used paddle crabs as bait during the pilot study, their presence in the adult rig stomachs is most likely the result of scavenging. Scavenging behaviour is known for smooth-hounds, and scavenging of teleosts was suspected for *M. mustelus* and *M. palumbes* from southern Africa due to the presence of fish heads in the diet (Smale and Compagno 1997; Simpfendorfer, Goodreid, and McAuley 2001).

Smale and Compagno (1997) concluded that larger sharks would be able to catch larger prey items, due to an increased ability to handle and crush larger crustaceans. They found a significant positive trend of shark total length and prey length for three crabs and one octopus from *M. mustelus* diets, and a similar trend with two crab species from *M. palumbes* diets (Smale and Compagno 1997). In addition to increasing prey size, several studies found a decrease in importance of Brachyura and an increase in importance of molluscs and teleosts with larger *Mustelus* spp. (Lipej et al. 2011; Saidi et al. 2009; Saidi, Bradai, and Bouain 2009). We did not observe adult sharks eating different prey items from YOY rig, but rather they appeared to consume larger individuals, however the prey were small in comparison to shark mouth width. Porirua Harbour may be a rich source of mud crabs which may explain their high incidence in adult and YOY rig diets. King and Clark (1984) discovered small prey items in the stomach of adult rig and concluded that abundance, rather than prey size, may be more important in determining prey composition.

Limitations

Samples for this study were collected for three consecutive days (two overnight sets) from each location and therefore only provide a snapshot of the YOY rig diets from New Zealand harbours and estuaries. Further, it took approximately one month to collect samples from all harbour locations and during this time, the tides, moon phase, and weather varied from place to place. Knowledge about YOY rig diet could benefit from future studies carried out in the same habitat across several months in order to document any seasonal changes and investigate whether any weather patterns, particularly tides and rainfall, are linked to YOY rig diet.

Sampling can only document what species are present. Species that are absent may be truly absent or they may not have been detected and are falsely absent. For this reason, emphasis on rare species in rig diets can be misleading. The majority of YOY rig diets in this study are made up of only a few species (*H. hirtipes, A. richardsoni, H. crenulatus*). Prey accumulation curves for samples from the six major harbours continued to increase steadily. This suggests we have not fully described YOY rig diets. Prey accumulation curves are based on occurrence of prey species. In theory, with infinite sampling effort, an infinite number of species could be detected, meaning the prey accumulation curve would continuously increase. On the other hand, the prey diversity curves are based on both occurrence and abundance of prey species. Therefore an asymptotic prey diversity curve would indicate the most important components of the diet were adequately described. Our data indicate approximately ten stomachs were needed from each area to adequately describe the most important components of the diet. The analysis for the YOY rig diets from Otago Harbour were based on only nine stomachs and the prey diversity curve does not show a clear asymptote. Otago Harbour was included in the analysis because it was the only South Island harbour to contain several YOY rig. While the most important components of the diet may not be fully described, the data are indicative of the diets of YOY rig from Otago Harbour.

Foraging-Safety Tradeoffs

We are still uncertain whether food or predation is the driving force for utilisation of harbours and estuaries. A high abundance of YOY rig in turbid areas suggests they may be trying to avoid predators (see Chapter 1: Natural Predators for information on rig predators); however these areas may also have a high abundance of prey species. The low percentage of empty stomachs in this study, along with stomachs containing prey at different stages of digestion, reveals YOY rig to be continuous feeders. Most studies on smooth-hound species found vacuity indices (i.e. percentage of empty stomachs) between 0 and 15% (Yamaguchi and Taniuchi 2000; Van der Molen and Caille 2001; Saidi, Bradai, and Bouain 2009; Saidi et al. 2009; Belleggia et al. 2011; Kamura and Hashimoto 2004; Lipej et al. 2011; Molina and Cazorla 2011; Morte, Redon, and SanzBrau 1997; Rountree and Able 1996; Talent 1982), however one study on *M. antarcticus* found a vacuity index of 46.7% (Simpfendorfer, Goodreid, and McAuley 2001). Vacuity indices tend to increase with shark size (Lipej et al. 2011; Chiaramonte and Pettovello 2000), therefore, a low vacuity index is not unusual for YOY rig. One way to test the trade-off between risk of predation and foraging is to measure the giving up density (GUD) of foraging individuals (Carrier, Musick, and Heithaus 2004). GUD assumes that under low risk of predation, there should be a low density of prey left behind after foraging (Brown 1988; Carrier, Musick, and Heithaus 2004).

Conclusions

Our results revealed: (1) young of the year rig from eight New Zealand harbours and estuaries consumed a variety of benthic crustaceans and polychaetes, including two recently introduced species; (2) diet of adult rig caught within Porirua Harbour appeared similar to the diet of YOY rig from the same area, (3) diet of YOY rig did not vary with sex; (4) the most important prey item of YOY rig was either the mud crab *H. hirtipes* or the snapping shrimp *A. richardsoni* depending on the harbour; and (5) of the variables measured, diet of YOY rig was most influenced by longitude, depth and temperature.

Chapter 3

Foraging Behaviour of Captive Juvenile Rig (*Mustelus lenticulatus*) on Two Substrates: Mud and Sand

3.1 Abstract

Smooth-hounds (*Mustelus* spp.) are known to feed on invertebrates on or within the sea floor. Juvenile smooth-hounds can often be found in harbours and estuaries close to human populations, making them vulnerable to habitat modification such as sedimentation. In this study we investigate how sediment type affects juvenile rig foraging behaviour. Six young of the year rig (*Mustelus lenticulatus*) captured from Porirua Harbour were fed stalk-eyed mud crabs (*Hemiplax hirtipes*) to determine whether foraging success and effort varied between sand and mud substrates. While no significant difference was found for foraging effort or success between mud and sand (P=0.79, P=0.69, respectively) there was an obvious difference in foraging effort when crabs were present compared to the control, when crabs were not present (P=0.004). Sedimentation can affect the abundance and diversity of macrobenthic communities in coastal areas, which in turn may affect the foraging behaviour and diet of rig living in these areas.

3.2 Introduction

Overview of shark and nursery ground conservation and management

Sharks typically have slow growth, low fecundity, late age at maturity, long gestation periods and long life spans (Compagno 1990; Cortés 2000; Speed et al. 2010) and these life history traits can increase the vulnerability of shark populations. The two main threats to shark populations world-wide are overexploitation and habitat degradation/destruction (Cortés 2000; Speed et al. 2010; White and Kyne 2010). One of the major causes of habitat degradation in coastal areas around the world is terrestrial sediment deposition (Thrush et al. 2003).

Sedimentation is a process by which suspended particles settle out of a fluid. The settlement of particles often occurs in coastal areas and can cause major changes in coastal ecosystems. These terrestrial sediments have a smothering effect on macrobenthic communities, reducing numbers of sensitive species and increasing abundance of opportunistic species, while also increasing turbidity (Thrush et al. 2004; Ellis, Norkko, and Thrush 2000). Lohrer et al. (2004) added 0, 1, 3, 5 and 7 mm of terrigenous sediment to the Whitford embayment, North Island, New Zealand, and found that as little as 3 mm of sediment caused significant changes in macrobenthic community structure, and that repetitive sediment deposition is more damaging then single events. While small amounts of sediment deposition are natural, rates of sedimentation have been exacerbated by human development in the form of deforestation, farming, mining and urbanization (Thrush et al. 2003; Thrush et al. 2004). While long-term effects of sedimentation are not fully understood, sedimentation in estuaries and coastal environments has the potential to alter habitat to a degree, which can affect rates of predation and habitat suitability for many shorebirds and predatory fish, including rig (Thrush et al. 2003). Impacts of sedimentation on coastal shark diets could occur through short-term or long-term changes in benthic communities, or through changes in prey availability or detectability through increased turbidity.

Biology of Study Species

Rig (*Mustelus lenticulatus*) is a small coastal shark species from the Triakidae family. It is endemic to New Zealand and commonly used in fish and chips (Ayling and Cox 1984). Adults can be found in many estuaries and harbours where they breed during spring and summer (Francis and Mace 1980). Rig are ovoviviparous and young are born in or near estuaries and large harbours at 25-35 cm total length (Francis and Francis 1992; Francis and Mace 1980). These new-born rig (also referred to as young of the year [YOY] or 0+ age class) spend the first 6-8 months living in these estuaries and harbours until autumn or winter when they leave (Francis and Francis 1992).

Young of the year rig captured during a nationwide rig survey in 2011 (Francis et al. 2012) ate primarily crustaceans and polychaetes (Chapter 2). The stalk-eyed mud crab (*Hemiplax hirtipes*) and the snapping shrimp (*Alpheus richardsoni*) were the two most important prey items nationally, however there were some differences regionally. While stalk-eyed mud crabs were the most important species (F=100%, W=72.4%, N=51.8%, IRI=86.6%; Chapter 2, Table 2.3) found in YOY rig stomachs from Porirua Harbour, in a few of the northern harbours and estuaries (i.e. Waitemata, Raglan and Tamaki), snapping shrimp were equally or more important.

Stalk-eyed mud crabs are common burrowing crabs which can be found between mid-tide level and sub-tidal areas in many inlets, lagoons and estuaries throughout New Zealand. Stalk-eyed mud crabs were found in sandy sediments containing less than 37% mud and between 0.7-2.9% organic matter in the Avon-Heathcote Estuary, Christchurch, New Zealand (Jones and Simons 1981). They construct temporary burrows which they use as protection against predators. However, when they are threatened and cannot reach a burrow, they will bury into the sediment. This behaviour is only possible in thixotropic sediments.

Shark Foraging Behaviour

Due to the inherent difficulties of studying shark foraging behaviour, many behaviour studies occur in the laboratory setting. Kalmijn's (1971) study of foraging behaviour in sharks and rays revealed that electroreception, rather than smell or vision, produces a more accurate strike response for the small-spotted catshark (*Scyliorhinus canicula*) and the thornback ray (*Raja clavata*). Smale and Compagno (1997) described searching behaviours of wild-caught, captive *M. mustelus* and *M. palumbes* from South Africa. Both species were observed typically swimming 50 mm from the sandy tank floor, presumably searching for prey. Kalmijn (1971) observed the small spotted catshark to spontaneously explore the tank when hungry, swimming just above the sand in search of food. Rather than starving the sharks and rays for over a week, Kalmijn discovered that adding a few drops of whiting (*Gadus merlangus*) juice to the tank at the start of each experiment produced a 'frenzied feeding behaviour'. He described smell to be a primary stimulus for eliciting a foraging response, and vision did not appear to play an important role (Kalmijn 1971). Given YOY rig are typically found in turbid, muddy harbours and estuaries, sight is probably not an important sense used by rig to locate prey. Sediment type could potentially impact rig foraging behaviour by interfering with the sharks' ability to detect and capture their prey (e.g. affecting vision and digging abilities) or through changes in prey activity.

Study Aim

The aims of this study are to: (1) determine the effects of sedimentation on young of the year rig foraging effort and success, and (2) describe young of the year foraging behaviour in captivity. Foraging effort is measured as the amount of time spent in the foraging behaviour state (Table 3.2), while foraging success is measured by the number of strikes at the prey.

3.3 Materials and Methods

Capture and Containment of Shark Subjects

Eight juvenile rig were caught using two 60 x 1.85 m nylon nets with a 76 mm (3") mesh size and 0.5 mm diameter in Porirua Harbour, Wellington on 16 March 2011 (Figure 3.1) according to the Massey University Animal Ethics Committee approved protocol 11/13. Due to injuries sustained, observed after capture, one shark was immediately euthanized, and a second shark jumped from the tank during the acclimation period, leaving three male and three female juvenile rig to enter the feeding trial.

Figure 3.1: Map of Porirua Harbour, Pauatahanui Arm indicating collection sites for mud and sand samples (indicated by white bullets), as well as capture and release sites for rig (indicated by white arrows).

Four identical circular black plastic tanks with a diameter and height (from bottom to drain) of 1.44 x 0.37 m, were used throughout the acclimation period and trial. Seawater was pumped continuously from Evans Bay, Wellington, and filtered before entering the tanks. Once water passed through the tanks, the overflow was returned to Evans Bay. Each tank was fitted with an air stone which provided continuous aeration of the tanks, except during feeding times and trials when the air supply was turned off to improve visibility for the observer. Two holding tanks allowed for the separation of the three smaller sharks from the three larger sharks during the adjustment period. Sharks were weighed weekly prior to the start of the trial (Figure 3.1). Sharks were kept in tanks without sediment during the acclimation period.

Each experiment tank contained 8-10 cm of substrate and was used only during the trials. Sediments were collected from Porirua Harbour (Figure 3.1). The collection off

Gray's Road was subjectively classified as mud according to the six-point scale used during the nationwide rig survey (Francis et al. 2012) and the sand collected from Bradley's Bay was classified as muddy-sand but will be referred to as sand throughout this chapter. In addition, samples from both locations underwent particle-size analysis (see Appendix Table 2 and Figure 1).

Table 3.1: Pit tag number, sex, capture total length (TL) and weekly weight during five weeks of captivity of juvenile rig (*Mustelus lenticulatus*) captured from Porirua Harbour on 16 March 2011.

Shark	Pit tag	Sex	TL (cm)	Weight (g)				
				18/03/11	28/03/11	4/04/11	11/04/11	18/04/11
1	154336	F	50	530	454	450	466	468
2	154347	F	45	390	384	378	398	400
3	154489	M	41	260	242	236	244	242
4	154588	F	47.5	480	422	406	424	417
5	154653	M	39.5	260	232	228	248*	244
6	154682	M	39.5	250	244	236	234	250

*water was splashed from the weighing bucket

Quarantine Period

During the first five days in captivity, sharks were kept together in one holding tank while they underwent a quarantine treatment to kill any parasites or bacteria that may affect their health during the trial. At the start of the quarantine treatment, the water level in the tank was halved to facilitate quick dilution of chemicals at the end of the treatment; then either Formalin or Chloramine-T (see below) was added to the tank and left for an hour. After an hour, the chemical was flushed from the tank while slowly filling the tank back to the normal height. The chemicals and amounts added were as follows:

Day 1: Formalin at 150 ppm for 1 hour

Day 2: Chloramine-T at 5 ppm for 1 hour

Day 3: Formalin at 150 ppm for 1 hour

Day 4: Chloramine-T at 5 ppm for 1 hour

Day 5: Formalin at 150 ppm for 1 hour

On the third day of captivity, a PIT-tag (ENSID 12mm FDX food safe polymer tag) provided by National Institute of Water and Atmospheric Research (NIWA) was inserted just below the dorsal fin on the left side of each shark. While scars and markings were often used for identification, PIT-tags ensured accurate identification throughout the period of captivity. Sharks were then weighed using a bucket of water (weight of shark = weight of bucket, water and shark – weight of bucket and water), and total length was measured to the nearest 0.5 cm.

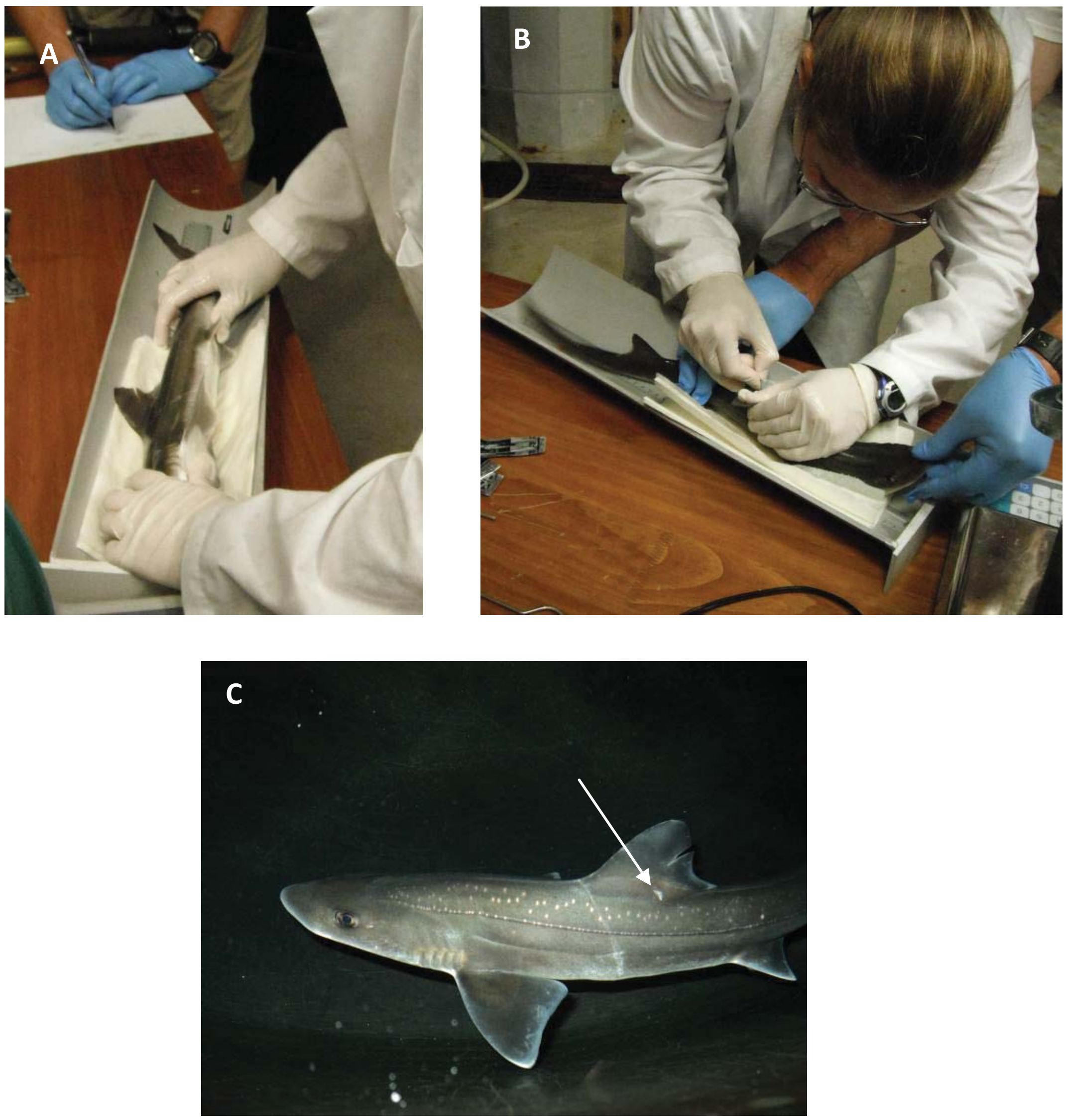


Figure 3.2: (A) Measuring shark total length, (B) inserting a microchip in the muscle on the left side just below the dorsal fin, and (C) arrow pointing to position of microchip.

Acclimation Period

Sharks remained in captivity for more than one month before feeding trials began, in order to acclimate them to their new environment. From the first day in captivity, 2-3 live stalk-eyed mud crabs (*Hemiplax hirtipes*) caught from Porirua Harbour were provided in each tank. In addition, thawed whole pilchard (*Sardinops* sp.) and peeled and deveined shrimp (*Penaeus* sp.) from the supermarket were provided. Enough shrimp and pilchard were prepared each day to provide approximately 3-5% of the combined body weight of all sharks.

During the daily tank maintenance, food and excrement was removed using nets and siphons prior to the next feeding event. Once the sharks had started feeding regularly, the amount of food prepared was reduced to approximately 2-3% shark body weight and the number of crabs was increased to 1-2 crabs per shark. The number of crabs remaining in the tank, total amount of food in grams, and the number of pieces eaten by each shark was recorded in the logbook at each feeding event.

Environmental parameters including dissolved oxygen (DO), temperature, salinity and pH were measured 4-5 times each day for the first three days to ensure a relatively stable environment for the sharks. During the following week, temperature, pH and ammonia levels were tested daily. Once these levels were determined to be stable, testing only occurred 2-3 times per week during the acclimation period. Before and after each feeding trial, temperature, DO, salinity and pH were recorded.

Measuring Rig Behaviour

Observations during the acclimation period were used to create an ethogram of juvenile rig behaviour to be used during the feeding trials (Table 3.2). Six days prior to the start of the trial, all six sharks were placed in a holding tank which contained a mixed substrate. This mixed substrate was created by taking one bucket of substrate from each experiment tank (sand and mud) and mixing them together. In the mixed substrate holding tank, the sharks were fed only mud crabs (*Hemiplax hirtipes*) every other day. For sharks about to be tested, food was withheld for approximately 24-48 hours and sharks were moved to the experiment tanks at least 24 hours prior to the start of each feeding trial.

Table 3.2 Ethogram of Juvenile Rig (*Mustelus lenticulatus*) behaviour in captivity.

STATE BEHAVIOUR		DESCRIPTION
Rest		Remaining in one place with very little movement. This includes opening and closing of gill slits and an occasional tail wave. Sharks may be lying in contact with the bottom or have their head propped up along the side of the tank.
Swim		Moving through the water column, either by using sinusoidal body waves or gliding.
Forage	Hunting/Searching	Swimming within five centimetres of the substrate. Rostrum typically one to two centimetres from the substrate. Often associated with quick, tight turns (more than 90°).
	Striking	Ranges from a quick tap of the mouth on substrate surface with suction, to digging a few centimetres into the substrate, using rostrum, jaws and pectoral fins. This state ends with a capture bite of the prey item.
	Ingestion	This state only occurs if a strike has been successful. Movements associated with the ingestion state are for the purpose of repositioning and breaking down the prey item for easier swallowing. Once the capture bite has occurred in the strike state a number of manipulation/processing bites begin the ingestion state. These bites may be associated with vigorous shaking of the head and body or simply opening and closing of the jaws with quick movements of the head in the same direction (usually to the left or right but sometimes vertically).

Each shark was filmed in four experimental treatments (mud without crabs, mud with crabs, sand without crabs and sand with crabs) for one hour. However, each control treatment (without crabs) was tested immediately prior to the prey condition (i.e. with crabs) because of time constraints. Two sharks could be tested each day so each shark was allocated to AM (09:00-11:00) or PM (12:00-14:00). Sharks were randomly assigned a substrate (mud or sand) for their first trial. The first hour of every trial was the control. At the end of the control hour ten crabs were dropped into the centre of the tank, marking the beginning of the treatment with crabs present, which lasted another hour. To avoid any carry-over effects, each shark was tested once on each substrate six days apart and was returned to the mixed sediment holding tank between trials where they were able to feed on crabs in a mixed substrate. At the end of the trial, all six sharks were released back into Porirua Harbour at Bradley's Bay.

Measurement and Analysis

Only the first ten minutes of each trial was used for analysis since approximately 80% of crabs were eaten during this time. Total time spent in three main behaviour states (foraging, swimming and resting) was recorded during the first ten minutes of each trial. Foraging effort was measured as the time spent in the foraging behaviour state, while foraging success was measured by the number of strikes (Table 3.2). A repeated measures analyses of variance within subjects design was used to investigate the effects of prey presence and substrate type. The assumptions for such a test include a normal distribution and homoscedasticity across conditions. Because rig spent almost no time foraging when there were no crabs present, there was little variance and therefore the controls were heteroscedastic compared to the treatments with crabs present. As a result we undertook paired t-tests of the treatments with crabs present.

3.4 Results

Description of Young of the Year Rig Foraging Behaviour

Young of the year rig displayed specific foraging behaviours during the acclimation period as well as during the feeding trial. The foraging state was split up into three phases: hunting/searching, striking, and ingesting. The hunting/searching behaviour involved sharks swimming close (<5cm) to the substrate (Figure 3.3). As the searching continued, the sharks eventually started making several tight turns (less than 90 degrees), often passing over the same area of sediment, until they finally struck. On the occasion when the crabs were on the substrate surface, the strike was relatively quick, with the rig taking less than a second to snatch up the crab. Sharks also tended to make fewer turns when crabs were on the surface. On a couple of occasions, when the crabs were on the substrate surface, the sharks did not turn at all but simply swam straight to a crab and struck. When the crabs were buried in the sediment, the sharks made more turns, investigating the area before they would strike and begin digging in the sediment. Digging usually only lasted 1-2 seconds before the shark swam off chewing the crab. The sharks typically used their mouth and pectoral fins to dig through the sand while expelling sand through their gills. Once digging finished and the ingestion phase commenced, the sharks often swam away shaking their entire body vigorously. Frequently sharks jerked their head to one side, or up and down, repetitively while chewing on a crab. The ingestion phase lasted anywhere between 5 and 41 seconds, however it was difficult to measure the duration accurately due to blind spots relative to the camera position (see field of view in Figure 3.3).

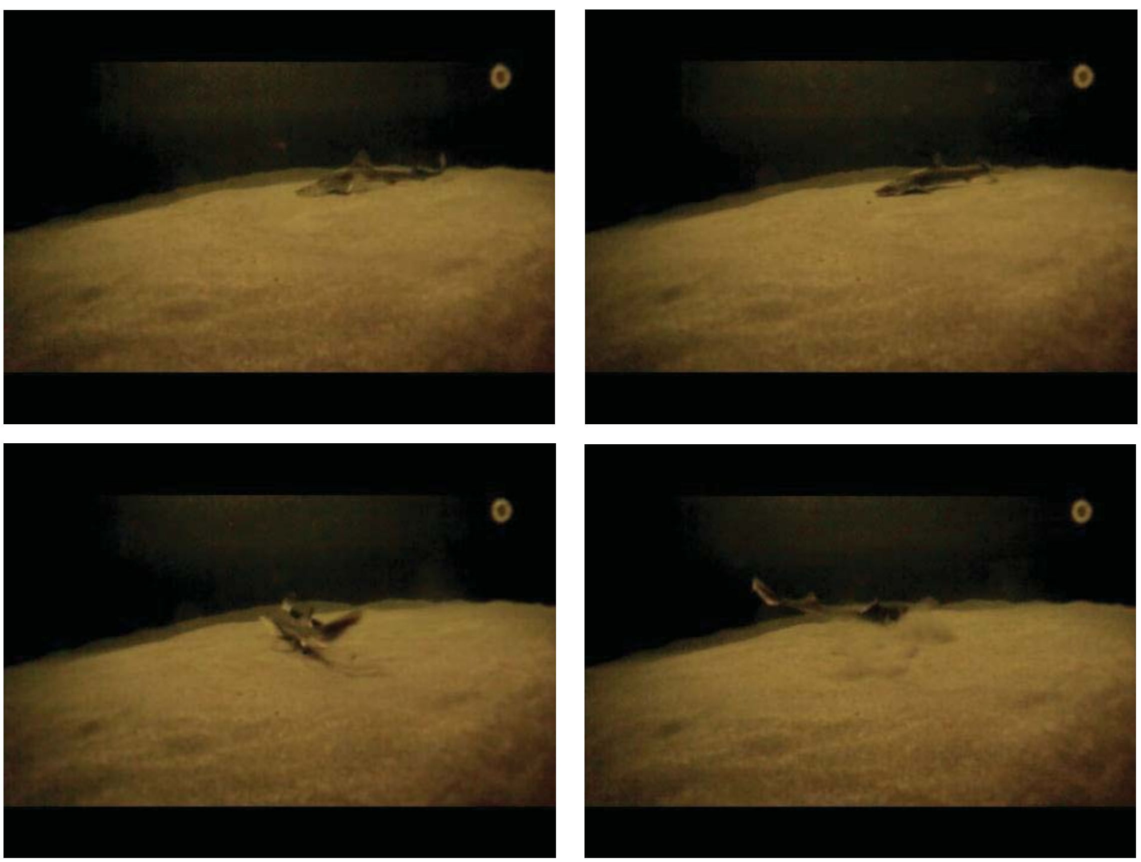


Figure 3.3: Time series from feeding trial showing a YOY rig hunting, striking and digging for a mud crab.

Behaviour States

A two-way repeated measures analysis of variance was used to statistically analyse the time spent in each behaviour state (rest, swim, forage, hunt and strike, ingest; Table 3.4). However, due to several zeroes in the control data, the data (see Appendix B, Table 1) violate the assumptions for the ANOVA and the results may not be statistically robust. Therefore, a paired t-test was applied to the treatments with crabs present and the treatments without crabs were ignored (Table 3.4). The paired t-test may be more statistically robust but lacks the ability to test the effect of crab presence/absence on the time spent in each behaviour state. Both statistical tests (two way repeated measures ANOVA and the paired t-test) revealed no significant difference for the time spent foraging on sand versus mud (Table 3.4 and 3.5). Shark behaviour did, however, vary in the presence and absence of prey, with foraging increasing and resting behaviour decreasing when crabs were present (Table 3.4).

Table 3.3: Mean behaviour states (forage, swim and rest) and standard error (SE) of six captive YOY rig during a feeding trial on two different substrates (sand and mud). Food offered during trials consisted of ten stalk-eyed mud crabs. No crabs were offered during either of the controls.

Behaviour State	Mud Control		Mud with Crabs		Sand Control		Sand with Crabs	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forage	0.00	0.00	82.33	17.08	1.50	0.96	83.83	27.03
Swim	315.33	98.75	353.67	60.88	292.67	99.10	367.17	53.71
Rest	284.67	98.75	164.00	53.10	305.83	60.78	149.00	60.78

Table 3.4: Results from two-way repeated measures ANOVA for behaviour states of six captive YOY rig.

	Substrate		Prey Presence		Substrate x Prey Condition	
Behaviour	F(df)	P	F(df)	P	F(df)	P
Swim	0.013(1)	0.913	1.577(1)	0.265	1.210(1)	0.322
Rest	0.004(1)	0.950	7.195(1)	0.044	2.591(1)	0.168
Forage	0.009(1)	0.929	25.931(1)	0.004	0.000(1)	1.000
Forage - Hunt&Strike	0.113(1)	0.750	17.187(1)	0.009	0.211(1)	0.665
Forage - Ingest	3.555(1)	0.118	9.056(1)	0.030	3.555(1)	0.118

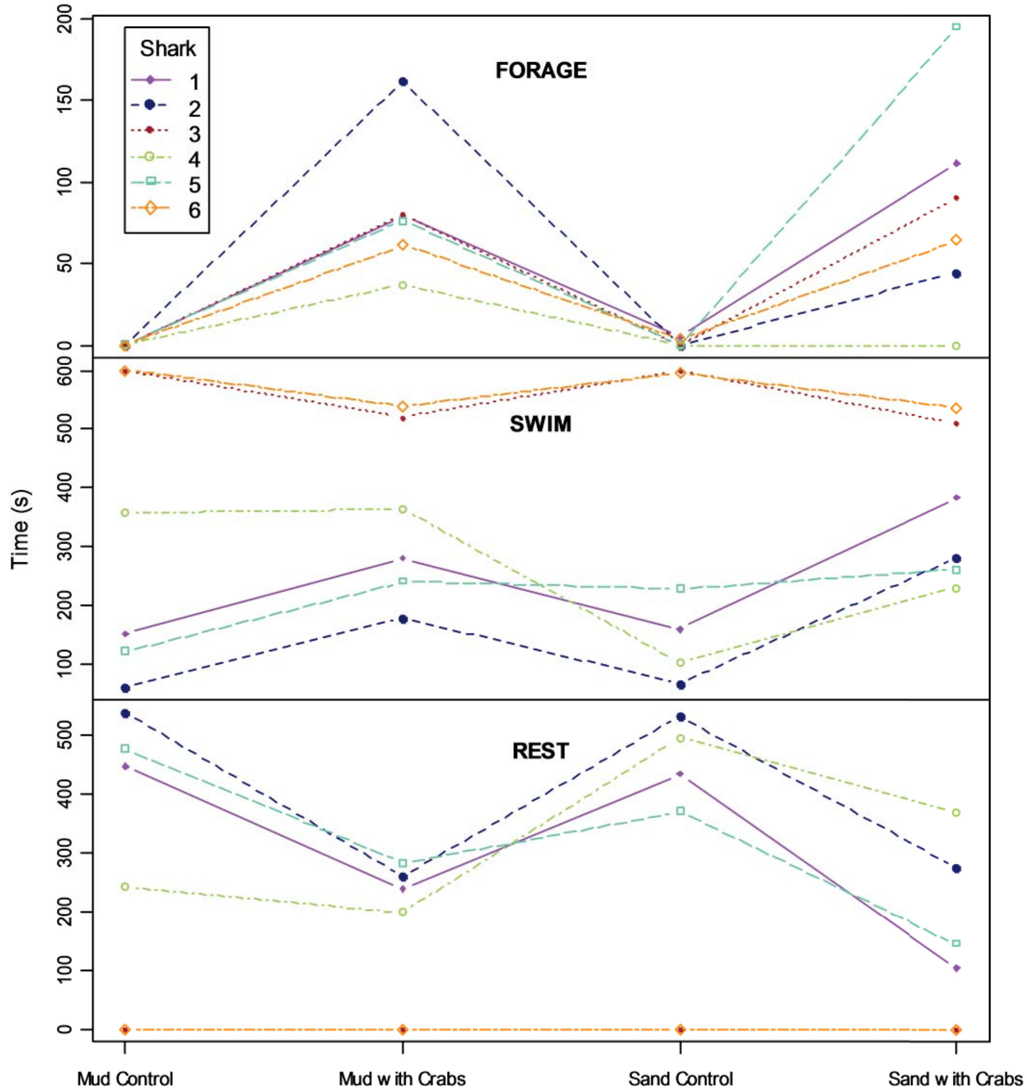


Figure 3.4: Time spent foraging, swimming and resting for six juvenile rig (*Mustelus lenticulatus*) when offered ten stalk-eyed mud crabs on two different substrates: mud and sand (Control=no crabs).

Table 3.5: Results from paired t-tests of time spent in behaviour states and number of strikes on two different substrates (sand and mud) of six captive YOY rig on mud versus sand.

Behaviour State	Mean of the differences	t (df)	P-value
Rest	15.0	0.32 (5)	0.76
Swim	-13.5	-0.38 (5)	0.72
Forage	-1.5	-0.05 (5)	0.96
Forage - Hunt&Strike	10.2	0.40 (5)	0.71
Forage - Ingest	-13.0	-1.89 (5)	0.12
Number of Strikes			
Successful Strikes	-0.5	-0.89 (5)	0.42
Total Strikes	-1.0	-1.46 (5)	0.20

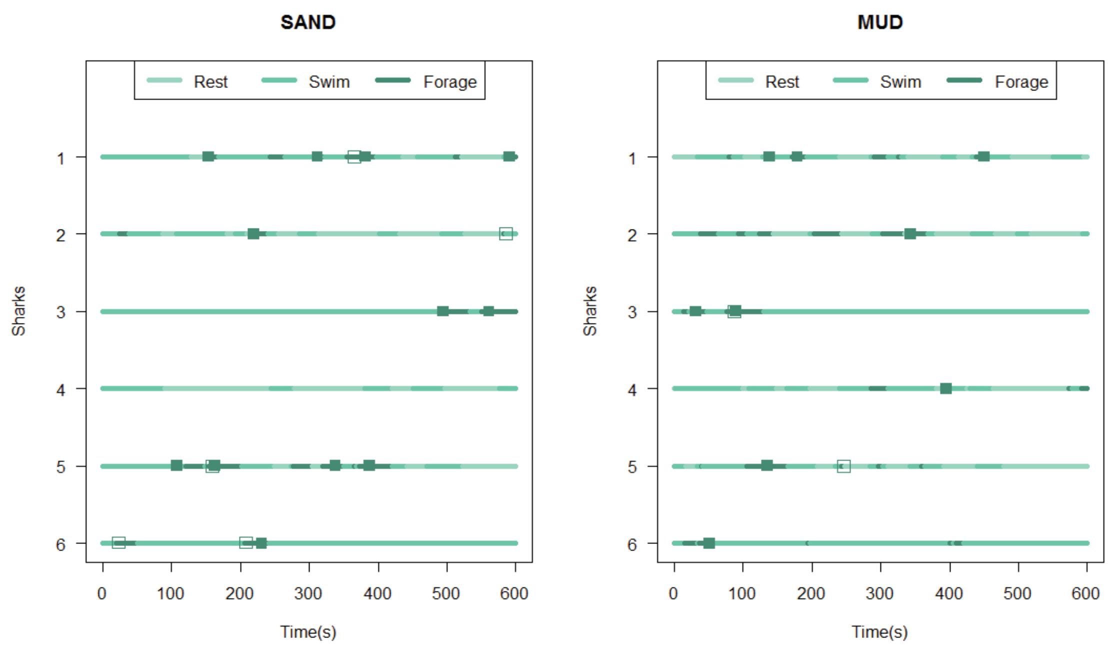


Figure 3.5: Time series of feeding trial with mud crabs displaying successful strikes (solid squares) and unsuccessful strikes (hollow squares) of six juvenile rig (*Mustelus lenticulatus*) on mud and sand substrates (legend shows behaviour states represented by different tones of green).

Behavioural states and foraging strikes (successful and unsuccessful) during the first ten minutes of the feeding trials with crabs present are shown in Figure 3.5 for both sand and mud substrates. There was high variability between sharks, however two strike patterns were observed. One, which occurred in three of the sharks, was a pairing of strikes occurring about a minute apart. The second was a successful strike immediately followed by an unsuccessful strike. It is also apparent from Figure 3.5 and

3.1 that certain individuals (sharks 3 and 6) spent a lot of time swimming and little to no time resting during the trial.

Foraging Success: Strike Analysis

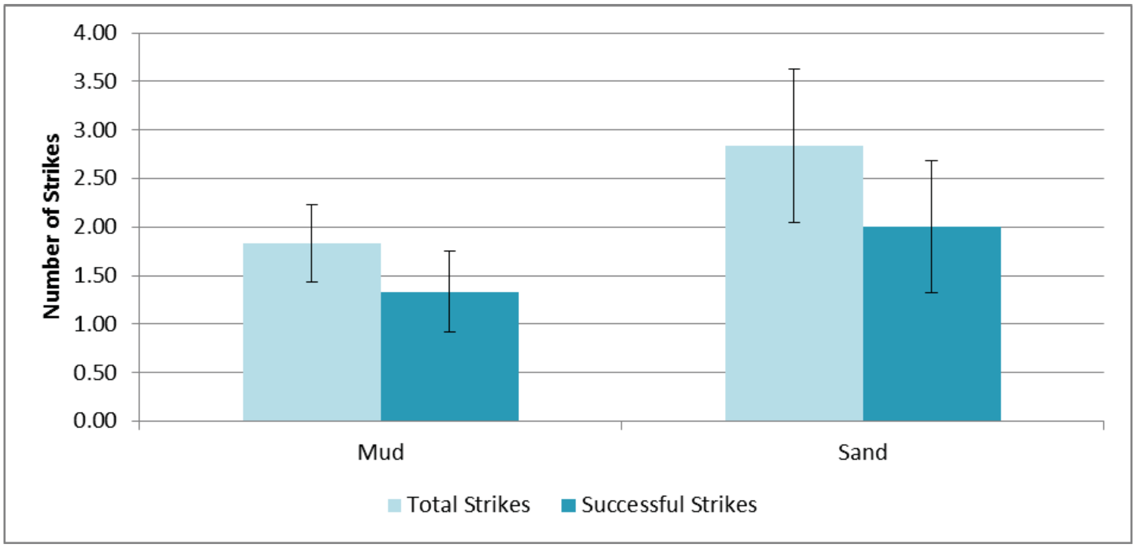


Figure 3.6: Foraging success of six captive juvenile rig (*Mustelus lenticulatus*), measured by the mean number of total strikes and successful strikes ± SE on two different substrates: mud and sand. Ten live crabs (*Hemiplax hirtipes*) were offered as prey.

The average number of successful strikes on mud was 1.3 ± 0.4 and on sand was 2.0 ± 0.7 (Figure 3.6). A paired t-test of successful strikes on mud versus sand revealed no significant difference (t_5=-1.464, p=0.203). Mean total strikes on mud and sand was 1.8 ± 0.4 and 2.8 ± 0.8 respectively (Figure 3.6). Similar results were found for the total number of strikes on mud versus sand (Wilcoxon signed-rank test: Z=1.342, p=0.500).

Mean number of strikes for sharks during the AM trials was higher than the mean number of strikes for the PM trials (Total Strikes: AM=3.2 ± 0.7, PM=1.5 ± 0.4; Successful Strikes: AM=2.3 ± 0.6, PM=1.0 ± 0.4), yet this could be skewed by individual shark behaviour. Successful and total strikes for the second feeding trial were on average higher than the first feeding trial but differences were not significant (Total Strikes: First=1.8 ± 0.5, Second=2.8 ± 0.8; Successful Strikes: First=1.3 ± 0.4, Second=2.0 ± 0.7).

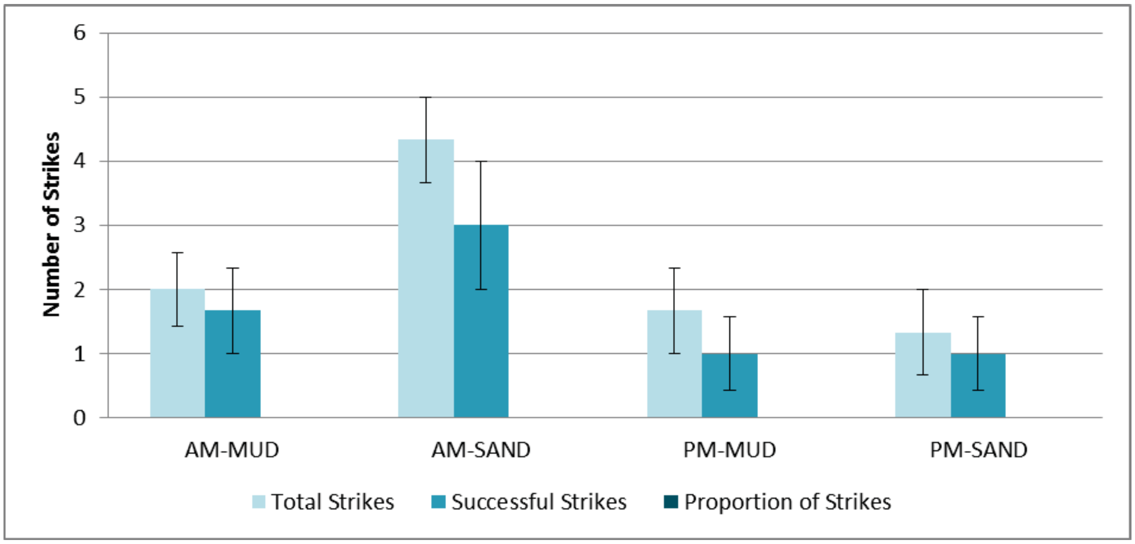


Figure 3.7: Relationship between AM and PM feeding trials by substrate. Three sharks were always fed in the morning while the other three sharks were always fed in the afternoon.

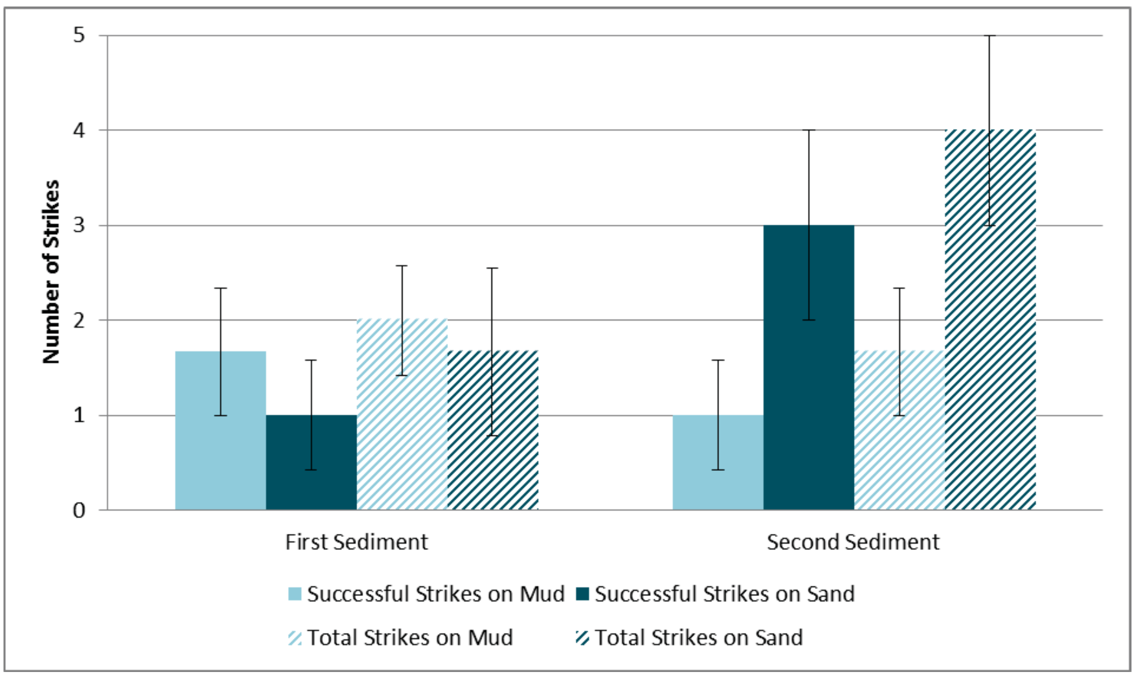


Figure 3.8: Relationship between the mean number of strikes (successful and total) for six captive rig tested on mud substrate first and sand substrate second and vice versa.

Parametric and non-parametric tests revealed that time of day (AM: 9-11 and PM: 12-14) had no significant effect on foraging success (see Appendix Table 2). An order effect was also not apparent in this study. The number of successful and total strikes on the shark's first sediment did not differ significantly from the second sediment (see Appendix Table 2).

Crab Behaviour and Survival

Ten stalk-eyed mud crabs were used as prey for the YOY rig on both sediment types. Different burrowing behaviours were observed from crabs on both sand and mud sediments. Crabs placed in the sand tank when a shark was present typically buried within seconds of contact with the sediment until completely inconspicuous. While most of the crabs remained buried when sharks were present, a few individual crabs did emerge from the sediment and crawl around the tank. No burrows were constructed in the sand tank throughout the feeding trial, yet stalk-eyed mud crabs and burrows had been present at both collection sites in Porirua Harbour (Figure 3.1). Crabs in the mud sediment behaved similarly to the crabs in the sand sediment for the first few minutes of the trial. Upon contact with the mud sediment, the crabs began to bury themselves, however it took them longer in the mud and they were not always completely concealed. Most crabs in the mud sediment remained buried yet a few individuals began constructing burrows after a few minutes. Once a burrow was complete, the crab usually did not appear again.

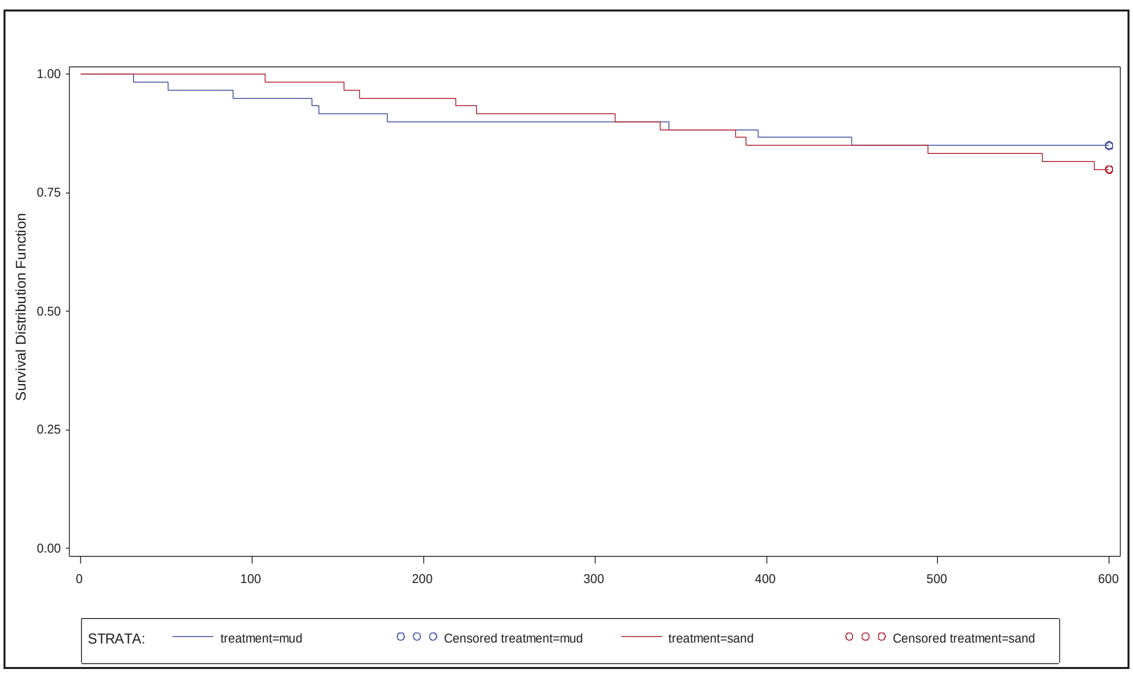


Figure 3.9: Crab survival during the first ten minutes of the feeding trials on mud and sand.

Crab survival was analysed on mud and sand as another means of determining differences in foraging behaviour of YOY rig. The Lifetest was applied to the crab survival patterns on mud versus sand substrates and no significant differences were detected (Wilcoxon test: chi-square = 0.274, P = 0.601; Figure 3.9).

3.5 Discussion and Conclusions

Overview

Six sharks were successfully acclimated to captivity where they began exhibiting normal feeding behaviours after only a few weeks. These sharks were subjected to a feeding trial on two different substrates (sand and mud) using stalk-eyed mud crabs as prey.

Results from feeding trial

Results from the feeding trials revealed that substrate did not have an effect on the foraging effort (time spent foraging) of captive YOY rig. However, the trials revealed that the presence of crabs elicited a feeding response. When crabs were present in the tank, the time sharks spent foraging increased significantly compared to the control trials when crabs were absent. Resting behaviour was also affected by the presence of crabs, resulting in a significant decrease in time spent resting. The amount of time spent swimming did not differ significantly between all four treatments. Foraging success, measured as the number of successful and total strikes, did not significantly differ for each substrate. Crab survival was also unaffected by substrate type.

Effects of sedimentation on other species

Sedimentation in coastal environments can significantly alter macrobenthic communities (Thrush et al. 2003) influencing their structure and function (Ellis, Norkko, and Thrush 2000), while changing abundances and behaviour of rig prey species could influence rig foraging success and effort. Our feeding trials, however, failed to detect any significant differences in the foraging effort and success of YOY rig on sand and mud. During the feeding trials there was high variability in the behaviour of individual sharks. Sharks 3 and 6, in particular, appeared "stressed" and swam near the surface during a large proportion of the trial (Appendix B: Figure 2A). The variability in behaviour, along with small sample sizes, could have masked any differences in foraging behaviour between substrates. Future studies may want to exclude individuals that appear not to have acclimated to captivity.

Feeding Response and Location of Prey

During the feeding trial, rig exhibited increased foraging behaviours when stalk-eyed mud crabs were added to the tank. We know that sharks can use visual, chemical, electrical and mechanical stimuli to locate their prey (Kalmijn 1971) and it is generally accepted that they use a combination of methods rather than relying on only one sense. When YOY rig were fed crabs during the feeding trial, there was often a delay to the onset of the searching/hunting behaviour once crabs entered the tank. When rig were fed defrosted pilchard and shrimp pieces during the acclimation period the same delay was apparent, however the rig often swam past the obvious food before turning back to strike and would occasionally bite the air stone which sat on the bottom of each tank. Similar observations were observed with wild-caught, captive small-spotted catshark (*Scyliorhinus canicula*) and thornback ray (*Raja clavata*) in Kalmijn's (1971) study of electric senses. The fact that rig live in muddy, turbid estuaries and their main prey items are buried in the sediment, leads us to believe vision is not an important means of locating prey for rig. This is further supported by the fact that YOY rig often swam past unburied pieces of pilchard and shrimp and would occasionally bite abiotic objects such as the air stone. On the other hand, rig may rely on smell or electroreception to locate live prey items. The delay in foraging response following the addition of crabs to a tank points towards smell as the primary stimulus eliciting foraging behaviour in rig. The smell of prey dropped in the tank would take a few seconds to disperse causing a delayed reaction. Hobson (1963) found that grey (*Carcharhinus menisorrah*) and white tip (*Triaenodon obesus*) sharks appeared to use olfactory cues to locate bait, with 9 out of 10 sharks approaching prey from downstream. For the rig trials we used round tanks so it was difficult to record the direction of approach in relation to the water current. Electroreception is likely a secondary means of locating prey and may become more important as the sharks move closer to their prey. Mechanical stimuli, as lateral line detection of vibrations, is often more important for sharks feeding on pelagic prey such as fish, however the movements made by crabs while digging may be detectable to rig. If sharks were using mechanical senses to detect the crabs, we would have expected a more immediate response to the addition of crabs to the tank. YOY rig consistently showed a foraging response to the presence of crabs and it appears that the stimulus is most likely smell. However further investigation is needed to determine the roles visual, chemical, electrical and mechanical stimuli play in prey location by YOY rig.

Crab Behaviour

The stalk-eyed mud crab *H. hirtipes* is common throughout New Zealand harbours and estuaries. Stalk-eyed mud crabs dig burrows as a means of protection against predators, however they also have the ability to bury into the sediment when they are unable to reach a burrow. In our experiment, we found the mud substrate was more conducive to permanent burrow construction, while the sand substrate was more conducive to immediate crab burying. No significant difference in rig foraging success and effort was observed on sand and mud.

Latham and Poulin (2002) found *Profilicollis* spp. parasites altered the hiding behaviour of *H. hirtipes*. The mean number of cysts in crabs exposed or partially exposed at low tide was almost double that of crabs hidden during low tide (Latham and Poulin 2002). Both *H. crenulatus* and *H. hirtipes* are intermediate hosts of *Profilicollis* spp. in New Zealand (Latham and Poulin 2002; Brockerhoff and Smales 2002), while the pied oystercatcher (*Haematopus ostralegus*), bar-tailed godwit (*Limosa lapponica*) and southern black-backed gull (*Larus dominicanus*) are definitive hosts of *Profilicollis* spp. in New Zealand (Brockerhoff and Smales 2002; Latham and Poulin 2002). This could affect shark foraging success if crabs affected by parasites are more easily detected by sharks. Crabs used in the current study were not tested for parasites but this could explain the differences in crab behaviour observed during the trial. In a larger study, it may be worth investigating whether foraging success of rig preying on crabs at the substrate surface differs significantly from foraging success of rig preying on crabs buried in the sediment.

Prey Capture Methods

While we determined that YOY rig have the ability to dig in the sediment for their prey, there is still a lot that is unknown about how they capture their prey. We do know that rig can dig in the sediment for prey but we do not know how deep they dig and whether substrate has any effect on their digging behaviour. Heupal and Bennett (1998) discovered epaulette sharks (*Hemiscyllium ocellatum*) were able to submerge their snouts into the substrate up to the first gill slit in order to capture prey items. Smale and Compagno (1997) observed hermit crabs in the stomachs of *Mustelus s*pp. without any signs of shells. It is unknown whether the sharks crushed up the shells and spat them out or whether they captured hermit crabs while out of their shells. A master's student from Auckland University, Sunkita Howard, described adult rig from the East Coast North Island having a particular technique for consuming paddle crabs (pers. comm. Howard 2011).

Study Design and Limitations

Laboratory experiments have an advantage over field experiments due to the greater control one has over experimental conditions. However, there were still limitations to the study design based on practicality and welfare of the study subjects. When testing the same subjects in two different treatments (i.e. sand and mud) a study design of ABB/BAA is ideal to ensure no order or learning effects are confounding the results. Due to time constraints and limited resources sharks were only tested once on each substrate (i.e. AB/BA). Order/learning effects were tested and revealed no significance (Table 3.4, Figure 3.7); however, sample numbers were very small. Carry-over effects are also of concern with crossover trials. In the case of the current study, we could not test sharks on one substrate immediately followed by the second substrate in case sharks became satiated during the first trial. A six-day period between trials was used as a washout period where sharks were returned to the holding tank, fed crabs on mixed sediment and then fasted before the next trial.

Conclusions

Feeding trials involving six captive YOY rig from Porirua Harbour revealed foraging behaviour of the sharks were not affected by sand and mud substrates. Feeding trials did reveal sharks elicited a feeding response when stalk-eyed mud crabs were present and resting behaviour was negatively affected by the presence of crabs. Sharks were observed digging for prey in both sediments. Smell appears to be the sense which elicits a 'frenzied' foraging response in YOY rig; however they seem to use a combination of senses to locate their prey.

Chapter 4

General Discussion

4.1 Introduction

Habitat destruction is a major cause of declines in coastal shark populations (Cortés 2000; Knip, Heupel, and Simpfendorfer 2010; White and Kyne 2010; Speed et al. 2010; Field et al. 2009). Nursery areas such as harbours and estuaries can provide both avoidance from predators and an important food source for young sharks (Castro 1993; Heupel and Hueter 2002; Simpfendorfer and Milward 1993). In recent years, there has been emphasis on the identification and protection of particular habitats important to coastal shark species such as nursery areas; while this is important, further research is necessary to understand the value of these important habitats to the recovery of shark populations (Kinney and Simpfendorfer 2009). It is known that harbours and estuaries around New Zealand act as nursery areas for juvenile rig (Francis et al. 2012), but little is known about how these areas contribute to rig populations in New Zealand. Specific threats to nursery areas, such as habitat destruction as a result of sedimentation, can pose a threat to rig populations. Prior to this study, little was known about the diet and predators of juvenile rig within harbours and estuaries, or how sedimentation might affect rig behaviour. The aims of our study were to (1) determine the diet of young of the year (YOY) rig in New Zealand harbours and estuaries, (2) describe differences in the diet of YOY rig among sampling locations compared to physical and environmental variables, (3) determine the effects of sediment type on captive YOY rig foraging effort and success, and (4) describe captive YOY rig foraging behaviour.

4.2 Summary of Results

Chapter 2: Diet of Young of the Year Rig (*Mustelus lenticulatus*) from New Zealand Harbours and Estuaries

While a few studies have examined rig diets from Otago Harbour, Blueskin Bay, Golden Bay and Avon-Heathcote estuary (King and Clark 1984; Graham 1939, 1956; Thomson

1921; Webb 1972); this is the most extensive study, examining 130 YOY rig from eight different harbours and estuaries from the North and South Islands of New Zealand. YOY rig diets consisted of benthic crustaceans and polychaetes, in particular the stalk-eyed mud crab (*Hemiplax hirtipes*) and the snapping shrimp (*Alpheus richarsoni*). While YOY rig from all locations consumed *H. hirtipes*, some of the lesser common crustaceans and polychaetes contributed to a diet which varied by harbour. Latitude, temperature and depth explained the most variation between individual rig stomachs, while substrate type and turbidity had little influence. A comparison of YOY rig diets and ten adult rig diets from Porirua revealed similar diets. Overall, harbours and estuaries appear to provide an abundant food source for YOY rig and possibly older individuals. We have not yet been able to determine the extent of selectivity of rig diets; to do this, further studies involving simultaneous stomach analysis and benthic sampling would be required.

Chapter 3: Foraging Behaviour of Captive Juvenile Rig (*Mustelus lenticulatus*) on two substrates: sand and mud

A behaviour study examining the effects of substrate type on the foraging behaviour of six captive juvenile rig revealed no significant differences in foraging behaviour for rig on sand and mud. However, the presence of stalk-eyed mud crabs significantly increased juvenile rig's time spent foraging and decreased their time spent resting. We also captured video evidence of juvenile rig digging in both sand and mud for live and dead prey items. Further studies are required to determine exactly which senses juvenile rig use to locate their prey but it is fairly certain that smell (chemoreception) is a key stimulus for rig to begin searching/hunting for prey. Crab hiding strategies appeared to vary with substrate type. Future studies require larger numbers of individuals in both laboratory and field experiments to determine the effects of sedimentation on young of the year rig populations.

4.3 Discussion

Smooth-hounds as crustacean feeders

At least 19 different species of Crustacea were identified from YOY rig stomachs collected during the 2011 rig survey. It was determined that YOY rig diets consisted primarily of benthic crustaceans; this has also been documented with several other juvenile smooth-hounds around the world (Saidi, Bradai, and Bouain 2009; Chiaramonte and Pettovello 2000; Molina and Cazorla 2011; Van der Molen and Caille 2001). Smooth-hounds are described as having strong jaws and pavement-like teeth designed for crushing (Compagno 1990; Yamaguchi and Taniuchi 2000), which accords with their inclusion of hard-shelled prey in their diets.

Polychaetes in the Diet of Rig

A number of studies examining the diet of smooth-hound species around the world have found polychaetes at frequencies greater than 10% (Chiaramonte and Pettovello 2000; Rountree and Able 1996; Smale and Compagno 1997; Van der Molen and Caille 2001). However, calculated importance (%IRI) of polychaetes is generally low due to their small size and mass. Polychaetes also have the tendency to be underestimated in diet studies because they are quickly digested and leave little in the way of identifiable remains. Polychaetes are often overlooked in smooth-hound diets. Their relatively high frequency in rig diets suggests they are an important part of their diets, perhaps providing specific nutrients not found in other prey, or readily digestible prey without a large indigestible load to be processed.

Vegetable, Shell and Other

Vegetable matter was found quite frequently but these items were most likely incidentally ingested and typically reflected the habitat of the prey items found in the same rig stomach (i.e. pieces of sea grass with stalk-eyed mud crabs or mangrove with snapping shrimp). Very small bivalves (<2mm wide) and one small whelk were found in YOY rig diets; due to their size it is highly unlikely the sharks were targeting these items. Abiotic items, including pieces of plastic, were occasionally found in the YOY rig stomachs. All these items were assumed to be incidentally ingested while rig foraged for other species. Identifying the species of plant matter found in the stomachs of rig may give insight into the types of habitats rig prefer to forage in (i.e. seagrass beds or mangroves).

Parasites

Acanthocephalans, nematodes and cestodes were found in YOY rig stomachs. The cystic phase of *Profilicollis* spp. was identified most frequently, followed by nematodes. A high incidence of *Profilicollis* spp. was observed in the diets of rig from Porirua Harbour. *H. hirtipes* and *H. crenulatus* have been identified as intermediate hosts of *Profilicollis* spp. and the pied oystercatcher (*Haematopus ostralegus*), bar-tailed godwit (*Limosa lapponica*) and southern black-backed gull (*Larus dominicanus*) are definitive hosts (Latham and Poulin 2002, 2002), but it is unclear whether rig is also an intermediate or definitive host to the parasite. Both species of crab were identified in the diets of rig from Porirua Harbour along with all three bird species. Parasites are often ignored in diet studies but they can provide important information about trophic levels and community structures (Thompson, Mouritsen, and Poulin 2005).

Ontogenetic Changes in Rig Diets

We did not deliberately set out to investigate ontogenetic changes in the diet of rig, but we did observe similarities in diets between YOY and adult rig in Porirua Harbour. This observation is worth investigating further. Some studies of smooth-hounds observed obvious changes in the diet as sharks grew in size, usually with an increase in size of prey (Smale and Compagno 1997) and diversity (Lipej et al. 2011; Saidi et al. 2009; Saidi, Bradai, and Bouain 2009), but occasionally observing a decrease in diversity presumably reflecting a diet that becomes more specialised with age (Yamaguchi and Taniuchi 2000). However, extrapolation of diet studies from a single area is precarious. For example, Yamaguchi and Taniuchi (2000) found significant ontogenetic changes in *M. manazo* diets from three locations but no significant differences in the diet from the two other locations.

Presence of Invasive Species in the Diet

Our study discovered two recently introduced species, the Japanese Mantis (*Oratosquilla oratoria*) and the greentail prawn (*Metapenaeus bennettae*), in the diet of young of the year rig. This greentail prawn was only just recorded the previous year during a biodiversity survey. This may indicate that rig are not as selective in their prey choice or else these introduced prey species fill similar niches as the native species typically found in rig stomachs. Determining the extent of prey selectivity of rig will require further research and analysis of rig diets with concurrent analysis of benthic communities. Rig may eat species that are most abundant or easiest to catch, on the other hand, rig may select species that are more palatable. Yamaguchi and Taniuchi (2000) discovered that *M. manazo* did not prey on the most abundant crustacean in Tokyo Bay, the southern rough shrimp (*Trachysalambria curvirostris*), but rather consumed many mantis and mud shrimps within the substrate. One possible explanation is that southern rough shrimp may be more difficult to catch than mantis or mud shrimps. Prey selectivity of juvenile lemon sharks was examined by Reeve et al. (2009) by offering two fish species at ratios from 10:0 to 2:8 while analysing the results using a relative electivity index (E_i*). Prey selectivity/preference in juvenile rig can be examined in the laboratory setting by offering multiple prey species and analysing the results using a rank test and/or relative electivity index. Information about prey catchability may be possible through comparisons of dead and live prey selectivity.

Diet from Different Locations

We discovered that while the diet was largely dominated by only a few species, YOY rig diets varied with location. Only in a few harbours, typically in close proximity to each other, did we see similar diets (Kaipara-Raglan, Tamaki-Waitemata, Otago-Porirua). Otago and Porirua are geographically much further from each other than are other pairs of harbours that had similar diets; however only nine stomachs were examined from Otago Harbour, this may not have been sufficient to describe the main components of YOY rig diets. Had there been more stomachs to analyse from Otago Harbour, we may have discovered a unique diet from that location. Examining the environmental variables associated with the stomach collection sites, we found that latitude, temperature and depth explained most of the variation between the diets. The changes in latitude were most likely confounded by the increasing temperatures in the northern harbours. Depth was somewhat surprisingly correlated with stomach contents, in the same direction as temperature; this is most likely confounded due to a tendency for the southern harbours (Otago and Porirua) to be shallower than the northern harbours. On the other hand, substrate type, salinity and turbidity had little effect on the diets of YOY rig ($r < 0.3$). However, only one stomach came from an area with sand while all other samples were from muddy, sandy-mud and muddy-sand areas. The two substrates used during the feeding experiment were most similar to mud and muddy-sand, and no significant differences in rig foraging effort and success were observed with substrate type.

Interpreting these types of environmental variables can be difficult. Changes in depth and benthic substrate can occur over small areas, and rig are quite mobile species, known to make diurnal migrations. Just because rig were caught in a muddy area does not mean they had not foraged in an adjacent area of sand. Animal-borne video systems attached to the dorsal fin of some shark species have been used to collect data about habitat use (Carrier, Musick, and Heithaus 2004, Chapter 19); yet these cameras are quite large and until smaller cameras are developed, this type of data collection will not be available for small shark species such as rig. In order to determine habitat preferences of rig, we must first have a better understanding of the physical and biotic factors influencing prey selection (i.e. Physical: temperature, salinity, depth and substrate type; Biotic: benthic vegetation, prey distribution and availability, predator distribution, social organization and reproductive activity) (Carrier, Musick, and Heithaus 2004, Chapter 19). Models may be helpful in identifying habitat preferences in future diet studies.

CONSERVATION OF COASTAL SHARKS

Overexploitation and habitat destruction/degradation are the biggest threats to coastal shark populations (Cortés 2000; White and Kyne 2010), especially for sharks with limited distribution or those that use a particular habitat (Speed et al. 2010; Walker 1998). The New Zealand National Plan of Action for the Conservation and

Management of Sharks (NPOA-Sharks) was introduced in 2008 and only in 2011 has there been action to identify important rig nursery habitat. While identifying these habitats is important, what is more important is understanding how these habitats contribute to the success of the species, whether it be increasing growth rates by providing an important food source or increasing recruitment by providing a low mortality area for the young. Learning more about the biology and role sharks play in a particular ecosystem can help use mitigate some of the threats affecting coastal shark populations.

Sedimentation

In this study we focused on an aspect of sedimentation occurring in New Zealand harbours and estuaries and how this might affect rig. Several harbours and estuaries around New Zealand have been identified as nursery areas for rig in a recent survey conducted by the National Institute of Water and Atmospheric Research (NIWA) (Francis et al. 2012). Several studies have shown sedimentation to drastically affect estuarine ecosystems. Large sediment deposition events are known to have a smothering effect on macrobenthic communities within harbours and estuaries while also changing abundance and diversity (Thrush et al. 2003; Ellis, Norkko, and Thrush 2000; Thrush et al. 2004), however smaller repetitive sediment deposition can be more damaging than single events (Lohrer et al. 2004). Sedimentation also increases turbidity, which can block light transmission affecting plants and phytoplankton reliant on sunlight for photosynthesis and clog feeding structures of suspension feeders (Thrush et al. 2004). This can begin a bottom-up trophic cascade that causes imbalances in the entire ecosystem (Field et al. 2009).

Sedimentation could cause direct changes to rig foraging behaviour by altering their ability to locate or capture prey, or through indirect changes resulting from an imbalance in the ecosystem, particularly changes in the benthic community. In our laboratory study we did not find that substrate type had any significant effects on foraging effort or success however our sample size was limited (n=6), and our experimental approach could only address immediate, direct impacts of sediment type on the ability of rig to locate and capture one type of prey.

Crab Presence

The presence of crabs had significant effects on the behaviour of rig. When crabs were present in the tank, the sharks significantly increased their foraging behaviour and decreased the time spent resting. This indicates the ability of the sharks to be able to sense the presence or absence of crabs. Thus, reassuringly, demonstrates that our experimental set-up had the potential to measure foraging activity differences. It also indicates that rig could sense the presence and absence of crabs.

Prey Location and Foraging Stimulus

Sharks use a number of senses to locate prey items including visual, mechanical, chemical, or electrical stimuli (Kalmijn 1971). Further investigation is needed to identify which senses YOY rig use to locate their prey but we postulate that smell is responsible for eliciting the feeding response because of a delay in response made by the sharks. Kalmijn (1971) discovered that the small-spotted catshark (*Scyliorhinus canicula*) and thornback ray (*Raja clavata*) produced a 'frenzied feeding behaviour' in response to a few drops of whiting (*Gadus merlangus*) juice added to the tanks. The ability to produce a feeding response to a chemical stimulus may be useful for future studies.

Laboratory versus Field Experiment

Observing rig foraging behaviour underwater, at night and in turbid areas can be quite problematic, which is why we decided to observe foraging behaviour of wild-caught captive YOY rig in a laboratory setting. The advantage of conducting experiments in a laboratory setting meant that we had greater control over certain conditions, but extrapolating our results from the laboratory setting to the natural environment must be done with caution. Lighting, which was set to match the natural diurnal cycle, and the absence of tides enabled some control over the experimental conditions, yet many of the water properties such as temperature and salinity varied with the conditions in Evans Bay. In an ideal laboratory experiment, all variables other than the one being studied would be controlled for and tested separately. In order to better understand the interactions between predator and prey (crab and shark) we would need to imitate these conditions of high and low salinity, temperature, pH, tides and light levels in the laboratory setting to determine the factors most influencing YOY rig diets.

4.4 Conclusions

Harbours and estuaries around New Zealand appear to provide a rich source of food for young of the year rig. While living in these harbours and estuaries YOY rig eat invertebrates, mostly crustaceans, living on top of or within the substrate. YOY rig have the ability to dig for their prey within the substrate and appear to use a combination of chemical, visual, electrical and mechanical stimuli to locate their prey. Changes in substrate type might directly affect rig foraging behaviour by altering their ability to locate prey or indirectly affect rig foraging behaviour by changing macrobenthic community structure and function, however this relationship between substrate and rig foraging behaviour appears complicated. Further research into rig biology, their use of coastal habitats and the major threats affecting these areas is required if we are to ensure their long-term sustainability.

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Appendix A

Table 1: Summary table of data collected from young of the year rig, including stomach content details. Kaipara I and II refer to Arapaoa River and Oruawharo River respectively. Shaded rows indicate rig which were excluded from diet analysis due to empty or decomposed stomachs. Shaded columns represent estimated total length (ETL), weight-stomach content (also known as adjusted total weight), and stomach content weight (n=137).

ID	Harbour or Estuary	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
K1 11-1	Kaipara I	M		27.5	28.1	8.2	6.22	2.22	2.12	1.66	0.93	75.47	70.51	1.94	6.35	1.39	4.96	6.57	3	6	1.15
K1 11-2	Kaipara I	M		37.7	38.6	11.3	7.99	2.79	2.73	2.28	1.10	203.54	198.38	6.93	9.18	4.02	5.16	2.54	2	6	0.93
K1 11-3	Kaipara I	F		35.2	36.0	11.1	7.63	2.75	2.70	2.18	1.17	184.65	169.60	4.27	18.54	3.49	15.05	8.15	4	8	2.69
K1 11-4	Kaipara I	M		40.3	41.2	12.4	8.18	2.96	2.68	2.15	1.15	252.34	245.39	7.80	12.02	5.07	6.95	2.75	2	0	0.00
K1 11-5	Kaipara I	M		46.3	47.4	13.7	9.70	3.49	3.21	2.49	1.51	373.48	359.36	11.36	22.30	8.18	14.12	3.78	3	3	1.28
K1 11-6	Kaipara I	F		35.7	36.5	10.7	7.97	2.90	2.73	2.13	1.19	196.46	184.62	5.58	14.97	3.13	11.84	6.03	3	12	1.80
K1 11-7	Kaipara I	F		39.1	40.0	11.6	8.30	3.27	2.87	2.35	1.25	256.04	246.00	8.48	15.20	5.16	10.04	3.92	3	12	4.73
K1 12-1	Kaipara I	M		36.8	37.6	11.5	7.87	2.74	2.89	1.88	1.26	213.43	211.82	6.54	5.41	3.80	1.61	0.75	1	2	0.04
K1 12-2	Kaipara I	F		43.2	44.2	12.9	9.14	3.13	3.13	2.48	1.28	339.15	321.92	9.47	25.55	8.32	17.23	5.08	3	9	0.39
K1 12-3	Kaipara I	M		42.7	43.7	12.6	8.71	2.88	2.98	2.30	1.21	333.48	327.16	15.50	13.15	6.83	6.32	1.90	1	0	0.00
K1 12-4	Kaipara I	F		40.4	41.3	12.0	8.20	2.85	2.79	2.14	1.24	287.51	275.20	8.08	17.23	4.92	12.31	4.28	3	21	5.73
K1 3-1	Kaipara I	F		44.5	45.5	13.1	8.34	2.80	2.97	2.59	1.25	348.46	336.04	11.60	19.16	6.74	12.42	3.56	2	8	6.44
K1 3-2	Kaipara I	F		42.9	43.9	12.6	8.20	2.79	2.79	2.44	1.19	323.37	315.02	16.91	14.21	5.86	8.35	2.58	2	3	0.14
K1 3-3	Kaipara I	M		39.7	40.6	11.5	8.32	3.02	2.91	2.15	1.15	245.90	232.54	7.38	17.04	3.68	13.36	5.43	3	9	3.29
K1 3-4	Kaipara I	M		41.4	42.3	12.0	8.32	2.92	2.87	2.27	1.23	305.82	287.11	13.10	23.64	4.93	18.71	6.12	4	19	5.50

ID	Harbour or Estuary	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
K2 3-1	Kaipara II	F		37.0	37.8	11.2	7.96	2.77	2.69	2.34	1.03	206.92	202.53	6.72	8.66	4.27	4.39	2.12	2	4	0.77
K2 3-2	Kaipara II	M		38.2*	-	11.2	7.66	3.09	2.60	2.42	1.11	220.67	213.25	5.02	10.84	3.42	7.42	3.36	3	1	0.03
K2 3-3	Kaipara II	M		40.2	41.1	11.5	8.10	3.08	2.80	2.21	1.28	280.21	274.13	8.24	10.20	4.12	6.08	2.17	2	8	2.83
K2 3-4	Kaipara II	M		37.8	38.7	11.4	7.97	2.87	2.66	2.24	1.14	199.97	194.32	5.67	10.45	4.80	5.65	2.83	3	9	3.22
K2 3-5	Kaipara II	M		38.8	39.7	11.4	7.70	2.76	2.50	2.28	1.05	230.18	226.27	9.42	7.74	3.83	3.91	1.70	2	6	1.15
K2 4-1	Kaipara II	F		42.7	43.7	12.8	8.78	2.8*	2.87	2.61	1.23	268.50	253.40	7.55	18.28	3.18	15.10	5.62	3	17	6.02
K2 4-2	Kaipara II	F		40.8	41.7	12.2	8.33	3.09	2.92	2.28	1.24	283.11	275.74	10.95	12.22	4.85	7.37	2.60	2	5	1.25
K2 4-3	Kaipara II	F		39.3	40.2	11.5	8.10	2.76	2.81	2.43	1.19	275.03	254.95	8.38	24.64	4.56	20.08	7.30	4	28	11.15
KN 11-1	Kenepuru	F		42.6	43.6	12.5	8.85	3.08	2.93	2.42	1.45	346.93	331.87	15.33	21.22	6.16	15.06	4.34	3	7	5.89
KN 11-2	Kenepuru	M		42.9	43.9	12.8	9.20	3.06	3.05	2.39	1.36	356.33	330.62	15.53	31.79	6.08	25.71	7.22	4	14	7.28
M 3-1	Manukau	F		40.1	41.0	11.7	8.34	3.05	2.72	2.37	1.28	236.33	230.11	5.71	9.86	3.64	6.22	2.63	2	6	2.34
M 3-2	Manukau	F		38.8	39.7	11.6	8.00	2.74	2.79	2.24	1.25	251.81	243.39	7.50	12.23	3.81	8.42	3.34	3	6	1.32
M 6-1	Manukau	F		38.0	38.9	11.6	7.69	2.28	2.78	2.21	1.32	226.92	218.53	6.33	12.38	3.99	8.39	3.70	3	5	0.77
O 2-1	Otago	F		37.2*	-	11.0	7.62*	2.48	2.83	2.00	1.02	193.90	189.53	1.75	7.83	3.46	4.37	2.25	2	4	0.72
O 8-1	Otago	M		37.0*	-	11.4	7.83	2.82	2.81	2.12	1.04	234.34	220.54	13.72	17.81	4.01	13.80	5.89	3	4	4.02
O 8-2	Otago	F		40.5	41.4	12.1	8.79	3.02	3.11	2.42	1.27	313.09	286.77	15.24	33.21	6.89	26.32	8.41	4	2	1.34
O 8-3	Otago	M		40.5*	-	12.4	8.45	3.04	2.92	2.25	1.23	299.12	276.42	12.48	28.66	5.96	22.70	7.59	4	10	6.80
O 8-4	Otago	F		34.5*	-	10.5	7.12	2.97	2.62	2.17	0.94	172.06	159.55	5.75	16.29	3.78	12.51	7.27	3	4	1.94
O 8-5	Otago	F		38.9*	-	12.0	8.14	3.06	2.91	2.24	1.23	258.45	247.19	12.15	17.62	6.36	11.26	4.36	3	3	1.60
O 8-6	Otago	M		40.1	41.0	11.7	8.26	2.99	3.00	2.36	1.06	279.93	262.57	14.77	23.53	6.17	17.36	6.20	4	4	5.88
O 8-7	Otago	M		36.7	37.5	11.3	7.61	2.91	2.62	2.09	0.95	196.52	181.12	8.03	19.09	3.69	15.40	7.84	3	4	2.94
O 8-8	Otago	F		40.6	41.5	12.3	8.83	3.20	3.06	2.57	1.14	289.33	272.11	15.71	21.78	4.56	17.22	5.95	3	3	2.96

ID	Harbour or Estuary	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
P 11-1	Porirua	M		41.4	42.3	8.6	12.20	2.70	2.97	2.13	1.12	305.91	293.91	13.67	16.10	4.10	12.00	3.92	2	5	3.22
P 12-1	Porirua	M		39.5*	-	8.0	11.70	2.77	2.78	2.02	1.28	224.15	214.93	8.54	12.33	3.11	9.22	4.11	2	2	3.40
P 12-2	Porirua	F		38.9	39.8	8.0	11.46	2.87	2.75	210.00	1.31	223.50	216.22	7.64	11.10	3.82	7.28	3.26	2	1	0.54
P 12-3	Porirua	M		39.9	40.8	8.7	12.23	2.97	2.86	2.28	1.28	258.16	251.52	13.07	10.69	4.05	6.64	2.57	2	3	2.52
P 12-4	Porirua	M		37.0*	-	8.0	11.15	2.62	2.72	2.14	1.16	196.90	190.67	8.20	9.17	2.94	6.23	3.16	2	6	2.01
P 12-5	Porirua	M		41.5	42.4	7.85*	11.80	2.51	2.84	2.19	1.28	286.69	270.28	11.64	19.99	3.58	16.41	5.72	3	3	5.46
P 3-1	Porirua	F		36.9	37.7	7.7	10.80	2.58	2.72	2.26	1.10	212.80	199.25	8.56	16.86	3.31	13.55	6.37	3	10	2.39
P 3-2	Porirua	M		34.7	35.5	7.1	10.10	2.35	2.61	2.27	0.99	165.90	153.12	6.64	15.72	2.94	12.78	7.70	2	8	0.79
P 3-3	Porirua	F		36.2*	-	7.4	11.80	2.49	2.81	2.14	0.95	182.20	-	-	-	-	-	-	-	0	0.00
P 3-4	Porirua	M		38.2	39.1	7.6	10.70	2.82	2.81	2.30	1.15	212.30	207.25	9.43	8.45	3.40	5.05	2.38	2	2	0.30
P 3-5	Porirua	F		35.1	35.9	7.3	10.60	2.31	2.50	1.89	1.21	176.30	167.60	7.57	11.96	3.26	8.70	4.93	2	3	0.84
P 3-6	Porirua	M		38.3	39.2	7.7	11.00	2.65	2.68	2.07	1.16	227.80	215.45	8.65	15.50	3.15	12.35	5.42	3	15	5.78
P 3-7	Porirua	M		39.8	40.7	7.7	12.00	2.87	2.87	2.26	1.14	280.00	266.92	-	17.84	4.76	13.08	4.67	3	16	4.84
P 4-1	Porirua	F		39.8	40.7	8.1	11.80	3.05	2.78	2.19	1.24	239.14	230.69	9.35	11.72	3.27	8.45	3.53	2	6	2.96
P 4-2	Porirua	M		40.5	41.4	8.1	11.60	2.87	2.82	2.30	1.17	260.44	248.38	10.46	16.46	4.40	12.06	4.63	2	4	1.25
P 4-3	Porirua	F		37.4	38.3	8.2	11.20	2.78	2.81	2.20	1.20	224.88	215.12	9.40	13.97	4.21	9.76	4.34	2	4	0.73
P 5-1	Porirua	M		38.2	39.1	8.0	10.70	2.82	2.85	2.39	1.09	260.85	243.07	10.93	22.96	5.18	17.78	6.82	4	3	1.31
P 5-2	Porirua	F		40.4	41.3	8.6	12.10	3.38	2.82	2.14	1.34	277.96	259.50	13.40	24.46	6.00	18.46	6.64	4	20	4.96
P 5-3	Porirua	M		34.8*	-	7.2	10.30	2.72	2.43	1.84	0.99	148.16	143.36	6.28	8.08	3.28	4.80	3.24	1	3	0.41
P 5-4	Porirua	F		36.7	37.5	7.9	10.90	2.73	2.62	2.07	1.15	202.31	189.84	8.53	15.83	3.36	12.47	6.16	3	10	2.91
P 5-5	Porirua	M		37.3	38.2	7.5	10.90	2.62	2.71	2.41	1.06	211.47	205.60	10.00	9.67	3.80	5.87	2.78	3	6	0.91
P 6-1	Porirua	M		35.6	36.4	7.4	10.60	2.88	2.59	2.22	112.00	171.3*	-	4.71	-	2.71	-	-	3	3	0.16
P 7-1	Porirua	F		36.0	36.8	7.4	10.31	2.50	2.55	2.10	1.09	181.12	172.62	7.40	10.98	2.48	8.50	4.69	2	1	1.21
P 7-2	Porirua	M		37.8	38.7	7.8	10.52	2.92	2.79	2.30	1.17	248.26	230.48	11.06	21.64	3.86	17.78	7.16	3	1	1.73

ID	Harbour	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
P 8-1	Porirua	M		40.3	41.2	8.2	11.67	2.90	2.83	2.28	1.15	284.64	273.39	12.01	15.50	4.25	11.25	3.95	2	1	0.76
P 9-1	Porirua	F		37.5	38.4	8.0	10.71	2.91	2.74	2.20	1.18	217.99	208.93	7.70	12.18	3.12	9.06	4.16	2	7	2.21
P 9-2	Porirua	M		36.2	37.0	7.7	10.69	2.83	2.40	2.27	1.00	179.44	170.33	6.56	11.58	2.47	9.11	5.08	2	9	3.90
P 9-3	Porirua	F		36.5*	-	8.2	11.80	3.06	2.85	2.34	1.17	259.33	244.20	9.30	19.12	3.99	15.13	5.83	3	2	4.61
P 9-4	Porirua	M		32.5*	-	6.8	9.26	2.45	2.45	2.10	0.99	138.94	134.95	5.88	6.39	2.40	3.99	2.87	2	5	1.57
P 9-5	Porirua	F		39.1	40.0	8.22*	11.47	2.94	2.84	2.22	1.08	209.68	202.51	7.45	10.50	3.33	7.17	3.42	2	6	5.25
P 9-6	Porirua	F		33.6	34.4	7.4	9.79	2.31	2.56	2.33	0.98	150.18	141.09	4.73	12.14	3.05	9.09	6.05	2	3	2.74
P 9-7	Porirua	M		38.0*	-	7.6	11.11	2.68	2.83	2.24	1.10	203.50	191.56	6.36	14.84	2.90	11.94	5.87	2	10	4.50
P 9-8	Porirua	F		40.7	41.6	8.5	12.17	2.92	2.89	2.38	1.18	291.71	281.44	11.58	15.31	5.04	10.27	3.52	2	5	0.71
P 9-9	Porirua	F		38.5*	-	8.22*	11.42	2.65*	2.80	1.97	1.16	211.71	206.45	9.63	8.59	3.33	5.26	2.48	2	7	1.76
R1-1	Raglan	M		38.2	39.1	11.8	8.19	2.82	2.82	2.22	1.23	253.06	235.03	9.77	22.36	4.33	18.03	7.12	4	12	2.03
R1-2	Raglan	F		37.8	38.7	11.9	7.87	2.82	2.82	2.16	1.12	228.20	209.58	7.17	22.30	3.68	18.62	8.16	4	20	8.49
R1-3	Raglan	F		37.6	38.5	11.4	7.97	2.70	2.94	2.36	1.11	241.13	228.91	8.14	16.90	4.68	12.22	5.07	4	7	3.36
R1-4	Raglan	F		40.6	41.5	12.6	8.58	3.16	2.97	2.39	1.17	285.59	271.51	10.40	18.43	4.35	14.08	4.93	3	7	1.48
R1-5	Raglan	F		39.5	40.4	12.1	8.25	2.86	2.89	2.41	1.22	272.71	260.91	9.31	15.96	4.16	11.80	4.33	4	9	4.27
R1-6	Raglan	F		37.2	38.1	11.2	7.76	3.14	2.84	2.03	1.19	240.59	229.46	10.14	15.21	4.08	11.13	4.63	3	10	2.52
R1-7	Raglan	F		41.6	42.6	12.6	8.71	3.32	2.94	2.45	1.09	283.46	281.44	10.78	7.32	5.30	2.02	0.71	1	4	0.67
R2-1	Raglan	M		37.8	38.7	11.6	7.68	2.91	2.71	2.16	1.12	208.83	201.80	7.55	11.36	4.33	7.03	3.37	2	8	1.82
R2-2	Raglan	F		40.1	41.0	12.0	8.67	3.14	2.89	2.49	1.17	268.26	256.95	9.04	16.16	4.85	11.31	4.22	3	11	4.20
R2-3	Raglan	F		36.4	37.2	11.2	7.87	2.72	2.60	1.94	1.09	196.84	183.46	7.36	17.04	3.66	13.38	6.80	3	9	1.42
R2-4	Raglan	M		48.5	49.6	14.5	9.83	3.59	3.47	2.62	1.46	379.79	350.81	11.56	37.47	8.49	28.98	7.63	4	0	0.00
R2-5	Raglan	M		40.7	41.6	11.9	8.18	3.23	3.00	2.23	1.12	242.33	237.16	7.10	8.44	3.27	5.17	2.13	2	13	1.97
R2-6	Raglan	M		47.3	48.4	14.1	9.96	3.62	3.35	2.57	1.30	372.21	356.59	12.77	23.21	7.59	15.62	4.20	4	13	2.01
R2-7	Raglan	M		38.9	39.8	11.3	8.10	2.81	2.80	2.26	1.05	260.41	250.47	-	12.67	2.73	9.94	3.82	2	12	2.61
R4-1	Raglan	F		39.6	40.5	11.7	8.21	2.97	2.86	2.11	1.22	238.99	228.04	8.05	15.78	4.83	10.95	4.58	3	9	1.20
R4-2	Raglan	M		41.8	42.8	12.0	8.44	3.08	2.84	2.23	1.35	287.67	280.33	10.45	12.36	5.02	7.34	2.55	3	6	0.97
R4-3	Raglan	F		46.1	47.2	13.7	9.59	3.66	3.25	2.50	1.38	401.23	372.24	10.47	38.00	9.01	28.99	7.23	4	8	3.42
R4-4	Raglan	M		41.3	42.2	12.4	8.34	3.05	2.77	2.18	1.30	268.01	255.93	7.57	17.86	5.78	12.08	4.51	4	12	2.47
R4-5	Raglan	F		41.4	42.3	12.5	8.56	3.07	2.88	2.06	1.31	308.60	293.80	11.44	19.62	4.82	14.80	4.80	3	14	4.68
R4-6	Raglan	M		41.1	42.0	12.8	8.53	3.13	2.89	2.53	1.11	271.79	260.73	8.72	16.09	5.03	11.06	4.07	3	10	2.27

ID	Harbour or Estuary	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
T 1-1	Tamaki	UNK		42.8	43.8	12.7	8.61	3.16	2.91	2.62	1.35	332.90	323.18	15.52	14.31	4.59	9.72	2.92	3	11	1.79
T 1-2	Tamaki	M		43.2	44.2	13.0	8.47	2.75	2.85	2.70	0.99	330.98	327.66	14.22	7.78	4.46	3.32	1.00	2	4	0.74
T 3-1	Tamaki	F		40.9	41.8	11.8	8.35	3.17	2.83	2.09	1.21	270.06	264.25	9.37	10.11	4.30	5.81	2.15	2	1	1.46
T 3-2	Tamaki	M		45.8	46.8	13.6	9.42	3.39	3.23	2.43	1.35	394.55	384.72	14.19	14.95	5.12	9.83	2.49	3	3	3.64
T 3-3	Tamaki	F		40.3	41.2	11.7	8.04	2.68	2.85	2.31	1.19	265.26	256.04	8.06	13.28	4.06	9.22	3.48	3	7	1.28
T 3-4	Tamaki	M		43.3	44.3	12.5	8.75	3.14	2.94	2.31	1.31	304.40	300.13	9.19	7.81	3.54	4.27	1.40	2	5	0.35
T 3-5	Tamaki	M		42.7	43.7	12.4	8.60	3.37	2.94	2.18	1.30	297.98	294.86	13.34	7.98	4.86	3.12	1.05	1	5	0.87
T 7-1	Tamaki	F	41.4	40.3	41.2	12.3	8.64	3.25	2.95	2.57	1.26	303.77	282.45	12.38	25.31	3.99	21.32	7.02	4	13	2.82
T 7-2	Tamaki	F	39.6	38.5	39.4	11.7	8.15	2.88	2.72	2.36	1.16	250.12	241.37	7.65	12.54	3.79	8.75	3.50	3	4	1.41
T 7-3	Tamaki	F	39	37.9	38.8	11.4	7.71	3.13	2.94	2.28	1.21	246.50	240.36	10.56	9.56	3.42	6.14	2.49	2	4	2.11
T 8-1	Tamaki	F	40.9	40.4	41.3	12.0	7.95	2.60	2.75	2.65	1.29	268.70	264.78	10.09	7.36	3.44	3.92	1.46	1	2	0.12
T 8-2	Tamaki	M	44.7	43.9	44.9	13.5	8.86	2.95	3.13	2.73	1.08	350.70	339.83	13.02	15.68	4.81	10.87	3.10	3	8	0.76
T 8-3	Tamaki	F	43*	42.5*	-	13.2	8.51	2.91	3.00	2.48	1.17	317.00	306.42	10.35	15.42	4.84	10.58	3.34	3	4	1.94
T 8-4	Tamaki	M	44.4	43.0	44.0	13.0	8.89	2.92	3.02	2.61	1.21	319.50	314.61	14.97	10.24	5.35	4.89	1.53	2	5	0.83
T 8-5	Tamaki	F	41.7	40.7	41.6	12.7	8.07	2.86	2.73	2.46	1.29	244.96	237.55	11.87	10.94	3.53	7.41	3.02	3	6	2.60
T 8-6	Tamaki	F	43.6	41.9	42.9	13.0	8.48	2.90	2.91	2.48	1.22	289.17	282.07	13.87	11.96	4.86	7.10	2.46	3	4	0.56
T 8-7	Tamaki	M	44.7	43.1	44.1	12.0	8.66	3.16	3.07	2.44	1.29	302.40	294.18	12.57	12.74	4.52	8.22	2.72	3	6	3.69
T 9-1	Tamaki	M	38.4	37.6	38.5	10.9	7.56	2.92	2.75	2.04	1.16	226.70	210.56	7.47	19.56	3.42	16.14	7.12	4	9	3.05
T 9-2	Tamaki	M	40.1	39.2	40.1	11.6	7.83	2.81	2.88	2.14	1.16	261.75	253.72	9.22	13.92	5.89	8.03	3.07	2	8	4.64
T 9-3	Tamaki	M	38.9	38.6	39.5	11.5	8.16	2.91	2.81	2.33	1.24	263.19	245.50	10.49	22.13	4.44	17.69	6.72	3	31	8.28
T 9-4	Tamaki	F	40.4	39.8	40.7	11.7	8.07	2.94	2.84	2.35	1.16	262.30	245.65	10.43	21.00	4.35	16.65	6.35	4	14	10.21

ID	Harbour or Estuary	Sex	Fresh Total Length	Total Length (TL)	Estimated TL (ETL)	Head Length	Dorsal Length	Pre-Orbital Length	Pre-Oral Length	Mouth Width	Mouth Depth	Total Weight	Weight - Stomach Content	Liver Weight	Full Stomach Weight	Empty Stomach Weight	Stomach Content Weight	Stomach Content Wt as %BW	Stomach Fullness (0-4)	Number of Prey Items	Weight of Measured Prey
W 10-1	Waitemata	M		39.2	40.1	11.6	8.44*	2.97	2.94	2.36	1.28	191.58*	-	-	-	-	-	-	-	0	0.00
W 10-2	Waitemata	F		38.2	39.1	11.3	7.92	2.77	2.77	2.18	1.15	222.11	216.68	5.79	9.18	3.75	5.43	2.44	2	6	0.76
W 10-3	Waitemata	M		41.8*	-	12.7	8.56	2.83	2.96	2.38	1.30	328.12	310.62	11.04	22.71	5.21	17.50	5.33	4	10	1.01
W 1-1	Waitemata	F		37.7	38.6	10.9	7.81	2.85	2.72	2.14	1.18	225.11	214.85	9.34	13.53	3.27	10.26	4.56	3	5	1.13
W 11-1	Waitemata	F		38.9	39.8	11.6	8.13	2.73	2.80	2.28	1.13	234.38	228.68	7.61	8.74	3.04	5.70	2.43	2	5	0.57
W 11-2	Waitemata	M		40.7	41.6	12.2	8.39	3.01	2.93	2.23	1.19	290.21	277.03	8.75	17.08	3.90	13.18	4.54	4	6	1.35
W 11-3	Waitemata	M		43.1	44.1	12.5	8.71	2.80	2.98	1.99	1.32	292.37	285.34	8.23	11.01	3.98	7.03	2.40	2	4	0.95
W 11-4	Waitemata	M		42.4	43.4	12.5	8.63	2.87	2.93	2.26	1.29	-	-	-	-	-	-	-	-	4	0.43
W 11-5	Waitemata	M		40.1	41.0	11.6	8.35	3.06	2.89	2.19	1.28	-	-	-	-	-	-	-	-	11	1.23
W 2-1	Waitemata	F		40.4	41.3	12.3	8.54	3.06	2.80	2.17	1.31	263.36	257.36	8.79	10.12	4.12	6.00	2.28	2	6	0.76
W 2-2	Waitemata	F		35.5	36.3	10.4	7.60	2.71	2.70	2.09	1.11	168.57	165.14	5.47	5.93	2.50	3.43	2.03	1	5	1.10
W 2-3	Waitemata	F		35.8	36.6	10.6	7.56	2.52	2.68	2.03	1.20	191.89	-	6.02	11.94*	2.49	-	-	4	5	0.69
W 2-4	Waitemata	F		38.6	39.5	11.6	7.94	2.72	2.86	2.37	1.10	257.99	244.33	8.41	18.40	4.74	13.66	5.29	4	6	2.32
W 2-5	Waitemata	M		40.8	41.7	12.0	8.30	3.14	2.84	2.29	1.26	282.29	268.36	6.39	17.77	3.84	13.93	4.93	4	9	5.40
W 2-6	Waitemata	M		37.0*	-	11.0	7.79	2.98	2.67	2.07	1.13	163.26	-	-	-	-	-	-	-	0	0.00
W 2-7	Waitemata	M		39.5	40.4	12.0	8.24	3.00	2.88	2.20	1.17	250.25	240.91	7.60	13.03	3.69	9.34	3.73	3	3	1.18
W 2-8	Waitemata	F		39.6	40.5	11.9	8.38	2.92	2.80	2.16	1.27	254.64	244.57	8.56	13.90	3.83	10.07	3.95	3	5	1.16
W 2-9	Waitemata	F		37.8	38.7	11.3	7.90	2.71	2.83	2.11	1.22	217.07	206.39	6.80	14.45	3.77	10.68	4.92	3	7	0.88
W 2-10	Waitemata	F		39.3	40.2	11.6	8.30	2.74	2.74	2.48	1.06	252.21	242.46	8.42	13.86	4.11	9.75	3.87	3	4	0.95
W 2-11	Waitemata	F		39.0	39.9	12.6	8.35	2.98	2.83	2.08	1.22	264.92	256.01	8.85	12.79	3.88	8.91	3.36	3	11	1.51
W 3-1	Waitemata	M		38.5	39.4	11.0	7.38	2.69	2.66	2.15	1.17	248.20	238.14	11.50	13.64	3.58	10.06	4.05	2	3	0.32
W 5-1	Waitemata	M		34.8	35.6	10.4	7.26	2.60	2.55	2.04	1.16	196.95	182.02	6.03	18.83	3.90	14.93	7.58	4	14	1.75
W 8-1	Waitemata	M		39.2	40.1	11.5	7.91	2.68	2.81	2.25	1.02	271.40	259.59	10.48	15.78	3.97	11.81	4.35	3	10	3.24
W 8-2	Waitemata	F		40.2	41.1	12.1	8.74	3.17	2.87	2.11	1.20	305.50	289.24	10.98	22.22	5.96	16.26	5.32	4	12	5.07
W 9-1	Waitemata	M		40.5*	-	12.0	8.80	3.64	2.94	2.33	1.22	287.37	282.34	7.66	9.78	4.75	5.03	1.75	1	0	0.00
Average				39.65	40.56	10.99	8.99	2.90	2.83	3.78	1.99	255.59	246.39	9.40	15.31	4.32	10.96	4.29	2.74	7.01	2.36
Standard Deviation				2.90	2.97	1.92	1.39	0.26	0.18	17.75	9.47	55.16	52.54	2.95	6.10	1.27	5.38	1.86	0.85	5.24	2.14
Standard Error				0.25	0.25	0.16	0.12	0.02	0.02	1.52	0.81	4.71	4.49	0.25	0.52	0.11	0.46	0.16	0.07	0.45	0.18

*measurements may not be accurate due to damage or decomposition

Appendix B

Table 1: Summary of time spent in each behaviour state (rest, swim, forage, forage – hunt and strike, forage – ingest) of six captive juvenile rig (*Mustelus lenticulatus*). Data were collected for the first ten minutes (600 seconds) of each trial. Final column indicates the substrate on which each shark was tested first.

		Mud					Sand					
	Shark	Rest	Swim	Forage	Forage - Hunt & Strike	Forage - Ingest	Rest	Swim	Forage	Forage - Hunt & Strike	Forage - Ingest	First Substrate Tested
No Crabs	1	448	152	0	0	0	435	160	5	5	0	Mud
	2	539	61	0	0	0	533	67	0	0	0	Mud
	3	0	600	0	0	0	0	600	0	0	0	Sand
	4	243	357	0	0	0	496	104	0	0	0	Sand
	5	478	122	0	0	0	371	229	0	0	0	Mud
	6	0	600	0	0	0	0	596	4	4	0	Sand
	Mean	284.7	315.3	0	0	0	305.8	292.7	1.5	1.5	0	
	SD	241.9	241.9	0	0	0	243.2	242.8	2.3	2.3	0	
Crabs	1	240	281	79	53	26	105	384	111	62	49	Mud
	2	261	178	161	135	26	274	282	44	23	21	Mud
	3	0	520	80	14	58	0	510	90	13	77	Sand
	4	199	364	37	37	0	370	230	0	0	0	Sand
	5	284	240	76	46	30	145	261	194	125	69	Mud
	6	0	539	61	53	8	0	536	64	54	10	Sand
	Mean	164	353.7	82.3	56.3	24.7	149	367.2	83.8	46.2	37.7	
	SD	130.1	149.1	41.8	41.2	20.1	148.9	131.6	66.2	45.4	32	

Table 2: Results of parametric and non-parametric testing of foraging success (number of total and successful strikes) for six captive YOY rig.

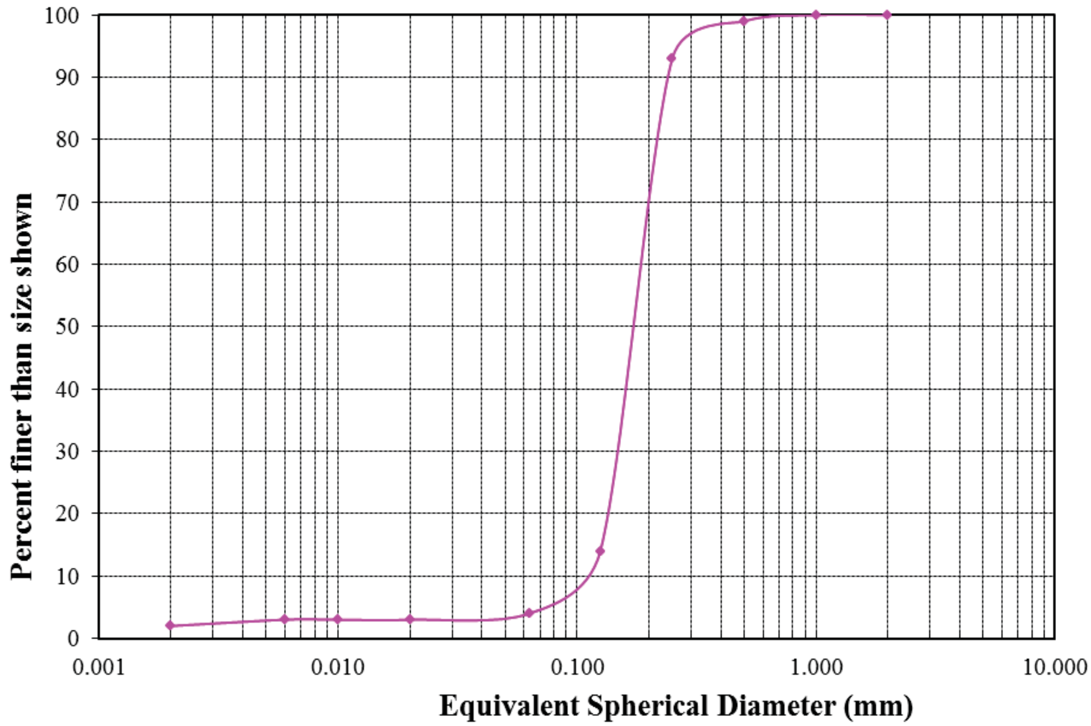
	Successful Strikes			Total Strikes		
	Test Statistic (df)	P-value	Test	Test Statistic (df)	P-value	Test
Mud vs Sand	1.342	0.500	Wilcoxon signed-rank test	-1.464 (5)	0.203	Paired t-test
Time of Day						
AM vs PM	9	0.180	Mann-Whitney rank sum	2.132 (10)	0.059	t-test
AM: Mud vs Sand	-1.512 (2)	0.270	Paired t-test	1.633	0.250	Wilcoxon signed-rank test
PM: Mud vs Sand	<0.001	1.000	Wilcoxon signed-rank test	-0.577	0.750	Wilcoxon signed-rank test
Sediment Order						
First vs Second Sediment	1.342	0.500	Wilcoxon Signed-rank test	-1.464 (5)	0.203	Paired t-test
First: Mud vs Sand	0.756 (4)	0.492	t-test	0.316 (4)	0.768	t-test
Second: Mud vs Sand	-1.732 (4)	0.158	t-test	-1.750 (4)	0.155	t-test

Table 3: Fine-Earth particle size distribution for the sand and mud used in the experiment tanks.

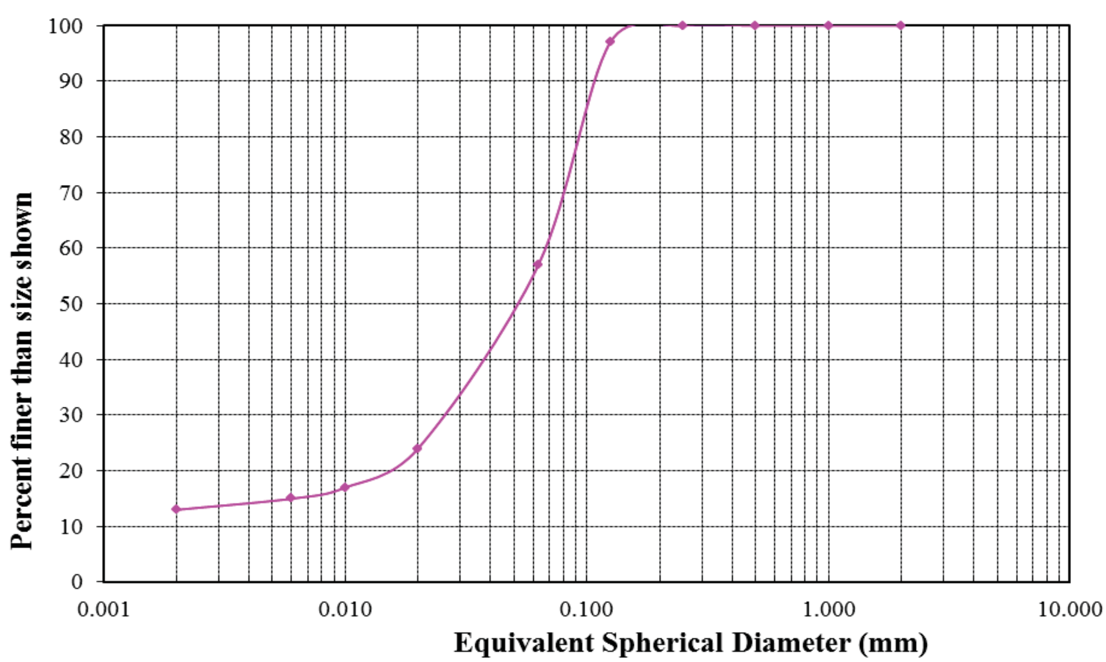
Sample	Coarse Sand (2-0.6 mm)	Medium Sand (0.6-0.2 mm)	Fine Sand (0.2-0.06 mm)	Silt (0.06-0.002 mm)	Clay (<0.002 mm)
Sand	1	32	63	2	2
Mud	0	1	45	41	13

Figure 1: Sand (A) and mud (B) particle diameter.

A



B



Appendix C

Behavioural Observations

Figure 1: (A) head-up swimming behaviour, and (B) head-up resting behaviour. Photo B by Jess Costal.

A few odd behaviours were observed while juvenile rig were kept in captivity. The head-up swimming behaviour (Figure 1: A) involves swimming near the water surface, sometimes at an almost vertical angle with the end of the rostrum out of the water. All six sharks exhibited this behaviour at some point during captivity, however, certain individuals seemed more prone to display this swimming behaviour compared to other individuals. It was often triggered by loud noises or vibrations from doors slamming or from observers bumping into the tanks.

Rig sharks spent the majority of their time lying on the bottom of the tank, resting. Sometimes sharks were observed resting in odd positions, such as lying with their head and fore-body propped up against the tank walls (Figure 3: B) or lying on top of each other.