

Diets and feeding relationships of deep-sea fish from central and
southern New Zealand.

Matthew Richard Langdon Jones

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ATTESTATION OF AUTHORSHIP

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material that, to a substantive extent, has been submitted for the award of any other degree or diploma from a university or institute of higher learning.

Matthew R.L. Jones

Foreword

When I started this I knew nothing about deep-sea fish. Now I can say that with some confidence.

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Abstract

Current New Zealand fisheries management policy is directed towards a more ecosystem-based approach to fisheries management. Any ecosystem-based approach to fisheries management requires an understanding of the feeding interactions within and between fish species; both those commercially and non-commercially exploited. Despite the existence of several decades-old deep-sea commercial fisheries for orange roughy, little is known of the feeding interactions of non-commercially exploited mid-slope deep-sea fishes in New Zealand waters. As a consequence, understanding the roles these fish species play in this ecosystem is of great importance.

To investigate the feeding interactions between New Zealand's deep-sea fish, the diets of 2888 fish attributed to 76 species, of a combined weight of 779 kg, were procured from two New Zealand mid-slope locations: northeastern Chatham Rise 901–1196 metres depth; Puysegur Bank, southern New Zealand, 1020–1072 metres depth; and one upper slope area off the Wairarapa coast, 239–448 metres depth. The stomachs of 1078 and the intestines of 695 of these fish contained food.

Fish with everted stomachs tend to be excluded from dietary analyses, resulting in an underestimation of their role in the ecosystem. Investigation of the intestinal contents permitted partial reconstruction of the diets of fish species with high rates of stomach eversion, or infrequent feeding periodicity. Many of the fish with everted stomachs were benthic feeders, suggesting that their exclusion from dietary studies could underestimate the significance of benthic trophic pathways in the deep-sea: this was highlighted by differences between feeding guilds based on stomach and all gut contents from the northeastern Chatham Rise.

Overall fish diets were from a variety of benthic and/or benthopelagic sources: with some species exhibiting ontogenic dietary shifts, larger bodied food items (often fish, prawns or squid) became more important in the diets of larger fishes. There was some evidence for scavenging in several species, and its role in the diets of these deep-sea species is likely to be underestimated. There were high levels of dietary overlap within species size classes, but not between most species. The fish species at either upper or mid-slope depths do not appear to compete very much for food, indicating a high level of niche partitioning. Niche breadths also were generally low for most species. Scampi was not an important source of food for benthic feeding upper-slope fish species from off the Wairarapa coast.

Stomach parasite analysis and the percentage of empty stomachs (PES) could both be useful dietary metrics. Serrulate rattail had significantly more stomach parasites than four-rayed rattail. The parasite loading correlated with the composition of the diet in both species, and an ontogenic shift in diet for serrulate rattail. Parasite analysis could be a useful addition to stomach content analysis in the absence of stomach contents. Several species did not appear to have fed recently, having a high percentage of individuals with empty stomachs. The percentage of empty stomachs (or intestines) could be a useful indicator of the surrounding food supply, and as such a proxy for the productivity of surface waters.

This thesis addresses some of the gaps in knowledge that are impeding an ecosystem-based approach to the management of New Zealand orange roughy fisheries. This approach is possible for New Zealand orange roughy fisheries, but is still some way in the future, and will require further investigation regarding the interactions between these fish species and their environment.

1.0 Introduction

1.0. General introduction

The deep oceans of the world are as mysterious as they are fascinating. They are the largest living spaces on earth (Rowe 1983, Gage & Tyler 1992, Haedrich 1996, Webb et al. 2010), and they contain one of the largest daily migrations in the animal kingdom (Badcock & Merrett 1976, Forward 1988, Hay 2003, Robison 2009, Ramirez-Llodra 2010). The oceans have an average depth of approximately 4000 metres with waters over 1000 metres deep covering at least 60 percent of the earth's surface (Roberts 2002, Glover & Smith 2003, Ramirez-Llodra et al. 2010), and a maximum recorded depth of 10,924 metres at the Challenger Deep, in the Marianas Trench (Ramirez-Llodra et al. 2011). Only a small fraction of this vast habitat has been explored, and the deep oceans can be considered to be the last undiscovered frontier on earth (Ramirez-Llodra et al. 2010, 2011, Webb et al. 2010).

As the sea becomes deeper, light is gradually absorbed so that by about 1000 metres depth, all solar light is gone. Water pressure also increases with depth; for about every five metres there is an increase of one atmosphere of pressure, so at 1000 metres the pressure exerted by the weight of the overlying water is immense. The deep-sea is cold, and in most places (the Mediterranean Sea being a notable exception) it is below 10°C (Food and Agricultural Organization of the United Nations (FAO) 2011). It was believed until late in the 19th Century that given these inhospitable conditions (lack of light for photosynthesis, immense pressure and cold) life would not be found in the deep-seas of the world (Forbes & Austin 1859, cited in Koslow 2007). However, the Challenger Expedition of the 1870s clearly showed that even though the amount of life decreased almost exponentially with depth, the deep oceans of the world contained much life (Günther 1887, Hamilton 1896, Jamieson et al. 2009).

The deep oceans can be described as layered vertical zones which, for the most part, have indistinct boundaries (Angel 2003). Primary productivity is largely restricted to the upper 200 metres where enough light penetrates for photosynthesis to occur (Rowe 1983, Angel 2003). For organic matter to reach the sea bed thousands of metres below, it has to run the gauntlet of thousands of jaws, tentacles, and other feeding apparatus (Koslow 2007, Smith et al. 2008). For the vast majority of the oceans, only a tiny fraction of surface productivity reaches the deep-sea floor (Gage & Tyler 1992, Buesseler et al. 2007, Ramirez-Llodra et al. 2010). As a consequence, the deep-oceans of the world tend to be food-poor oligotrophic regions (Glover & Smith 2003, Smith et al. 2008, Ramirez-Llodra et al. 2011). Despite the low levels of biomass in the deep-sea,

there are high levels of biodiversity, especially in the sediments (Gage & Tyler 1992, Gage 1996, Danovaro et al. 2008, Smith et al. 2008, Leduc et al. 2010).

The passive falling of organic matter as detrital 'rain' or 'marine snow', which is the basis of the detrital food web (**Fig. 1**), is not the only way organic material is transported downwards (Robinson et al. 2010). Energy is also transported downwards in the form of vertically migrating animals that rise towards the surface to feed, and are eaten once they return to the depths. This has become known as the biological pump (Longhurst & Harrison 1989, Angel 2003, Buesseler et al. 2007, Robison 2009). Many of these vertically migrating organisms have a specific depth range within which they migrate, forming a ladder of overlapping migrations from the surface down to the depths. These vertically migrating animals transfer energy downwards when they are eaten at depth (Percy & Laurs 1966, Iseki 1981, Bathmann et al. 1988, Moku et al. 2000, McClatchie et al. 2005, Robison et al. 2005, Robison 2009), and form the basis of many deep-sea food webs (Koslow 1996, 2007; Drazen et al. 2008).

Although large expanses of the deep-sea floor are made up of oligotrophic muddy abyssal plains fed by the detrital food web, not all deep-sea habitats are low energy (**Fig. 1**). There are some notable exceptions including hydrothermal vents (Shank et al. 1998, Henry et al. 2008, Bachraty et al. 2009), and cold seeps (Foucher et al. 2009, Baco et al. 2010, Law et al. 2010). These examples of high productivity are driven by chemoautotrophic bacteria that reduce hydrogen sulphide (**Fig. 1**) (Pond et al. 2008, Ramirez-Llodra et al. 2011). Hydrothermal vents and cold seeps have attracted much scientific interest as production is not directly driven by the sun (Kolsow 2007, Foucher et al. 2009). Hydrothermal vents are found around continental margins and/or near volcanic hotspots (Desbruyères et al. 1994, Wright et al. 2002, Bachraty et al. 2009), while cold seeps are found around subduction zones, where organic matter on the subducting plate is piled up against the edge of an overriding plate (Foucher et al. 2009) (**Fig. 1**).

New Zealand's complex geography has produced hydrothermal vents in the Bay of Plenty northeast along the Kermadec Ridge (de Ronde et al. 2001, Wright et al. 2002), and zones of subduction, most notably off the east coast of the North Island (Hikurangi Margin) and off the south western tip of the South Island on Puysegur Bank (Lewis & Marshall 1996, Baco et al. 2010, Crutchley et al. 2010). These subduction zones are known for the occurrence of several cold seeps (Carey 1993, Lewis & Marshall 1996, Baco et al. 2010, Barnes et al. 2010, Law et al. 2010).

Enhanced local productivity is also caused by food falls, whether these are from plant matter (often wood and seaweed) (Duperron et al. 2008, Jefferies et al. 2010, Hoyoux et al. 2009, Nishimoto et al. 2009), or animals such as pyrosomes and salps (Lebrato & Jones 2009, Lebrato et al. 2012), jellyfish (Billett et al. 2006, Yamamoto et al. 2008), giant larvacean houses (Robison et al. 2005, 2010), fish (Soltwedel et al. 2003), or the bodies of dead whales (Jones et al. 1998, Baco & Smith 2003, Lundsten et al. 2010). Food falls become localised areas of enhanced productivity (Stockton & DeLaca 1982), and can have specialised fauna (e.g., mussels and worms that are found on whale bone (Marshall 1994, Rouse et al. 2004)). These small islands of productivity can be relatively short-lived, from months up to several years depending on the size and type of fall.

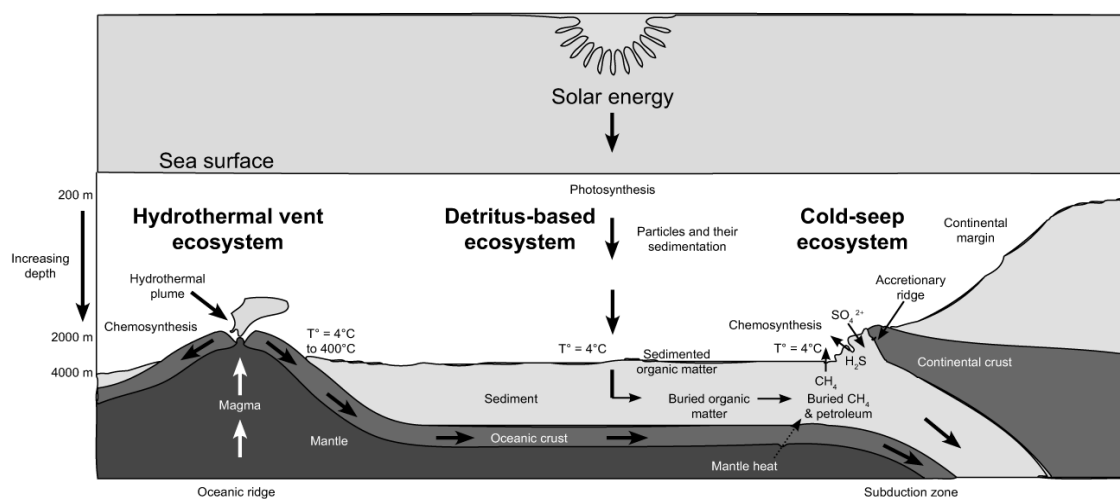


Figure 1. Generalised energy sources in the deep-sea (after Ramirez-Llodra et al. 2010).

Other habitats formed by variations in the bathymetry of the seabed can also provide exceptions to the general low productivity of the deep-sea. Seamounts, undersea mountains of varying sizes and shapes, have summits of limited extent, but do not reach the sea level (Rogers 1994, Yesson et al. 2011), and are considered to be areas of enhanced productivity, regardless of the productivity of the surrounding water (Genin et al. 1986; Fock et al. 2002; Rowden et al. 2010a, b). Definitions of what constitutes a seamount vary, but generally speaking any bathymetric feature rising >50 to 100 vertical metres from the surrounding seabed has been termed a seamount feature (e.g., Tracey et al. 2004, Staudigel & Clague 2010, Wessel et al. 2010). Seamounts increase local current flow and become attractive habitat for sessile filter feeders (typically hard and soft corals and sponges), which take advantage of the hard substrates for

attachment, and the increased current flow to feed and proliferate (Genin et al. 1986; Rowden et al. 2010a, b). Seamounts have become the focus of several commercial fisheries worldwide, most notably orange roughy (*Hoplostethus atlanticus* Collett, 1889) (Clark 1999, 2001, Clark & Rowden 2009, New Zealand Ministry of Fisheries (Mfish) 2011).

Other areas of variable bathymetry such as canyons and drop-offs can be localised areas of enhanced productivity (Genin et al. 1986, Koslow 1997, Vetter & Dayton 1998, Morato et al. 2008, De Leo et al. 2010, Mamouridis et al. 2011). Seamounts and canyons have become commercially important, for the enhanced productivity has often been found to support commercial fisheries of great value (Koslow 2007, Amaro et al. 2009, De Leo et al. 2010, Mfish 2011). Off the south eastern coast of New Zealand's South Island, the Kaikoura Canyon has become the focus of a lucrative commercial whale-watching enterprise (Curtin 2003, Richter et al. 2006) and a now-depleted orange roughy fishery (Mfish 2011).

1.1.1. Global fisheries issues

Historically, fisheries worldwide have been poorly managed in terms of sustainability, with cycles of boom and bust frequent (e.g., Pauly 1995, Jackson et al. 2001, Myers & Worm 2003, Pauly et al. 2005, Caddy & Seijo 2005, Jackson 2008, Mora et al. 2009, Worm et al. 2009, Srinivasan et al. 2012). It has become clear that most marine ecosystems that can be exploited by commercial fishing are being exploited, from the shallows to the depths (Morato et al. 2006, Devine et al. 2006; Tacon & Metian 2009; FAO 2008, 2011; Baker et al. 2009; Link 2010). Global catches appear to have peaked, as the global catch taken by marine capture fisheries has remained mostly static over the last decade (Pauly & Froese 2012), and in 2009 was estimated to be 79.9 million tonnes (FAO 2011). The FAO (2011) also report that there is little room, if any, for further expansion, with approximately 75 percent of global fisheries considered either fully, or over-exploited.

Apart from the overall reduction in the biomass of the exploited species, there are concerns regarding the effects commercial fishing has on the surrounding environment (Jennings & Kaiser 1998, Pauly et al. 1998a, Bailey et al. 2009, Watters et al. 2010). There are concerns that commercial fishing alters the structure of food-webs/ecosystems (Pauly et al. 1998a, Pinnagar et al. 2000, Quinn & Collie 2005, Morato et al. 2006), through the reduction of fish stocks, non-targeted species (bycatch) and their subsequent

discard (Hall, 1996, Hall et al. 2000), damage to habitat (Jones 1992, Dayton et al. 1995, Watling & Nourse 1998, Collie et al. 2000, Clark & O'Driscoll 2003), and the fishing-down (Pauly et al. 1998a, 2001), or through (Essington et al. 2006), or otherwise (Branch et al. 2010) of food webs, resulting in unpredictable changes in species composition (trophic cascades) (Pauly et al. 1998a, Parsons & Lalli 2002, Casini et al. 2008). These effects are compounded by illegal, unregulated or unreported fishing (IUU), which occurs outside of (or despite) fisheries management control (le Gallic & Cox 2006, Sumaila et al. 2006, Agnew et al. 2009, Field et al. 2009). These changes in ecosystem structure are unpredictable, inhibit the sustainability of fisheries (Quinn & Collie 2005, Lynam et al. 2006, Watling et al. 2010), and may be non-reversible (Hutchings 2000, Conover & Munch 2002, Pauly et al. 2002, Hutchings & Reynolds 2004).

1.1.2. Management strategies

One management strategy put forward to help to alleviate these problems has been to allocate fishers a share of the total catch as a property right, or quota (Moloney & Pearse 1979, Annala 1996, Grafton 1996, Pauly 1996, Kearney 2001). By so doing, this passed the responsibility of maintaining stock sustainability to the fishers. In other words, it became in the fisher's interest to spread their catch over the whole year, giving them stable work, and the market a stable supply. These quotas were managed as the summed parts of a total allowable commercial catch (TACC), and a TACC was assigned to the species being exploited. This single species model using TACCs split into quota, then assigned as a tradable property right, has been the basis of fisheries management in New Zealand since 1986 when the quota management system (QMS) was introduced (Lock & Leslie 2007).

However, it has become increasingly evident that this single species management model is not suitable, or effective, for the sustainable management of marine living resources (Copes 1986, Beverton 1998, Walters et al. 2005, Gibbs 2010, Link 2010). Single species management fails to take into account interactions between fishers and the ecosystem; or interactions between species within the ecosystem (Copes 1986, Pauly 1996, Walters et al. 2005, Casini et al. 2008, Branch 2009, Link 2010). The debate fell into two broad camps (Leslie et al. 2008). Advocates of single species management claim that single species management would work if it were followed rigorously (Mace 2004, Hilborn 2004; Hilborn et al. 2005, 2006; Leslie et al. 2008;

Gibbs 2010; Powers & Monk 2010). However, it is increasingly believed that single species approaches can never fulfil sustainability aspirations and that for the future sustainability of fisheries a new paradigm is needed (Pauly 1996, 1997; Francis et al. 2007; Link 2002a, 2010; Hilborn 2011, Hobday et al. 2011).

The new paradigm advocated is ecosystem-based fisheries management (EBFM) (Brodziak & Link 2002, Pikitch et al. 2004, Arkema et al. 2006, Francis et al. 2007). Ecosystem-based fisheries management takes a more holistic view of the fishery (Francis et al 2007, Link 2010, Hobday et al. 2011), focusing on desired states rather than produced outcomes (Morishita 2008), and acknowledges humans as a functional part of the ecosystem (Chuenpagdee et al. 2006). Humans act as a top predator, removing fish from the ecosystem through fishing (Pauly et al. 1998a, Myers & Worm 2003), as well as having a major structuring effect on the ecosystem through habitat modification (Turner et al. 1999). Further to this, an EBFM program considers the interactions between species, especially predator/prey relationships and the interconnectivity of marine ecosystems (Cury et al. 2005, Francis et al. 2007). One of the building blocks of EBFM is the precautionary principle; that is to say, in the absence of data to the contrary, give the benefit of the doubt to the environment (Trouwborst 2009). Another building block is the use of marine protected areas (MPAs) by EBFM (Francis et al. 2007, Wood et al. 2008). As such EBFM is strongly place-based, and specific to the ecosystem under consideration; it also promotes constant and adaptive management so that, as more information regarding the ecosystem is gained, management plans can be altered to accommodate change (Levin et al. 2009, Link 2010, Curtin & Prellezo 2010).

The advantages of EBFM are that it gives more precautionary management recommendations (e.g., Hobday et al. 2011), with particular consideration given to non-target and protected species and their habitats, and trade-offs between user groups are directly addressed and incorporated into management plans (Levin et al. 2009, Link 2010). Ecosystem-based fisheries management also provides improved short, and long-term returns for fishers, and in doing so promotes sustainability over the long term (Link 2010). The main disadvantage with EBFM is that it has intense data requirements, and as such, can be difficult to implement (Brodziak & Link 2002, Pitcher et al. 2009, Hobday et al. 2011). As a consequence, a specific EBFM program requires a great deal of study and analyses before it can be implemented in a practical sense (Arkema et al. 2006, Pitcher et al. 2009, Tuck et al. 2009, Link 2010, Hobday et al. 2011).

In order to understand the ecosystem interactions in a fishery, it is necessary to understand the processes that occur within that fishery (Francis et al. 2007). These include the physical processes such as currents, tides, and climate cycles (on varying temporal scales) (Link 2010). The biological interactions amongst the ecosystems' inhabitants are just as important as the physical interactions, and arguably the most important of these is predation (Cury et al. 2005). Predation plays an important role in the structuring of marine ecosystems (Bax 1998, Pauly et al. 2002, Hay 2006, McCauley et al. 2012). Therefore, it becomes vital to understand predation to enable an understanding of ecosystem processes (Francis et al. 2007). It is necessary to analyse the food and feeding of the ecosystem inhabitants. In a fisheries context, this means the interactions between the fish species must be understood, not only at an inter-specific level, but also at the intra-specific level, as small fish eat different food than bigger fish of the same species do (Pauly et al. 2001).

1.1.3. Global deep-sea fisheries issues

As shallow water fisheries have become fully exploited, deep-sea ecosystems have become the targets of commercial fishing (Koslow et al. 2000; Gordon 2001a, b, c; Morato et al. 2006; Bensch et al. 2009; Nourse et al. 2012). Deep-sea fisheries have been defined as those occurring deeper than the shelf break, where the relatively gentle slope of the continental shelf transitions to the steeper continental slope (Morato et al. 2006, FAO 2011, Drazen & Haedrich 2012). This is demonstrated in the north Atlantic by the mean depth of commercial fishing, which has been increasing by a rate of 32.1 metres per decade since 1990 (Morato et al. 2006). Deep-sea fisheries are not a new occurrence, and originated as small-scale artisanal fisheries on coastlines with narrow, steep continental shelves (Moore 1999, Koslow et al. 2000, Gordon 2001a, Gordon et al. 2003, Morato et al. 2006), e.g., the black scabbard fish *Aphanopus carbo* Lowe, 1839, fishery of Madeira Island, the in North Atlantic (Martins & Ferreira 1995, Gordon 2001a). However, the expansion of commercial fisheries into deep water has been a general worldwide trend over the past 50 years (Merrett & Haedrich 1997, Roberts 2002, Gordon et al. 2003, Morato et al. 2006, Koslow 2007, Baker et al. 2009).

The expansion of fisheries into deeper waters has not been without its challenges and failures, as few deep-sea fisheries have proved to be sustainable (Gordon 2001a, Morato et al. 2006, Bensch et al. 2009, Dunn & Forman 2011, Nourse et al. 2012). There have been 'boom and bust' fisheries in the deep-sea and notable examples include

the fisheries for pelagic armourhead *Pseudopentaceros richardsoni* (Smith, 1844)¹ in the Pacific (Koslow et al. 2000, Koslow 2007, FAO 2011); round-nosed grenadier *Coryphaenoides rupestris* Gunnerus, 1765 in the north Atlantic; rock fish *Sebastes* spp. off Alaska (Moore 1999, Koslow et al. 2000, Gordon 2001a, Bensch et al. 2009); and orange roughy in New Zealand (Clark 1999, O'Driscoll & Clark 2005, Francis & Clark 2005, Dunn & Forman 2011), southern Australia (Koslow 2007), the north Atlantic (Foley et al. 2011), Indian Ocean (Strutt 2000, 2001), and Namibia (Branch 2001). There is now considerable debate regarding the sustainability of deep-sea fisheries (Clark 1999, Francis & Clark 2005, Hilborn et al. 2006, Heymans et al. 2011, Watling et al. 2010, Nourse et al. 2012).

In general the problems regarding the lack of sustainability of deep-sea fisheries have been caused by science lagging behind exploitation (Gordon 2001a, Haedrich et al. 2001, Sissenwine & Mace 2007, Sovacool 2009). There has been a 'fish first, ask questions later' approach to deep-sea fisheries worldwide, with fishers all too eager to exploit new grounds and species before adequate scientific life-history data were collected (e.g., Strutt 2000, 2001, Nourse et al. 2012). This lack of knowledge has been compounded by a lack of regulation for some deep-sea fisheries, as they have often straddled the boundaries of some national exclusive economic zones (EEZs), or occurred outside of them (Bensch et al. 2009), e.g., pelagic armourhead on Hawaiian seamounts (Moore 1999, FAO 2011).

Bycatch and discarding are also issues with deep-sea fisheries, as virtually all bycatch is dead by the time it reaches the surface from mid-slope (approx. 1000 m) depth, and many species of bycatch are discarded (e.g., Anderson 2009). Discards in shallower waters are known to affect the structure of food webs (e.g., Kaiser & Spencer 1994, Dayton et al. 1995), but in deep water this effect is less clear. It is very hard to discern 'scavenging' from 'scavenging on fisheries discards', unless very strict criteria are used (for example: pelagic species that normally would not be available to deep-sea demersal fish, cleanly severed fish heads and filleted fish skeletons (frames) can all indicate discards). Also there is a lack of baseline data to compare the ecology of fishes before exploitation to assess the role discards could now play in the diets of these deep-sea species.

¹ Note: *P. wheeleri* is a misidentification of pelagic armourhead (Froese & Pauly, 2011).

There has been difficulty reconciling the rate of exploitation with the ecology of deep-sea animals (fish and invertebrates). This is especially true when considering habitat disturbance. Deep-sea habitats are often fragile and not adapted to cope with mobile trawl gear (Engel & Kvitek 1998, Watling & Nourse 1998, Cryer et al. 2002, Clark & Koslow 2007, Clark & Rowden 2009). Trawling effectively removes biogenic three-dimensional complexity from the seabed and recovery times may not be measurable on human time scales (Probert et al. 1997, Clark & Rowden 2009). It is also not clear what effect, if any, the removal of this biogenic habitat has on the sustainability of deep-sea fish populations (Fössa et al. 2002, Tracey et al. 2011).

Illegal, unreported, and unregulated (IUU) fishing is also considered to be a major impediment to not only the sustainability of global fisheries, but also their recovery once depleted (Sumaila et al. 2006, Agnew et al. 2009, Sovacool 2009). Illegal, unreported, and unregulated fishing is also a significant issue for deep-water fisheries as many are located offshore where monitoring is often difficult and expensive (e.g., Agnew 2000, Sumaila et al. 2006, Agnew et al. 2009, Bensch et al. 2009). Illegal, unreported, and unregulated fishing also occurs outside national EEZs where the resource is open-access, leaving it open to the potential of a 'tragedy of the commons' situation (Hardin 1968, le Gallic & Cox, 2006, Agnew et al. 2009). Most high seas fishing for deep-sea fish would not be economically viable without subsidies (Sumaila et al. 2010), and some of the problems associated with unregulated high-seas deep-sea fishing would cease if the nations that supported these subsidies could be convinced to cease funding them (Jacquet et al. 2010).

Hannesson (2011) suggests that a possible way of alleviating the problem of the exploitation of stocks occurring outside of national jurisdictions would be to extend national EEZs. Extending the national EEZ would then take some of these high-sea fisheries in under the control of regional management plans, and governmental control. New Zealand and Australia have in effect done this for the orange roughy fisheries in the international waters of the Tasman Sea (Bensch et al. 2009). In this area, catches by Australian and New Zealand vessels have at times been restricted by a total allowable catch (TAC) imposed under a Memorandum of Understanding between the two countries (Bensch et al. 2009).

An example of a positive response to IUU fishing has been the management of the Southern Ocean's toothfish fisheries by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The CCAMLR has taken a proactive

stance on IUU fishing with member states taking an active role in the protection and prosecution of vessels caught fishing illegally within the CCAMLR-managed areas (le Gallic & Cox 2006). For example, Australian naval vessels chased and captured two Russian vessels in 2002 (Bialek 2003). This resulted in prosecutions, and revealed a high degree of organisation behind the IUU fishing, something described as akin to organised crime (Österblom & Sumaila 2011). Other countries have confiscated vessels, most notably France, which subsequently converted one of the captured/confiscated vessels into a patrol boat (Österblom & Sumaila 2011).

One of the problems with exploiting deep-sea fish species is that deep-sea fish often have some life history characteristics that predispose them to being vulnerable to over-exploitation (Gordon 2001a, Koslow 2007, Drazen & Haedrich 2011, FAO 2011). These tend to be a combination of long life, slow growth, high age at maturity, low fecundity, and with some species, a tendency to regularly aggregate around known underwater features, making large catches easier (Clark 1995a, Gordon et al. 1995, Gordon 2001a, b, Merrett & Haedrich 1997). These problems have been compounded by the fish biology being incompletely known at the commencement of the fishery. Ecosystem interactions within these fisheries are also often fairly unknown: be they interactions between the target species and habitat, or other fish species, prey or predation (Uiblein et al. 2003, Baker et al. 2009, Watling et al. 2010). All of these interactions, when coupled with relative ease of capture and powerful ocean-going fleets, have meant that these fisheries have been prosecuted for a relatively short time, over areas which have been serially depleted (e.g., southwestern Chatham Rise seamounts during the late 1980's (Clark et al. 2000, Clark & O'Driscoll 2003)); until the fishery concerned (in the case of pelagic armourhead, and north Atlantic orange roughy) has reached commercial extinction (Moore 1999, Koslow 2007, Foley et al. 2011, Nourse et al. 2012).

It is interesting to note that the biomass of several North Atlantic deep-sea species has been reduced to the level at which they meet the World Conservation Union (IUCN) criteria for endangered species (Devine et al. 2006, Baker et al. 2009). This reduction of biomass could be seen as a clear indication that these species have been overexploited. Several New Zealand orange roughy fisheries would also fit the IUCN criteria but for that species, high age at maturity and long life span (Mfish 2011, International Union for Conservation of Nature and Natural Resources 2001).

1.1.4. New Zealand deep-sea fisheries

New Zealand has developed several highly profitable deep-sea fisheries, some of which are considered to be amongst the most sustainably managed in the world (Townsend et al. 2006, Mora et al. 2009, Worm et al. 2009, Marine Stewardship Council (MSC) 2010). In 2009 New Zealand hoki (*Macruronus novaezelandiae* Hector, 1871) fisheries had an asset value of \$815 (millions of NZD), and orange roughy \$282 (Statistics New Zealand 2010), making orange roughy the second most valuable deep-water trawl fishery after hoki in New Zealand (**Table 1**). These fisheries are of great value to New Zealand not only in the export dollars they generate, but also in the jobs and income they provide (Helson et al. 2010). Consequently, the sustainability of these fisheries is of great importance to the future of the New Zealand economy.

New Zealand's deep-water fisheries can be broadly divided into two groups: fisheries that exist on the upper-slope between depths of between approximately 200 and 800 metres (middle-depth fisheries), and those that occur in deeper water on the mid-slope, at approximately 800 to 1200 metres (deep-sea fisheries) (**Table 1**). The two major mid-slope fisheries are those for orange roughy and oreos (*Oreosomatidae*) (Mfish 2011, Anderson 2011a, b). The orange roughy fisheries are divided into ten major fisheries management areas (FMAs). These are loosely based on the spawning stocks they contain, although it is thought that some of the areas may contain more than one spawning stock (Mfish 2011). The largest stock is on Chatham Rise (3B) and the fisheries there are based around seamount features (Clark 1995a, 1999, Clark et al. 2000, Clark and Rowden 2009, Mfish 2011).

Table 1. Major New Zealand commercial deepwater fisheries by asset value in 2009. Mid-slope fisheries are in bold typeface (Statistics New Zealand 2010, New Zealand Ministry for Primary Industries (MPI), 2012) (na: data not available).

Species	Scientific name/s	Approximate depth range fished (m)	Predominant method of fishing	Asset value in 2009 (millions of NZ dollars).
Hoki	<i>Macruronus novaezelandiae</i>	200–800	Mid-water, and bottom trawl	815
Orange roughy	<i>Hoplostethus atlanticus</i>	750–1200	Bottom trawl	282
Ling	<i>Genypterus blacodes</i>	200–800	Long-line, and bottom trawl	246
Hake	<i>Merluccius australis</i>	250–800	Mid-water, and bottom trawl	135
Scampi	<i>Metanephrops challengeri</i>	250–450	Bottom-trawl	132
Oreo	Three main species: <i>Allocyttus niger</i>, <i>Neocyttus rhomboidalis</i>, <i>Pseudocyttus maculatus</i>	450–1500	Bottom-trawl	74
Southern blue whiting	<i>Micromesistius australis</i>	250–600	Bottom-trawl	74
Squid	Two species: <i>Nototodarus gouldii</i> and <i>N. sloanii</i>	300–500	Jigging and trawling	na
Jack mackerel	Three species: <i>Trachurus declivis</i> , <i>T. murphyi</i> , <i>T. novaezelandia</i>	0–500	Bottom trawl, mid-water trawl, or by purse seine targeting surface schools	54
Deepwater crabs	Several species: <i>Chaceon bicolor</i> <i>Lithodes murrayi</i> <i>Neolithodes brodiei</i>	800–1100 120–700 800–1100	Pots Pots, and as bycatch in orange roughy fisheries.	na

The oreos (Oreosomatidae) are the focus of the other major mid-slope fin-fish fishery in New Zealand waters, and are fished in deeper waters (approx. 600–1300 m) than orange roughy (Mfish 2011, Anderson 2011b). There are three main oreo species caught, and as they are largely caught together they are treated as a species group (Table 1). Of the three main oreo species, black oreo (*Allocyttus niger* James, Inada & Nakamura, 1988) is a southern species and is very abundant on the southern flanks of the Chatham Rise; smooth oreo (*Pseudocyttus maculatus* Gilchrist, 1906) occurs slightly deeper at 650–1500 metres, and has a similar distribution to black oreo; spiky oreo (*Neocyttus rhomboidalis* Gilchrist, 1906), is less common than the previous two species (Anderson et al. 1998, Mfish 2011, Anderson 2010b). A further oreo species, warty oreo (*A. verrucosus* (Gilchrist, 1906)) is still less abundant than the previous two species, and is thought to have a more northerly distribution (James et al. 1988, Koslow et al. 1994, Anderson et al. 1998, Bulman et al. 2002).

The oreo fishery differs from the orange roughy fishery in that it has a more southern focus, and occurs in slightly deeper waters (Anderson 2010b, Mfish 2011). It is speculated that the more southerly distribution of oreos is related to their preference for slightly colder water than orange roughy, reflected in the relative distributions of the two groups of species on Chatham Rise, with orange roughy more common on the

northern flanks and oreos on the southern (Tracey & Fenaughty 1997, Dunn et al. 2009, Anderson 2010a).

Hoki is the most important of New Zealand's trawl fisheries (**Table 1**) (Francis et al. 2006, Connell et al. 2010, Mfish 2011). It is an upper-slope fishery and is fished generally between depths of 200 and 800 metres (Livingston & Schofield 1996, Livingston 2002, Bull & Livingston 2001). There are considered to be two main stocks; eastern and western (Bull & Livingston 2001). Hoki migrate to spawn and the western stock is thought to originate on the Campbell Plateau, and migrate northwards to spawn off the west coast of the South Island. The eastern stock migrates from Chatham Rise to Cook Strait to spawn. Although hoki are caught throughout New Zealand waters (Mfish 2011), the main fishing grounds are their two spawning grounds on the west coast near the Hokitika Canyon, on the east coast of South Island in Cook Strait, and on Chatham Rise (Mfish 2011). The hoki fishery was certified as sustainable by the MSC in 2001, and re-certified in 2006 (MSC n.d., New Zealand Ministry of fisheries (Mfish) 2011). Other notable upper-slope trawl fisheries exist for several other crustacean and finfish species, for example, hake, ling, alfonsino (**Table 1**). However, they are not the focus of this study, and they are not discussed in detail.

Currently the New Zealand Ministry of Fisheries has an ambition to have the orange roughy fisheries similarly certified as sustainable, with a view to using ecosystem-based fisheries management approaches (Mfish 2010). Management of orange roughy fisheries using these approaches requires knowledge of the ecology of the other fishes that occur on the mid-slope; their feeding, and interactions with their environment (Francis et al. 2007). While much is known regarding the biology of orange roughy (Rosecchi et al. 1988, Clark et al. 2000, Branch 2001, Dunn & Forman 2011) and other commercially exploited deep-sea species (Mfish 2011, Stevens et al. 2011), comparatively little is known regarding the ecology of the other fish species that inhabit the mid-slope waters off New Zealand (Clark & King 1989, Clark et al. 1989, Clark et al. 2000). Before any ecosystem-based approach to management can be successfully attempted, this is an issue that needs to be addressed.

An upper slope crustacean trawl fishery exists in New Zealand waters for scampi, *Metanephrops challengeri* (Balss, 1914) (MPI n.d.). This small clawed-lobster occurs around New Zealand in upper slope depths between approximately 140 and 640 metres (Wear 1976), and is typically fished between approximately 200 and 500 metres (Cryer & Stotter 1999). Scampi live in burrows in soft sediments, and a commercial fishery for

them has developed since the mid 1980s (Cryer et al. 2002, Hartill et al. 2006, Mfish 2011). This fishery had an asset value of \$132 million NZ dollars in 2009, and produced about 11 million (NZ) dollars in exports in 2008 (Mfish: scampi n. d.). The central (east) scampi fisheries management area (SCI2) (of which the Wairarapa coast is a part) has had a TACC of 200 Tonnes since its introduction into the QMS in 2004 (Mfish 2011). However, this TACC has not been achieved since then, with catches usually being less than half this value (Mfish: scampi, n. d.).

Although there is no current plan to have scampi MSC certified, any ecosystem-based management plan would require knowledge of the demersal ecosystem in this region, starting with the major trophic interactions (Francis et al. 2007). At the time of this study these data did not exist, as there was no information regarding the trophic interactions of fish species from a scampi fishery from the Wairarapa coast. It was not known if scampi was important as food for any of the fish species, or what fish species it was important to.

For both the New Zealand mid-slope orange roughy and upper slope scampi fisheries there is currently a lack of knowledge regarding biological ecosystem interactions. Most particularly these are the feeding interactions between the non-commercially exploited fish species. For many of these species their feeding ecology is very incompletely known (or unknown), with previous studies being few in number, based on large adult fish from one region, time of year, and carried out decades ago (e.g., Clark 1985a, b; Kerstan 1989; Clark & King 1989; Clark et al. 1989). While more recent work has focussed on the diets of non-commercially exploited fish species from upper slope depths on Chatham Rise, it is not clear that the results of these studies can be extrapolated to deeper mid-slope waters on Chatham Rise or to other New Zealand regions (e.g., Dunn et al. 2010a, b, c; Horn et al. 2010a, b, 2011; Forman & Dunn 2010, 2012).

This research programme provides the most comprehensive account of mid-slope deep-sea trophic relationships in New Zealand waters to date. It provides fundamental information that advances our appreciation and understanding of deep-sea ecosystem functioning, and these data are fundamental to the development of any future plan for sustainable ecosystem-based fisheries management in New Zealand waters.

1.1.5. The aims of this thesis:

1. construct a literature review of New Zealand deep-sea fisheries issues using orange roughy as a case study
2. describe the diets of deep-sea bycatch species from three geographic regions: mid-slope soft-sediment of northeastern Chatham Rise, seamount habitat of the Puysegur Bank, and upper slope, soft sediment off the Wairarapa Coast, New Zealand
3. describe feeding relationships between bycatch species within and between regions
4. discuss the diet and feeding relationships of bycatch from northeastern Chatham Rise, seamount habitat of the Puysegur Bank, and upper slope, soft sediment off the Wairarapa Coast in terms of EBFM and potential future management

1.1.6. Chapter outlines

Chapter two contains a literature review, which focuses on the creation of the New Zealand quota management system (QMS), the shortcomings of single species approaches to fisheries management and a move to more ecosystem-based approaches to fisheries management, using orange roughy as a case study. This chapter also outlines the methods used, and the challenges faced when trying to describe the diets of deep-sea fish.

Chapter three describes the dates, depths and locations from where the fish were obtained. This chapter describes the methods used to calculate the percentage of empty stomachs and the calculations used to ascertain the efficacy of the samples to describe the dietary variation within each species. This chapter also describes the methods used to compare fish gut contents within species (ontogenically) and between species (dietary overlap); the methods used to analyse the differences between stomach and intestinal contents for selected fish species; the methods used to calculate the approximate trophic level and the feeding guilds of these species; and the analyses of stomach parasites in serrulate and four-rayed rattail. Finally, the limitations of this study are described.

Chapter four provides the results of the analyses described in the previous chapter. The results are laid out by region and by depth range: firstly northeastern Chatham Rise; then Puysegur Bank; and off the Wairarapa coast. Results are then provided for the number of stomachs and/or intestines necessary to describe the diets of each species, depending on which dietary classification was used. Results are provided for fish species with greater than ten stomachs or intestines containing food; then comparisons between stomach and intestinal contents for selected fish species from the three study areas. Then the results of the parasite analysis of serrulate and four-rayed rattail are provided. Finally, the results of the multivariate analysis of diet similarity and feeding guild analysis are provided.

Chapter five provides a discussion regarding the results found in the previous chapter. The structure of this chapter follows the previous chapter. The diets of these deep-sea fish are described in relation to their ecology and morphology.

2.0 Literature review

2.0.1. New Zealand deep-sea fisheries for orange roughy and the quota management system (QMS)

This chapter will review deep-sea fisheries issues and fisheries management in New Zealand and international waters. The focus of this review is on the management of species in relation to their ecology, using orange roughy (*Hoplostethus atlanticus* Collett 1889) as a case study. This chapter will also briefly describe the biology of orange roughy, the history of the quota management system in New Zealand fisheries, and the advantages and disadvantages of single-species-based management.

2.1. Biology of orange roughy and a brief history of orange roughy fisheries in New Zealand waters

2.1.1. Biology of orange roughy

In order to understand why orange roughy fisheries have a poor history of sustainability it is important to understand major aspects of this species' biology. Orange roughy has a nearly global distribution, and is found throughout the temperate oceans of the southern hemisphere (Kotlyar 1996), also occurring in the temperate north and western Atlantic (Laptikhovsky 2006, White et al. 2009), the southern Indian Ocean (Strutt 2000, 2001), and appearing to be most abundant around New Zealand and the waters off southern Africa (Branch 2001). It is found on the mid-continental slope between depths of 450–1900 metres (Kotlyar 1996, Branch 2001), although is typically fished at circa 1000 metres (Gordon & Duncan 1987, Branch 2001, Mfish 2011). A notable discontinuity in the distribution of orange roughy is its absence from north Pacific and tropical waters. It has been considered that a possible driver for this distribution of species was the circum-Antarctic conveyor current that encircles the southern hemisphere in the Southern Ocean at about 1000 metres water depth, and then passes up into the north Atlantic (Rintoul 1991). This current is also used as a possible explanation for why orange roughy is not found in the northern Pacific, as the loop of current that extends up into the north Atlantic is not duplicated in the north Pacific. Its vertical distribution is thought to be related to ambient water temperature, where it is most commonly found between 3.9–6.5°C (Branch 2001, Dunn et al. 2009).

Orange roughy is a slow-growing fish, thought to live 120–130 years (Tracey & Horn 1999, Andrews et al. 2006). Bulman & Koslow (1992), and Koslow (1996, 1997) have shown that orange roughy has a relatively high metabolic rate for a deep-sea fish. High levels of the enzyme lactate dehydrogenase, a glycolytic enzyme that mediates

anaerobic metabolism, and citrate synthase, an enzyme mediating aerobic metabolism, consistent with an elevated metabolic rate have been recorded, which confirm this (Koslow 1996). Koslow (1997) linked the high estimates of metabolic rate to body plan and the firmness of the flesh, and suggests that orange roughy consumes most of its energy through activity. The seamount habitat this species favours is one of high current flux (often greater than 40 cm s^{-1}), and Koslow (1997) concluded that orange roughy were likely to use up energy simply by maintaining position in a high current environment. As such, orange roughy can be considered a high-energy/high-expenditure fish, a combination resulting in a very low growth rate.

There is a small amount of evidence for colour change in orange roughy and that this appears to be linked to metabolism. Lorance et al. (2002) observed white orange roughy from a submersible off the Bay of Biscay. This phenomenon had been observed previously on video recordings, but was assumed to be an artefact caused by the lighting of the submersible. Tissue samples from orange roughy have shown the presence of a tissue layer rich in melanocytes, which have the ability to open and close and hence change the colour of the fish. It is suggested that the colour change is linked to metabolic activity, but at present this white colouration is incompletely understood.

Orange roughy have few natural predators and the rate of natural mortality is low (0.0045 year^{-1}) (Clark et al. 2007). There is some evidence for sperm whale (*Physeter macrocephalus* Linnaeus, 1758) predation of orange roughy, as Gaskin & Cawthorn (1967) report “*Hoplostethus* sp.” (most probably orange roughy) in stomachs of sperm whales caught off the east coast of South Island New Zealand. Kotlyar & Lipskaya (1980) also report orange roughy in the stomachs of sperm whales, and Koslow et al. (1995a) report observing sperm whales diving over known locations of orange roughy spawning aggregations. It would be interesting to speculate on the size of orange roughy populations before the reduction of sperm whale biomass due to whaling.

Orange roughy has low fecundity, with 20,000–70,000 eggs kg body mass^{-1} (Pankhurst & Conroy 1987, Pankhurst et al. 1987, Clark et al. 1994, Minto & Nolan 2006, Mfish 2011) and, in New Zealand and Australian waters, forms large spawning plumes between June and August (Bell et al. 1992, Clark et al. 2000, Koslow et al. 1995b). Orange roughy is a group-synchronous spawner and in New Zealand waters spawning generally occurs from June–August and is linked to day length (Pankhurst et al. 1987). It possesses retinal adaptations that maximise visual sensitivity, enabling it to determine diurnal changes in ambient light at depths to 900 metres, which may aid in

the formation of spawning aggregations (Pankhurst 1987). Estimates on the age at first spawning range between 23 and 31.5 years; and the species is not believed to spawn every year (Francis & Clark 1998). Sex ratios vary greatly within spawning aggregations, and depend not only on where, but when the catches were taken (Pankhurst 1988, Clark & King 1989, Anderson 2000, Langley 2001, Anderson & Langley 2002). There is also vertical stratification between the sexes, with females tending to predominate at the bottom and males at the top of these aggregations. This is thought to facilitate fertilisation of the eggs, which are positively buoyant upon hatching (Pankhurst 1988, Grimes & Zeldis 1993, Zeldis et al. 1995a, 1998).

Orange roughy are thought to migrate hundreds of kilometres to spawn (Francis & Clark 1998). In a review of Australian orange roughy fisheries, Koslow (1997) inferred that the size and density of the spawning aggregations is such that they could not be maintained by the productivity of the surrounding water. It was concluded that spawning aggregations of orange roughy were not from the standing stock and probably migrated in from other areas to spawn. However, orange roughy tend not to feed during spawning (Liwoch & Linkowski 1986), so the productivity of the water surrounding an aggregation may not be important to spawning fish. Conversely, they may not be feeding due to the lack of food. On Chatham Rise, Francis & Clark (1998) used the length at which 50 percent of mature females are spawners (L_{50}) to infer migration into spawning areas. By comparing the L_{50} at different times of the year, it was shown that fish were larger during spawning in June–July than other times, thus inferring that fish were migrating to spawning grounds from elsewhere to spawn.

There are conflicting reports regarding the juvenile ecology of orange roughy, with reports from the north Atlantic suggesting that juveniles are mesopelagic (Shephard et al. 2007), while on Chatham Rise nursery grounds are thought to be demersal (Dunn et al. 2009). Juvenile orange roughy are almost unknown and only recently have nursery grounds been found on Chatham Rise (Dunn et al. 2009). In the north Atlantic juveniles are thought to be mesopelagic, later settling near the seabed (Shephard et al. 2007).

Orange roughy are benthopelagic foragers and broadly speaking have a diet consisting of (in order of importance) vertically migrating fish (Stomiidae and Myctophidae), prawns (Oplophoridae, Pasiphaeidae and Sergestidae) and squid (Cranchiidae, Mastigoteuthida and Onychoteuthidae). Diet varies with ontogeny (more squid are eaten by larger fish and fewer small crustaceans), and by depth (more squid

are eaten in deeper water) (Rosecchi et al. 1988). They have a slight diel variation in feeding, with more full stomachs being found in the afternoon (Bulman & Koslow 1992), and seasonally they feed more in the austral spring, and least in the austral winter (Liwoch & Linkowski 1986).

2.1.2. Fisheries for orange roughy

The New Zealand bottom-trawl fishery for orange roughy developed in 1978 (Clark 2001), and the first grounds to be exploited were on Chatham Rise (Clark 1995a), with others subsequently found and exploited throughout the 1980s on Challenger Plateau (Clark & Tracey 1994), off the east coast of South Island north of Kaikoura, and on Wairarapa and Ritchie Banks (Mfish 2011). In the 1990s, fisheries expanded further into southern areas off Puysegur Bank, the Bounty Platform and Campbell Plateau, and northern areas, such as those north of East Cape, within Bay of Plenty, and Northland (Clark et al. 2000). Fisheries also developed outside New Zealand's 200 nautical miles EEZ, notably on Louisville Ridge (Clark & Anderson 2003), Lord Howe Rise, northwest Challenger Plateau (O'Driscoll 2001), South Tasman Rise, and West Norfolk Ridge (Mfish 2011).

Catches in New Zealand waters were initially high, with 40–50,000 tonnes caught annually throughout much of the mid 1980s (Clark 1995a). However, catches began to decline in the late 1980s, in a response to a reduction in total allowable catch (TAC) limits, and this trend of reduction has continued throughout the 1990s and into the new millennium (Mfish 2011). Originally, spawning “plumes” were the targets of commercial fishers, limiting catch to mostly mature fish, but more recently fishing has been undertaken all year round and immature fish are now regularly taken by trawls (Clark et al. 2000, Clark 2001, Branch 2001, Dunn et al. 2009). Although during the 1990s catches continued to decline, the overall catch was maintained at a relatively high level due to the almost continuous discovery of new fishing grounds, with fishing fleets transferring effort further afield, moving progressively offshore from New Zealand into international waters (Clark 1999, Clark & Anderson 2003, Clark et al. 2007). For example, the Chatham Rise fishery in the late 1980s saw a period of decline in catch rates, offset by a progression eastward as new seamount features (mostly hills and knolls (Rogers 1994)) were discovered and exploited elsewhere (Clark 1999, Clark et al. 2000). This serial depletion of orange roughy also occurred on hills and knolls throughout the Bay of Plenty (Annala et al. 2004) and has also been observed with

seamounts in the Louisville Ridge fishery (Clark 1999, Clark & Anderson 2003). Many of these hills, knolls, and seamounts were only fished for a short period before they became depleted and fishing effort was directed elsewhere (Clark 1999, Clark & Koslow 2007).

Bottom trawling for orange roughy also produces bycatch (Probert et al. 1997, Anderson & Clark 2003). In the early years of New Zealand orange roughy fishing, bycatch was minimal as the fishers targeted spawning plumes that occurred off the seabed (Clark 2001). However, as the fishery expanded and sounding equipment and trawl gear improved, fishers were able to trawl along the sea bed and fish more difficult terrain, such as that occurring on seamounts and other rough ground (Probert et al. 1997, Branch 2001); the amount of bycatch initially increased, then decreased with the reduction of fishing effort (Clark & Koslow 2007). Most fish and invertebrates retained from approximately 1000 metres water depth are dead or dying by the time they reach the surface (Boyle et al. 2012). This mortality is attributable to changes in pressure, temperature shock, the physical trauma of being caught in the net and physical crushing by the sheer weight of fish retained in the cod end of the trawl.

Some steps have been made, both within New Zealand's EEZ and in the international waters surrounding New Zealand, to mitigate the effects of bottom trawling. Within New Zealand's EEZ, areas have been set aside as benthic protection areas (BPAs) where bottom trawling is banned and mid-water trawling is limited (Helson et al. 2010). It was hoped that the creation of these BPAs would both mitigate some of the effects of trawling and allow for the study of the recovery rates of previously impacted benthic areas (Clark & Rowden 2009).

Outside New Zealand's EEZ, protocols have been put in place for high seas deep-sea fisheries, whereby a 'move-on' rule has been put forward for fishers encountering vulnerable marine ecosystems (VMEs) (FAO 2008, Penney et al. 2009). When evidence of a VME is encountered (e.g., deep-sea corals) fishers are required to record the location of that VME, but to 'move-on' to another area. This enables the continued fishing on well-known grounds but limits the expansion of high seas bottom trawling fishing onto more VMEs. As the most productive orange roughy fishing grounds in New Zealand's EEZ have tended to coincide with VMEs (Clark et al. 2010a, Tracey et al. 2011), this has effectively put a moratorium on the discovery and exploitation of new orange roughy fishing grounds outside New Zealand's EEZ.

At present there is ongoing debate regarding whether orange roughy can be fished sustainably (Clark 1999, Francis & Clark 2005, Hilborn et al. 2006, Watling et al. 2010, Nourse et al. 2012). Its slow growth, longevity, low fecundity, non-annual spawning, and high age at maturity have rendered orange roughy susceptible to over-exploitation, and this has been the case not only in New Zealand waters, but everywhere it has been fished (Koslow 1997; Koslow et al. 2000; Branch 2001; Strutt 2000, 2001; Francis & Clark 2005, Hilborn et al. 2006, Foley et al. 2011, Dunn & Forman 2011).

2.1.3. Functional role of orange roughy

As a predator, orange roughy performs an important role in the structuring of the mid-slope demersal community it inhabits. Orange roughy has been depleted in many New Zealand fisheries (Mfish 2011) but there is little evidence to suggest that either its functional role in the ecosystem has been filled by other species (Clark et al. 2000), or that there has been a measurable increase in the abundance of its prey, or any form of trophic cascade. Bulman et al. (2002) suggested that the species with diets most similar to that of orange roughy (from off Tasmania) were warty oreo (*Allocyttus verrucosus*), and serrulate rattail (*Coryphaenoides serrulatus* Günther, 1878). In New Zealand waters the diets and functional ecology of these two species remain unknown, so it is not yet possible to speculate on what species (if any) could benefit from a reduction in orange roughy biomass. On Chatham Rise, acoustic estimates of small mesopelagic fish (common prey of orange roughy on Chatham Rise (Jones 2007), showed no significant biomass trends over a seven-year period (O'Driscoll et al. 2009). However, this study was targeting the food of hoki (which is a shallower-living species), so it may not be possible to translate these data to the deeper seamount-focused orange roughy fisheries. As a consequence, there are data deficiencies in these two areas.

2.2. Characterisation of New Zealand deep-sea species assemblages

While orange roughy is one of the most abundant mid-slope fish species in New Zealand waters, it is part of a much larger assemblage of demersal deep-sea fish species. On the New Zealand continental slope there is a faunal shift in the demersal fish species assemblage at around 800 metres water depth, where the upper-slope assemblage gradually transitions into a mid-slope assemblage (Jacob et al. 1998, Francis et al. 2002). Francis et al. (2002) demonstrate this ichthyofaunal transition, using samples taken from research trawls around New Zealand, and Bull et al. (2001) show it to a

lesser degree on Chatham Rise (their sampling was carried out to a depth of 800 m, so some species with deeper distributions have their vertical depth range truncated).

Leathwick et al. (2006) found the highest level of fish species richness in New Zealand waters was on the northern flanks of Chatham Rise between the depths of 800–1000 m. These demersal ichthyofaunal transitions are most obviously correlated with increasing depth, and to a lesser degree latitude (Francis et al. 2002).

New Zealand and Australia have very similar continental slope fish communities, with many species common to both areas (Bulman et al. 2001, 2002, Francis et al. 2002, Clark et al. 2010b). Across the Tasman Sea in Australian waters, Koslow et al. (1994) also found a faunal transition between characteristic upper and mid-slope ichthyofaunal assemblages on the southeastern Australian slope. They contended that there was no distinct boundary between the two assemblages, and as in New Zealand waters there was more a transition between them between depths of approximately 700–800 m.

Differences between the upper and mid-slope fish assemblages in New Zealand waters are further reflected by the composition of the bycatch of the major commercial fisheries that occur there. Hoki is characteristically an upper slope fishery (approx. 200–800 m), (Connell et al. 2010, Mfish 2011), while orange roughy is mid-slope (approx. 750–1200 m, Mfish 2011). While there is some overlap in species composition between the two fish assemblages, generally speaking the bycatch species taken in each fishery are different (Anderson et al. 1998, Bull et al. 2001, Francis et al. 2002, Blackwell 2010). For example, on northeastern Chatham Rise the most abundant orange roughy bycatch species (**Table 2**) were not listed amongst the ten most abundant upper-slope species reported by Bull et al. (2001), further outlining the difference in fish species composition between the two depth ranges (Doonan et al. 2009).

The reasons for the separation of assemblages within these depths ranges are unclear, although Gordon et al. (1995) suggested that enzyme function under conditions of high pressure and low temperature would preclude shallower water shelf species from extending their depth ranges beyond about 500 metres. Early views on deep-sea fish assemblages suggested that there were no controlling factors regarding deep-sea fish species assemblages and that they (species assemblages) were effectively random (Haedrich & Merrett (1990). However, this view was challenged by more recent work by Koslow et al. (1994) and Francis et al. (2002), who considered that depth and latitude were contributing factors to species assemblage composition. Overall, the reasons for the depth distribution of deep-sea fishes are complex, and relate to a combination of life

history characteristics and physical factors (Siebel & Drazen 2007, Drazen & Haedrich 2012).

In New Zealand waters there are many species, both fishes and benthic invertebrates, which are characteristic of either the upper or mid-slope (Probert & McKnight 1993, Probert & Grove 1998, Bull et al. 2001, Francis et al. 2002, Probert et al. 1996, 2009). Much research has been devoted to the ecosystem interactions in the shallower (and more valuable) hoki fishery (e.g., Murdock 1990, Murdock & Quigley 1994, Bull & Livingston 2001, Livingston 2002, Francis et al. 2006, Mfish 2011), and the diets of fish that inhabit the surrounding ecosystem (e.g., Dunn et al. 2010a, b, c; Connell et al. 2010; Horn & Dunn 2010; Horn et al. 2010a, b, 2011, Forman & Dunn 2012, Horn et al. 2012). But there is only indirect evidence that data collected for the management of this fishery is applicable to the deeper orange roughy fisheries. The fish species are mostly not the same (although there are some which are common to both (Francis et al. 2002)), nor are the areas in which the orange roughy fisheries occur (Clark 2009). Consequently the functional roles of mid-slope species (apart from those commercially exploited (e.g., Rosecchi et al. 1988, Clark et al. 1989, Anderson & Fenaughty 1996, Stevens et al. 2011) are largely unknown in New Zealand waters. When they are known, samples have been homogenised to species and general region so that environmental and/or ontogenic shifts in diet are obfuscated (Clark & King 1989, Clark et al. 1989). Whether the mid-slope fish species fulfil the same functional roles as upper slope species is also unknown.

Table 2. Estimates of the total numbers and biomass (Tonnes) from the TAN0709 orange roughy trawl survey, for the eight most prevalent species (other than orange roughy) on northeastern Chatham Rise (cv: coefficient of variation) (after Doonan et al. 2009).

Species code	Species	Estimated population size		Abundance	
		Numbers in millions	cv (%)	Tonnes	cv (%)
CSU	Four-rayed rattail	63.2	39	3275	22
CIN	Notable rattail	16.8	14	904	10
CSE	Serrulate rattail	11.5	8	1618	6
BEE	Basketwork eel	8.9	13	4560	9
SND	Shovel-nosed dogfish	8.1	23	16184	20
SBI	Big-scaled brown slickhead	7.3	22	3660	16
HJO	Johnson's cod	3.8	10	2342	11
SSM	Small-scaled brown slickhead	1.8	26	1019	32

2.3. Establishment of New Zealand's quota management system (QMS)

New Zealand has an advantage over most other countries in implementing fisheries legislation, in that it has sole sovereign control over its surrounding waters (New Zealand Government 1996). Since 1986, New Zealand commercial fisheries have been governed under the quota management system (QMS) (Lock & Leslie 2007). The QMS was established for three main reasons: the formation of the 200 nautical mile (nm) EEZ; over-exploitation of inshore fisheries; and the free market policies of the Labour Government in the mid-1980s.

Firstly, the formation of the 200 nm EEZ in 1978 (the fourth largest in the world at 4.4 million km² (Blezard 1980, Gordon et al. 2010)), and the exclusion of other countries from fishing within it (Clark et al. 1988, Lock & Leslie 2007, Bess 2010), gave New Zealand fishers exclusive rights to essentially new and exclusive fishing grounds. It was implicit that once the EEZ was set up, New Zealand was then expected to 'use it or lose it' (Clark et al. 1988, Johnson & Haworth 2004). This opened up new fishing areas and target species.

Secondly, the quota system for orange roughy was used as a model for the subsequent introduction of the QMS to the shallow water fisheries, which at the time were under considerable exploitative stress (Johnson & Haworth 2004, Gibbs 2008). The creation of the QMS would alleviate problems caused by the open access policies of the past (Crothers 1988, Johnson & Haworth 2004, Bess 2005, Lock & Leslie 2007), which had been implemented to encourage the expansion of the New Zealand fishing industry (Johnson & Haworth 2004). By the 1970s this expansion had worked a little too well and many of the inshore fisheries had become fully exploited, while some were showing signs of depletion and over-capitalisation, with too many vessels chasing too few fish (Clark et al. 1988, Clark 1993, Sharp 1997, Johnson & Haworth 2004, Lock & Leslie 2007).

Thirdly, the free market policies of the fourth Labour Government encouraged greater economic efficiency and sustainability within the industry (Clark et al. 1988, Clark 1993, Crothers 1988, Sharp 1997, Johnson & Haworth 2004, Bess 2006). The QMS is based upon the concept of economic sustainability, and is now the basis for most commercial fisheries management in New Zealand waters (Gibbs 2007, 2008, Lock & Leslie 2007, Mfish 2011).

2.3.1. New Zealand fisheries quota management system (QMS) legislation

The QMS exists within the framework of the Fisheries Act 1996. Section eight (p 54) of this Act outlines that its purpose is to: “provide for the utilisation of fisheries resources while ensuring sustainability”. It defines sustainability as being both economic “maintaining the potential of fisheries resources to meet the reasonably foreseeable needs of future generations”, and biological by “avoiding, remedying, or mitigating any adverse effects of fishing on the aquatic environment”. This second part is important as it formalises the link between economic and biological sustainability. Section nine (p 54) of the Act further defines this link by describing three environmental principles:

- (a) associated or dependent species should be maintained above a level that ensures their long-term viability;
- (b) biological diversity of the aquatic environment should be maintained;
- (c) habitat of particular significance for fisheries management should be protected.

The Fisheries Act (1996) also controls and applies guidelines to the setting of TACs. The responsibility for setting the TAC resides with the Minister for Primary Industries, who acts on advice received from the Ministry for Primary Industries (formally the Ministry of Fisheries).

The QMS is based on individual transferable quotas (ITQs), which are a form of property right (Moloney & Pearse 1979, Annala 1996, Pauly 1996, Sharp 1997, Kearney 2001). Each ITQ refers to a portion of an exploitable fish stock and each stock is managed within a quota management area (QMA). These stock areas are determined through a combination of regional and biotic factors and are a subset of the ten fisheries management areas (FMAs) that make up the New Zealand EEZ (Mfish 2011). Species are generally managed singly, using a single species approach (Lock & Leslie 2007, Mfish 2011). Occasionally, species that are caught together or are difficult to identify at sea are treated collectively as species groups for convenience. Examples of species groups include jack mackerel (three closely related species, **Table 1**), oreos (a mixture of black and smooth, and to a lesser extent spiky and warty oreo), and arrow squid (two species of Omastrephidae) (Mfish 2011). New Zealand currently has 97 species (or species groups) in the QMS and they are divided into 636 stocks (or sub-stocks).

Of the 636 stocks (or sub-stocks) managed by the Ministry for Primary Industries (MPI) in 2010, there was enough information to provide stock assessment data for 123.

Of these, 83 were considered to be at or near their management targets, with the rest either unknown or below management targets. Nineteen stocks were considered to be below the 'soft limit' outlined in the Harvest Management Strategy, and of these nine were deep-sea stocks: three stocks of black cardinal fish and six stocks or sub-stocks of orange roughy (MPI 2011).

Each quota management area (QMA) has a total allowable catch (TAC) for the species (or species group) managed in that area. The TAC encompasses all forms of fishing-related mortality for that species (or species group), and includes non-commercial catches, either recreational and/or customary Māori catches. The remainder comprises the total commercial catch (TACC) and this is divided up amongst those eligible to hold quota (Bess & Harte 2000, Bess 2005, Lock & Leslie 2007). In this way the total allowable catch (TAC) encompasses the ITQs (Lock and Leslie 2007). Originally, holders of quota paid a resource rental to the crown for the right to harvest fish (Linder et al. 1992), but this was replaced by a cost recovery levy in 1994, which helps to pay for stock assessment science (Harte 2001, 2007; Wyatt 2003; Stokes et al. 2006; McKoy 2007; Helson et al. 2010). During the 2007/8 financial year, the New Zealand Ministry of Fisheries spent \$15.3 million on stock assessment research services, and of this \$13.7 million NZD were expected to be recovered from industry under the cost recovery system (Allen et al. 2007).

In New Zealand's deep-water fisheries for orange roughy there is no customary catch, so the TACC is effectively the same as the TAC. The TAC is set at a level that will give the maximum sustainable yield (MSY) for that species (or species group) for that fisheries management area (FMA) (Batstone & Sharp 1999, Mace 2001, Lock & Leslie 2007). The New Zealand Ministry of Fisheries sets TACs within the framework of the Harvest Management Strategy (Mfish 2008a). The Harvest Management Strategy (Mfish 2008) defines two minimum biomass limits, a soft and a hard limit. "Essentially, the soft limit is half of the MSY-compatible biomass or 20 percent of the unfished biomass, whichever is higher; while the hard limit is a quarter of the MSY-compatible biomass or 10 percent of the unfished biomass, whichever is higher." (Mfish 2008a, p1). The Ministry of Fisheries considers these to be limits to avoid. Stocks can still be exploited if they fall below the biomass necessary to support MSY, but obviously at a reduced rate, and with management steps taken to ensure the rebuilding of that stock (Mfish 2011).

Under New Zealand legislation, most fisheries undergo a regular formal stock assessment process, which estimates the MSY of the target species (Allen et al. 2007, Mfish 2011). Ideally, these stock assessments are undertaken each year, but often they are not (Mfish 2011, Weeber 2012). For finfish, squid and some shellfish, scientific trawl surveys are the usual method of fisheries stock assessment (Mfish 2011). Acoustic methods have also been used to estimate the biomass of several species (e.g., orange roughy (McClatchie et al. 1999; McClatchie & Coombs 2005; Doonan et al. 2006, 2009)). However, orange roughy have a wax-filled swimbladder and this has led to problems discerning it from other species with gas-filled swimbladders (which are easier to see and then differentiate acoustically) (Francis & Clark 2005). Egg production surveys have also been used in the estimation of orange roughy spawning biomass, but these proved to be inconclusive owing to the uncertainty surrounding the mortality of the eggs, and have not been continued (Clark 1996).

These relative biomass surveys are used to estimate the current stock biomass, with the original biomass (B_0) then back-calculated from these yearly estimates of relative stock biomass (Mfish 2011). The total allowable commercial catch (TACC) is based on the concept of maximum sustainable yield (MSY), which is a theoretical level of exploitation (Gilbert et al. 2000, Mfish 2011). In actuality, it is represented by the maximum constant yield MCY, which is a constant level (tonnage) of the biomass of the species exploited. However, a problem with using MCY is that if the biomass of the target species decreases, then the proportion of the biomass removed by MCY increases relative to the original biomass. As a result, the constant annual yield (CAY), which is a proportional amount, is used instead. As the CAY is proportional to the available biomass it can increase or decrease with the estimated biomass of the exploited species (Lock & Leslie 2007).

As orange roughy was a newly discovered fishery in the 1970s, very little was known regarding the virgin biomass, the location and distribution of the stocks, or the biology of the species (Clark 1995a). Prior to the discovery of large quantities of this species off the coast of New Zealand, it was regarded more as a deep-sea curiosity (Clark 1995a, Kotlyar 1996), occasionally turning up in the stomachs of sperm whales (Gaskin & Cawthorn 1967, Kotlyar & Lipskaya 1980). As a consequence, certain assumptions were made regarding the level at which it could be exploited, and these were based on models for shallow water species (Clark 1995a, 1996). As more was discovered regarding the longevity, low fecundity, slow growth, and high age at

maturity of orange roughy, it was realised that these assumptions had been too optimistic, and that the productivity of orange roughy was much lower than that of shallow water fish (Mace et al. 1990, Clark et al. 1994, Clark 1995a, 1996). Once this was discovered, TACs for orange roughy fisheries were reduced in a stepwise fashion during the late 1980s and early 1990s (Clark 1996, 2001; Mfish 2011). However, this was too late to stop the overexploitation of some stocks, for example Cook Canyon, Challenger Plateau and Puysegur Bank², and these fisheries were eventually closed to allow the recovery of the stocks (Mfish 2011). Calculations regarding the rate of sustainable exploitation were revised downwards, so that once the virgin biomass had been fished down to approximately 30 percent of the original estimated biomass, an annual estimate of the MSY was 1–2 percent of the original virgin biomass (Clark 1995a, Hilborn et al. 2006). Recent work on the North Island mid-east coast orange roughy stocks has suggested that even these estimates were too high, as the expected stock recovery had not occurred, continuing a downwards trend in biomass (Dunn & Forman 2011).

Recovery of orange roughy stocks is thought to be extremely slow, due to their high age at maturity, low fecundity, and intermittent spawning (Mace et al. 1990, Clark et al. 1994, Clark 1995a, Francis & Clark 2005). Given that orange roughy in New Zealand waters do not reach maturity until approx 23–30 years of age (Fenton et al. 1991, Francis & Horn 1997), it is probable that the various New Zealand fisheries have been exploiting the virgin stock until very recently (Dunn et al. 2009). This was shown by Clark & Tracey (1994) and Francis & Smith (1995), who found no change in the size structure of exploited orange roughy populations on Challenger Plateau or Chatham Rise (respectively), despite large reductions in biomass, a common trait of exploited fish populations (Bianchi et al. 2001, Clark et al. 2000, Pauly et al. 2002, Shin et al. 2005, Shackell et al. 2010, Endberg et al. 2012). In the north Atlantic, targeted orange roughy fishing has ceased and it is now thought that it will take at least a century for those exploited stocks to recover (Watling et al. 2010).

²The Challenger Plateau and Puysegur Box fisheries were recently re-opened (2009 and 2010 respectively) with a TACs of 500 and 150 tonnes (respectively) to assess the possible rate of recovery after many years of closure, although the Cook Canyon fishery remains closed (Ministry of Fisheries: Deep water plan 2010).

2.3.2. Advantages of individual transferable quotas (ITQs)

2.3.2a. Conceptually easy to understand

Individual transferable quotas have some advantages over the management regimes they replaced. They are conceptually simple, are designed to optimise economic efficiency and are transferable, enabling fishers to change their quota, hence optimising their fishing operations to suit prevailing conditions (Grafton 1996, Kearney 2001, Bess 2005, Harte 2007, Costello et al. 2008). Through owning a property right (to fish for a particular species/species group), the responsibility to ensure the sustainability of fish product is placed firmly on the fisher. In other words, it is in the best interests of the fisher to do whatever is necessary to ensure their continued income. In this way, the sustainability of the fishery becomes of paramount importance, so that ecological sustainability is encouraged through the function of economic sustainability (Grafton 1996, Dewees 1998, Costello et al. 2008).

2.3.2b. Ownership of quota in perpetuity

The allocation of ITQs in perpetuity is a major feature of the QMS (Sissenwine & Mace 1992). It ensures a regular income and enhanced employment stability for fishers throughout the fishing year, enabling them to plan for the future, and in doing so to ensure a regular supply of product. This helps to avoid gluts, and potential wastage through any inability to process oversupply (Kearney 2001). The classic “race to fish” (Pauly et al. 1998a) is then (as much as practical) avoided (Bess & Harte 2000, Kearney 2001, Emery et al. 2012). Safety is improved through the reduction of unsafe practices caused by the necessity to “race to fish” (Branch et al. 2006). Also, the crown receives income from the right to access quota (Sinner & Fenemor 2005). Individual transferable quotas have generally been considered an improvement on the management regimes they superseded (Annalla 1996, Batstone & Sharp 1999, Costello et al. 2008, Chu 2009, Branch 2009).

2.3.3. Disadvantages of ITQs

2.3.3a. Social concerns

The introduction of individual transferable quotas was not universally accepted into New Zealand fisheries management (Johnson & Haworth 2004). Concerns over the adoption of ITQs included the perception that the fisheries resource would be swallowed up by large corporations and that small-scale fishers would lose out (Pauly

1996, Johnson & Haworth 2004, Memon & Kirk 2011). This did happen to some degree, with many small part-time fishers being removed from the industry (Johnson & Haworth 2004, Stewart et al. 2006, Lock & Leslie 2007, Stewart & Walsh 2008), but it was offset with the allocation of large amounts of quota to Māori (Memon & Cullen 1992, Bess 2001). It has been argued that the removal of these small-scale fishers was a logical prerequisite to making the industry more efficient (Sissenwine & Mace 1992, Kearney 2001, Johnson & Haworth 2004). Moving forward, the industry has become more concentrated, with a trend towards fewer owners/holders of quota (Stewart & Callagher 2003). Stewart et al. (2006) further confirmed this, finding that most of the fishers who left the industry after the establishment of the QMS were small-scale operators.

2.3.3b. Cost of fishing

Fishing the deep-sea is an expensive business, as often the grounds are far offshore and the vessels needed to exploit them are large, and have a correspondingly large crew (Gordon et al. 2003, Durán Muñoz & Sayago-Gil 2011, Stewart & Callagher 2011, Watling et al. 2010). As a result of this, New Zealand deep-sea fisheries have also seen a contraction in the ownership of quota in the middle-depth and deep-water fisheries, where four organisations own 90 percent of the annual catch entitlement (ACE) for orange roughy (Mfish 2011), reflecting the expense related to fishing the deep-sea and subsequent attempts to make efficiency gains through economies of scale (Ratnayake 1999, Stewart & Callagher 2011). The Deepwater Group Ltd. is a group of quota owners that owns approximately 90 percent of the quota for deep-water and middle depth fisheries in New Zealand and is the point of contact between quota owners and the New Zealand Government (Helson et al. 2010).

2.3.3c. Narrow focus

Several authors have criticised the implementation of ITQs (Deweese 1998, Costello et al. 2008, Emery et al. 2012). Gibbs (2010, p 708) described ITQs as a “narrowly-focused policy instrument that are not explicitly designed to manage the ecosystem effects of fishing”. This is possibly because the ITQ system has its roots as a model of economic sustainability, not biological sustainability (Deweese 1998, Costello et al. 2008, Emery et al. 2012). However, it could be argued that the two concepts operate "hand in glove". Individual transferable quotas (ITQs) are essentially a

relatively simple economic model being applied to a complex and incompletely understood biological system: a fishery, where the primary methods of stock control are either mediating the level of extraction of the targeted species, the gear used for extraction, or the closure of the fishery (Mfish 2011).

The exploitation of a target species does not only affect that species, as there are cascading effects throughout the ecosystem where the removal of higher trophic level species can have profound effects on the populations of other, lower trophic level species (Dayton et al. 1995, Pauly et al. 1998a, Pinnegar et al. 2000, Lynam et al. 2006, Baum & Worm 2009). One example of this is the concept of compensation/depensation, where the adults of an exploited species control potential predators of its juveniles. The removal of the adults removes this control mechanism, so the population is further reduced through the proliferation of predators of the target species' juveniles, thus further reducing the numbers of the exploited population (Walters & Kitchell 2001). This can mean that exploited populations are under pressure from more than just the direct fishing pressure on them.

2.3.3d. Bycatch and discards

Fisheries bycatch, and its associated discarding, are also important consequences of ITQs (Copes 1986, Alverson et al. 1994, Turner et al. 1999, Quinn & Collie 2005). If the ITQ system is controlled by the weight of the quota species, it becomes in the interest of the fishers of that quota to only retain the largest fish they catch (as these will provide the largest return for the effort of catching them). The incentive is then created to discard smaller, less valuable fish (Turner 1997, Kearney 2001, Hatcher 2005). This is often termed "high grading" (Copes 1986, Arnason 1994, Squires et al. 1998, Branch 2009, Branch et al. 2009). This is wasteful, as in many fisheries the smaller fish are dead and/or dying when caught and are lost to the fishery anyway (Johnsen & Eliassen 2011). It is especially true in deep-sea fisheries, where virtually all fish brought to the surface are killed by the change in pressure and temperature (Gordon 2001c, Allain et al. 2003). In New Zealand's QMS all quota fish are expected to be landed, which was intended to act as a disincentive to high-grading and the discarding of fish at sea (New Zealand Fisheries Act 1996). Turner (1996) suggested that high grading was a result of weight-based ITQs. He argued that if ITQs were value-based rather than weight-based this would disincentivise high grading and associated discarding.

Individual transferable quotas continue to be weight-based in New Zealand's QMS (Mfish 2011).

Bycatch that is discarded at sea can be fish or other marine life for which there is no market value, or fish that have been damaged through the actions of fishing (being crushed or dropped, or deterioration of fish through delays in processing) (Sánchez et al. 2004, Anderson & Smith 2005, Stockhausen et al. 2012). In a quota management sense, discards can also be quota species caught in excess of the vessel's quota for that species. In the North Sea there is considered to be a serious problem with the discarding of bycatch at sea (Johnsen & Elliasen 2011). Worldwide, it has been estimated that 7.3 million tonnes of dead or dying fish are discarded annually (Kelleher 2004).

Fisheries discards can have unforeseen effects on the trophic structure of exploited fisheries and the marine ecosystems that contain them, through the alteration of the abundance of target and bycatch species abundance (e.g., Hall 1996, Clark et al. 2000, Hall et al. 2000, Pinnagar et al. 2000, Cryer et al. 2002, Bugoni et al. 2010, Rice 2011, Forman & Dunn 2012). The consumption of discards can redirect trophic pathways within ecosystems (Ramsay et al. 1996, Hall et al. 2000, Jackson et al. 2000). On the Patagonian shelf and slope, Laptikhovskiy & Fetisov (1999) found that 20–40 percent by volume of the diets of common hake (*Merluccius hubbsi*), southern cod (*Notothenia ramsayi*) and hollow-snout rattail (*Macrourus holotrachys*) comprised squid fishery discards. Bozzano & Sardà (2002) suggested that a constant influx of carrion, in the form of bycatch discards, could permanently alter benthic ecology and community stability, through the positive feedback of extra food availability. Most discarded material is consumed at or near the surface but some of it can sink to deep waters (Laptikhovskiy & Fetisov 1999, Erzini et al. 2003). Zhou (2008) argues that while it would be beneficial to reduce the amount of fisheries discards overall, it is important to realise that a reduction in discards could in turn cause a reduction of the biomass of species that have come to rely on them. Bycatch and its associated discarding are considered to be a major global challenge facing fisheries (Alverson et al. 1994, Hall et al. 2000, Zeller & Pauly 2005, FAO 2011, Soykan et al. 2008, Watling et al. 2010, Johnsen & Elliasen 2011, Lewison et al. 2011).

Bycatch is present to varying degrees in many New Zealand deep-sea fisheries, and it ranges from comparatively little in the orange roughy fisheries (at least when fishers are targeting spawning plumes during the winter spawning season) (Clark et al. 2000), to other times of the year when it can be considerable (Anderson 2009, 2011c).

In New Zealand waters, bycatch species not part of the QMS or having no other commercial or curio value are discarded at sea (Mfish 2011). In New Zealand orange roughy fisheries between 1999 and 2005, bycatch estimates ranged between 6300 and 13,500 tonnes (t), compared with catches of targets species of 16,000 to 21,000 t during this time (although most of this bycatch was oreo and other commercial species) (Anderson 2009).

Historical assessments of the levels of fish bycatch in New Zealand's deep-sea fisheries have revealed some trends in the biomass of several fish species (Livingston et al. 2003). Estimated biomass levels of several bycatch species taken in deep-water fisheries on Chatham Rise were shown to decrease over time, in both the middle depth (200–800 m) hoki fishery (Livingston et al. 2003), and in the deeper (approx. 800–1200 m) orange roughy fishery (Clark et al. 2000). In an examination of bycatch from Chatham Rise orange roughy fisheries, Clark et al. (2000) found that the estimated biomass of several bycatch species (as well as the target species orange roughy) had decreased between 1984 and 1994, when detailed records ceased (M. Clark pers. com.). However, Clark et al. (2000) also found that some species' biomass had not changed (e.g., four-rayed rattail, *Coryphaenoides subserrulatus* Mashukok 1976), and one had increased (long-nosed velvet dogfish, *Centroselachus crepidater* (Bocage & Capell 1864)). The main difficulty with interpreting this data set is that fishing for orange roughy on Chatham Rise had been undertaken for several years previous to 1984 and subsequently from 1994 (Mfish 2011). Although change had occurred in the biomass of several species over that period of time, it is difficult to do more than speculate on the cause of that change (Tuck et al. 2009).

The identification of bycatch species has also been a problem in New Zealand's deep-sea fisheries, as many of the fish species are morphologically similar (McMillan & Paulin 1993), and/or undescribed (Paulin et al. 1989, Anderson et al. 1998). Anderson (2011) reports that differences in the level of identification of deep-sea bycatch species between scientific observers and skippers have confounded comparisons between non-commercially exploited species: meaning that several species were grouped (dogfishes, rattails and morid cods), making comparisons between them impossible.

Anderson (2009) reported that the amount of fish bycatch in the orange roughy fisheries increased between 1999 and 2005, and suggests that this is due to an increase in the duration and length of trawls. The length of trawls is thought to have increased in

this time in an effort to offset falling catch rates. The amount of bycatch taken from New Zealand's orange roughy fisheries is thought to represent 0.16 kilogram, per one kilogram of orange roughy landed (Anderson 2009).

Fisheries discards have been perceived to be at least a potential problem in New Zealand's deep-sea fisheries, although it has been difficult to quantify the amount or their potential effects, as most research has focused on the upper slope hoki fisheries (Anderson 2009, Connell et al. 2010, Forman & Dunn 2012). Little is known regarding the fate of discards from the orange roughy fisheries. However, there has been concern in the shallower hoki fisheries that discards might sink to the bottom, decompose there, and create an anoxic layer, killing off benthic life (Livingston & Rutherford 1988). Hoki frames (filleted and discarded hoki bodies) have been reported on the bottom at depths of approximately 800 metres off the west coast of the South Island adjacent to hoki fishing grounds (Grange 1993), but there has been no evidence of an anoxic layer forming due to their decomposition (Livingston & Rutherford 1988). There was also concern that since deep-sea ecosystems are less tolerant to disturbance than shallow water ones (Probert et al. 1997, Probert 1999, Freese 2001, Rowden & Clark 2009, Watling et al. 2010), any large influx of carrion could have a detrimental effect on the demersal ecosystem.

There is little information regarding the fate of bycatch from orange roughy fisheries once it has been discarded, although it is likely that some of it reaches the seabed. However, there are data to suggest that discards from other New Zealand deep-sea fisheries do find their way into the demersal food web. Clark et al. (1989) report hoki frames from the stomachs of basketwork eels (*Diastobranchus capensis* Barnard, 1923) from oreo fisheries on southwestern Chatham Rise, from depths of 600–1100 m. Horn et al. (2010) suggested that offal from shallower fisheries on Chatham Rise has become an important part of the diet of ling (*Genypterus blacodes* (Forster 1801)) on the upper slopes of Chatham Rise, as do Forman and Dunn (2012) for smooth skate (*Dipturus innominatus* (Garrick & Paul 1974)). Cryer et al. (2002) suggest that the increase in abundance of scavenging species in scampi bycatch from the upper slopes of the Bay of Plenty is likely to be due to an historical influx of bycatch discards. However, elsewhere there is little information regarding the fate of discards in New Zealand deep-sea fisheries, or what potential food-web contribution they make. This is because there have been very few investigations into the feeding of non-commercially-exploited mid-slope fish species in New Zealand waters (Clark & King

1989, Clark et al. 1989); resulting in a lack of baseline feeding data.

Whether scavenging in these fish species has always occurred, or is facultative in response to bycatch discards is also largely unknown. Knowledge regarding the role of scavenging in the other fish species found in the orange roughy fisheries is very incomplete.

In New Zealand waters, all quota species caught under the QMS are to be landed, not only to aid enforcement of the system, but also to help remove the incentive to “high grade” (New Zealand Fisheries Act 1996). However, there is evidence to suggest that this does not always occur (Annala 1996, Burns & Kerr 2008, Bremner et al. 2009). In the ling fishery, Burns & Kerr (2008 p31) found significant differences in the bycatch reported when a scientific observer was aboard ship, compared to when one was absent. Much less bycatch was reported when no observers were aboard. They suggest that unreported bycatch (and its implied discarding at sea) could have “serious implications for fishery sustainability.” Bremner et al. (2009) found discrepancies of a similar nature to Burns & Kerr (2008) in New Zealand’s hoki fishery.

2.3.3e. Seasonal pressure

In some ITQ fisheries there is still the potential for a “race to fish”. Where temporal factors influence the harvest, such as a spawning season, there will be incentives for fishers to maximise their catches when the going is easiest (Bess & Harte 2000, Bisark & Sutinen 2006). An example of this in New Zealand waters is the orange roughy fisheries, where despite there being a yearlong season and associated TACC, the largest catches occur during the austral winter months between June and August (Mfish: orange roughy, n. d.). This is when orange roughy aggregate to spawn, and are easiest to catch (e.g., Clark 1999, Clark et al. 2000). Orange roughy are known to spawn over known underwater features (seamounts, canyons) (Koslow 1996, Clark 1999, 2001, Branch 2001), so being able to get to the closest of these first, and to catch as much of one's quota allocation before the cessation of the spawning period, would be an advantage. This suggests that even if there is no actual “race to fish”; then the potential for one to occur certainly exists.

2.3.3f. Multi-species fisheries

Heterogeneous fisheries, where many species may be taken at one time, also pose a challenge for ITQ-based fisheries (Copes 1986, Pauly 1996, Link 2002a, Quinn &

Collie 2005, Sanchirico et al. 2006, Prellezo & Gallastegui 2008). The problem is that catching a full quota of one species may require over-catching the quota of another, or catching species for which the fisher has no quota allocation. This can become a problem if one of the bycatch species is vulnerable (Soykan et al. 2008), protected (Chilvers 2008), or already depleted (Squires et al. 1998, Prellezo & Gallastegui 2008). In an ITQ context, solutions to this problem have been to aggregate species under one combined quota (Squires et al. 1998, Mfish 2011) or to set an overrun percentage to the allocated quotas. In New Zealand's QMS this value is 10 percent of the allocated quota (Mfish 2011). Another solution has been to allocate an upper limit to a particular bycatch species and close the fishery once this has been reached, as has been done for rattails in the Antarctic toothfish fishery (Mfish 2011). It has been predicted by Pauly (1996) that ITQs will fail to provide sustainability in multi-species fisheries, a sentiment echoed by Sanchirico et al. (2006), who maintain there is no solution to quota overruns in ITQ-based multispecies fisheries. Link (2010) also does not believe that ITQs can work in multi-species fisheries, because it is energetically impossible for B_{msy} to be achieved for multiple species concurrently. The fate of catch overruns is also an issue, which overlaps that of discards, and as a consequence also impacts marine ecosystems in currently unforeseen ways.

2.3.3g. Lifespan of quota species

There are also some species for which determining a TAC at the beginning of each season/year is problematic. An example of this is arrow squid in New Zealand waters (actually two species, managed as one for most of New Zealand's EEZ). According to New Zealand's Ministry of Fisheries (Mfish 2011) website, "arrow squid live about one year, spawn and die", which makes predicting biomass on a yearly basis uncertain (Mfish 2011), as the future population is directly related to the success of the previous year's spawning. At the other end of the temporal spectrum there are also problems in determining the TAC for long-lived species, as these can also be slow-growing and have low productivity, rendering them vulnerable to over-exploitation (Clark & Tracey 1994, Francis & Smith 1995, Clark 1995a). Orange roughy, a long-lived and slow-growing species, is an example of this (Mace et al. 1990, Clark & Tracey 1994, Francis & Smith 1995, Clark 1995a, 1999, 2001, Clark et al. 2000).

2.3.3h. Migratory species

Migratory species are also problematic as they can only be managed inside the QMAs under the jurisdiction of the regime concerned, for example, big eye tuna (Mfish, 2011), although efforts are now being considered to manage these species at migratory ‘choke’ points (Game et al. 2009). Obviously, outside these areas they are available to anyone with the ability and motivation to exploit them, and to whatever level they can. Attempts have been made to apply rights-based fishing models to the high seas, but these have so far met with very limited success (Sumaila et al. 2010, Hannesson 2011).

2.3.3i. Straddling stocks

There are some deep-water fish stocks that exist across regulatory boundaries. In the New Zealand region these typically straddle the boundaries of the EEZ. One example of this is the orange roughy fishery on northwestern Challenger Plateau, much of which is outside New Zealand's EEZ (Mfish 2011). Straddling stocks can be difficult to manage if a significant proportion of the stock is being exploited outside of any regulation. In this case, the New Zealand and Australian governments have jointly agreed to manage this area under a memorandum of understanding between the two countries, and there is a TAC for this area (**Table 3**).

Table 3. International agreements and regional agreements to which New Zealand is a signatory, that influence the Ministry of Fisheries management of the effects of fishing on the aquatic environment (after Mfish 2008).

International Agreements	Regional Fisheries Agreements
<ul style="list-style-type: none"> • Convention on the Conservation of Migratory Species of Wild Animals (CMS). Aims to conserve terrestrial, marine and avian migratory species throughout their range. • Agreement on the Conservation of Albatrosses and Petrels (ACAP). Aims to introduce a number of conservation measures to reduce the threat of extinction to the albatross and petrel species. • Convention on Biological Diversity. Provides for conservation of biological diversity and sustainable use of components. States accorded the right to exploit resources pursuant to environmental policies. • United Nations Convention on the Law of the Sea (UNCLOS). Acknowledges the right to explore and exploit, conserve and manage natural resources in the State’s EEZ. With regard to the protection and preservation of the marine environment including associated and dependent species, pursuant to the State’s environmental policies. • Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES). Aims to ensure that international trade in wild animals and plants does not threaten their survival. • United Nations Fish stocks Agreements. Aims to lay down a comprehensive regime for the conservation and management of straddling and highly migratory fish stocks. • International Whaling Commission (IWC). Aims to provide for the proper conservation of whale stocks and thus make possible the orderly development of the whaling industry. • Wellington Convention. Aims to prohibit drift net fishing activity in the convention area. • Food and Agriculture Organisation - International Plan of Action for Seabirds (FAO - IPOA Seabirds). Voluntary framework for reducing the incidental catch of seabirds in longline fisheries. • Food and Agriculture Organisation - International Plan of Action for Sharks (FAO - IPOA Sharks). Voluntary framework for the conservation and management of sharks. • Noumea Convention. Promotes protection and management of natural resources. Parties to regulate or prohibit activity likely to have adverse effects on species, ecosystems and biological processes. • Food and Agriculture Organisation - Code of Conduct for Responsible Fisheries provides principles and standards applicable to the conservation, management and development of all fisheries, The be interpreted and applied to conform to the rights, jurisdiction and duties of States contained in UNCLOS. 	<ul style="list-style-type: none"> • Convention for the Conservation of Southern Bluefin Tuna (CCSBT). Aims to ensure, through appropriate management, the conservation and optimum utilisation of the global Southern Bluefin Tuna Fishery. The convention specifically provides for the exchange of data on ecologically related species to aid in the conservation of these species when fishing for southern bluefin tuna. • Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). Aims to conserve, including rational use of Antarctic marine living resources. This includes supporting research to understand the effects of CCAMLR fishing on associated and dependent species, and monitoring levels of incidental take of these species on New Zealand vessels fishing in CCAMLR waters. • Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean (WCPFC). The objective is to ensure, through effective management, the long-term conservation and sustainable use of highly migratory fish stocks in accordance with UNCLOS. • South Tasman Rise (STR) Orange Roughy Arrangement. The arrangement puts in place the requirement for New Zealand and Australian fishers to have approval from the appropriate authorities to trawl or carry out other demersal fishing for any species in the STR area. • A South Pacific Regional Fisheries Management Organisation (SPRFMO) is being negotiated to facilitate management of non-highly migratory species in the South Pacific. • Environmental Performance Indicators (EPI) (Ministry for the Environment (MfE). The purpose of the EPI programme is to “develop and use indicators to measure and report how well we are looking after our environment”. Seamount communities have been identified within the EPI project as key habitats for which extent and condition should be measured as indicators.

2.3.3j. Fisheries impacts

One of the frequent criticisms of the ITQ system is that since it is single stock focused it takes very little account of the ecosystem effects of fisheries activity (Copes 1986, Link 2000, Gibbs 2010). The impact of mobile trawl gear on the seabed (bottom trawling) is a well-known example of this (e.g., Jones 1992, Jennings & Kaiser 1998, Watling & Norse 1998, Hall 1999, Jennings et al. 2001, Coleman & Williams 2002, Cryer et al. 2002, Armstrong & Falk-Peterson 2008, Althaus et al. 2009, Clark & Rowden 2009, Nourse et al. 2012). The action of trawling can not only crush marine life the trawl gear passes over, it can scour the sediment and smother sea life through the creation of sediment plumes, which in turn can alter the chemistry of near-bottom waters (Riemann & Hoffmann 1991, Freese 2001).

Trawling can reduce biodiversity through the homogenisation of bottom habitats (Jennings & Kaiser 1998, Turner et al. 1999, Cryer et al. 2002, Kaiser et al. 2002, Danovaro et al. 2008) and the replacement of large long-lived species with small forms, which are able to grow and reproduce between trawling episodes (Dayton et al. 1995, Cryer et al. 2002, Bremner et al. 2005). Bottom trawling also damages or destroys sessile habitat-forming biogenic substrates, for example, deep-sea corals (Probert 1999, Clark & Hill 2001, Fosså et al. 2002, Althaus et al. 2009, Clark & Rowden 2009, Tracey et al. 2011). In shallow waters the removal of this three-dimensional habitat can cause unforeseen trophic cascades (Dayton et al. 1995, Jennings & Kaiser 1998, Pinnagar et al. 2000, Link 2002b), and in deeper waters the effects are unpredictable. The timeframes required for the recovery of trawled areas is dependent on the growth rate, rate of recruitment, and ability of impacted animals to repair their biogenic structures (Morrison et al. 2008, Astles et al. 2009). As waters get deeper, the time taken for benthic ecosystems to recover from the effects of trawling is thought to increase, and for deep-sea (approx. 1000 m) ecosystems impacted by fisheries the recovery times are thought to be measured in decades or centuries, if recovery is possible (Probert et al. 1997, Althaus et al. 2009, Clark & Rowden 2009, Watling et al. 2010, Williams et al. 2010).

In New Zealand the destruction of three-dimensional biogenic habitat has been shown to have a detrimental effect on shallow water species (Bradstock & Gordon 1983, Turner et al. 1999, Carbines et al. 2004, Morrison et al. 2008). In deeper waters (with the notable exception of Cryer et al. (2002)), studies have focused on the impacts of trawling on specialised habitats, particularly seamounts (Probert et al. 1997,

O'Driscoll & Clark 2005, Rowden et al. 2008, Clark & Rowden 2009). Seamounts are considered to be vulnerable habitats, especially to deep-sea bottom trawling (Clark & O'Driscoll 2003, FAO 2008, Clark & Rowden 2009, Rowden et al. 2002, 2010a).

New Zealand has over 800 seamounts of varying sizes and bathymetry (Rowden et al. 2002, 2003, 2004, 2005; Yesson et al. 2011). New Zealand seamounts are volcanic and/or tectonic in origin (Wright 1999) and are usually associated with the boundary between the Australian and Pacific plates, although few have been studied in any detail (Rowden et al. 2005, 2010a, Yesson et al. 2011). They range in size from the small hill features, found on the Chatham Rise to the much larger Bollons' Seamount (Wright 1999, Clark et al, 2011). Much effort regarding seamount research in New Zealand has been in regards to fisheries management, and/or research into fisheries impacts (e.g., Probert et al. 1997, Probert 1999, Clark 2001, Clark & O'Driscoll 2003, Clark & Rowden 2009).

One group of seamounts that have been studied in detail is the Graveyard Complex of hills on the northern flank of Chatham Rise (Clark & Rowden 2009, Clark et al. 2010a, Rowden et al. 2002, 2010a) that have been the focus of a fishery for orange roughy since the early 1990s (Rowden et al. 2002, Clark et al. 2010a). Three features in this complex were closed to commercial fishing in 2001 (Clark et al. 2010a, Helson et al. 2010). One feature, "Morgue", had been heavily trawled, and the other two, "Pyre and Gothic", had not. They were closed to provide a comparison between trawled and untrawled seamounts, and to ascertain how long it would take for the trawled seamount feature to recover from the effects of previous trawling (Clark & Rowden 2009, Clark et al. 2010a).

Cold-water corals are common in the deep-waters around New Zealand (Squires 1965, Clark & Rowden 2009, Tracey et al. 2011). In the north Atlantic and Mediterranean Sea it is recognised that these corals provide habitat for fish and invertebrates (Fössa et al. 2002, Costello et al. 2005, D'Onghia et al. 2010, Quattrini et al. 2012), and it is very likely that they perform a similar role in New Zealand waters (Tracey et al. 2011). It is currently unknown if the removal of these deep-sea corals from New Zealand deep-sea habitats has any effect on demersal fish or invertebrates (Francis & Clark 2005). Clark and Rowden (2009) used a deep towed imaging system (DTIS) to show that after nearly a decade of protection there had been little change in the coral cover on the trawled seamount feature "Morgue". This lends weight to the assertion that not only are seamounts fragile habitats, but the recovery of their benthic

fauna from disturbance can be measured in at least decades (Probert et al. 1997, Williams et al. 2010).

Deep-sea trawling is also thought to have a detrimental effect on soft-sediment communities, through the homogenisation of bottom sediments, and the removal of large sessile and mobile invertebrate species (Cryer et al. 2002). Cryer et al. (2002) investigated the effects of scampi trawling on benthic invertebrate species in the Bay of Plenty, northern New Zealand, and found that there was an increase in some species of invertebrates in areas repeatedly trawled, and a decrease in large bodied benthic animals. There is little information regarding the impacts of trawling on deeper mid-slope soft sediment communities, but the effects are likely to be similar, and possibly more pronounced and longer lasting (Watling et al. 2010).

Fishing can reduce the genetic diversity of the exploited population by removing the largest individuals, first reducing the level of genetic variability on the exploited population, and often these can be the most fecund females (Pauly et al. 2001, Francis et al. 2007, Link 2010). Francis et al. (2007) contend that the removal of these large females can have effects on the egg production of the fish population, especially in longer-lived species, as larger females can spawn earlier, for longer, and can produce larger eggs, which can develop more quickly than the eggs of smaller females. Under current ITQ fisheries management practice there is no protection for these females within fishing grounds. Nor is there the financial or legislative incentive to do so, as larger fish are more valuable. The preferential protection of larger female fish would represent a paradigm shift in fisheries, and presents a significant logistical challenge (Francis et al. 2007). In shallow water fisheries it might be possible to return these females once caught, assuming that they are not mortally harmed by the method of capture (Butcher et al. 2012). However, this is not the case with deep-water fisheries, as most fish caught are dead or dying once brought to the surface, so this is not practicable. In New Zealand's orange roughy fisheries there is conflicting evidence for a reduction of genetic diversity (Smith et al. 1991, Smith & Benson 1997). However, there is no evidence that larger females produce larger eggs, or are significantly more fecund than smaller individuals (Pankhurst & Conroy 1987).

A further criticism of ITQs is that they do not enhance the sustainability of previously exploited fisheries. Gibbs (2008) has argued that ITQs have done little to ensure the recovery and sustainability of fish stocks in New Zealand waters. He argued that these populations had little chance of recovery as ITQs were based on historical

catch levels, and that many remain at low levels when compared to historical maxima. He further states that recent biomass gains in some species only represent incremental gains when compared with historical biomass estimates. In addition to this, when new species are added to the QMS fishers will intentionally target that species to build up a catch history for that species (Mfish 2011). By doing this when the species enters the QMS, its TAC is then based on historical catches, which could be too high as fishers sought to maximise their share of the incoming TAC (Squires et al. 1998).

Overall, even though single species approaches to fisheries management using ITQs have been considered to be an improvement on the open access, command and control regimes they replaced, they still have some significant drawbacks. Individual transferable quotas based on single species TACs do not appear to have served New Zealand orange roughy stocks well. Despite millions of dollars worth of research over many years, orange roughy catches have declined, and fisheries have collapsed (Dunn & Forman 2011), leaving sustainability an, as yet, elusive goal.

2.4. Ecosystem-based fisheries management (EBFM)

2.4.1. Introduction to EBFM

The shortcomings of single-species based fisheries management have led to the consideration of other forms of management, and an alternative to the single species management approach is to attempt to manage the ecosystem as a whole (Larkin 1996, Francis et al. 2007, Curtin & Prellezo 2010, Link 2010). This ecosystem-based approach to fisheries management (EBFM) aims to manage the fishery in a more holistic way, and by doing so mitigate some of the adverse affects of commercial fishing whilst ensuring/enhancing the sustainability of the fishery (Pauly et al. 1998a, 2005; Garcia & Staples 2000; Garcia et al. 2003; Pikitch et al. 2004; Francis et al. 2007; Curtin & Prellezo 2010; Link 2010). This approach has developed hand-in-hand with the precautionary principle: in that when decisions are required in the absence of suitable information, caution is recommended (González-Laxe 2005). In other words, the precautionary principle gives the benefit of the doubt to the environment “*in dubio pro natura*” (Trouwborst 2009, p 27). Ecosystem-based fisheries management (henceforth EBFM) has become the prevailing paradigm in fisheries management worldwide (Pitcher et al. 2009, Link 2010, Hobday et al. 2011), and has generated much controversy regarding what exactly it is (e.g., Link 2000, 2002a, 2010; Brodziak & Link 2002; Murawski 2007, Morishita 2008; Curtin & Prellezo 2010), and how and why it

can/should be implemented (e.g., Browman & Stergiou 2004, Caddy & Seijo 2005, Jennings 2005, Livingstone et al. 2005, Arkema et al. 2006, Francis et al. 2007, Smith et al. 2007, Le Heron et al. 2008, Pauly 2009, Link 2010, Rice 2011). However, despite the debate there is still a large gap between the countries talking about it and those actually practising EBFM (Pitcher et al. 2009).

The FAO describes EBFM as having its roots in terrestrial natural resource management and wildlife management (Garcia et al. 2003). Definitions of terrestrial ecosystem-based management have evolved over the years and are overlapping, with Cortner et al. (1994) defining ecosystem-based management as “a management philosophy which focuses on desired states rather than system outputs and which recognises the need to protect or restore critical ecological components, functions and structures in order to sustain resources in perpetuity”. Lackey (1998) defined ecosystem-based management, as “the application of ecological and social information, options, and constraints to achieve desired social benefits within a defined geographic area and over a specified period.” In a fisheries context, the International Council for the Exploration of the Sea (ICES) has defined the ecosystem-based approach to fisheries management as,

the comprehensive integrated management of human activities based on the best available scientific knowledge about the ecosystem and its dynamics, in order to identify and take action on influences, which are critical to the health of marine ecosystems, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity (ICES 2000).

Link (2000) suggested that EBFM was fisheries management in an ecosystem context rather than managing ecosystems, as it is not really possible to manage an ecosystem. Further to this, Fluharty (2005) defined EBFM in common-sense terms as: “using what is known about the ecosystem to manage fisheries”. Morashita (2008) characterised EBFM into four main types; bycatch mitigation, multi-species management, protection of vulnerable ecosystems, and the use of an integrated approach to management. A critical feature of EBFM is that it is place-based (Grumbine 1994, Lackey 1998, Arkema et al. 2006, Rice 2011, Link 2010), and is therefore defined by the location and range of the fishery (e.g., Agnew 1997, Fabra & Gascón 2008).

2.4.1a. Ten commandments for EBFM

Francis et al. (2007) generally summarised EBFM by providing “ten commandments” for scientists wishing to embark on an EBFM programme, and these are briefly summarised below:

1. Keep a perspective that is holistic, risk-averse, and adaptive

By holistic this commandment means that obviously more than just the target species needs to be considered. Not just the biological components of the ecosystem are important, but also the physico-chemical and climate cycles, from diel, to seasonal, to decadal cycles. This first commandment is clearly linked to the precautionary principle. Also, it suggested that as new information comes to light then it should be acted on quickly.

2. Question key assumptions, no matter how basic

Briefly, this means that any assumptions previously used in earlier management regimes need to be questioned, no matter how entrenched. Just because something has worked in the past does not necessarily mean it will work in the future, and vice versa.

3. Maintain old-growth age structure in fish populations

This is because larger older females can produce many more eggs than smaller adult females (Francis et al. 2007). This makes them very important for future recruitment of the exploited population (Edwards & Plagányi 2011).

Unfortunately, maintaining old growth structure in exploited fish populations is very hard to achieve, as larger fish are often the first to be removed from a population (Pauly et al. 2001). Marine protected areas could alleviate this situation (Edwards et al. 2009, Edwards & Plagányi 2011), but their success has proved hard to empirically quantify (Hinnink et al. 2008), and in the deep-sea may need monitoring on time scales longer than human lifespans (Baker et al. 2009, Clark et al. 2010a).

4. Characterise and maintain the natural spatial structure of fish stocks

This basically states that you need to know what your stocks are before you can manage them effectively. Are you dealing with one or two large stocks (e.g., NZ hoki), or are you dealing with several or many smaller discrete stocks (e.g., NZ orange roughy (Francis & Clark 2005, Mfish 2011))? This is important, as what you do to one stock may or may not affect another, depending on whether or not

there is a link between them. The consequence is that if a stock is small and isolated then it could be locally 'fished-out' while being within the management province of a much larger area. Something, which may have happened to some New Zealand orange roughy stocks with the serial depletion of seamounts, although this is difficult to confirm (Clark et al. 2000, Francis & Clark 2005).

5. Characterise and maintain viable fish habitats

This is an extension of the previous commandment. Put bluntly, if your fish stock needs a particular type of habitat for protection, feeding, (while juvenile or adult) or reproduction, then any practice that inhibits that habitat function (or destroys that habitat) is probably not a good thing (Watling et al. 2010), especially if you have designs on sustainably exploiting that fish stock over any length of time. Also, it is useful if you know what these habitat preferences are. The habitat preferences of non-commercially exploited fish species in New Zealand's mid-slope waters are only known in very broad terms (Anderson et al. 1998, Francis et al. 2002, Tracey et al. 2004, Clark et al. 2010a), and their interactions with these habitats are largely unknown.

6. Characterise and maintain ecosystem resilience

This is where the commandments become data intensive, as to understand an ecosystem requires a great deal of information and analysis. This basically asks how much this ecosystem can be altered before it changes its configuration and a regime shift occurs (Kraberg et al. 2011). Once this regime shift has happened, how long will it take to return to its previous configuration? Can it actually return to its previous configuration? Models have become useful tools for describing the broad scale interactions within ecosystems (Plagányi 2007). They range from the simple to the complex, and this complexity is related to the questions being asked of them (Butterworth & Punt 1999, Fulton et al. 2005). Two of the most popular complex ecosystem models are Ecopath with Ecosim (EwE) (Polovina 1984, Christensen & Pauly 1992, Walters et al. 2000, Christensen & Walters 2004, Coll et al. 2009), and ATLANTIS (Fulton et al. 2004, 2011). Ecopath with Ecosim is older than ATLANTIS, and is composed of two parts. Ecopath (Ecological Pathways Model) is based on the concept of mass balance (based on the laws of thermodynamics), and is used to model the trophic interactions within an ecosystem (Polovina 1984, Christensen & Pauly 1992, Walters et al. 2000, Christensen & Walters 2004, Coll et al. 2009). Ecosim

enables various permutations of that modelled ecosystem to be modelled over a period of time (usually a year) (Walters et al. 1999, Coll et al. 2009). Another important part of this commandment is to know how close the ecosystem in question is to changing its configuration (i.e., no longer giving you what you want from it).

7. Identify and maintain critical food-web connections

This commandment leads directly from the last, because in order to address ecosystem resilience one needs to understand the linkages within the ecosystem. This is possibly the most data-intensive of the commandments, as to understand the critical food-web connections a considerable amount of effort (time and money) need to be expended to describe them. Regardless of whether this is done by direct methods (i.e., gut content analyses, e.g., Clark et al. 1989; Bulman et al. 2002; Jones 2007, 2008a, b, 2009; Connell et al. 2010; Dunn et al. 2010a, b, c; Horn et al. 2010a, b, 2011), or indirect methods (stable isotopes (Drzen et al. 2008), cross-reacting anti-sera (Feller et al. 1985), crossed immunoelectrophoresis (Grisley & Boyle 1985), fatty acids (Drzen et al. 2009; Connan et al. 2010; Pethybridge et al. 2010, 2011), DNA, (Dunn et al. 2010c), or indirect methods, then validated by direct methods (Drzen et al. 2008, 2009; Dunn et al. 2010c; Stowasser et al. 2009; Hirsch & Christiansen 2010; Pethybridge et al. 2010, 2011). These data can then be fed into complex whole ecosystem models (e.g., Ecopath (Christensen & Pauly 1992) with Ecosim (Walters et al. 1999), or ATLANTIS (Fulton et al. 2004, Fulton 2010), to provide a representation of the general linkages within the ecosystem being modelled (Plagányi 2007; Fulton et al. 2004, Fulton 2010).

8. Account for ecosystem change through time

Ecosystems change over time, and over different temporal scales, from climatic changes: diel, to the seasonal, decadal, assuming that they were in an approximately steady state before exploitation (in most fisheries it is unlikely that there was a "before exploitation") (Pauly 1995, Jackson et al. 2001, de Juan et al. 2009, Poulsen 2010). This commandment links to the last, in that the diets of fish and hence the food-web connections will change over time, and over spatial scales. For instance, small fish eat different food from big fish, and as such their position within the food web may change as they grow (Pauly et al. 2001, 2002). Also, the diets of fish are linked to food availability, which is in turn linked to

levels of primary and secondary production (e.g., Arrington et al. 2002, McClatchie et al. 2005, Vinson & Angradi 2011) and as this varies both with the seasons and annually, the diets of fish also vary (e.g., Liwoch & Linkowski 1986, Horn et al. 2010a).

9. Account for evolutionary change caused by fishing

Fishing changes the genetic structure of fish populations by removing larger fish, and by selecting for a smaller size at maturity. This means that over time the mean adult size of the population will decrease. If fish are not allowed to get large, then they may not be able to feed on large prey, causing their trophic level to decrease over time (Pauly et al. 2001).

10. Implement an approach that is integrated, interdisciplinary, and inclusive

Put simply (if indeed this is possible), ecosystem-based management is a complex issue and cannot be carried out successfully by one discipline alone (Lackey 1998, Degnbol et al. 2006). As Link (2010) states, “Economic objectives shall be subordinate to social objectives, which will be subordinate to biological objectives, which shall be subordinate to human existence.” So for EBFM to succeed, involved parties are going to have to work together towards a common (clearly articulated) goal, and there will be trade-offs between them in order to reach said goal (Link 2010, Hobday et al. 2011). A recent New Zealand example of this cooperation would be the industry-led creation of the benthic protection areas in New Zealand’s EEZ (Helson et al. 2010). The industry sought relief from levies paid to cover the cost of research on the effects of bottom trawling and habitat damage, so they suggested some areas that they would be happy to see closed. Consultation with the government resulted in some trade-offs being made, but the benthic protection areas were created. There have been some criticisms of the areas chosen (e.g., Leathwick et al. 2008), but overall the BPAs are considered to enhance New Zealand’s reputation in fisheries management (Helson et al. 2010).

Most of the Francis et al. (2007) “ten commandments” are common sense, but the common thread is that in order to attempt to manage something as complex as an ecosystem you need to know what you are dealing with, and what you are trying to achieve; echoing the views of Brodziak & Link (2002) and Link (2002a, b). As a consequence, a successful ecosystem-based management (and by extension EBFM)

programme will necessarily be a multi-disciplinary one, involving policy makers, management agencies and scientists, all working towards a common set of clearly defined goals (Arkema et al. 2006, Piet et al. 2008, Link 2010, Shin et al. 2010a, b; Hobday et al. 2011).

2.4.2. Ecosystem-based fisheries management from within single species approaches

Single species management and EBFM can be considered to be two extremes along a continuum (Link 2000, Link 2002a, b). It could be argued that ecosystem-based approaches to fisheries management are already happening within the confines of single-species-based regimes, or at least that it is possible (Mace 2001, 2004; Hall & Mainprize 2004; Hilborn et al. 2006; Lock & Leslie 2007; Froese et al. 2008; Le Heron et al. 2008; Gibbs 2010). Hall and Mainprize (2004), and Daan (2005) have suggested that many ecosystem-based attributes could be added to existing single-species management plans, and that this is the most practical way forward for existing single-species fisheries. Gibbs (2010) suggests that TACs could be continuously reduced until they reach a level where ecosystem objectives (these will likely be ecosystem/fishery specific) are attained. Given that the primary method for the mediation of single-species fisheries is the TAC, this is probably the simplest and most easily executed concession to EBFM (Hilborn 2011). Mace (2004) contends that failure of single species approaches are due more to a lack of political will to curtail allowable catches than the concept itself; a view shared by Cardinale & Svedäng (2008). Further to this, Mace (2004) suggests that any ecosystem-based approach will not make any difference if the political will to enforce it is not forthcoming, especially if the TACs are reduced under an ecosystem-based regime as Gibbs (2010) suggests. Daan (2005) also suggested that some solutions could be found within existing single-species management structures, particularly those which involve benthic impacts to habitat. However, Daan (2005) stresses that these measures would only be successful if applied in a fleet-wise manner, echoing the sentiments of Mace (2004).

Powers and Monk (2010) also suggest that ecosystem-based management objectives could be achieved from within single-species regimes. They suggest more species be introduced into single-species management regimes; species that might not necessarily be economically important, but are ecologically important (*sensu* Hall & Mainprize 2004, Link 2007). Although it could be argued that if a species contributes to

the sustainability of a commercially exploited fishery then it has some economic value, even though it is not harvested. This indirect value to the fishery of these species may be hard to quantify, and would require knowledge of the ecology of those species (Wainger & Boyd 2009, Hilborn 2011).

There is evidence of EBFM principles augmenting existing New Zealand single species fisheries management programmes. Black cardinal fish (*Epigonus telescopus* (Risso, 1810)) is an example of the addition of a commercially valuable species to an existing single-species management plan. Black cardinal fish are taken as bycatch in orange roughy fisheries in New Zealand waters and they have recently included in the management plan for orange roughy as key bycatch species (Mfish 2010, 2011). Also, individual feature limits have been given to orange roughy TACs on seamounts off the North Island of New Zealand, and this could be said to reflect the place-based nature of EBFM.

2.4.3. Ecosystem-based fisheries management from within multi-species approaches

Pikitch et al. (2004 p 346) state “EBFM reverses the order of management priorities so that the objective of sustaining ecosystem structure and function supersedes the objective of maximizing fisheries yields”. To do this requires information regarding ecosystem structure. It seems likely that most deep-sea ecosystems (and possibly all aquatic ecosystems) will be defined according to what can be exploited from them, and the limits thereof. More specifically, a marine ecosystem is likely to be spatially defined by its fishery (Link 2002a, b, 2010; O’Boyle et al. 2005; Hobday et al. 2011). For example, in New Zealand waters the mid-slope ecosystem could be defined as the orange roughy/oreo ecosystem, as these are the main species being exploited (Mfish 2011). This is a convenient way of defining an ecosystem, as obviously if there is a commercial fishery for a species it is probably a safe assumption that the species is a numerically dominant member of that ecosystem. If the ecosystem is to be defined by its fishery, it is also physically constrained by it, although the effects of fishing can be much deeper than the depth of the fishing itself (Bailey et al. 2009).

2.4.4. Ecosystem structure

Link (2000) suggests that ecosystems continue to function regardless of fishing pressure, but in altered states: that the collapse of a fishery is the ecosystem moving

from one state to another due to an external force; in this case commercial fishing pressure. Whether or not that ecosystem will return to its original configuration depends on many factors, including the frequency of disturbance, and how many other external forces are involved (Jackson 2008, Kraberg et al. 2011). This raises several questions regarding the ecosystem. What was the structure of the ecosystem before it was fished (Dayton et al. 1995, Pauly 1995, Parsons et al. 2009), does anybody remember, or have the baselines shifted (e.g., Baum & Myers 2004, Bunce et al. 2008, Parsons et al. 2009)?

Ecosystem function and regime shifts are difficult to identify in deep-sea fisheries owing to the slow rate of the biological activity of the inhabitants, especially when compared to the rate of human-induced change through commercial fishing (Watling et al. 2010). This is illustrated to a degree in many New Zealand deep-sea orange roughy fisheries, as records are often patchy (Anderson & Fenaughty 1996, Clark et al. 2000, Anderson & Haworth 2004, Tuck et al. 2009). Limited comparisons are only possible for fish species with a history of commercial exploitation (Mfish 2011), and very little can be concluded regarding change in the abundance of non-commercially exploited species from orange roughy fisheries (Clark et al. 2000). As a result, it is highly unlikely that any fishing-induced regime change will have been observed, and this is a major challenge in deep-water fisheries (Clark et al. 2000, Tuck et al. 2009). How to decide what is important to measure leads to determining what ecological (or otherwise) indicators are the most relevant for what is trying to be achieved (Daan et al. 2005, Bundy et al. 2010, Shin et al. 2010a, b).

2.4.5. Ecological indicators

The choice regarding what to measure and the metrics used in an ecosystem depend upon what management outcome is desired (Rice 2003, Jennings 2005, Fulton et al. 2005, Methratta & Link 2006, Link 2010). The concept of an ecological indicator is similar to the keystone species concept, where a species or species group has a disproportionate effect on its surrounding ecosystem relative to its biomass or abundance (Paine 1969, Coleman & Williams 2002). An ecological indicator is used as a proxy for the health of an ecosystem or a predetermined desired ecosystem state: whereby an ecological indicator becomes an ecosystem indicator (Libralato et al. 2006, 2008).

For individual ecological indicators to be useful, they first have to be sensitive to the ecosystem properties they measure; those properties then have to be relevant to the functioning of the ecosystem (and this, in turn, is inextricably linked to the desired outcome), and one must be able to distinguish metrics solely affected by fishing and those affected by the natural variability of fish populations (Rice 2000, Link et al. 2010, Powers & Monk 2010). For ecological indicators to be successful, there also needs to be a way of applying control rules for when actions fail to mitigate undesirable reference-point values or trends (Bundy et al. 2010). Whatever ecological indicators are chosen, it is important to realise that there are going to be trade-offs between economic and ecological goals (Link 2010, Fulton 2010). These trade-offs will ultimately depend on the management outcomes desired, and the political will to achieve them (Mace 2004, Link 2010).

2.4.6. Types of ecological indicators

There have been many attempts at describing appropriate ecological indicators to measure the ecosystem effects of fishing (Pauly et al. 1998a, Rice 2000, Link et al. 2002, Fulton et al. 2005, Jennings 2005, Methratta & Link 2006, Piet et al. 2008, Blanchard et al. 2010, Bundy et al. 2010). It has been considered that no one indicator will be sufficient in describing for the purposes of EBFM, and consequently a suite of ecological indicators will be necessary, and these will depend on the ecosystem in question (Link et al. 2002; Libralato et al. 2006, 2008; Link 2010; Bundy et al. 2010). Probably the most obvious choice would be a size-based indicator, for example, the size of the fish caught over time. These have the advantage of being relatively easy to measure, and would probably have a reasonable amount of historical context if applied to a commercial fishery (as these data are routinely recorded) (e.g., Mfish 2011). A size-based ecological indicator could give information on the size structure of an exploited population, and the most obvious trend that a size-based ecological indicator would be likely to express would be decreasing adult size in response to exploitation (Jennings & Kaiser 1998). A disadvantage of size-based ecological indicators is evident with deep-sea fisheries where the target species are often long-lived and slow growing (e.g., orange roughy). Exploitation has been shown to decrease the biomass of this species over insufficient generations for their adult size to be selected against (Clark & Tracey 1994, Francis & Smith 1995).

Biodiversity has also been evaluated as an ecological indicator (Norberg 2004), the premise being that the more species in an ecosystem, the healthier it is (Coleman & Williams 2002, Danovaro et al. 2008, Link 2010). With more species comes greater redundancy of ecological function within the ecosystem, and greater resilience to change, be that environmental- or human-induced (Worm et al. 2006, Link 2010). Biodiversity would only be an appropriate measure if the biodiversity of the area under management were well-known. With many deep-sea ecosystems there are high levels of undiscovered biodiversity (Sogin et al. 2006, Danovaro et al. 2008, Gordon et al. 2010). This is especially the case in New Zealand, where there is a great deal of undescribed marine biodiversity and a dearth of taxonomists to describe it (Gordon et al. 2010).

Link (2000) has suggested that biodiversity is not necessarily a good measure of the health of an ecosystem, as groups of species (functional groups) can maintain essential ecosystem functions (a point reinforced by Norberg 2004), especially so in the deep-sea, where the large degree of biodiversity may render a single ecological indicator species impractical; the role of one species could be taken by another without effecting the functioning of the ecosystem.

Deep-sea corals have been considered to be a potential ecological indicator for deep-sea fisheries (Campbell & Gallagher 2007). However, these would not necessarily make a good ecological indicator, as once they are removed from the ecosystem they are no further indicative use. As stated by Anderson and Clark (2003), a reduction in deep-sea coral bycatch is not necessarily a good thing, as it just means that the coral is gone, and areas are being repeatedly trawled. Deep-sea corals highlight an important issue with deep-sea ecological indicators, in that for an ecological indicator to be relevant it needs to be able to measure something on a time scale meaningful to humans. Because two (and most probably more) of the important components of this fishery, orange roughy and deep-sea corals, are extremely long-lived (see previous references) it is difficult to find a suitable metric for an ecological indicator (Clark & Rowden 2009, Williams et al. 2010).

Clark and Rowden (2009) demonstrated the difficulty in using deep-sea corals as ecological indicators for a benthic-protected area (BPA) on Chatham Rise. A previously fished seamount feature, "Morgue", was assessed for coral regrowth nearly a decade after the cessation of bottom trawling for orange roughy, but no stony deep-sea coral regrowth was found. However, Clark and Rowden (2009) found small (approx. 20 mm) styastrid hydrocorals on heavily trawled seamounts in the Graveyard complex, and

suggested that these might be examples of re-growth, but they were unsure if this was the case. They state that coral cover could be used as a potential ecological indicator, but at present it is not known what amount of coral cover indicates a healthy or unhealthy ecosystem. This would be further complicated on soft sediment areas (much of Chatham Rise is flat bottomed soft sediments (Probert et al. 1997)), where deep-sea corals are less common (Probert et al. 1997, Tracey et al. 2011).

Functional groups could be used as an ecological indicator. The loss of a functional group could be where ecosystem functions would change (Bundy et al. 2010). Most of the deep-sea bed is made up of soft sediments and the bioturbation of those sediments is an important process (Danovaro et al. 2008, Loreau 2008). As a consequence, bioturbators could be a suitable source of ecological indicator for deep-sea soft sediments.

On a human scale, the loss of a functional group is important if the ecosystem becomes incapable of producing exploitable resources of commercial or social value (Link 2010). Wainger & Boyd (2009) argue that the value of an ecosystem can only be measured by the goods and services it provides. If this rationale is applied to a fishery, its value is a combination of the market value of the extracted resource, and the wages they generate.

Cury et al. (2005) used tropho-dynamic indicators as ecological indicators. These follow the premise that as fish get larger their trophic level increases (Pauly et al. 2001). Fishing pressure removes the largest individuals from a population selectively over time; so one would expect the mean trophic level of an exploited population to decrease in response to prolonged exploitation (Pauly et al. 2001, 2002). Tropho-dynamic indicators are extremely data-intensive, as they require not only the collection of many fish from many areas, but also the dissection and identification of those fishes, stomach contents. These stomach contents are then assigned a trophic level, and a mean trophic level is then calculated for whatever subset of the fish population is being analysed (Pauly et al. 2002). For this method to be effective, the trophic levels of the prey need to be known, and often this is not possible. In the deep-sea many small invertebrates are undescribed and their trophic status is uncertain (Danovaro et al. 2008, Probert et al. 2009).

It could be argued that it should be possible to assume the trophic functioning of small deep-sea invertebrates based on their morphology, using the morphology of similar, shallow water forms (for which trophic information is available) as a guide.

However this is not always the case, for example Hicks & Marshall (1985) demonstrated that propaemussid bivalves (scallops) were carnivores, preying on male harpacticoid copepods, when the prevailing view regarding deep-sea bivalves has been that they are either filter or deposit feeders (e.g., Bulman et al. 2002). A more obvious example would be the chemosynthetic communities of vents, cold seeps and food-falls, which do not directly rely on the sun for energy (Koslow 2007). Tropho-dynamic ecological indicators are data-intensive and require knowledge of ecosystem components, which can be challenging to obtain (e.g., Bradford-Grieve et al. 2003, Libralato et al. 2006, 2008), and while these data can be inferred from shallow water studies, it is not always appropriate.

2.4.7. Limitations of ecological indicators

Scientific trawl surveys have also been investigated as a possible source of ecological indicators (Jouffre et al. 2010). In a New Zealand fisheries context these surveys have some advantages, in that they have often been undertaken over a period of years, and with consistent methodologies (Mfish 2011). As such, they may represent the only reliable historical dataset for many species, especially those from the deep-sea (e.g., Anderson & Fenaughty (1996) for orange roughy). The main disadvantage with using trawl surveys is that the data are being used for a purpose for which they were not originally designed, and the metrics they measure may not be appropriate to serve as ecological indicators (Tuck et al. 2009).

In New Zealand, Tuck et al. (2009) have investigated the use of trawl surveys as potential sources of ecological indicators. They found that measuring ecological indicators was a data-intensive task, and could only find reliable datasets for three areas in New Zealand: Hauraki Gulf, Chatham Rise middle-depth, and Southland and sub-Antarctic waters surveys. They focused on three fish-based ecological indicators gathered in trawl surveys: size-based, species-based, and tropho-dynamic-based. Like Shin et al. (2005), they found that size-based indicators were not that useful in detecting changes in relation to fishing pressure, and that species diversity indices (based on presence/absence data) were more effective ecological indicators. Tuck et al. (2009) encountered problems when trying to analyse trawl surveys from deeper mid-slope orange roughy and oreo fisheries. They found that the New Zealand orange roughy surveys were numerous but “many of these have not been consistent enough, or

repeated enough, to generate a useful series of data for this study” (Tuck et al. 2009, p 20).

Tuck et al. (2009) recommended that consistent deepwater survey series be developed, and that data on fish diet consumption and trophic level in New Zealand be compiled to identify knowledge gaps and research needs. This last recommendation was in response to the then lack of dietary data regarding many of New Zealand’s fish species, especially deeper water mid-slope fish species. As a result, they used single trophic values for some species, which, given that some species change their diet annually and seasonally (Laptikhovsky 2005, Horn & Dunn 2010), or as they grow (Horn et al. 2010a; Stevens & Dunn 2011), may not have been appropriate (Pauly et al. 2001, Piraino et al. 2002). Also, when dietary data was not available, Tuck et al. (2009) used estimates from related species sourced from Fishbase (Froese & Pauly 2011). These values also may not have been appropriate, as Fishbase often uses data that assumes diets are homogenous over temporal and spatial scales. Tuck et al. (2009) did not find that tropho-dynamic ecological indicators were well described by their datasets.

2.4.8. Process of implementing EBFM through integrated management

Levin et al. (2009) advocate the use of integrated ecosystem assessments (IEA) to provide a way forward for the implementation of EBFM. They outlined five steps that they believed necessary for the facilitation of EBFM: scoping; development and validation of appropriate indicators; risk analysis; management strategy evaluation; and monitoring. Scoping is where the goals of EBFM and the threats to achieving those goals are assessed and decided on. In terms of the New Zealand orange roughy fisheries, the Ministry of Fisheries has expressed an ambition to have these fisheries MSC-certified as a goal (Mfish 2010). The main threats to achieving these goals would appear to be the perceived unsustainability of deep-sea fisheries (Hilborn et al. 2006, Watling et al. 2010, Nourse et al. 2012), the damage to fragile benthic habitats (most notably deep-sea corals) by bottom-trawling (Campbell & Gallagher 2007, Clark and Rowden 2009, Tracey et al. 2011), and the lack of information regarding the relationships within the ecosystem at these depths (trophic links) (Campbell & Gallagher 2007).

Once the scoping step is completed, the second step is the development and validation of appropriate ecological indicators (Link 2010). These can include size-based, species-based and tropho-dynamic-based indicators.

The following process is that of risk analysis. Here the risks to those indicators posed by both human activities and natural processes are assessed. A good New Zealand example of this is the risk analysis of Campbell & Gallagher (2007), who applied a risk analysis framework to a dataset based on several of New Zealand's orange roughy fisheries. Although this study was not conceived as part of any overall EBFM plan for orange roughy, it highlighted some of the issues that would need to be addressed if such a plan was to be implemented. Most particularly, Campbell & Gallagher (2007) revealed that the two major risk factors that the orange roughy fisheries posed to the environment were the impacts on habitat (deep-sea corals), which they considered to be extreme, and the trophic interactions between species (considered to be significant). A limitation of the Campbell and Gallagher (2007) study is the lack of appreciation for the longevity and the time taken for the re-growth of deep-sea corals, but this was not an explicit aim of their study. The risk assessment is used to evaluate each ecological indicator, and then, through the use of models, the ecosystem is assessed relative to historical baselines (status), and compared to desired EBFM goals.

The fourth step in this five-step process is that of management strategy evaluation. In this step, a plan or management strategy evaluation (MSE) is established based on appropriate ecological indicators, and aimed at addressing the desired EBFM goals. Once this plan is in place, the final (fifth) stage is that of monitoring the aforementioned plan, and assessing its success relative to the EBFM goals outlined at the start. A brief outline of this process using New Zealand's orange roughy fisheries as a possible functional example is shown in **Figure 2**.

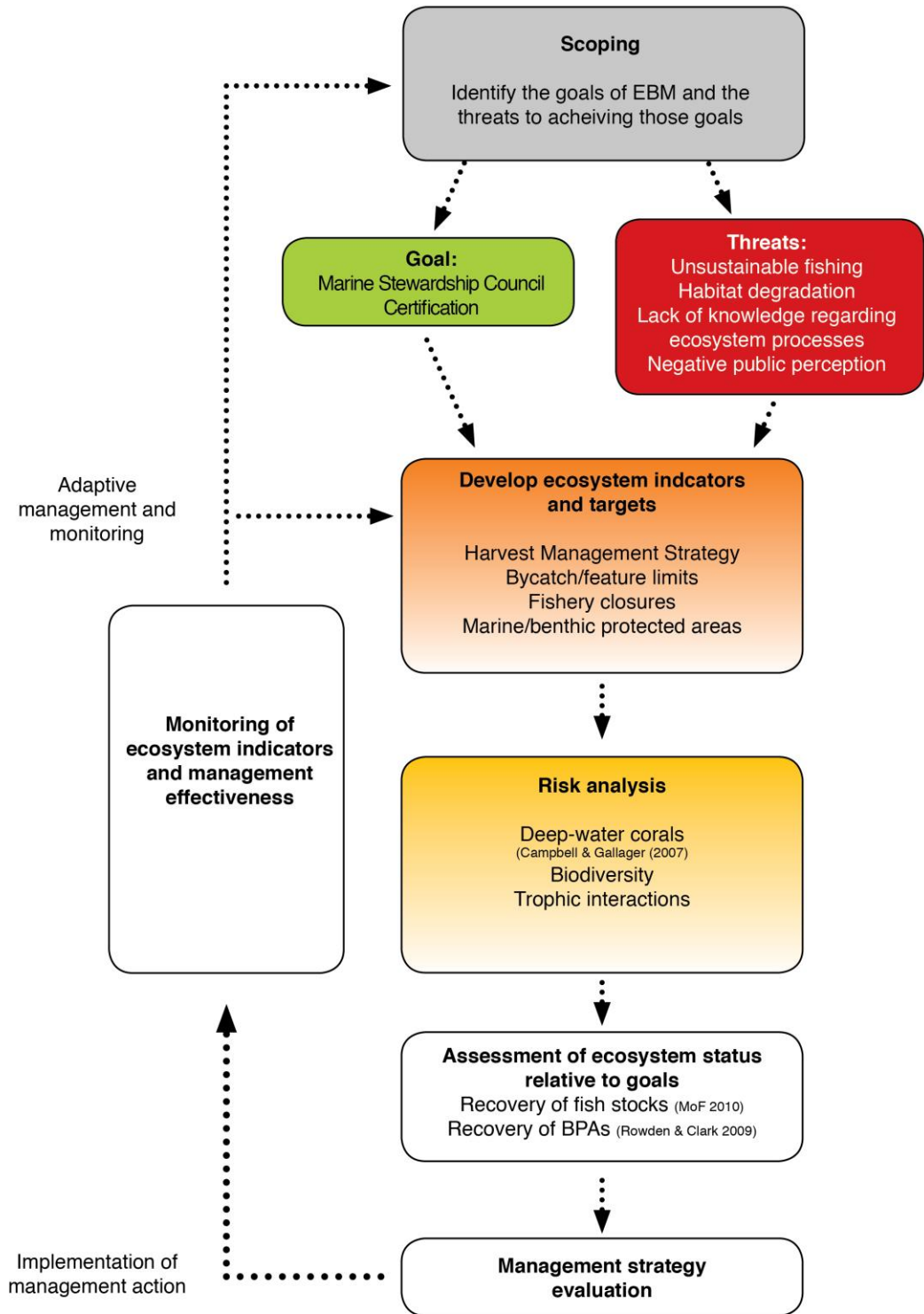


Figure 2. The five-step process of integrated ecosystem assessment, applied to New Zealand's orange roughy fisheries (after Levin et al. 2009).

2.4.9. Example of an existing EBFM programme

The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) is an organisation responsible for the management and conservation of Southern Ocean marine resources (Constable et al. 2001, Schiffmann 2009). Established in 1982, CCAMLR is a pioneer in the implementation of ecosystem-based fisheries management (Fabra & Gascón 2008). Ecosystem-based principles were embedded in its convention; so it was not necessary to make the transition from a single species-based management structure to an ecosystem-based one (Constable 2011). The convention has as central to its operation Article 2, which states:

- A. The prevention of decrease in harvested populations to levels below those which ensure stable recruitment;
- B. The maintenance of ecological relationships between harvested, dependent and related populations;
- C. The prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two to three decades. (Agnew 1997, p 235).

The mandate of the CCAMLR is to control the management of all marine species in the Southern Ocean. Exceptions are whales and seals south of 60°S, which are covered by other agreements (Ruckelshaus et al. 2008). One of the challenges facing CCAMLR was the management and monitoring of fisheries in the international waters of the Southern Ocean. The major fin fisheries are long-line fisheries for Patagonian and Antarctic toothfish (*Dissostichus eleganiodes* Smitt, 1898, and *D. mawsoni* Norman, 1937), and trawl fisheries for mackerel icefish (*Champsocephalus gunnari* Lönnberg, 1905) (Kock et al. 2007, Mfish 2011, Brooks et al. 2011). These fisheries are managed using single species TACs, but with ecosystem-based considerations added (Mfish 2011). For example, there are limits placed on the levels of rattail (Macrouridae), and skate (Rajidae) bycatch, and if these limits are exceeded the fishery can be closed for that season (Mfish 2011). Steps have also been taken to reduce the bycatch of seabirds (Waugh et al. 2008, Delord et al. 2010). The other major issue facing the fisheries managed by the CCAMLR has, and continues to be, illegal, unreported, and unregulated fishing (IUU) (Agnew 2000, Agnew et al. 2009, Brooks et al. 2011, Österblom & Sumaila 2011).

2.4.10. Legislative context of EBFM in deep-sea fisheries in New Zealand

New Zealand fisheries management in the form of the New Zealand Ministry of Fisheries has made a commitment to EBFM and is signatory to several international

agreements (**Table 3**). In New Zealand, goals have been set regarding EBFM, and these have been framed within the Fisheries Act (1996) as: the sustainability of fish-stocks and mitigation of the negative effects of fisheries activity on the associated environment. The act itself is rather vague regarding exactly how these goals are to be achieved. However, further policy statements have built upon this framework: the Strategy for Managing the Environmental Effects of Fishing (SMEEF) (Mfish 2005). The SMEEF was initiated in 2005 and has four main goals

1. The health of the aquatic environment is protected.
2. People are able to realise the best value from the sustainable and efficient use of fisheries.
3. Crown obligations to Māori with respect to fisheries are delivered.
4. Credible fisheries management.

More recent policy statements by the Ministry of Fisheries (Fisheries 2030) have further refined these objectives (Mfish 2008b). Fisheries 2030 outlines its main goal as “New Zealanders maximising benefits from the use of fisheries within environmental limits”. It does this through describing two main policy outcomes: use, and environment. Use outcomes are described as fisheries outcomes that give the “greatest overall economic, social and cultural benefit”. These are balanced by environment outcomes, which are the maintenance of the capacity and integrity of the aquatic environment for present and future use. More recently, the New Zealand Ministry of Fisheries has released the National Deepwater Plan (Mfish 2010), which provides their vision of the future for deep-sea fisheries in New Zealand waters. At the time of writing only the chapters for hoki and orange roughy have been released.

2.4.11. Potential for EBFM for orange roughy

The Deepwater Plan for orange roughy details an aspiration to have the fishery MSC certified as sustainable (Mfish 2010). This is interesting, as the sustainability of orange roughy fisheries is already legislated as a condition of the Fisheries Act (1996). So the desire for the further MSC certification of orange roughy as sustainable highlights a perception that these fisheries have been badly managed (Hilborn et al. 2006), and are unsustainable (Clark 1999, 2001, Francis & Clark 2005, Watling et al. 2010, Dunn & Forman 2011, Weeber 2012, Nourse et al. 2012). The New Zealand non-government organisation (NGO) Forest and Bird lists the two major New Zealand mid-slope fisheries (oreos and orange roughy) as their two worst-choice fisheries for sustainability in their Best Fish Guide (Weeber 2012). The Marine Conservation

Society of the United Kingdom goes even further and recommends not eating any deep-sea fish species (Marine Conservation Society 2011).

If it were possible to get orange roughy MSC certified, this may not do much to change current perceptions, as it has been argued that the MSC certification is a weak, ineffectual and poorly adopted standard (Kaiser & Edwards-Jones 2006; Jacquet & Pauly 2007, Jacquet et al. 2010; Ward 2008; Gulbrandsen 2009; Blight et al. 2010). Jacquet et al. (2010) go so far as to suggest that money spent on MSC certification would be better used on lobbying for the creation of marine protected areas. Additional fisheries certification (to demonstrate sustainability) could also be seen as an admission of the failure of current management practices (Shelton 2009). Therefore, the need for eco-labeling in New Zealand fisheries could be seen as unnecessary, given that sustainability of the fishery is already legislated for in the Fisheries Act (1996). However, as Shelton (2009) suggests, ecolabelling could provide a synergy building on the foundations laid by the Fisheries Act (1996), and subsequent policy documents.

2.5. Foundations of EBFM — fish dietary analysis

Effective ecosystem-based fisheries management requires knowledge of the ecosystem under consideration and an understanding of the trophic (feeding) links within that ecosystem (Fulton et al. 2004, Francis et al. 2007, Plagányi 2007, Fulton 2010, Link 2010). In marine ecosystems, this is usually investigated through the use of fish gut contents (e.g., Bulman et al. 2002; Madurell & Cartes 2005a). In shallow water this involves the analysis of fish stomach contents, which is reasonably straightforward and merely requires collecting enough fish for the desired objectives (e.g., Pinkas et al. 1971). However, studying the diets of deep-sea fish is a more challenging exercise, as in orange roughy fisheries samples are collected from between depths of 800 and 1200 metres (Anderson & Fenaughy 1996, Bulman et al. 2002, Doonan et al. 2006, 2009). Many species of fish recovered from these depths suffer from stomach eversion (due to the change in pressure as the net is brought to the surface), especially oreo dories (Oreosomatidae) (Clark et al. 1989), morid cods (Moridae) (Mauchline & Gordon 1984b) and rattails (Macrouridae) (Iwamoto et al. 1999, Bailey et al. 2006). The latter two common, and in the case of the rattails, specious deep-sea fish families (McMillan & Paulin 1993, McMillan et al. 2011) can have stomach eversion rates as high as 100 percent (Mauchline & Gordon 1984b).

Stomach eversion is not the only issue facing dietary reconstruction of deep-sea fish. Deep-sea research is expensive, and samples from deep-sea fisheries can be hard to obtain, as commercial vessels often have to travel great distances to trawl grounds and are reluctant to give up freezer space to fish of no commercial value (Bremner et al. 2009). As a consequence, samples are often from opportunistic sources (Pethybridge et al. 2010, 2011). On one hand this can limit the scope of possible research as the collection of samples was not the focus of the voyage, nor the gear used (Doonan et al. 2006, 2009, Tuck et al. 2009). On the other, it can force researchers to innovate, and find novel solutions to these sampling issues.

Fish with everted stomachs usually are ignored in dietary studies (e.g., Mauchline & Gordon 1984b, Blaber & Bulman 1987, Clark et al. 1989, Laptikhovsky 2005, Madurell & Cartes 2006, Stevens & Dunn 2011, Horn et al. 2012), so these families can be under-represented in feeding studies. The macrourids are often (but not always) benthic feeders and their exclusion from feeding studies can lead to a potential bias toward fish species with lower rates of stomach eversion that feed in the water column (Bulman et al. 2002, Bradford-Grieve et al. 2003).

2.5.1. Methods of studying the diets of deep-sea fish

2.5.1a. Direct methods

The most common direct method used to study the diets of deep-sea fish is gut content analysis, most commonly stomach contents (e.g., Clark 1985a; Macpherson 1985; Clark et al. 1989; Laptikhovsky 2005; Anderson 2005a, b; Connell et al. 2010; Dunn et al. 2010a, b, c; Horn et al. 2010a, b, Stevens & Dunn 2011; Forman & Dunn 2012), and rarely intestinal contents (Merrett & Marshall 1981, Jones 2008a). Stomach content analysis involves the examination, identification, and quantification of the contents of a fish's stomach. This can be a challenge as the systematics (identities) of many deep-sea species are unknown, exacerbated by the fragmented and partially digested nature of stomach contents, and intestinal samples, and small size of many prey items (otherwise poorly sampled in deep-sea fishing nets or scientific sampling devices) (Robison et al. 2005, 2010; Boyle et al. 2012).

Stomach content analysis can be used (in conjunction with levels of stomach fullness) to assess cycles of feeding, and to provide an estimate of the daily food intake (daily ration) of a species (Macpherson 1985, Bulman & Koslow 1992, Madurell & Cartes 2005b). Daily ration is important when calculating the influence a species has on

the trophic level below it. However, this method requires multiple sampling episodes at predetermined times, over several days, for adequate data (Bulman & Koslow 1992, Williams et al. 2001). The percentage of empty stomachs (PES) can give a rough estimate of feeding periodicity, and can also be used to provide other data on the feeding of fishes, as fish that feed at higher trophic levels (usually piscivorous feeders) feed less frequently than those lower in the food web (Arrington et al. 2002, Vinson & Angardi 2011). Also the PES can be a rough proxy of the productivity of the ecosystem as high PES values could indicate low productivity and vice-versa.

A common method of analysing stomach contents is through the use of the index of relative importance (IRI) (Pinkas et al. 1971, Hyslop 1980, Bowen 1996, Cortez 1997). The IRI is a compound index combining the mass, abundance and frequency of food items to provide a numerical metric of the importance in the diet of each food item. It can be expressed either as a numerical value or as a percentage. Its advantages are that it is simple to calculate, and is widely used (e.g., Pinkas et al. 1971; Matallanas 1982; Clark 1982, 1985a; Clark et al. 1989; Anderson 2005a, b; Connell et al. 2010; Dunn et al. 2010a, b; Horn et al. 2010a, b, 2011; Stevens & Dunn 2011, Pethybridge et al. 2010, 2011, Forman & Dunn 2012, Horn et al. 2012).

The IRI does have some disadvantages in that each metric has an associated error, and combining the three metrics combines the error. Also, the number of food categories can have a direct bearing on the value of the IRI, as a large number of categories can decrease the IRI (Hansson 1998, Cortez 1998). However, it is still a useful metric if displayed as a three-dimensional figure (*sensu* Matallanas 1982; Anderson 2005a, b; Madurell & Cartes 2005b, 2006), as each of the three measures is displayed in turn on three axes. As a consequence, in this thesis the IRI is only used as an indication of diet.

Food items taken from the intestines (intestinal contents) provide a different challenge from stomach contents, and so one has to be very careful when dealing with the two sources of dietary information. Firstly, intestinal contents have already been through the stomach and have been partially (or fully) digested. This means that large, fragile or gelatinous items (with some exceptions, e.g., thaliaceans in the Alepocephalidae) do not go through to the intestines whole, or in an identifiable form. Often, food items are represented by hard-parts, such as crustacean fragments (chela, copepod antennae, isopod heads/telsons, prawn mandibles, and other identifiable body parts), molluscan shells (also the gizzard-plates of benthic opisthobranch gastropods),

squid beaks, polychaete jaws and setae, and chaetognath jaw hooks. The identification of these dietary components can be quite challenging and time consuming. As a consequence material sourced from the intestines of deep-sea fish can present some unique analytical problems.

Secondly, there are problems with the periodicity of intestinal contents. Stomach contents are thought to represent a snapshot (what a fish has just eaten), although with deep-sea fish this can be problematic to evaluate, as gut evacuation rates are unknown for most species. Indeed, stomach fullness has been used to estimate the daily ration of several deep-sea fish (e.g., Macpherson 1985, Bulman & Koslow 1992, Madurell & Cartes 2005b). However, despite this, it is still unknown how long times are between feeding episodes. It is known from lipid studies on the deeper-living cosmopolitan rattail (*C. armatus*) that it can possibly live for at least 186 days without feeding (Smith 1978), so the duration between feeding episodes could be quite long. It is currently impossible to ascertain how many feeding episodes intestinal contents represent, or the time between them. Another issue regards the intestinal contents of (mainly) larger fish, the problem being that it is impossible to ascertain whether the intestinal contents came directly as result of the fish in question's feeding activity, or from the gut contents of another animal the fish has eaten. This is also a potential issue when using DNA or fatty acid profiles (Pethybridge et al. 2011).

As a consequence of these factors: lack of weight, uncertain periodicity, and uncertain origin of food items, analyses based on intestinal contents are best based on presence/absence data. While this method of addressing these data does not rectify the problems mentioned above, it does mitigate the potential errors as much as possible, thus enabling dietary analysis of fish species that would have been previously excluded from direct dietary analyses (e.g., Clark et al. 1989).

2.5.1b. Indirect methods

Indirect methods of fish dietary analysis can be quite simple, for example using the mouth position to predict where a fish is feeding (McLellan 1977). The premise is that fish with terminal mouths (at the end of the fish's body) will tend to feed in the water column, and fish with a mouth position under the head (inferior) will feed from the bottom. This can only be used as a rough indication of feeding preferences, as there are fish species with inferior mouths that feed in the water column, particularly dogfishes and catsharks (Mauchline & Gordon 1983a). Other head morphology has

been used to infer the diets of fish species in shallow waters: the number of gill rakers can be used to determine the size range of prey fish can manipulate (Pauly et al. 1998b), and the morphology and length of the alimentary canal can be used to infer diet (de Groot 1981).

The time of day a fish was caught can also be used to elicit dietary information; for example Kobayashi (1986) found that shovel-nosed dogfish were caught on longlines more frequently at night, suggesting that this species could be a nocturnal feeder. Scavenging can be inferred from the attraction/interaction of fishes to baited landers (Priede et al. 1994a, b; Priede & Bagley 2000; Uiblein et al. 2002; Yeh & Drazen 2011; Tales from Te Papa 2011), or from the nature (and condition) of the food in their stomachs (Clark et al. 1989, Horn et al. 2010a, Forman & Dunn 2012).

Another simple indirect technique has been the analysis of the percentage of empty fish stomachs in a given sample (Arrington et al. 2002). The percentage of empty stomachs of a given fish species, can reflect food availability: high food availability = low percentage of empty stomachs and vice-versa. Vinson & Angradi (2011) suggest that the PES could be used as a proxy for the productivity of an ecosystem.

The sensory apparatuses of fish have also been used to infer feeding behaviour (Kotrschal et al. 1998, Warrant & Locket 2004, Lisney 2010). Foraging activity has also been inferred from the morphology of the brains of some deep-sea species (Wagner 2001, 2002, 2003). Wagner (2002) examined the relative sizes of parts of the brains of the alepocephalids *Xenodermichthys copei* and *Alepocephalus productus*, and found a large optic nerve and optic tectum, and suggested that due to this they were likely to be optically focused foragers. Given the depths that the adults of these two species are found at (approximately 1000 m); this strongly suggests that bioluminescent animals are probably important in the feeding of these species.

Wagner (2002) also looked at deep-sea eels and found that two species (*Histiobranchus batybus*, and *Synaphobranchus kaupi*) had enlarged olfactory bulbs, and suggested that these two species were demersal foragers and/or scavengers. The olfactory bulbs of the previous two alepocephalid species were not greatly developed, which could suggest that scavenging is not important to these two species. Further to this, Wagner (2003) found an ontogenic change in the morphology of the brain of *C. armatus*, and linked this to an ontogenic shift in diet. He found that the optic tectum decreased in size, while the olfactory bulb increased in size, and related this to a behavioral change from optically- to olfactory-based foraging. He suggested this was

reflected in a shift to scavenging in larger individuals, and found further supporting evidence in their stomach contents.

Yopak & Montgomery (2008) have also inferred feeding activity in several species of deep-sea chondrichyans from brain morphology. They suggested that the small brain size of some deep-sea fishes was in response to the energetic expense of maintaining brain tissue, but also that small brain size inferred low activity. Such low activity inferred more passive behaviour than active foraging and probable scavenging. The species they identified as being likely to exhibit these behaviours were Baxter's, long-nosed velvet, and Owston's dogfishes. Yopak and Montgomery (2008) also suggested that deep-sea sharks with more complex brain morphology would probably be more active and thus active foragers.

Parasites have been used to deduce deep-sea fish diet, as certain parasites have particular intermediate hosts that need to be consumed in order to gain the aforementioned parasite (Clarke & Merrett 1972, Zubchenko 1981, Houston & Haedrich 1986, Palm & Klimpel 2008). Benthic feeding fish are considered to have a higher and more diverse parasite loading than those that feed in the water column (Houston & Haedrich 1986, Klimpel et al. 2006, 2010); therefore deep-sea fish diet and feeding habits can be inferred from the composition of their stomach parasites (Zubchenko 1981, Gibson & Bray 1986, Palm & Klimpel 2008).

More complex indirect techniques, such as using cross-reacting antisera, have been used to determine deep-sea fish diet, but these have been laboratory-intensive and have not been generally pursued (Feller et al. 1985). The use of stable isotopes of carbon and/or nitrogen has also become more popular (Stowasser et al. 2009), as well as other indirect methods using DNA and/or fatty acids (Stowasser et al. 2009; Drazen et al. 2008, 2009; Dunn et al. 2010a; Pethybridge et al. 2011). These methods have been used in conjunction with stomach contents to provide validation. Caution is necessary when interpreting the results of stable isotope analysis, as they represent a time-averaged representation of diet (O'Reilly & Hecky 2002, Suring & Wing 2009), and the time period is dependent on the turnover rate of the tissue chosen for analysis (Tieszen et al. 1983, Suring & Wing 2009). Isotopic values can also be misleading if proteins are routed to body synthesis and not to metabolism (Voigt et al. 2008, Boyle et al. 2012). Also, time-averaged methods can overlook opportunistic feeding episodes, and can have difficulty distinguishing between scavenging and predation (Jefferies et al. 2010, 2011). This last point has particular resonance in deep-sea fisheries bycatch species, as not only

is scavenging important to the diets of deep-sea fish (Drazen et al. 2008, 2009; Yeh & Drazen 2011; Jamieson et al. 2011), but scavenging on fisheries discards has become an important source of energy for several deep-sea species worldwide (Yamamura 1997, Laptikhovsky & Fetsov 1999, Forman & Dunn 2012, Boyle et al. 2012, Horn et al. 2012). As King et al. (2008 p 958) state for the elucidation of fish gut contents using DNA analysis: "The fact that a predator tests positive for a target prey species does not necessarily mean that it killed that prey animal nor even that it intended to eat it."

2.6. Role of scavenging in deep-sea fish

Food is often hard to come by in the deep-sea, and this is reflected in the low metabolisms and feeding rates of some deep-sea fish (Smith & Hessler 1974, Smith 1978, Drazen 2002, Drazen & Yeh 2012); therefore many fish species scavenge for at least part of their diets (Bailey et al. 2002; King et al. 2006, 2008, Drazen et al. 2008). Well-known examples of deep-sea scavengers are the cosmopolitan rattail *Coryphaenoides armatus* (Priode et al. 1994a, Jones et al. 1998, Drazen 2002, Bailey et al. 2007, Drazen et al. 2008), deep-sea dogfishes (e.g., *Etmopterus princeps*, *Centroscymnus coelolepis*) (Ebert et al. 1992, Priode et al. 1994b, King et al. 2006), hagfish (*Eptatretus deani*) (Smith 1985), and eels (e.g., *Synaphobranchus kaupi*) (Priode et al. 1994b, Gordon & Mauchline 1996, Jamieson et al. 2011).

Benthic feeding deep-sea fish species can utilise two trophic pathways (Drazen et al. 2008). One pathway is based on the recycling of phytodetritus, which sinks to the seafloor where it is eaten by deposit feeders (Corliss et al. 2009). These are in turn eaten by primary carnivores, which are also then eaten, and so on, until they are eaten by benthic-feeding fish (Drazen et al. 2008, Ramirez-Llodra 2010). This recycling of phytodetritus can result in augmented trophic levels for benthic feeding fishes (Drazen et al. 2008, Boyle et al. 2012). A second trophic pathway bypasses the detrital pathway: the dead bodies of surface dwelling animals and/or plant material rapidly sink to the seafloor and are then eaten by benthic-scavenging fish. Thus, the detrital food-web is bypassed through scavenging. This second pathway provides a rapid influx of food of pelagic origin that would usually be available to those benthic-scavenging fishes (e.g., Bathmann 1988; Robison et al. 2005; Jones & Leschen 2008; Lebrato & Jones 2009; Jefferies et al. 2010, 2011). The phytodetrital pathway has yet to be described for New Zealand deep-sea communities, although there is increasing evidence for the second carrion-based pathway (Clark et al. 1989; Jones 2008a, b, 2009; Forman & Dunn 2012).

In addition, this second pathway can be further augmented by the influx of fisheries bycatch discards (Forman & Dunn 2012, Horn et al. 2012).

In New Zealand waters, data regarding the scavenging behaviour of mid-slope deep-sea fish are sparse, and mostly restricted to inferences from their stomach contents (Clark et al. 1989, Jones 2008a). Although both *C. armatus* and *C. coelolepis* occur in New Zealand waters (Paulin et al. 1989), they are not commonly taken in research trawls (Francis et al. 2002), and there are no local studies on their trophic interactions. Some closely related species occur in New Zealand waters at mid-slope depths, so it is possible that they could fulfill a similar role. For example, serrulate and four-rayed rattail (*Coryphaenoides serrulatus* and *C. subserrulatus* respectively) could be scavengers, as could Baxter's dogfish (*Etmopterus baxteri* Garrick, 1957) and long-nosed velvet dogfish (*Centroselachus crepidater*), as well as basketwork eel (all common New Zealand mid-slope fish species (Clark et al. 1989, Anderson et al. 1998, Clark et al. 2000, Francis et al. 2002, Doonan et al. 2009)). Scavenging has been recently reported for several species of upper-slope fish species from New Zealand waters (Dunn et al. 2010a, b; Horn et al. 2010a; Forman & Dunn 2012), although the precise role scavenging plays in their diets is unclear.

In the deep-sea, large food falls are rare, but represent extremely important local sources of energy (Stockton & De Laca 1982, Baco & Smith 2003, Soltwedel et al. 2003). Food-falls have been reported as making up over ten percent of the respiratory requirements of the benthic community at a depth of 1310 metres in the Santa Catalina Basin (Smith 1985). Collins et al. (2005) suggest that since carrion can occur in larger pieces than manageable prey, and is more arbitrarily distributed, there is an evolutionary advantage to scavenging fish, in being of a larger size. They found that scavenging fish species were larger in size than predatory fish, and they related this to food availability. Being larger enables fish to swim faster, for longer, and have greater energy reserves, thus enabling them to survive on a sporadic food source. It has been estimated that cosmopolitan rattail can live on stored energy for up to 186 days without feeding (Smith 1978). This could also be a why larger deep-sea fish are often found with no food in their stomachs, as their feeding could be reflecting a sporadic and infrequent food source (hence possible evidence for scavenging, or feeding at a high trophic level). An ontogenic shift from benthic foraging to scavenging has been observed in *C. armatus* from abyssal depths (Wagner 2003), but prior to this study no corresponding

ontogenic shift in diet has been recorded for any deep-sea rattail in New Zealand waters at mid-slope depths (Jones 2008a).

2.7. Summary

In summary, New Zealand fisheries management (Mfish) has expressed a desire to move towards a more ecosystem-based approach to fisheries management. One of the major focuses of this desire is the valuable mid-slope deep-sea orange roughy fisheries. While much recent research has focused on the ecosystem interactions of commercial and non-commercial fish species in the shallower hoki fishery (particularly on Chatham Rise), very little similar work has been undertaken regarding the deeper mid-slope orange fisheries, rendering an ecosystem-based approach to orange roughy fisheries an as-yet-unrealised goal.

There is a faunal shift in fish species between upper and mid-slope depths on Chatham Rise, with few of the species common to one depth range occurring in the other. As a consequence, despite the large amount of recent work undertaken on Chatham Rise, there is a large data deficiency regarding the ecosystem interactions of non-commercial mid-slope fish species in New Zealand waters in general and Chatham Rise in particular. If EBFM is to be used, it is vital to understand the feeding relationships within and between the fish species that inhabit these deep-sea ecosystems.

This thesis will examine this knowledge gap and provides supplementary dietary data from a seamount complex off the southwestern tip of New Zealand for comparison. Further supplementary dietary data is provided from an upper-slope scampi fishery from off the Wairarapa coast to augment those dietary data obtained from similar depths on Chatham Rise by other researchers. The following chapter describes the materials and methods used to achieve this.

3.0 Materials and methods

3.0. Materials and Methods

3.1. Opportunistic methodology

"What is the function of research? Ultimately, all research is concerned with the creation of new knowledge. But the level of this knowledge varies, as do the methods which are used to reach it. Psychologist Colin Robson noted that research was generally concerned with producing knowledge that could meet one of three purposes. The first was *exploratory*, the second *descriptive* and the third *explanatory*." (Silke 2001 p1). Opportunistic exploratory research is important in gathering data on subjects or in regions where data is difficult to obtain. The deep-sea is an example of both. Often the deep regions of the world (and New Zealand is no exception) are far from shore, requiring days of steaming to reach. Once there, large vessels using kilometres of cabling can be required to obtain samples. Deep-sea research is expensive (Gordon et al. 2003, Durán Muñoz & Sayago-Gil 2011, Stewart & Callagher 2011, Watling et al. 2010), and quantitative samples of non-commercially important deep-sea species can be hard to obtain (Bremner et al. 2009). As a result, opportunistic sampling has been used previously in deep-sea studies, not only as a basis for the collection of samples (Clark et al. 1989, Pethybridge 2010, 2011), but also to augment existing research plans (e.g., Forman & Dunn 2012, Horn et al. 2012). As such, opportunistic sampling can provide novel and useful data that would not have normally been available through traditional means (Jones 2007, 2008a, b, 2009; Jones & Leschen 2008).

This thesis uses opportunistic sampling as a cost-effective methodology to provide exploratory data regarding the food and feeding relationships of deep-sea fish. These fish were collected through the medium of bycatch from orange roughy and scampi trawls.

3.2. Collection of material

Fish were opportunistically sourced from three separate regions, and two depth ranges. Fish were recovered from northeastern Chatham Rise as bycatch from four orange roughy trawls, between bottom depths of 901 and 1196 metres. These trawls were undertaken during July 2004 by the National Institute of Water and Atmospheric Research Limited (NIWA), from the RV *Tangaroa* (cruise number TAN0408), as part of a survey to assess the abundance of orange roughy on northeastern Chatham Rise (NIWA 2004a, Doonan et al. 2006). This area was mostly flat-bottomed soft-sediment,

adjacent to the "Andes Complex" of hills on northeastern Chatham Rise (Tracey et al. 2004).

The net used was the NIWA full wing trawl "ratcatcher". This net has upper and lower wings, a wingspread of approximately 25 metres, door spread of about 115 metres, with a headline height of approximately 3.3 metres. It had six-inch mesh in the wings and 40 mm mesh on the codend (full inside mesh), and low 200 mm bobbins. This net has smaller meshes and ground gear than standard orange roughly trawl gear, to ensure closer bottom contact so that smaller fish entering the net were retained (Doonan et al. 2006).

Additional orange roughly bycatch was procured from the Puysegur Bank (*sensu* Carey 1993, Taylor 2001), an area of seamount features (including the "Lady Godiva" Pinnacle) south west of New Zealand (**Fig. 3**) (Tracey et al. 2004). This material was sourced through the New Zealand Ministry of Fisheries Scientific Observer Programme, and was collected by Rick Guild aboard the FV *San Waitaki* during July 2006, between bottom depths of 1020 and 1072 metres (**Table 4**). The FV *San Waitaki* used a "Champion" two-panel bottom trawl, with a headline height of 3.8 m.

Fish were also opportunistically obtained from off the Wairarapa coast as bycatch from trawls used to assess the abundance of scampi (*Metanephrops challengeri* Balss). These trawls were undertaken by NIWA during January and February 2004 by the RV *Kaharoa* (cruise number KAH0401), between mean bottom depths of 239 and 448 metres (NIWA 2004b), using a "Florida Flyer" net with an 85 mm mesh, 35 mm cod-end and Bison doors (Cryer et al. 2002).

All samples were collected as sub-sets of trawls, but are broadly representative of the fish assemblages within each of these two depth ranges, in accordance with the bathymetric communities reported by Bull et al. (2001), Francis et al. (2002), and Doonan et al. (2006, 2009).

Trawl locations and depths are listed in **Table 4**. All fish species collected during these trawls are detailed in **Table 5**, in addition to the numbers, weights, size, depth and latitudinal ranges, of all individuals examined (after Anderson et al. 1998) (**Table 6**).

3.2.1. Description of the study areas, oceanography and sediments

3.2.2. Chatham Rise

The Chatham Rise is a large broad, relatively flat-topped submarine feature extending eastwards from New Zealand's South Island at about 43° South, roughly from

Christchurch in the west to the Chatham Islands and beyond to the east. It rises from the abyssal plain at approximately 3000 metres to its flat-topped ridge at approximately 250 metres (Probert et al. 1997). It is separated from the South Island to the west by the approximately 500 metres deep Mernoo Gap and reaches sea level at the Chatham Islands to the east, and then tapers down across the Arrow Plateau to abyssal depths. Sediments on the rise are varied, and can range from fine sand (e.g., Probert & McKnight 1993; Probert et al. 1996, 1997) to the rocky outcrops of “seamount-like” features (mainly pinnacles, hills, and knolls according to Rogers (1994)) (Probert et al. 1997, Anderson & Clark 2005, Clark & Rowden 2009). “Seamount-like” features are henceforth referred to as seamounts, for clarity. This variety in sediments has been reflected in the benthos extant, with significant faunal differences reported between the flat areas of soft sediment and the seamounts (Probert et al. 1997).

The Chatham Rise is under the influence of the subtropical convergence (STC): a major southern-hemisphere front separating subtropical water in the north from sub-Antarctic water in the south (Gilmore & Cole 1979, Heath 1985, Sutton 2001, Chiswell 2002a, Nodder et al. 2007). The STC is a continuous feature around southern New Zealand (Heath 1985). It bends down around the southwest tip of the South Island and then flows up the east coast of the South Island (Heath 1985, Chiswell 1996). It follows the edge of the continental shelf northwards (where it is known as the Southland Front) and then flows eastward between 43–44°S over the Chatham Rise, where it is a continuous feature over the southern flanks (Bradford-Grieve 1999, Chiswell 2001a, b; Sutton 2001). The STC mixes warmer and more saline water from the north, with colder and less saline sub-Antarctic water from the south (Chiswell 1994). It moves north during the Austral summer, but for the most part is found over the southern flanks of the Chatham Rise (Heath 1985), which as a result are considered to be more productive than the north (Uddstrom & Oien 1999, Murphy et al. 2001, Knox et al. 2012). Over the Chatham Rise, the temperature and salinity of the STC can be also influenced to some degree by water from the Wairarapa Eddy from the north (Chiswell 2002b), and the Southland Front from the south (Butler et al. 1992, Chiswell 1996, Sutton 2003). The STC is considered to be a region of enhanced primary productivity (e.g., Bradford 1980, Bradford-Grieve et al. 1997, 1998, 1999, Uddstrom & Oien 1999, Murphy et al. 2001, Hadfield et al. 2007, Knox et al. 2012), and considered to be the driving force behind the productivity of several major commercial fisheries that exist on Chatham Rise (Mfish 2011).

3.2.3. Puysegur Bank

Puysegur Bank also sits underneath the subtropical convergence (STC) (Heath 1985). It is thought that the bank itself influences the mixing of subtropical, sub-Antarctic, and freshwater sources (Butler et al. 1992). This mixing is thought to influence the relatively high productivity of the surrounding area (Vincent et al. 1991). The bank itself contains a complex of seamounts (Carey 1993, Tracey et al. 2004), on which has been a fishery for orange roughy (also known as the Puysegur Box) since 1991 (Mfish 2011). The fishery itself was closed in 2001 to allow stocks to recover and was recently reopened after several industry-based stock assessments (Mfish 2011). Puysegur Bank is adjacent to the tectonic boundary between the Australian Plate to the east and the Pacific Plate to the west, where the Australian Plate is undergoing subduction by the Pacific Plate (Sutherland et al. 2006, Clark et al. 2011). An area containing levels of gas hydrates (Crutchley et al. 2007), Puysegur Bank is also thought to be the location of cold-seeps (Lewis & Marshall 1996), particularly an area near the “Lady Godiva” pinnacle feature (Carey 1993).

3.2.4. Wairarapa coast

The water mass off the Wairarapa coast is under the influence of the East Coast Current (moving southwards) (Bradford-Grieve et al. 1991, Chiswell 2000), and within it the Wairarapa Eddy (Chiswell 2003, 2005). The Wairarapa Eddy is a mesoscale semi-permanent anti-cyclonic eddy constrained within a triangular wedge between the Wairarapa coast to the east, and the Chatham Rise to the south (Roemmich & Sutton 1998). Water from the Wairarapa Eddy eventually finds its way over to the Chatham Rise and subtropical convergence (STC) (Chiswell 2002b, Nodder et al. 2007). The Wairarapa Eddy is thought to be important to the local distribution and reproduction of spiny lobster larvae (*Jasus edwardsii*) by keeping them close to the coast as they develop, and then settle (Jeffs et al. 2001). It is likely that the Wairarapa Eddy is an influence on the distribution of many animals with a planktonic dispersal stage. The upper-slope off the Wairarapa Coast is considered to be relatively steep, with fine-grained sediments (Pantin, 1965). The Wairarapa coast is also an area where cold seeps have been found, although these have tended to be in deeper water (approx. 1000 m), mid-slope sediments further offshore (Lewis & Marshall 1996, Barnes et al. 2010, Klaucke et al. 2010).

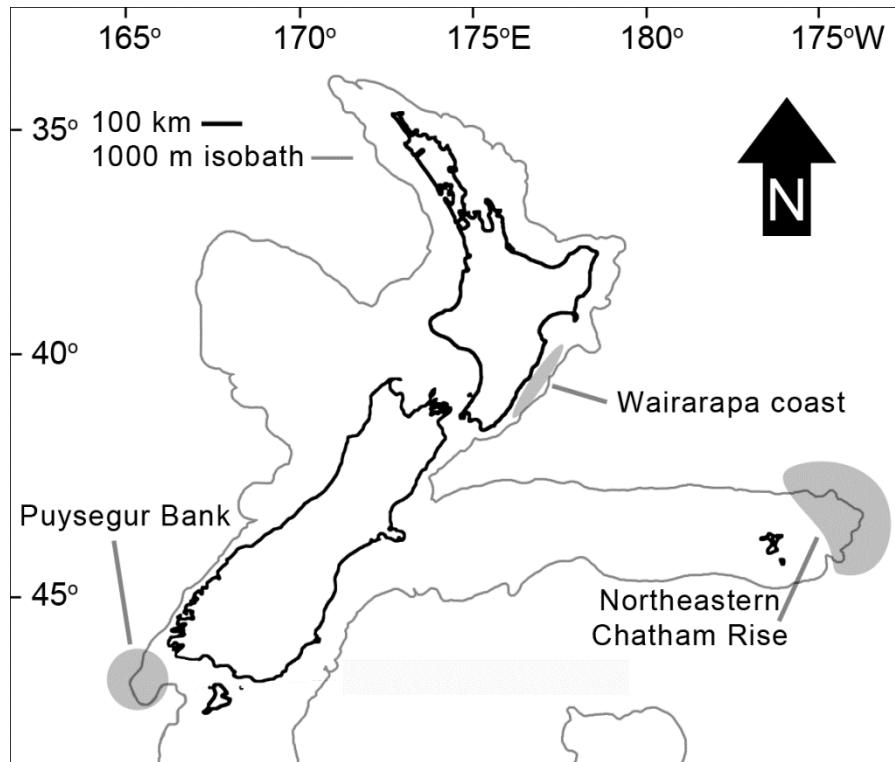


Figure 3. Locations of the sample areas.

Table 4. Northeastern Chatham Rise (NECH), Puysegur Bank (PUY), and Wairarapa coast (WAI) trawl stations.

Station number	Date	Location	Latitude (S)	Longitude*	Depth (m)**
36*	17/07/04	NECH	43.2	174.19W	901
42	17/07/04	NECH	43.03	174.04W	1196
44	22/07/04	NECH	44.04	174.37W	1117
61	25/07/04	NECH	43.28	174.59W	1093
na	11/07/06	PUY	46.55	165.26E	1050
na	12/07/06	PUY	46.59	165.25E	1050
na	12/07/06	PUY	46.54	165.25E	1072
na	12/07/06	PUY	46.54	165.29E	1053
na	12/07/06	PUY	46.53	165.28E	1055
na	13/07/06	PUY	46.55	165.26E	1020
na	13/07/06	PUY	46.56	165.24E	1062
na	13/07/06	PUY	46.59	165.24E	1062
39	30/01/04	WAI-start	39.96	177.17E	239.5
39	30/01/04	WAI-finish	39.80	177.48E	239.5
50	1/02/04	WAI-start	40.05	177.32E	365
50	1/02/04	WAI-finish	40.88	176.69E	365
52	1/02/04	WAI-start	40.68	176.87E	418
52	1/02/04	WAI-finish	40.72	176.74E	418
59	2/02/04	WAI-start	40.73	176.60E	448
59	2/02/04	WAI-finish	40.81	176.60E	448
60	3/02/04	WAI-start	40.84	176.64E	442.5
60	3/02/04	WAI-finish	39.93	177.19E	442.5
62	3/02/04	WAI-start	39.78	177.51E	329.5
62	3/02/04	WAI-finish	40.05	177.32E	329.5
63	4/02/04	WAI-start	40.86	176.73E	248
63	4/02/04	WAI-finish	40.71	176.86E	248
64	4/02/04	WAI-start	40.75	176.72E	281
64	4/02/04	WAI-finish	40.76	176.58E	281
65	4/02/04	WAI-start	40.85	176.59E	326
65	4/02/04	WAI-finish	40.87	176.62E	326

*NECH trawl locations were west of the meridian, all others were east. **Maximum gear depths are shown for NECH and PUY trawls. Mean gear depth is given for WAI trawls. na: not available. *Station 36 is now located within the East Chatham Rise benthic protected area.

Table 5. Location, identity, total number, weight, size range and measurement technique of 76 fish species examined from northeastern Chatham Rise (NECH), Puysegur Bank (PUY), and off the Wairarapa coast (WAI). Length measures: SL, standard length; PCL, pre-caudal length; TL, total length; PAL, pre-anal fin length.

Location	Family	Species	Species code	Total number	Total weight (g)	Size range (mm)	Measure
NECH	Somniosidae	<i>Centroselachus crepidater</i> (Bocage & Copell, 1864)	CYP	15	37384.3	530–885	PCL
	Centrolophidae	<i>Deania calcea</i> Lowe, 1839	SND	75	126157.9	252–894	PCL
	Etmopteridae	<i>Etmopterus baxteri</i> Garrick, 1957	ETB	34	30795.3	183–712	PCL
	Chimaeridae	<i>Chimaera</i> sp. C <i>sensu</i> Paulin et al. 1989	CHC	3	2591.9	220–224	SV
	Rhinochimaeridae	<i>Rhinochimaera pacifica</i> (Mitsukuri, 1895)	RCH	1	3912.7	675	SV
	Arhynchobatidae	<i>Bathyraja shuntovi</i> Dolganov, 1985	PSK	3	n/a	450–670	TL
	Synphobranchidae	<i>Diastobranchius capensis</i> Barnard, 1923	BEE	266	124775.7	392–1114	TL
	Notocanthidae	<i>Notocanthus sexispinus</i> Richardson, 1846	SBK	9	2167	440–638	TL
	Congridae	<i>Bassanago hirsutus</i> (Castle, 1960)	HCO	2	798.4	575–770	TL
	Alepocephalidae	<i>Alepocephalus australis</i> Barnard, 1923	SBI	196	59261.6	101–953	SL
		<i>Alepocephalus antipodanus</i> (Parrot, 1948)	SSM	101	706.1	165–601	SL
	Platyroctidae	<i>Xenodermichthys copei</i> (Gill, 1884)	BSL	86	13475	238–509	SL
		<i>Persarsia kopua</i> (Phillips, 1942)	PKO [‡]	8	159.6	123–139	SL
	Phosichthyidae	<i>Phosichthys argenteus</i> Hutton, 1872	PAR [‡]	3	142.6	165–280	SL
	Chauliodontidae*	<i>Chauliodon sloani</i> Bloch & Schneider, 1801	CSL [‡]	1	75	262	SL
	Myctophidae**	spp.	MYC	18	21.2	~50–117	SL
	Moridae	<i>Antimora rostrata</i> (Günther, 1878)	VCO	4	2649.5	468–500	SL
		<i>Halargyreus johnsonii</i> (Günther, 1862)	HJO	41	38348.2	118–630	SL
	Bathylagidae	<i>Lepidion microcephalus</i> Cowper, 1956	SMC	21	4958	210–419	SL
		<i>Bathylagus bercoides</i> (Borodin, 1929)	BBE [‡]	6	249.2	170–227	SL
	Sternoptychidae	<i>Agyropelecus gigas</i> Norman, 1930	AGI	3	38.2	71–95	SL
	Macrurionidae	<i>Macruronus novaezelandiae</i> (Hector, 1871)	HOK	3	2461.1	201–355	PAL
	Macrouridae	<i>Coelorinchus acanthiger</i> Barnard, 1923	CTH	21	2639	68–129	HL
		<i>C. fasciatus</i> (Günther, 1878)	CFA	1	108.3	72	HL
		<i>C. innotabilis</i> McCulloch, 1907	CIN	74	2481.7	41–79	HL
		<i>C. matamua</i> (McCann & McKnight, 1980)	CMA	2	103.7	51–76	HL
<i>C. trachycarus</i> McMillan, Iwamoto & Shcherbachev, 1999		CHY	17	3836.3	89–122	HL	
<i>Coryphaenoides dossenus</i> McMillan, 1999		CBA	5	1802.9	59–135	HL	
<i>C. serrulatus</i> Günther, 1878		CSE	101	11325.3	23–78	HL	
<i>C. subserrulatus</i> Mashukok, 1976		CSU	469	20358.8	26–69	HL	
<i>Gadomus aoteanus</i> McCann & McKnight, 1980		GAO [‡]	1	92.93	103	HL	
<i>Lepidorhynchus denticulatus</i> (Richardson, 1846)		JAV	1	319.7	122	PAL	

Table 5 (continued).

Location	Family	Species	Species code	Total number	Total weight (g)	Size range (mm)	Measure	
NECH		<i>Nezumia namatahi</i> McCann & McKnight, 1980	NNA	9	466.1	34–54	HL	
		<i>Macrourus carinatus</i> Günther, 1878	MCA	40	21765.9	52–166	HL	
		<i>Trachyrincus aphoydes</i> McMillan, 1995	WHX	21	12021.4	107–248	HL	
		<i>T. longirostris</i> (Günther, 1878)	WHR	8	2301.1	110–141	HL	
	Oreosomatidae	<i>Allocyttus verrucosus</i> (Gilchrist, 1906)	WOE	29	14450	160–301	SL	
		<i>Pseudocyttus maculatus</i> Gilchrist, 1906	SBL	14	3385.8	153–275	SL	
		<i>Neocyttus rhomboidalis</i> Gilchrist, 1906	SPO	1	394.3	251	SL	
	Trachichthyidae	<i>Hoplostethus atlanticus</i> Collett, 1889	ORH	96	77965.4	177–381	SL	
	Scorpaenidae	<i>Trachyscorpia capensis</i> (Gilchrist & von Bonde, 1924)	TRS	1	1038.2	303	SL	
	Epigonidae	<i>Epigonus robustus</i> (Barnard, 1927)	EPR	188	11333.1	115–205	SL	
	Psychrolutidae	<i>Psychrolutes microporos</i> Nelson, 1995	PSY	1	120.3	156	SL	
	PUY	Somniosidae	<i>Centroselachus crepidater</i> Bocage & Capello, 1865	CYP	9	8694.8	265–561	PCL
			<i>Centroscyrmus owstoni</i> Garman, 1906	CYO	4	1834.5	441–504	PCL
		Etmopteridae	<i>Etmopterus baxteri</i> Garrick 1957	ETBp	50	46670.9	224–580	PCL
Scyliorhinidae		<i>Apristurus</i> sp. A <i>sensu</i> Paulin et al. 1989	APA [‡]	1	1030	549	PCL	
		<i>Apristurus</i> sp. B <i>sensu</i> Paulin et al. 1989	APB [‡]	1	978.9	515	PCL	
		<i>Apristurus exsanguis</i> Sato, Nakaya & Stewart, 1999	AEX [‡]	1	900.3	527	PCL	
Synphobranchidae		<i>Diastobranchus capensis</i>	BEE	2	2172.4	935–945	TL	
Moridae		<i>Halargyreus johnsonii</i>	HJOp	23	9538.3	288–439	SL	
		<i>Lepidion microcephalus</i>	SMC	8	1954.8	320–367	SL	
Macrouridae		<i>Coelorinchus kaiyomaru</i> Arai & Iwamoto, 1979	CKA	3	303.55	101–116	PAL	
		<i>Coryphaenoides serrulatus</i>	CSE	6	1292.63	101–134	PAL	
		<i>C. subserrulatus</i>	CSUp	132	6667.02	50–95	PAL	
		<i>Lepidorhynchus denticulatus</i>	JAV	8	2044.17	106–128	PAL	
		<i>Macrourus carinatus</i>	MCA	7	8347.6	131–274	PAL	
WAI	Etmopteridae	<i>Etmopterus lucifer</i> Jordan & Snyder, 1902	ETL	1	28.2	182	PCL	
	Chimaeridae	<i>Hydrolagus novaeseelandiae</i> (Fowler, 1911)	HNO	8	3938	195–575	PCL	
	Scyliorhinidae	<i>Halaelurus dawsoni</i> Springer, 1971	DAW	2	456.4	231–301	PCL	
		<i>Cephaloscyllium isabellum</i> (Bonnaterre, 1788)	CAR	2	515.7	212–338	PCL	
	Congridae	<i>Bassanago hirsutus</i>	HCO	6	1755.7	521–692	TL	
	Argentinidae	<i>Argentina elongata</i> Hutton, 1879	ARE	21	405.3	127–192	SL	
	Moridae	<i>Pseudophycis bacchus</i> (Bloch & Schneider, 1801)	RCO	15	2412.67	123–353	SL	
		<i>Triperophycis gilchristi</i> Boulenger, 1902	TGI [‡]	1	26.1	185	SL	
		<i>Euclichthys polynemus</i> McCulloch, 1927	EPO [‡]	1	39.79	204	SL	
	Macrouridae	<i>Coelorinchus biclinozonalis</i> Arai & McMillan, 1982	CBI	11	2397.03	96–172	PAL	
		<i>C. bollonsi</i> McCann & McKnight, 1980	CBO	58	3926.3	39–195	PAL	
		<i>C. oliverianus</i> Phillips, 1927	COL	48	2492.2	60–103	PAL	
		<i>Lepidorhynchus denticulatus</i>	JAV	121	7825.09	26–113	PAL	
		<i>Lucigadus nigromaculatus</i> (McCulloch, 1907)	VNI	1	6.5	31	PAL	

Table 5 (continued).

Location	Family	Species	Species code	Total number	Total weight (g)	Size Range (mm)	Measure
	Trachichthyidae	<i>Beryx splendens</i> Lowe, 1834	BYX	2	1331.9	282–300	SL
		<i>Hoplostethus mediterraneus</i> Cuvier, 1829	SRH	82	1272.14	43–133	SL
	Ophiidae	<i>Genypterus blacodes</i> (Bloch & Schneider, 1801)	LIN	1	747.7	578	TL
	Zeonidae	<i>Capromimus abbreviatus</i> (Hector, 1875)	CDO	71	973.1	58–85	SL
	Scorpaenidae	<i>Helicolenus percooides</i> (Richardson, 1842)	SPE	124	11034.74	74–308	SL
		<i>Polyprion americanus</i> (Bloch & Schneider, 1801)	BAS	1	3027.6	485	SL
	Epigonidae	<i>Epigonus denticulatus</i> Dieuzeik, 1950	EPD	7	110.2	91–118	SL
	Triglidae	<i>Lepidotrigla brachiopertera</i> Hutton, 1872	SCG	2	100.94	119–147	SL
	Hoplichthyidae	<i>Hoplichthys haswelli</i> McCulloch, 1907	FHD	23	305.54	41–227	SL
	Psychrolutidae	<i>Neophrynichthys angustus</i> Nelson, 1977	NAN [‡]	1	123.5	159	SL
	Uranoscopidae	<i>Kathetostoma giganteum</i> Haast, 1873	STA	1	1536.9	380	SL
	Pentacerotidae	<i>Pentaceros decacanthus</i> (Günther, 1871)	YBO	3	93.3	90–93	SL
	Percophidae	<i>Hemerocoetus macrophalmus</i> Regan, 1914	HMA [‡]	4	31.3	129–148	SL
	Achiropsettidae	<i>Mancopsetta milfordi</i> (Penrith, 1965)	MAN	4	242.6	142–198	SL
	Pleuronectidae	<i>Azygopus pinnifasciatus</i> Norman, 1926	SDF	12	405.3	127–192	SL
				2888	779.4 kg		
*taken from the stomach of a CYP. **Includes 16 fish taken from the stomachs of SND. Species' authors are provided for the first incidence of that species only. ‡Indicates a non-standard New Zealand Ministry of Fisheries species code.							

Table 6. Depth ranges and distributions of fish examined in this study (after Anderson et al. 1998).

Species	Common name (where known)	Depth (m)			Range (m)	Latitude		
		Mean	Min	Max		Mean	°N	°S
<i>Argyropelcus gigas</i>	giant hatchet fish	na	300	1000	700			
<i>Alepocephalus australis</i>	big scaled brown slickhead	1272	610	1700	1090	44.02	32.41	54
<i>Alepocephalus antipodanus</i>	small-scaled brown slickhead	1292	560	1700	1140	40.06	32.31	53.73
<i>Allocyttus niger</i>	black oreo	924	461	1396	935	45.53	37.68	51.01
<i>Allocyttus verrucosus</i>	warty oreo	1224	607	1489	882	37.92	32.31	44.74
<i>Antimora rostrata</i>	violet cod	1322	435	1700	1265	48.84	37.3	54
<i>Apristurus</i> spp.	catsharks	1209	324	1516	1192	42.43	32.41	53.73
<i>Apristurus exsanguis</i>	catshark	*						
<i>Apristurus</i> sp. A	catshark	*						
<i>Apristurus</i> sp. B	catshark	*						
<i>Argentina elongata</i>	silverside	421	23	1185	1162	48.77	34.57	53.78
<i>Azygopus pinnifasciatus</i>	"flatfish"	413	148	803	655	48.33	42.45	53.41
<i>Bassanago hirsutus</i>	hairy conger eel	622	292	1183	891	48.81	34.87	53.73
<i>Bathylagus</i> spp.	deep-sea smelts	1163	571	1433	862	43.4	36.48	47.99
<i>Bathylagus bercoides</i>	deep-sea smelts	*						
<i>Bathyraja shuntovi</i>	long-nosed deep-sea skate	1134	345	1479	1134	44.92	34.92	53.73
<i>Coelorinchus acanthiger</i>	surgeon rattail	*						
<i>C. aspercephalus</i>	smooth-headed rattail	461	45	976	931	50.21	35.46	53.78
<i>C. biclinozonalis</i>	two-saddle rattail	296	19	722	703	37.68	33.94	47.55
<i>C. bollonsi</i>	Bollons' rattail	599	53	1489	1436	43.01	33.91	53.59
<i>C. caelanostomus</i>	black lipped rattail	786	490	1328	838	35.59	33.91	42.8
<i>C. fasciatus</i>	banded rattail	684	133	1271	1138	49.29	34.22	54
<i>C. innotabilis</i>	notable rattail	985	295	1490	1195	40.83	32.31	53.73
<i>C. kaiyomaru</i>	Kaiyomaru rattail	1029	347	1310	963	47.42	39.48	54
<i>C. matamua</i>	Mahia rattail	852	358	1246	888	42.5	34.47	53.73
<i>C. oliverianus</i>	Oliver's rattail	640	243	1357	1114	48.34	34.66	54
<i>C. trachycarus</i>	rough-headed rattail	*						
<i>C. sp.</i>	(<i>aca.</i> and <i>tra.</i>)	1287	490	1586	1096	38.14	32.31	48.8
<i>Capromimus abbreviatus</i>	capro dory	323	62	1088	1026	39.52	33.94	47.63
<i>Centroslachus crepidater</i>	long-nosed velvet dogfish	960	349	1480	1131	43.31	32.31	54
<i>Centrocyminus owstoni</i>	Owston's dogfish	1006	477	1459	982	40.28	32.31	53.71
<i>Cephaloscyllium isabellum</i>	carpet shark	172	7	673	666	42.56	34.3	48.83
<i>Chauliodus sloani</i>	viper fish	1069	412	1470	1058	41.21	33.94	44.02
<i>Chaanus pictus</i>	pink frog mouth	958	683	1401	718	35.94	32.31	46.82
<i>Chimaera</i> sp. C		1226	578	1480	902	42.95	34.5	51.19
<i>Chimaera</i> sp. B		*						
<i>Coryphaenoides dosseus</i>	humpback rattail	1084	542	1495	953	44.05	34.47	53.78
<i>C. serrulatus</i>	serrulate rattail	1036	295	1480	1185	41.2	32.31	54
<i>C. subserrulatus</i>	four-rayed rattail	1069	295	1497	1202	43.41	34.47	54
<i>Deania calcea</i>	shovel-nosed dogfish	881	107	1471	1364	41.69	32.31	53.78
<i>Diastobranchius capensis</i>	basketwork eel	1204	468	1610	1142	43.38	32.41	54.02
<i>Epigonus lenimen & robustus</i>	robust cardinal fish	989	229	1497	1268	42.17	33.91	53.56
<i>Etmopterus baxteri</i>	Baxter's dogfish	1055	220	1700	1480	46.03	34.47	54
<i>Etmopterus lucifer</i>	Lucifer's dogfish	611	158	1354	1196	41.1	33.91	52.84
<i>Gadomus aetanus</i>	filamentous rattail	1158	810	1469	659	35.87	32.31	47.02
<i>Genypterus blacodes</i>	ling	481	16	1308	1292	47.61	33.91	53.75
<i>Halaelurus dawsoni</i>	Dawson's catshark	478	50	789	739	50.64	41.88	53.42
<i>Halargyreus johnsonii</i>	Johnson's cod	1174	295	1700	1405	41.42	32.31	53.78
<i>Helicolenus percoides</i>	sea perch	436	23	1271	1248	41.61	33.12	49.15
<i>Hoplichthys haswelli</i>	deep-sea flathead	460	86	1098	1012	40.75	33.91	50.79
<i>Hoplostethus atlanticus</i>	orange roughy	1112	409	1586	1177	42.11	32.31	54
<i>H. mediterraneus</i>	silver roughy	609	119	1324	1205	37.36	32.31	54
<i>Hydrolagus novaezealandiae</i>	pale ghost shark	374	32	1282	1250	45.75	34.22	54.02
<i>Kathetotoma giganteum</i>	giant stargazer	318	12	1082	1070	44.31	34.12	51.48
<i>Lepidion microcephalus</i>	small-headed cod	970	229	1444	1215	42.67	34.47	52.48
<i>Lepidorhynchus denticulatus</i>	javelin fish	629	55	1444	1389	47.68	33.91	53.82
<i>Lepidotrigla brachyoptera</i>	scaly gurnard	158	16	499	483	40.58	34.49	48.74
<i>Lucigadus nigromaculatus</i>	black spot rattail	714	414	1372	958	45.03	32.31	53.78
<i>Macrourus carinatus</i>	ridge-scaled rattail	1164	295	1513	1218	47.58	37.69	54
<i>Macruronus novaezealandiae</i>	hoki	651	15	1445	1430	47.22	33.91	54.02

Table 6. (Continued).

Species	Common name (where known)	Depth (m)			Range (m)	Latitude		
		Mean	Min	Max		Mean	°N	°S
<i>Neophrymichthys augustus</i>	na	601	58	1489	1431	40.75	34.5	53.61
<i>Nezumia namatahi</i>	squashed face rattail	1180	296	1490	1194	37.97	32.41	47.26
<i>Notocanthus sexispinis</i>	spine back eel	789	168	1480	1312	47.58	34.51	54.02
<i>Pentaceros decacanthus</i>	yellow boar fish	466	186	722	536	37.79	34.12	43.9
<i>Persiparsia kopua</i>	tube shoulder	1193	735	1403	668	41.81	37.54	48.6
<i>Photichthys argenteus</i>	lighthouse fish	1217	450	1612	1162	45.99	34.85	53.72
<i>Polyprion americanus</i>	bass	366	93	564	471	42.07	34.9	48.57
<i>Pseudophycis bachus</i>	red cod	250	4	1056	1052	43.72	34.22	53.27
<i>Psychrolutes microporos</i>	blob fish	1147	452	1469	1017	46.35	34.51	54
<i>Rosenblattia robusta</i>	na	1107	732	1278	546	40.62	37.3	47.32
<i>Trachyrincus aphyodes</i>	white rattail	*						
<i>T. longirostris</i>	unicorn rattail	*						
<i>T. ap. & lon.</i>		1055	345	1481	1136	42.64	34.95	54
<i>Trachyscorpia capensis</i>	na	916	474	1370	896	39.3	34.48	48.76
<i>Tripterophycis gilchristi</i>	pelagic cod	699	131	1077	946	38.72	34.68	45.42
<i>Xenodermichthys copei</i>	black slickhead	1037	611	1700	1089	37.94	32.31	48.92

Mid-slope species are highlighted in dark grey rectangles with white text. na: not available.*These species were combined by Anderson et al. (1998).

3.3. Biological data

Fish were frozen onboard at -20°C and transported to the Auckland University of Technology, where they were stored in freezers at approximately -18°C until being processed. Once defrosted, each fish was identified, weighed ($\pm 1\text{ g}$) and measured ($\pm 1\text{ mm}$). Standard length (SL, the distance between the tip of the head to the fork of the tail) was used for most fish species, with the exception of rattails, which can lose the ends of their tails. For rattails, head length (HL), and later pre-anal fin length (PAL) was used as a length measure. Initially head-length was used to measure rattails, but pre-anal fin length has been considered to be a more sensitive length measure (Drazen et al. 2001), and was used to measure all rattails from the Puysegur Bank and Wairarapa coast data sets. To measure dogfishes, the pre-caudal fin length (PCL) was used, snout-vent length (SV) was used to measure chimaeras, and total length (TL) was used to measure eels.

Each fish was dissected, and where possible assigned a gender. When the sex of the fish could not be determined (where fish were either immature or too damaged), these individuals were excluded from gender-based analyses, but were included in the overall sample for dietary analysis. Most of the fish from the Wairarapa were immature, and for most, reliably assigning a gender was not possible. Accordingly, no gender-based analyses were attempted on the Wairarapa fish. A coefficient of variation (CV) was applied to all mean lengths and weights. One-way ANOVAs were used to compare mean length and weights versus the sex of the fish. The null hypothesis was that there was no significant difference between the weight and/or length of female and male fish

of the same species. Where data were of a non-normal distribution, non-parametric Kruskal-Wallis ANOVAs were applied to compare median lengths and weights (Kruskal & Wallis 1952). The same null hypothesis was tested using the Kruskal-Wallis ANOVAs. The normality of the raw data was tested using Minitab 14.

Three letter species codes were applied using standard New Zealand Ministry of Fisheries species codes. Where this was not possible (for example, where previously groups of closely related species were treated as a collective group), the first letter of the genus and the first two letters of the species name were used in accordance with Francis et al. (2002). Where the same combination of letters occurred, the next letter in the species name was used to provide a distinct name. Where species were yet to be described, the first two letters of the Genus was used, and then sequential letters of the alphabet to differentiate further species. For example: two species of the genus *Apristurus* gave *Apristurus* sp. B, (APB), and *Apristurus* sp. D, (APD).

The two *Alepocephalus* species proved difficult to identify. Their identifications were based on lateral line scale counts. Often all the scales were missing, so lateral line scale-pocket counts were substituted (one lateral line scale pocket was assumed to have held one lateral line scale). For the purposes of this study, the species with 50–55 lateral line scales/scale pockets, was named big-scaled brown slickhead, *Alepocephalus australis* Barnard, 1923, (SBI, **Fig. 26**), and the second species, with 57–61 lateral line scales/scale pockets was assigned the name small-scaled brown slickhead, *Alepocephalus antipodius* (Parrot, 1948), (SSM, **Fig. 34**). Conspecifics of northeastern Chatham Rise fish from Puysegur Bank were given the suffix p: Baxter's dogfish (EBAp), Johnson's cod (HJOp), and four-rayed rattail (CSUp). Fish from the family Myctophidae, which could not be identified further, were given the code MYC. All other fish species codes are provided in **Table 5**.

3.4. Dietary analyses

Dietary analyses were conducted using direct methods, that is, stomach contents. In default of stomach contents, where stomachs were everted (due to the expansion of the swim-bladder as the fish was brought to the surface, or was crushed by the weight of the trawl) intestinal contents were investigated.

3.4.1. Percentage of empty stomachs/intestines

The percentage of empty stomachs or intestines (PES/PEI) was calculated for species with greater than ten stomachs and/or intestines containing food, as a percentage of the total number of stomachs or intestines examined (*sensu* Arrington et al. 2002).

3.4.2. Stomach contents

Stomachs were removed and dissected, and their contents (when present) were blotted on tissue paper to remove excess moisture, weighed (± 0.01 g), counted, and either preserved in 70% ethanol if <30 mm greatest dimension, or 4% buffered formalin solution if larger. Fish that were found to have been obviously net feeding (e.g., fish with material in their mouths too big to be swallowed) were excluded from any analysis.

Diets were interpreted using an index of relative importance (IRI) (*sensu* Pinkas et al. 1971, Hyslop 1980) as

$$\text{IRI} = \text{F}(\text{W} + \text{N}),$$

where F is the frequency of occurrence percentage, expressed as the total number of occurrences of a food item as a percentage of the total number of stomachs; W is the percentage weight, expressed as the total weight of a food-item as a percentage of the total weight of all food items; and N is the numerical percentage, expressed as the total number of a particular food item as a percentage of the total numbers of all food items found in stomachs. For those species with only intestinal contents, the numbers and percentage frequency of occurrence of food items were recorded, but not their weight. The term food item is used instead of prey as some fish were thought to be scavenging.

Table 7. Fourteen functional food-item groups (sensu Bulman et al. (2001, 2002)) used to aggregate food-item data for 19 fish species from north eastern Chatham Rise (NECH), Puysegur Bank (PUY), and off the Wairarapa coast (WAI).

Some taxa may have species occurring in more than one group	
Functional group	Taxa comprising functional groups
Benthic invertebrates	Echinodermata, Gastropoda, Bivalvia, Holothuroidea, Foraminifera
Benthic crustaceans	Isopoda, Gammaridea, Caprellidea, Ostracoda
Polychaetes	Polychaeta
Megabenthos	Polychelidae, Galatheidea, Reptantia
Benthopelagic crustaceans	Crangonidae, Pandalidae
Benthopelagic fish	Alepocephalidae, Chimaeridae, Carangidae, Macrouridae, Moridae, Squalidae, Synphobranchidae, Trachichthyidae
Pelagic fish	Bathylagidae, Chauliodontidae, Myctophidae, Paralepididae, Phosichthyidae
Pelagic invertebrates	Pteropoda, Thaliacea, Teuthoidea
Pelagic crustaceans	Penaeidae, Sergestidae, Oplophoridae, Nematocarinidae, Pasiphaeidae, Euphausiacea, Mysida, Calanoida, Hyperidea, Ostracoda, lobster phyllosoma.
Insects	Insecta
Algae	Algae
Unidentified fish	Unidentifiable fish remains
Unidentified crustaceans	Unidentifiable crustacean remains
Unidentified	Unidentifiable remains

The IRI calculations were applied to two interpretations of the data, firstly, food items identified down to the lowest practical taxon. Food item categories were chosen in accordance with literature regarding predatory deep-sea fish diets (e.g., Mitchell 1984; Clark 1985a, b; Clark et al. 1989; Carrassón et al. 1992; Carrassón & Matallanas 2002; Pusch et al. 2004; Anderson 2005a, b; Madurell & Cartes 2005b). The food category ‘unidentified crustacean remains’ refers to fragments of crustaceans that could not be identified further, it does not refer to whole animals. Second, food items were classified to functional groups (*sensu* Bulman et al. 2001, 2002) (**Table 7**). Functional food items groups give information based on where a food item has been taken from, rather than a taxon-based description, which can be misleading.

Unknown items were not pro-rated across categories, as they were of inconsequential contribution to the diets of most fish. Graphical representation of the IRI equation as an area chart follows Anderson (2005a, b), Madurell & Cartes (2006), and Jones (2008a, b; 2009). The area charts depict three aspects of fish diet: percentage frequency of occurrence (x-axis), percentage abundance (upper y-axis) and percentage weight of food items (lower y-axis), with the resulting rectangle graphically depicting the IRI equation. A diet dominated by many small items of low mass results in a vertically compressed rectangle for that food-item, whereas a diet dominated by a few items of high mass results in a horizontally compressed rectangle (**Fig. 4**). Food taxa comprising less than one percent IRI were rounded to one percent and were pooled.

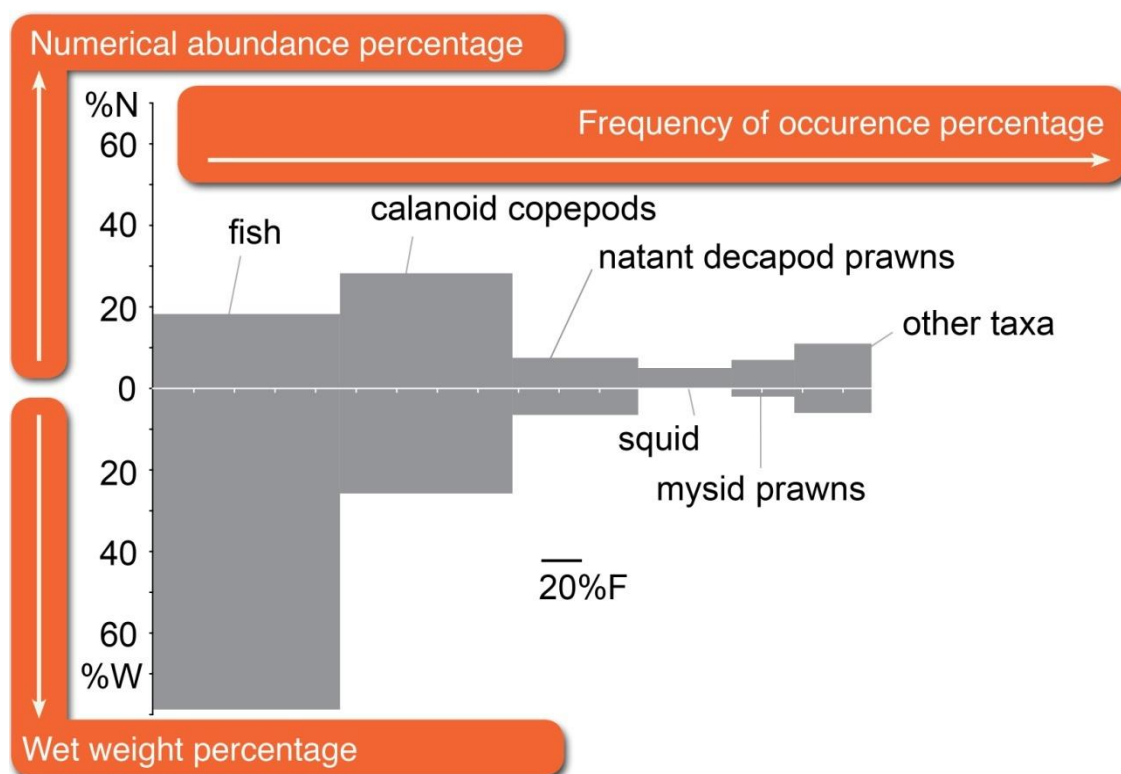


Figure 4. Sample index of relative importance (IRI) area chart. The vertically ascending arrow indicates the increasing value of the numerical abundance percentage of a particular food item. The vertically descending arrow indicates the wet weight percentage, and the horizontal arrow indicates the frequency of occurrence percentage.

3.4.3. Ontogenetic dietary analysis

The Spearman rank correlation (Spearman 1904) was applied to the whole sample to assess any relationship between the relative sizes of fish, and the number and weight of their food items. The null hypothesis was that there was no significant correlation (positive or negative) between either the weight or number of food items and the size of the fish. Species with >50 stomach samples containing food items were divided into arbitrary fish length size classes to investigate any ontogenetic change in diet (Jones 2008a, b, 2009).

3.4.4. Dietary overlaps and niche breadths

Dietary overlap was used to assess differences in diet between fish species, and between size-classes of individual species, C_{xy} was calculated using a similarity index (Schoener 1974):

$$C_{xy} = 1 - 0.5 \sum_{i=1}^n |p_{xi} - p_{yi}|$$

where C_{xy} is the similarity between diets of species x and y , p_{xi} is the proportion of food category i in the diet of species x , and p_{yi} is the proportion of food category i in the diet of species y . Using this formula, dietary overlap is given a value from 0 to 1, and while not a formal test of a hypothesis, it is considered to be biologically significant when this value exceeds 0.6 (Keast 1978, Wallace 1981). Dietary overlaps of <0.3 are considered to be low and those between 0.4 and 0.59, moderate. Input data to ontogenic and overlap calculations were based on percentage weight data (%W), *sensu* Madurell & Cartes (2005a, b). Percentage weight data were used, as weight has been considered to be a viable proxy for mass; since mass is related to energy it has been used to describe energy flow through an ecosystem (e.g., Bulman et al. 2001, 2002; Madurell & Cartes 2005a).

Niche breadths were calculated to assess the range of food items a particular fish was feeding on. A large niche breadth would indicate a large amount of different food items, whereas a narrow niche breadth would be indicative of a small range of food items. Niche breadth (B) was calculated using Levins' (1968) formula:

$$B = (\sum p_i^2)^{-1}$$

(where p_i is the proportion of each food category), and standardised (B_s) based on Hespeneide's (1975) method:

$$B_s = (B - 1) (N - 1)^{-1}$$

where N is the number of food-item categories consumed. Standardised niche breadth B_s , is expressed as a number between zero and one, with a number approaching zero

representing a narrow niche. Niche breadths below 0.3 are considered to be low, 0.3–0.59 moderate, and >0.6 high. The IRI, niche-overlap and niche-breadth calculations were applied to the total sample of species with >10 stomach contents, and the size classes within species with >50 stomach contents. The Spearman rank correlations (r_s) were applied to the total sample of species with >10 stomach contents. The Spearman rank correlation was also applied to assess the relationships between the number and weight of food items, and fish size. This analysis tested the null hypothesis that there was no significant correlation (positive or negative) between the numbers or weight of food items and the size of the fish. The software package Minitab (14.1) was used for ANOVA and Kruskal-Wallis tests, and SPSS (14.0) was used for the Spearman rank correlations.

3.4.5. Intestinal contents

Some fish species had everted stomachs, typically those fish possessing a gas-filled swim bladder, for example, Oreosomatidae, Macrouridae, and Moridae, or species that did not feed frequently, for example, Alepocephalidae. Intestinal contents were dissected from entire intestines, and identified in the same manner as stomach contents.

The composition of food items obtained from stomach contents was compared to that found in intestines using presence/absence data for those fish species with >10 stomach and intestinal samples with food. Where individual fish had both stomach and intestinal contents these were also compared. These data were entered into a matrix for each fish species, which consisted of stomach contents and intestinal contents identified to the lowest practical taxon. The data were transformed into presence/absence data to allow for the differences in levels of digestion between stomach contents and intestinal contents. The Plymouth Routines in Multivariate Ecological Research software package PRIMER-E (Clarke & Warwick 2001) was used to carry out analysis of similarity tests (ANOSIM) on these matrices. One-way analysis of similarities (ANOSIM) uses Bray-Curtis (1957) dissimilarities to test the sample statistic R , which is based on the difference between the average of all the rank dissimilarities between objects between groups (r_B) and the average of all the rank similarities between objects within groups (r_W):

$$R = \frac{\bar{r}_B - \bar{r}_W}{n(n-1)/4}$$

R is scaled to lie between the values -1 and +1. Values of $R = 0$ show that the null hypothesis (H_0) is supported (Quinn & Keough 2002).

Similarity percentages (SIMPER) were calculated to describe the percentage of which food category contributed most to the variance between stomach and intestinal contents for each species examined. SIMPER analysis is not a formal test of a hypothesis and in this case only provides the percentage contribution of various food items to the dissimilarities measured (Quinn & Keough 2002).

The following species were used in these analyses as they had sufficient numbers of stomachs and intestines to enable a comparison to be made: big-scaled brown slickhead (SBI), black slickhead (BSL), and warty oreo (WOE), from northeastern Chatham Rise, four-rayed rattail from northeastern Chatham Rise (CSU) and Puysegur Bank (CSUp), serrulate rattail from northeastern Chatham Rise, and Bollons' rattail (CBO) from off the Wairarapa coast (**Table 8**).

Table 8. Number of fish species with stomach or intestinal contents, and those fish with both, from northeastern Chatham Rise (NECH), Puysegur Bank (PUY), and off the Wairarapa coast (WAI). Fish codes as for Table 5.

Species code	SBI	BSL	CSU	CSUp	CSE	WOE	CBO
Number of fish with stomach contents	15	58	97	53	68	13	39
Number of fish with intestinal contents	86	25	112	54	85	11	53
Number of fish with both	6	16	10	17	62	1	34

3.4.6. Trophic level calculations

Trophic levels of fish species were calculated using the estimated trophic levels of prey species TL_g based on their proportion in the diets of the species studied P_g :

$$TL_g = 1 + \sum_{g=1}^N TL_g \cdot P_g$$

Primary producers, detritus and bacteria were defined as having a trophic level of one. All other consumers were given a trophic level based on the summed average of all the trophic levels of their prey items (*sensu* Mearns et al. 1981, Pauly et al. 2002, Bulman et al. 2002, Pinkerton 2011). The ecology of many small forms is largely unknown, so

assumptions were made regarding the trophic levels of many small prey items, and these are based on the work of Bulman et al. (2002), unless otherwise stated (**Table 9**).

Table 9. Estimated trophic levels of food items used in the calculation of trophic levels of fish from northeastern Chatham Rise, Puysegur Bank and off the Wairarapa coast.

Lowest practical taxonomic group	Estimated trophic level
Gammaridea	3
Hyperiidea	2.2 (Pinkerton 2011)
Caprellidea	2
Isopoda	3
Isopoda (parasitic)	4
Calanoida	3 (Bradford-Grieve 2004)
Natant decapoda	3 This study
Brachyura	3
Other reptantia (Palinuridae, Nephropidae, Polychelidae)	3
Ostracoda	2
Galatheidea	2
Paguridea	2
Mysidacea	3
Unidentified crustacean material	3
Insecta (Scarabidae)	2 (Steinbauer & Weir 2007)
Squid	4.8 (Pinkerton 2011)
Octopoda	4
Gastropoda	3
Pteropoda	2
Bivalvia	2
Polychaeta	3
Chaetognatha	4
Foraminifera	2
Echinoidea	2
Ophiuroidea	2
Crinoidea	2
Thaliacea	3.2 (Pinkerton 2011)
Mesopelagic fish	4.5 (Pinkerton 2011)
Unknown fish	4
Seaweed	1

3.4.7. Dietary comparisons between regions

To compare dietary similarity between fish from northeastern Chatham Rise and Puysegur Bank, a data matrix was created using the presence or absence of every food-item found in every fish, regardless of whether it was found in the stomach or the intestine. Presence/absence data were chosen to incorporate two species of cod and five species of rattail into the dataset; species with high levels of stomach eversion that would otherwise have been excluded from any analyses. The presence/absence data transformation was chosen to help alleviate biases, owing to the uncertainty regarding the feeding periodicity represented by intestinal contents. Fish species with <10 stomach or intestinal samples containing food were excluded from this analysis. This gave nineteen species from northeastern Chatham Rise, three from Puysegur Bank and eight from off the Wairarapa coast, three of which were common to northeastern Chatham Rise and Puysegur Bank (**Table 10**). No species (in sufficient numbers to enable meaningful analysis) were common to the Wairarapa coast and the other two sample areas.

A second dataset was based on stomach contents alone and comprised 21 species: 11 from northeastern Chatham Rise, two from Puysegur Bank and eight from the Wairarapa coast. This dataset was based on the wet-weight (g) of food items divided into 14 functional food-item groups *sensu* Bulman et al. (2001, 2002) (**Table 7**), with the addition of two further functional categories (insects and benthopelagic crustaceans). The category ‘benthopelagic crustaceans’ was chosen to differentiate pelagic (e.g., *Acanthephyra* spp.), and benthic prawns, for example, *Pontophilus acutirostratus* Yaldwyn, 1960 (Crangonidae) and *Notopandalus magnoculus* Bate, 1988 (Pandalidae). Justification for this split was drawn from Yaldwyn (1960), Houston & Haedrich (1986), and Fujita et al. (1995), who describe prawns from these families as predominantly benthic dwellers, but also found in the water column (Robertson et al. 1978). Food item weights ranged between 0.001 g (e.g., calanoid copepods) to 212.19 g (e.g., squid). Data were square root transformed to offset the bias caused by the large amount of zero values and the large range in weights (Clarke & Warwick 2001, Schaefer et al. 2002) and then averaged by species. A resemblance matrix was then calculated using the Bray-Curtis similarity measure (Bray & Curtis 1957). Agglomerated cluster analysis was then used to produce a dendrogram based on these values. From here clusters were identified at the 40 and 60 percent similarity level and displayed using nMDS plots.

Agglomerated cluster analysis (using Bray-Curtis similarity, (Bray & Curtis 1957)), and non-parametric multi-dimensional scaling (nMDS), were also used to graphically explore the variation in the diets between species and regions. These results were then used to build feeding guilds for the fish from northeastern Chatham Rise and the Wairarapa coast. To simplify the feeding guild analysis, Baxter's dogfish, Johnson's cod, and four-rayed rattail from Puysegur Bank were included in the cluster and nMDS analysis, but excluded from the final feeding guild analyses, as feeding guilds were described for the northeastern Chatham Rise and off the Wairarapa coast. Two-dimensional bubble plots were used to illustrate the major dietary components contributing to the distribution of the nMDS plot. Two-dimensional bubble plots display the square root transformed data of the average weight of each dietary classification for each fish species.

More specific dietary comparisons were made for conspecifics that occurred in both northeastern Chatham Rise and PUY. The null hypothesis tested was that there was no significant difference between the diets of conspecifics from the flat-bottomed soft sediments of northeastern Chatham Rise and the harder seamount terrain of Puysegur Bank. The species investigated here were ETB, ETBp, CSU, CSUp, and HJO, HJO_p. The diets of these species were obtained from either stomach or intestinal (or a combination) contents, often with quite small samples. As a consequence they were treated as separate species pairs. The null hypothesis was that there was no difference in diet between conspecifics from flat-bottomed soft sediment and harder seamount terrain.

Table 10. Twenty seven fish species with >10 stomach or intestinal samples containing food from northeastern Chatham Rise (NECH), Puysegur Bank (PUY), and off the Wairarapa coast (WAI).

Location	Species	Common name	Code
NECH	<i>Centroselachus crepidater</i>	Long-nosed velvet dogfish	CYP
	<i>Deania calcea</i>	Shovel-nosed dogfish	SND
	<i>Etmopterus baxteri</i>	Baxter's dogfish	ETB
	<i>Diastobranchius capensis</i>	Basketwork eel	BEE
	<i>Xenodermichthys copei</i>	Black slickhead	BSL
	<i>Alepocephalus australis</i>	Big-scaled brown slickhead	SBI
	<i>A. antipodians</i>	Small-scaled brown slickhead	SSM
	<i>Halargyreus johnsonii</i>	Johnson's cod	HJO
	<i>Lepidion microcephalus</i>	Small-headed cod	SMC
	<i>Coelorinchus acanthiger</i>	Surgeon rattail	CTH
	<i>C. innotabilis</i>	Notable rattail	CIN
	<i>C. trachycarus</i>	Rough-headed rattail	CHY
	<i>Coryphaenoides serrulatus</i>	Serrulate rattail	CSE
	<i>C. subserrulatus</i>	Four-rayed rattail	CSU
	<i>Macrourus carinatus</i>	Carinate rattail	MCA
	<i>Trachyrincus aphoydes</i>	White rattail	WHX
	<i>Alloctytus verrucosus</i>	Warty oreo	WOE
	<i>Hoplostethus atlanticus</i>	Orange roughy	ORH
	<i>Epigonus robustus</i>	Robust cardinal fish	EPR
	PUY	<i>E. baxteri</i>	Baxter's dogfish
<i>C. subserrulatus</i>		Four-rayed rattail	CSUp
<i>H. johnsonii</i>		Johnson's cod	HJOp
WAI	<i>Argentina elongata</i>	Silverside	SSI
	<i>Coelorinchus biclinozonalis</i>	Two-banded rattail	CBI
	<i>C. bollonsi</i>	Bollons' rattail	CBO
	<i>C. oliverianus</i>	Oliver's rattail	COL
	<i>Lepidorhynchus denticulatus</i>	Javelinfish	JAV
	<i>Hoplostethus mediterraneus</i>	Silver roughy	SRO
	<i>Capromimus abbreviatus</i>	Capro dory	CDO
	<i>Helicolenus percoides</i>	Sea perch	SPE

3.4.8. Dietary richness comparisons

Diet was assessed over three classifications: the raw data (RW), where every food item was described to the lowest possible taxon or enumerated unknown. Lowest practical taxon (LPT), where each food item was identified, and assigned to putative taxonomic groups, which were taken from recent literature (see earlier references). Functional food groups (FG), where each food item was allocated to a functional category (*sensu* Bulman et al. 2001, 2002). Classifications were also divided into stomach contents and intestinal contents for those species with an excess of ten of either. No attempt was made to split the samples into smaller groups within species.

Dietary data were analysed with EstimateS 8.2.0. (Colwell 2006), using the Chao 2 estimator to generate richness predictions with presence/absence data (Chao 1984, 1987, Watson 2010):

$$S_{\text{est}} = S_{\text{obs}} + a^2/2b;$$

where S_{est} is estimated food category richness; S_{obs} is the observed food category richness; a is the number of unique food categories and b is the number of duplicate food categories (Chao 1987). The minimum total (Min. total) number of fish required for the estimation of diet was chosen at the point where the standard deviation of the Chao 2 estimate continuously decreased (Watson 2010). The Chao 2 estimate compares the ratio between food categories occurring once, with food categories occurring twice. The number of food categories occurring once will decrease as sampling effort increases until no categories occur only once (Colwell 2006, Watson 2010).

Samples were randomised and the calculations performed 50 times to remove the influence of sample order and to provide estimates of variance. The Min. total derived from the Chao 2 estimate was applied to the S_{obs} curve for each dietary classification and these were used to calculate S_{max} , the number of fish required to describe 70, 80, and 90 percent of the dietary richness of each food classification for each species. The total number of singletons S_t , (food items occurring once only) per dietary classification was also calculated. Samples where the Chao 2 estimate food categories did not asymptote were considered not adequately described, and no assessments of S_{max} were attempted.

3.4.9. Parasitology

Parasites were opportunistically obtained from the stomachs of serrulate (CSE) and four-rayed rattail (CSU) from northeastern Chatham Rise. These were provisionally identified and enumerated. Comparisons were then made between counts of parasites within (ontogenically) and between these two species; the null hypotheses being that there was no difference between the numbers of parasites between size classes within each species, or between species. The number of parasites was also compared to the diet of each species. Where the data were not normally distributed, the median number of parasites per fish or size class was compared using Kruskal-Wallis ANOVAs as per previous analyses.

4.0. Results

4.0. Results

This chapter provides the results of all the dietary analyses, and is divided up into two main sections.

Section one provides the results of intraspecific biology and dietary analyses for fish species firstly from the mid-slope fish species from northeastern Chatham Rise, Puysegur Bank and then upper-slope fish from off the Wairarapa coast. Then the results for the comparisons between stomach and intestinal contents are provided. Finally, the results of the food accumulation curves are summarised.

Section two then provides the results of interspecific analyses between conspecifics from northeastern Chatham Rise and Puysegur Bank. The results of the analyses of the stomach parasites of serrulate and four-rayed rattail are given here. Dietary overlaps between fish species from Chatham Rise and Puysegur Bank, and overlaps between fish species from off the Wairarapa coast, followed by their feeding guilds, are presented.

4.1. Section one — Aspects of the biology and principal food items of fish from northeastern Chatham Rise (NECH), 901–1196 m

Overall 1,999 fish attributed to 43 species were examined from northeastern Chatham Rise, including 16 lantern fish (Myctophidae, MYC), which were taken from the stomachs of 14 shovel-nosed dogfish (SND). The lantern fish were represented by more than one species, but were too digested for further identification. In addition, one lantern fish (?*Lampanyctus* sp.) was taken from the stomach of a viperfish, which in turn was taken from the stomach of a long-nosed velvet dogfish (CYP). One notable rattail (*Coelorinchus innotabilis*, McCulloch, 1907) was also taken from the stomach of another long-nosed velvet dogfish. The intestines of the notable rattail contained gastropods.

For most species, females were significantly larger and heavier than males (**Table 11**). Exceptions were shovel-nosed dogfish, small-headed cod, ridge-scaled rattail, and white rattail, where there was no difference in size or weight between the sexes. For orange roughy (ORH), females were not larger but they were heavier than males. For black slickhead (BSL) only two males were recorded, and for long-nosed velvet dogfish (CYP) and Johnson's cod (HJO) only one male was recorded, so gender-based analysis was not attempted.

Table 11. Mean length (mm) and weight (g) of 19 fish species (male and female) from northeastern Chatham Rise, depths 901–1196 m, with >10 stomach or intestinal samples containing food. Length measurements: pre-caudal fin length, PCL; total length, TL; standard length, SL and head length, HL; co-efficient of variation (CV). Statistical tests for lengths and weights verses sex for each species: one-way ANOVA (F), and Kruskal-Wallis ANOVA (H). Significant differences are in bold.

Species Code	Gender	Number	Mean length (PCL) (TL ¹) (SL ²) (HL ³) (mm)	CV	Weight (g)	CV
<i>Centroselachus crepidater</i> CYP	Male	1	663		2518	
	Female	14	668.9	8.4	2490.5	22
	Unknown	0				
<i>Deania calcea</i> SND	Male	30	667.8	5.5	1708.6	15
	Female	34	641.7	19.9	1663.7	51.4
	Unknown	0				
			<i>H</i> = 1.08, <i>P</i> > 0.298		<i>H</i> = 1.49, <i>P</i> > 0.222	
<i>Etmopterus baxteri</i> ETB	Male	9	354	29.8	421.3	80
	Female	22	494.9	20.1	1227.4	56.9
	Unknown	0				
			<i>H</i> = 1.99, <i>P</i> < 0.001		<i>H</i> = 9.28, <i>P</i> < 0.002	
<i>Diastobranthus capensis</i> BEE	Male	91	698 ¹	16.4	389.9	60.6
	Female	138	784.7 ¹	17.1	557.1	58.8
	Unknown	37				
			<i>H</i> = 18.67, <i>P</i> < 0.000		<i>H</i> = 23.90, <i>P</i> < 0.000	
<i>Alepocephalus australis</i> SBI	Male	37	299.4 ²	9.6	196.7	30.6
	Female	151	338.6 ²	24.9	335.7	64.1
	Unknown	8				
			<i>H</i> = 10.46, <i>P</i> < 0.006		<i>H</i> = 11.75, <i>P</i> < 0.001	
<i>A. antipodanus</i> SSM	Male	50	407.8 ²	17.4	594.2	60.3
	Female	46	473.4 ²	16.7	875	50.4
	Unknown	5				
			<i>H</i> = 16.48, <i>P</i> < 0.000		<i>H</i> = 12.60, <i>P</i> < 0.000	
<i>Xenodermichthys copei</i> BSL	Male	2	315.2 ²	15.2	246.5	65.2
	Female	84	297.3 ²	7.3	150.1	30.2
	Unknown	0				
			<i>H</i> = 0.045, <i>P</i> > 0.500		<i>H</i> = 4.080, <i>P</i> < 0.043	
<i>Halargyreus johnsonii</i> HJO	Male	1	433.1 ²		636	
	Female	36	456.7 ²	22.6	939.1	36.8
	Unknown	4				

Table 11. (Continued).

Species Code	Gender	Number	Mean length (PCL) (TL ¹) (SL ²) (HL ³) (mm)	CV	Weight (g)	CV
<i>Lepidion microcephalus</i> SMC	Male	8	284.5 ²	13.6	755.2	42.8
	Female	12	318.3 ²	15.8	249.3	28.7
	Unknown	0				
			$H = 0.29, P > 0.589$	$H = 0.21, P > 0.643$		
<i>Coelorinchus acanthiger</i> CTH	Male	10	82.2 ³	15.6	89.7	101.4
	Female	10	99.9 ³	18.3	184.2	72.5
	Unknown	2				
			$F = 6.34, P < 0.022$	$H = 7.27, P < 0.007$		
<i>C. innotabilis</i> CIN	Male	17	59.7 ³	14	40	48
	Female	22	67.4 ³	11.6	59.1	27.3
	Unknown	35				
			$H = 8.61, p < 0.003$	$F = 11.39, p < 0.002$		
<i>C. trachycarus</i> CHY	Male	9	98.6 ³	7	221.8	16.7
	Female	7	105 ³	17.6	230	46.8
	Unknown	1				
			$F = 2.65, P > 0.124$	$F = 0.05, P > 0.827$		
<i>Coryphaenoides serrulatus</i> CSE	Male	65	58.4 ³	18.4	110.8	56.1
	Female	18	67.9 ³	12.4	160.5	32.8
	Unknown	19				
			$H = 10.56, P < 0.001$	$H = 11.53, P < 0.001$		
<i>C. subserrulatus</i> CSU	Male	157	249 ³	15.1	30.5	46.4
	Female	303	289.4 ³	15.5	51.1	41.1
	Unknown	9				
			$H = 73.48, P < 0.000$	$H = 95.0, p < 0.000$		
<i>Macrourus carinatus</i> MCA	Male	22	109.1 ³	21	618.7	95.1
	Female	17	107.1 ³	18.2	508.5	68.2
	Unknown	1				
			$F = 0.08, p > 0.776$	$H = 0.18, P > 0.671$		
<i>Trachyrincus aphoydes</i> WHX	Male	6	114 ³	5.6	260.9	9.7
	Female	11	132.8 ³	4.6	296.5	9.5
	Unknown	2				
			$H = 0.18, P > 0.671$	$H = 0.01, P > 0.920$		
<i>Allocyttus verrucosus</i> WOE	Male	9	227.1 ²	10.3	434.6	22.5
	Female	19	239.2 ²	12.4	531.1	32.3
	Unknown	2				
			$F = 0.96, P > 0.337$	$F = 2.01, P > 0.169$		
<i>Hoplostethus atlanticus</i> ORH	Male	52	284.5 ²	13.2	755.2	41.6
	Female	37	300.4 ²	15	892.5	39.3
	Unknown	7				
			$F = 3.27, P > 0.074$	$F = 4.40, P < 0.039$		
<i>Epigonus robustus</i> EPR	Male	63	149.7 ²	12.7	71.4	34.3
	Female	104	169.3 ²	11.6	47.1	41.6
	Unknown	21				
			$H = 32.08, P < 0.000$	$H = 37.25, P < 0.000$		

F: One way ANOVA, d. f. = 1, H: Kruskal-Wallis ANOVA, d. f. = 1, adjusted for ties

4.1.1. Long-nosed velvet dogfish (CYP), *Centroselachus crepidater* ($n = 15$)

Figure 5. Long-nosed velvet dogfish, (CYP), *Centroselachus crepidater*.

All but one of the long-nosed velvet dogfish examined were female (**Fig. 6**) and 12 contained identifiable food in their stomachs, giving a percentage of empty stomachs (PES) of 20 percent. All intestines were examined and were empty. Squid were the most important food items in the diet of this species (68% IRI) (**Fig. 7A**) and included *Histioteuthis* spp., *Chiroteuthis* sp., and *Cycloteuthis akimushkini* Filippova, 1968. Over the whole sample the trophic level was 4.68. The most important functional food-item groups were pelagic invertebrates and unidentified fish (**Fig. 7B**). Fish comprised the rest of the diet (32%), again usually highly digested, although it was possible to identify the remains of two fish, a notable rattail and a viperfish (*Chauliodus sloani*). There was no relationship between the number or weight of food items and increasing fish size (Spearman rank $r_s = 0.354$, $P > 0.129$ and $r_s = -0.168$, $P > 0.301$ respectively). Standardised niche breadth was moderate (0.48). The dietary variation within the stomach contents of long-nosed velvet dogfish was not adequately described by any of the dietary classifications (**Fig. 8**, **Fig. 9**), and there were singletons in all dietary classifications.

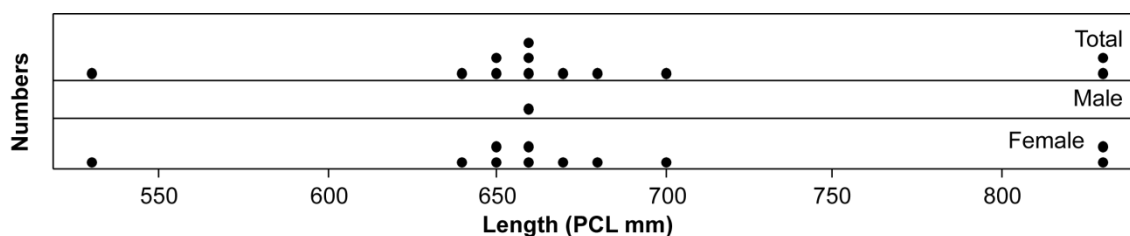
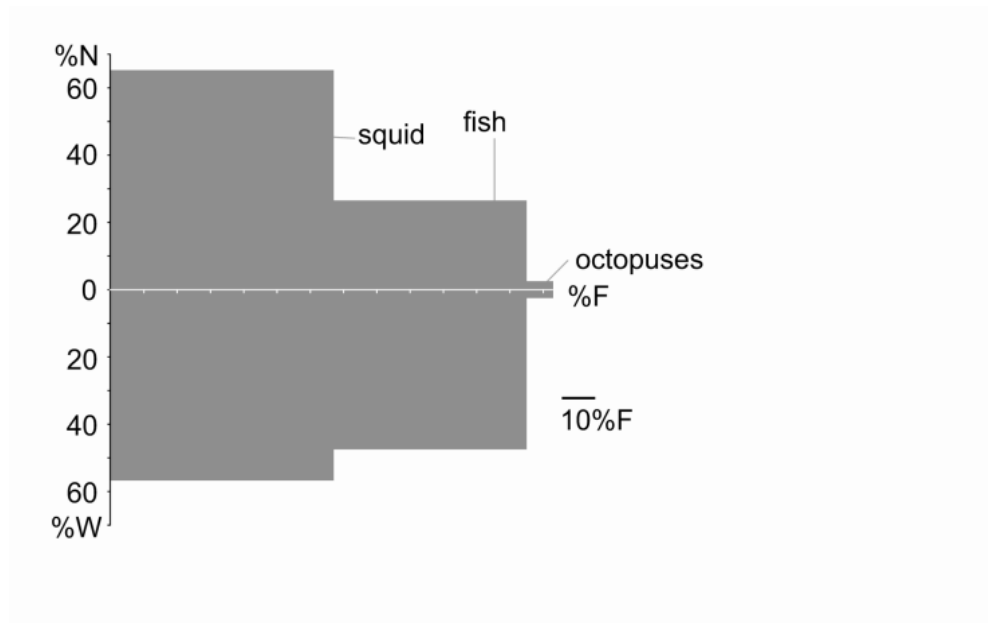


Figure 6. Size-frequency distribution for long-nosed velvet dogfish (stomachs containing food). (PCL mm).

A.



B.

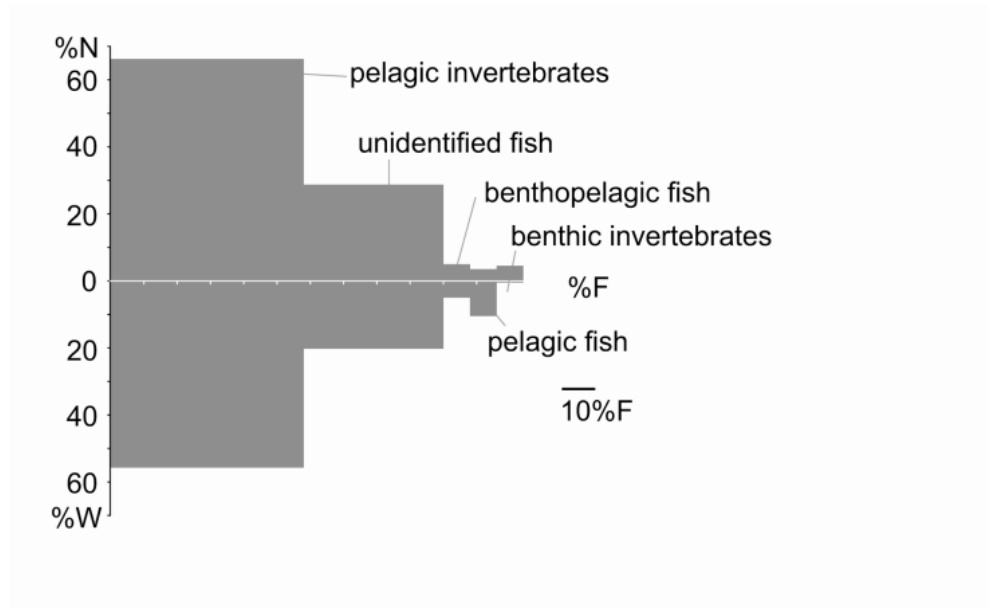


Figure 7. Diet of long-nosed velvet dogfish from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 12$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

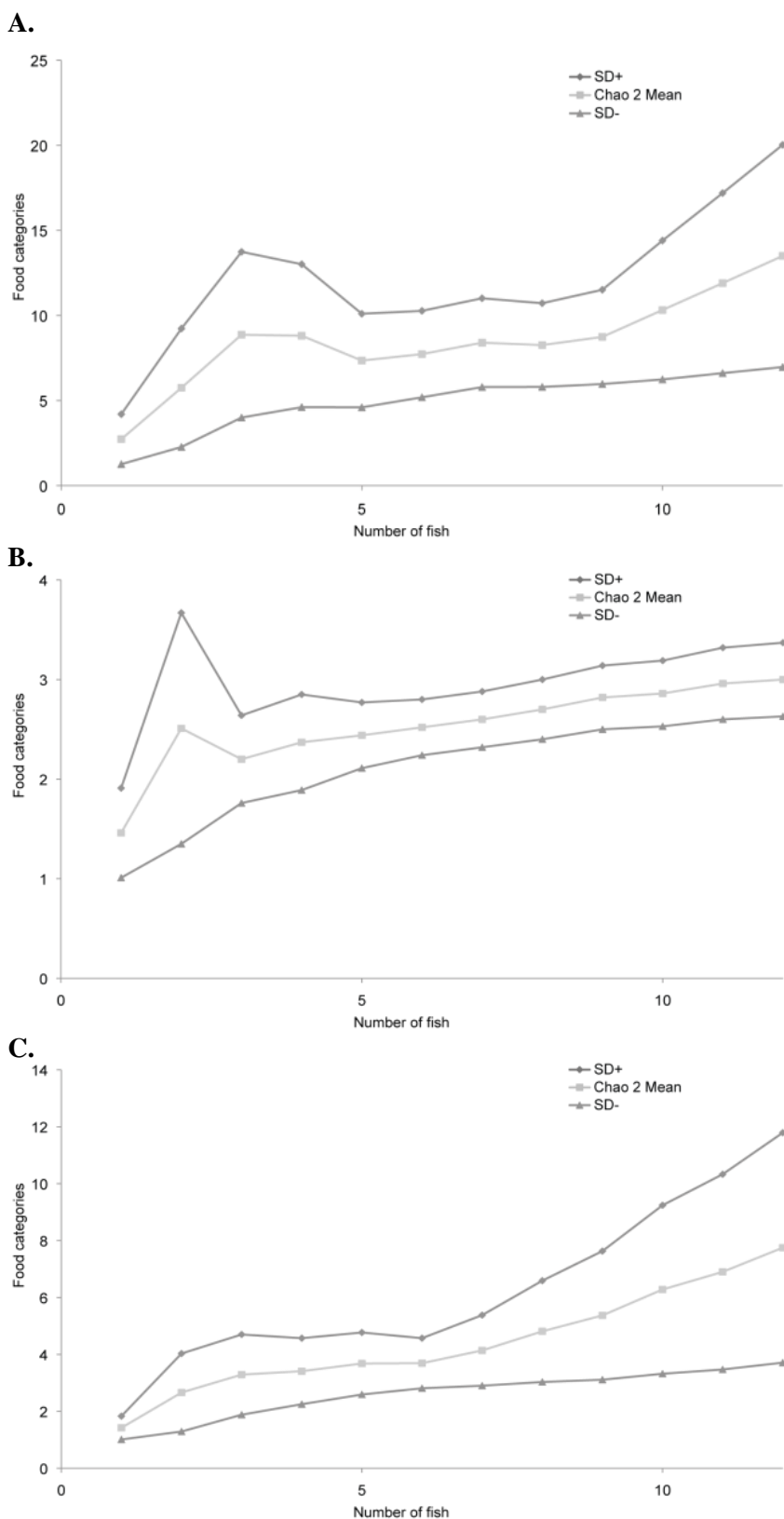


Figure 8. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of long-nosed velvet dogfish from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis). **A.** Raw data (7, 4). **B.** Lowest practical taxon (3, 1). **C.** Functional food groups (5, 3).

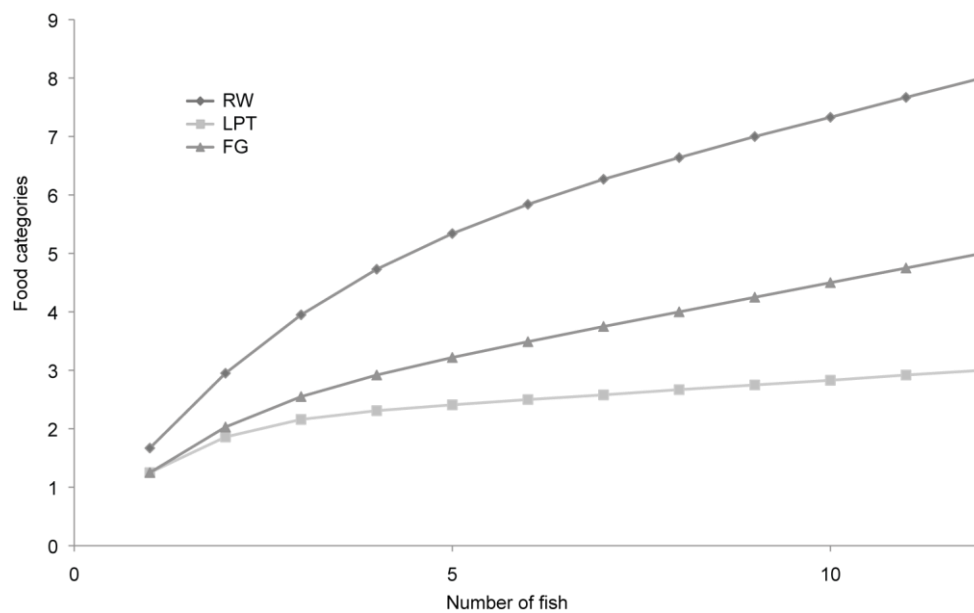


Figure 9. S_{obs} accumulation curves for the stomach contents of long-nosed velvet dogfish from northeastern Chatham Rise for three dietary classifications. Standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

3.1.2. Shovel-nosed dogfish (SND), *Deania calcea* ($n = 75$)

Figure 10. Shovel-nosed dogfish, (SND), *Deania calcea*.

Thirty one shovel-nosed dogfish stomachs contained food items (**Fig. 11**), which gave a PES of 57.7%. All intestines were examined but none contained any identifiable material. Fish were the most important food items (97% IRI) (**Fig. 12A**), and these were mostly pelagic lantern and light fishes from the families Myctophidae and Phosichthyidae, with slickheads (Alepocephalidae) and barracudinas (Paralepididae) present to a lesser extent. Over the whole sample, the trophic level was 4.92. ‘Pelagic fish’ was also the most important functional food-item category (**Fig. 12B**). Most of the fish and fish-remains recovered from stomach contents were too digested to be identified beyond familial level. There was no relationship between the number or weight of food items and increasing fish size (Spearman rank $r_s = -0.076$, $P > 0.343$ and $r_s = 0.052$, $P > 0.390$ respectively). Standardised niche breadth was very low (0.02).

The dietary variation within the stomach contents of shovel-nosed dogfish was adequately described by one dietary classification (RW) (**Fig. 13, Fig. 14, Table 11**). The minimum total number of fish needed to describe the dietary variation within the stomach contents of shovel-nosed dogfish was 28, and 24 were required for S_{\max} 90%. There were singletons in all of the dietary classifications (**Table 11**).

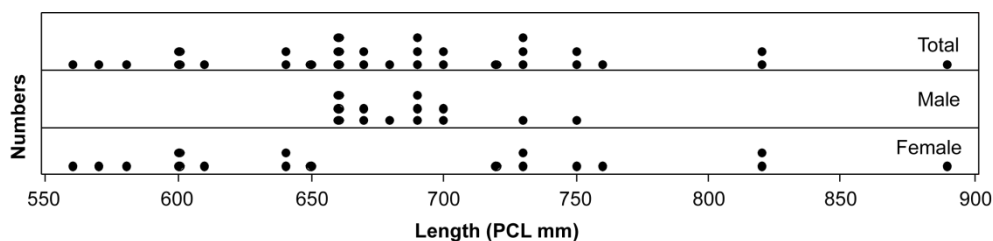
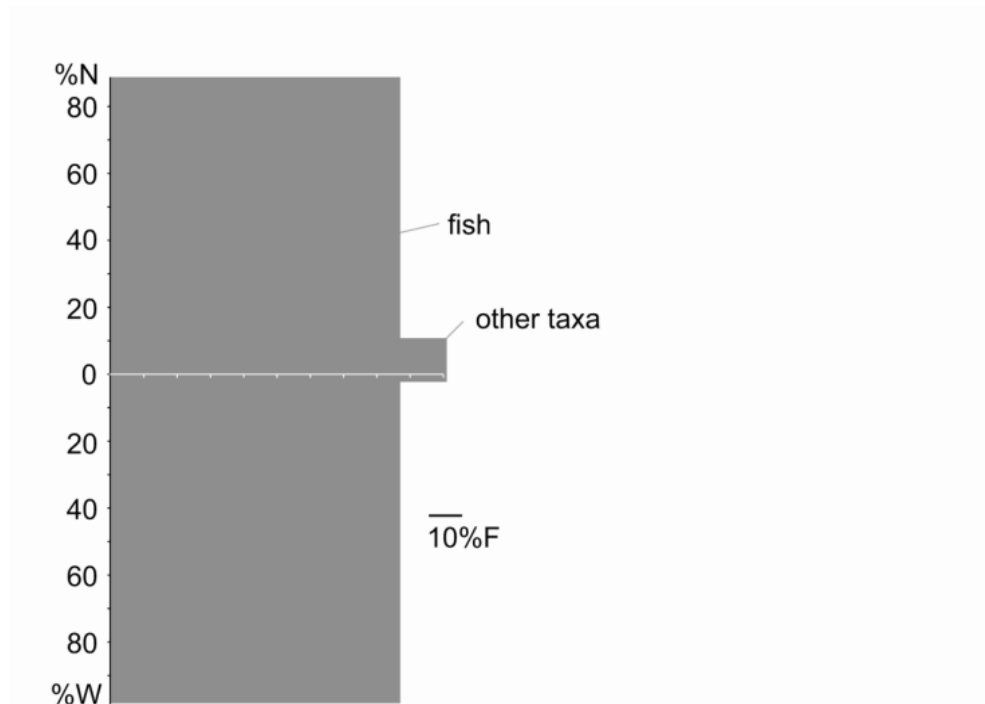


Figure 11. Size-frequency distribution for shovel-nosed dogfish (stomachs containing food). (PCL mm).

A.



B.

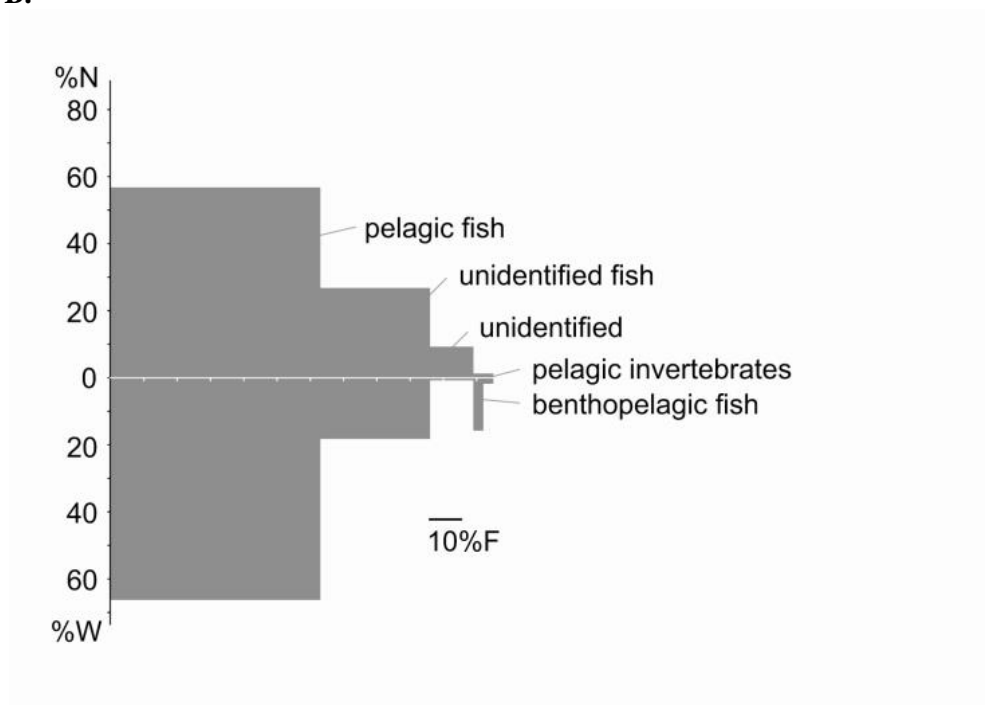


Figure 12. Diet of shovel-nosed dogfish from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 31$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

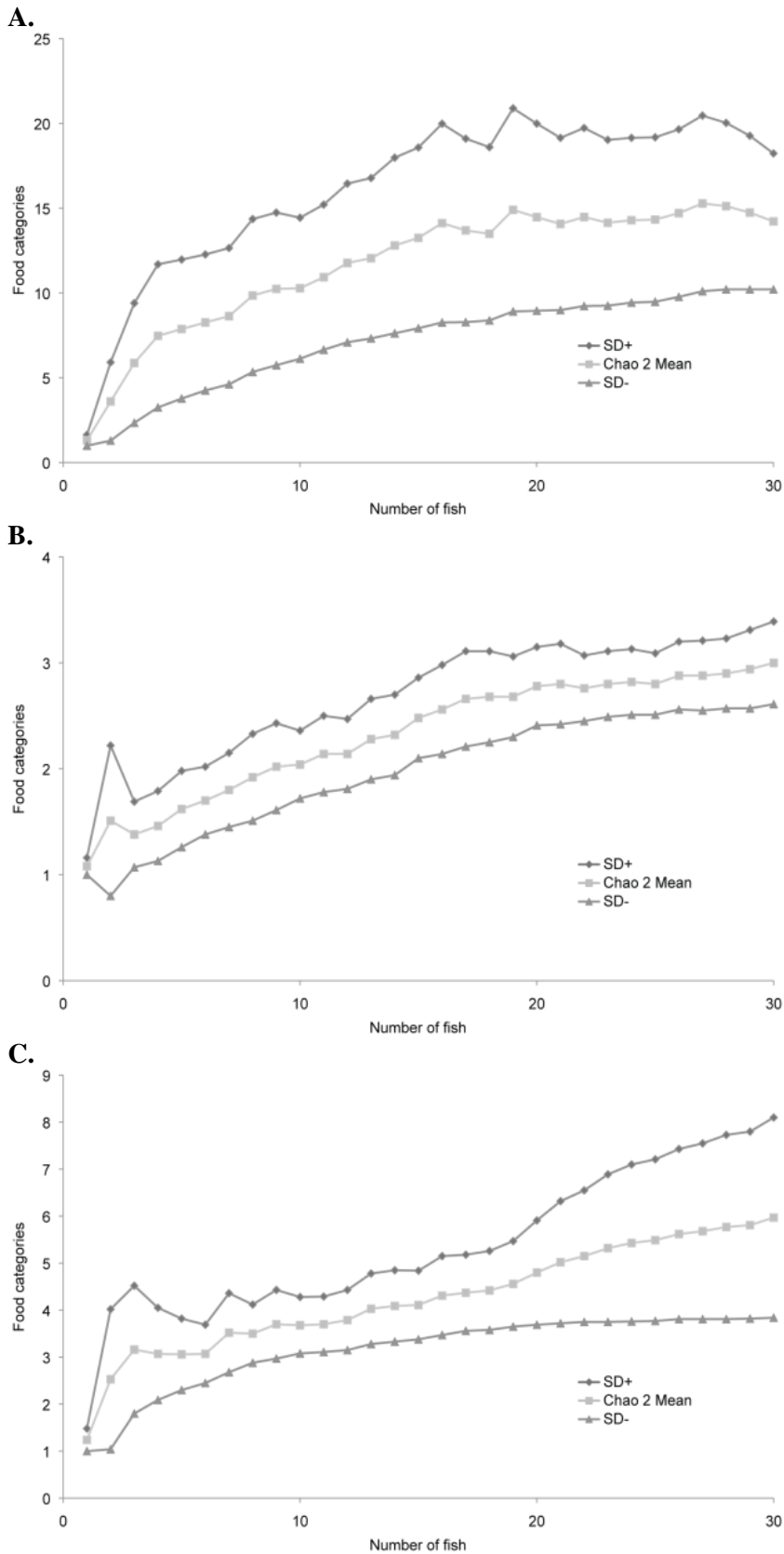


Figure 13. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of shovel-nosed dogfish from northeastern Chatham Rise. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis). **A.** Raw data (5, 11). **B.** Lowest practical taxon (3, 1). **C.** Functional food groups (5, 2).

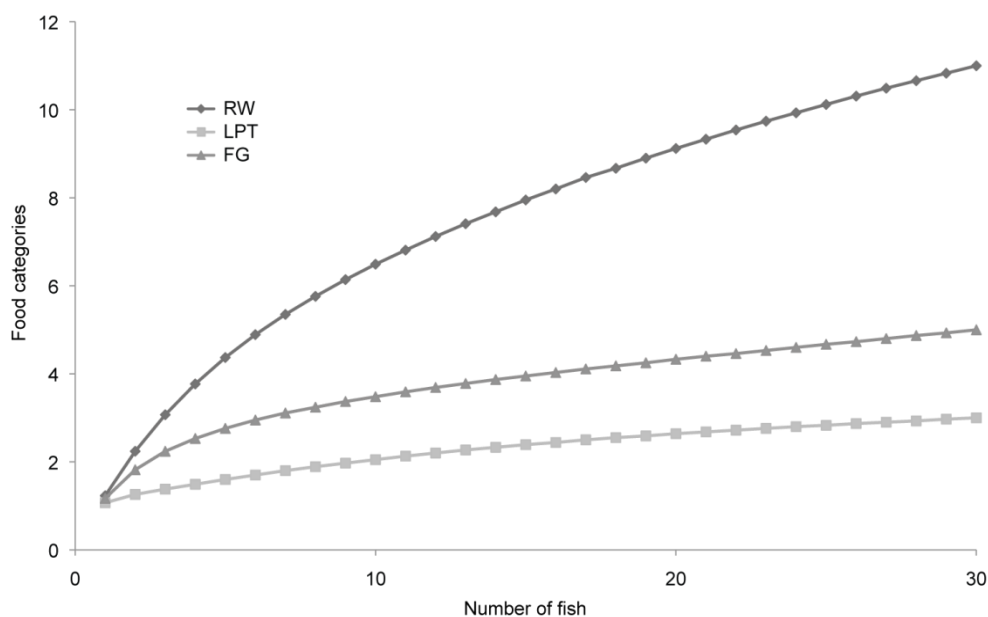


Figure 14. S_{obs} accumulation curves for the stomach contents of shovel-nosed dogfish from northeastern Chatham Rise for three dietary classifications. Standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 12. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of shovel-nosed dogfish from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease. n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups, NA: no asymptote reached, S_t : total number of singletons in each food category).

STOMACHS	RW	LPT	FG
S_{max} 70%	14		
S_{max} 80%	18		
S_{max} 90%	23		
Min. total	28	NA	NA
S_t	5	1	2
n	11	3	5

4.1.3. Baxter's dogfish (ETB), *Etmopterus baxteri* ($n = 31$)

Figure 15. Baxter's dogfish, (ETB), *Etmopterus baxteri*.

Ten Baxter's dogfish had identifiable material in their stomachs (**Fig. 16**); little material was found in the intestines (some fish remains), and the PES was 67.7%. The diet of Baxter's dogfish consisted mainly of squid (53.8% IRI) (**Fig. 17A**) (*Onykia* sp., *Abraliopsis* sp. and *Chiroteuthis* sp.), fish (38%) and natant decapod prawns (8.2%). The fish and prawns were too digested for further identification. Over the whole sample, the trophic level was 5.05. Pelagic invertebrates and unidentified fish were the two most important functional food-item groups (**Fig. 17B**). There was a significant negative relationship between the numbers of food items per stomach and the size of the dogfish (Spearman rank correlation $r_s = -0.503$, $P < 0.033$), but not for the weight of food and dogfish size ($r_s = 0.57$, $P > 0.423$). Standardised niche breadth was high (0.63). The dietary variation within the stomach contents of Baxter's dogfish was not adequately described by any dietary classification (**Fig. 18, Fig. 19**), and there were multiple singletons in one of the dietary classifications (RW).

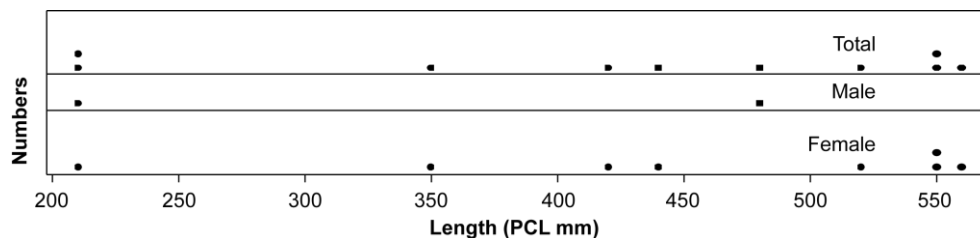
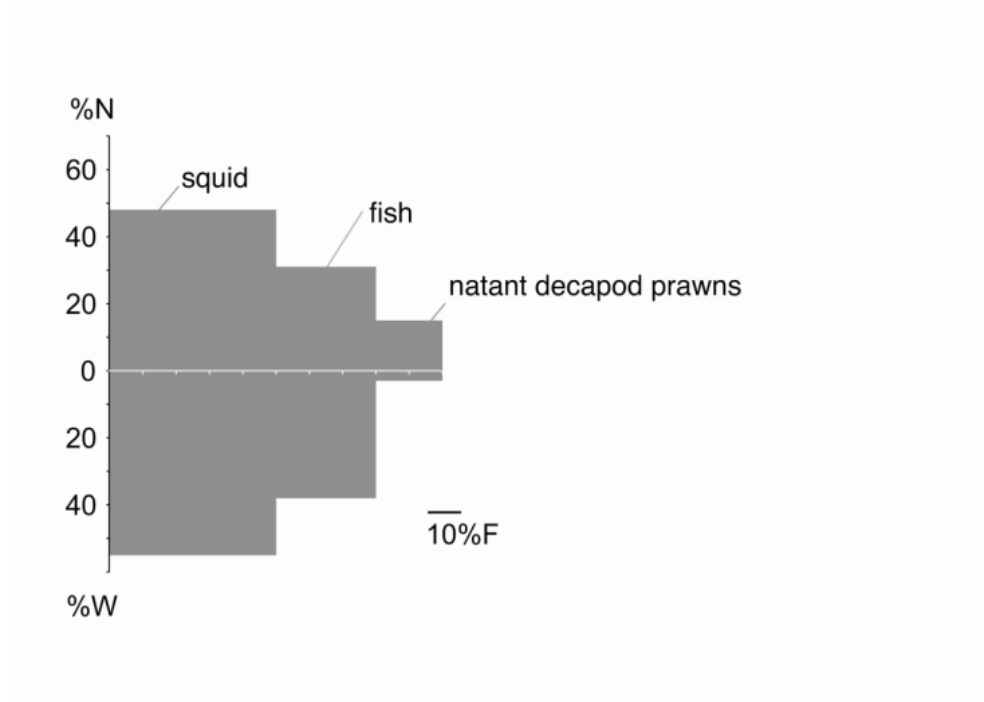


Figure 16. Size-frequency distribution for Baxter's dogfish (stomachs containing food) (PCL mm).

A.



B.

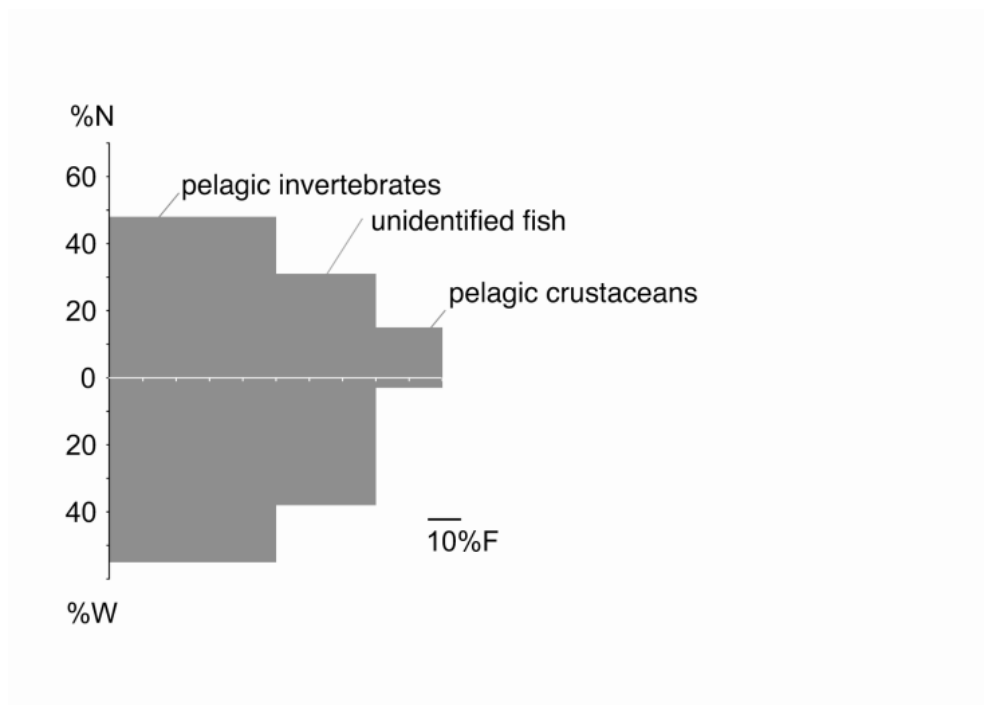
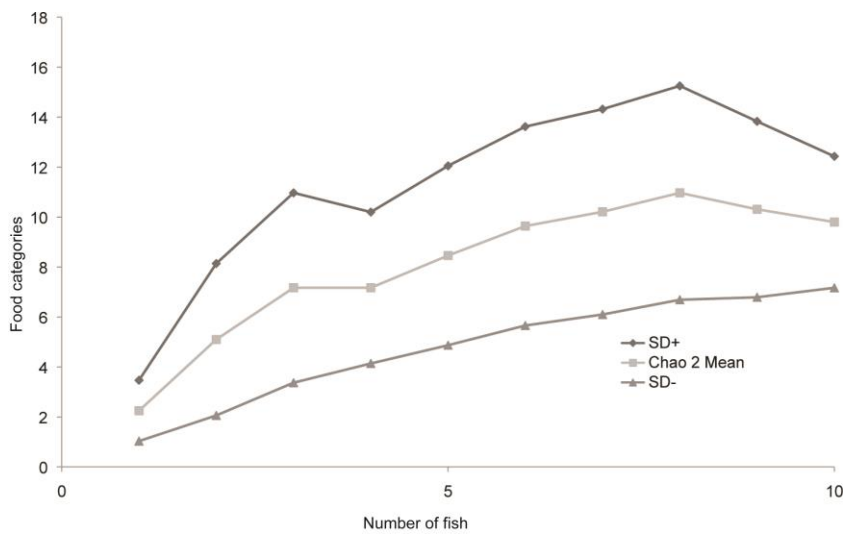


Figure 17. Diet of Baxter's dogfish from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 10$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

A.



B.

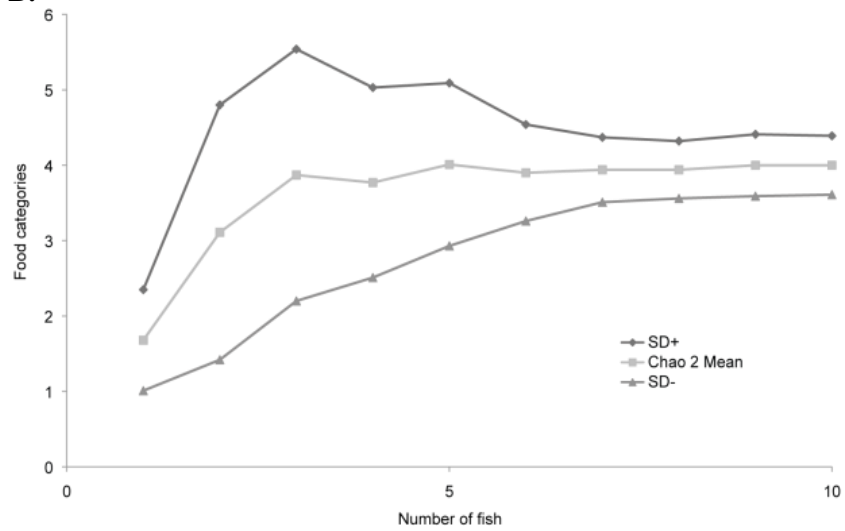


Figure 18. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents Baxter’s dogfish from northeastern Chatham Rise. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis). **A.** Raw data (8, 4). **B.** Lowest practical taxon, functional food groups (3, 1).

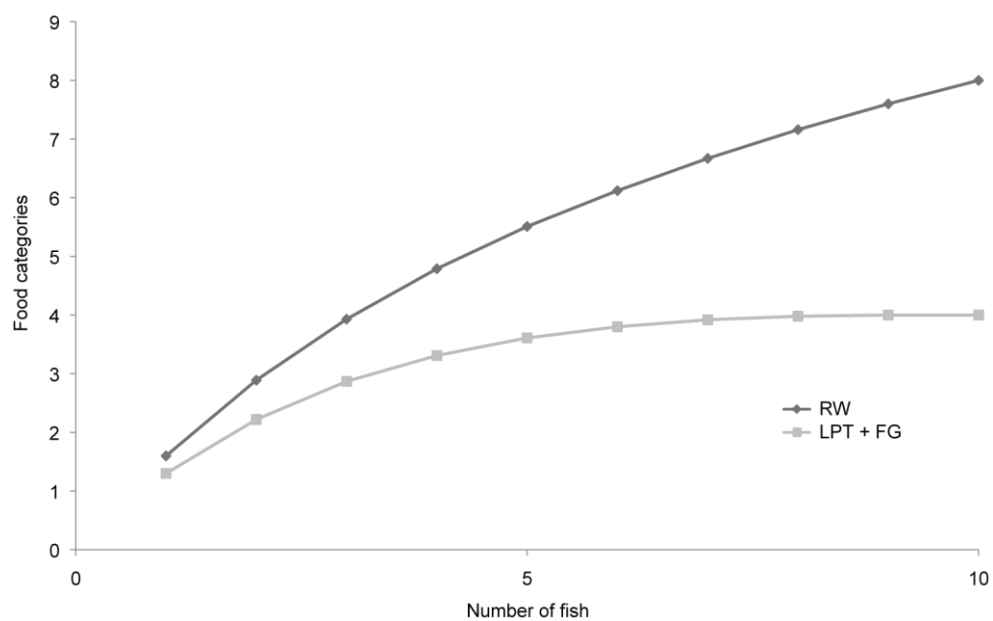


Figure 19. S_{obs} accumulation curves for the stomach contents of Baxter's dogfish from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, FC: lowest practical taxon, FG: functional food groups).

4.1.4. Basketwork eel (BEE), *Diastobranchus capensis* ($n = 266$)



Figure 20. Basketwork eel, (BEE), *Diastobranchus capensis*.

One hundred and thirty six basketwork eels were found to have material in their stomachs (**Fig. 21**), and this gave a PES of 49.2%. Overall, the remains of fish (most often sections and not whole individuals) dominated the diet of basketwork eel (76.6% IRI) (**Fig. 22A**). These included: lighthouse fish *Phosichthys argenteus* Hutton, 1872, Johnson's cod, cardinal fish (Epigonidae), lantern fish (Myctophidae) and rattails (Macrouridae). Squid also were important in the diet of basketwork eel (20.8%), and these included warty squid *Onykia ingens* (Smith, 1881), *Onychoteuthis* sp., and violet squid *Histioteuthis atlantica* (Hoyle, 1885). Natant decapod and mysid prawns (*Gnathophausia* sp.), and brown seaweed supplemented the diet. Over the whole sample, the trophic level was 4.34. Unidentified fish and pelagic invertebrates were the two most important functional food-item groups (**Fig. 22B**). The number of food items and their weight did not increase with fish size (Spearman rank $r_s = 0.74$, $P > 0.199$ and $r_s = 0.115$, $P > 0.094$ respectively). There was a slight ontogenic shift in diet, with squid becoming more important in the diets of the largest size class of basketwork eel (**Fig. 23**). There were high levels of dietary overlap between all size classes (**Table 13**). Over all sizes, standardised niche breadth was low (0.25).

The dietary variation within the stomach contents of basketwork eel was adequately described by all dietary classifications (**Fig. 24, Fig. 25, Table 14**). The minimum total number of stomachs required to describe the dietary variation within the stomachs ranged between 122 and 130 (LPT & RW respectively), with between 68 and 93 stomachs required for S_{\max} 90% (FG and RW respectively) (**Table 14**). There were singletons in all dietary classifications. Fewer stomachs were required to describe the variation within the diet of basketwork eel when the number of food categories within each classification decreased (**Table 14**).

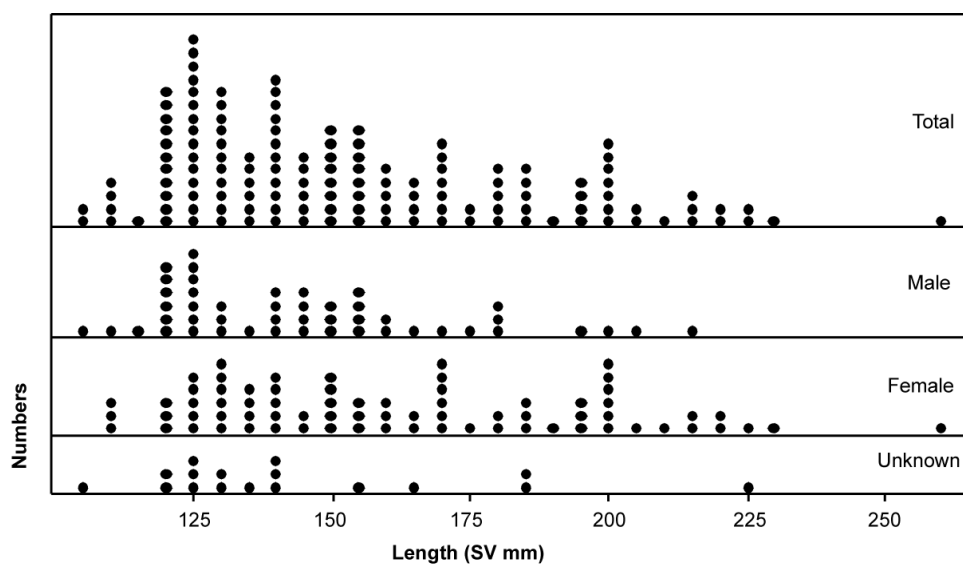
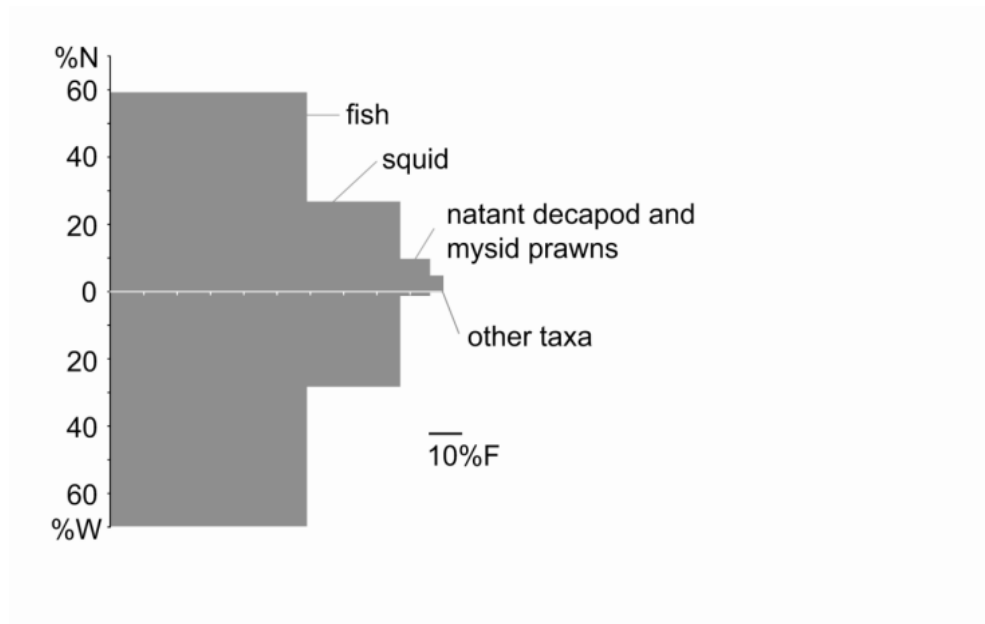


Figure 21. Size-frequency distribution for basketwork eel (stomachs containing food) ($n = 136$, SV mm). The Unknown category includes damaged and/or immature fish.

A.



B.

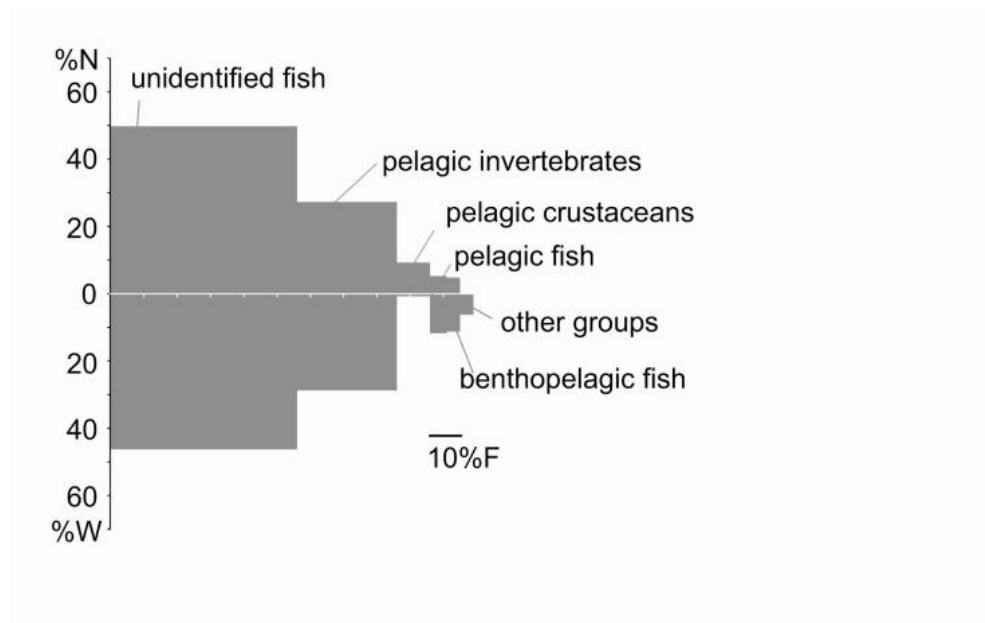


Figure 22. Diet of basketwork eel from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 136$). **A.** Lowest practical taxon: other taxa; unidentified crustaceans and seaweed. **B.** Functional food-item groups: other groups, unidentified crustaceans and algae. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

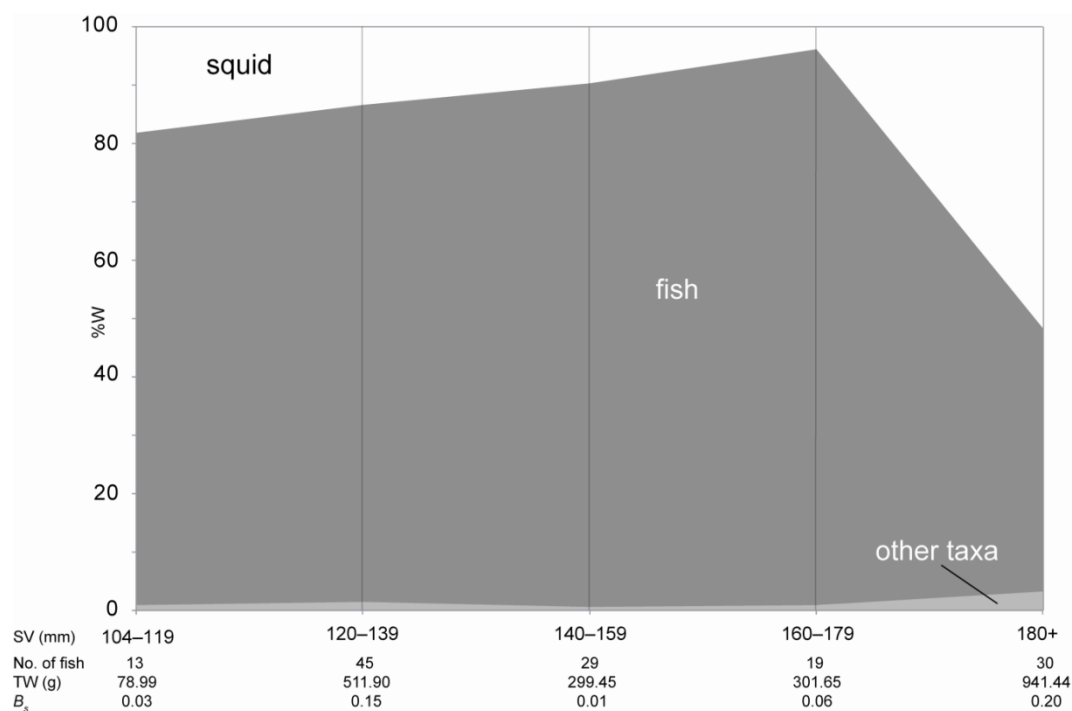


Figure 23. Diet of basketwork eel from northeastern Chatham Rise over five size classes ($n = 136$, SV mm) (%W); number of fish (No.) in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on lowest practical taxon. Other taxa: natant decapod and mysid prawns, unidentified crustaceans, and seaweed.

Table 13. Dietary overlap values for basketwork eel from northeastern Chatham Rise, over five size classes ($n = 136$, SV mm). Food categories are based on lowest practical taxon. Dark grey rectangles indicate biologically significant levels of dietary overlap (>0.6). Calculations are based on %W.

Length (SV mm)	104–119 ($n = 13$)	120–139 ($n = 45$)	140–159 ($n = 29$)	160–179 ($n = 19$)	180+ ($n = 30$)
104–119		0.7	0.8	0.9	0.6
120–139			0.8	0.8	0.9
140–159				0.8	0.7
160–179					0.7
180+					

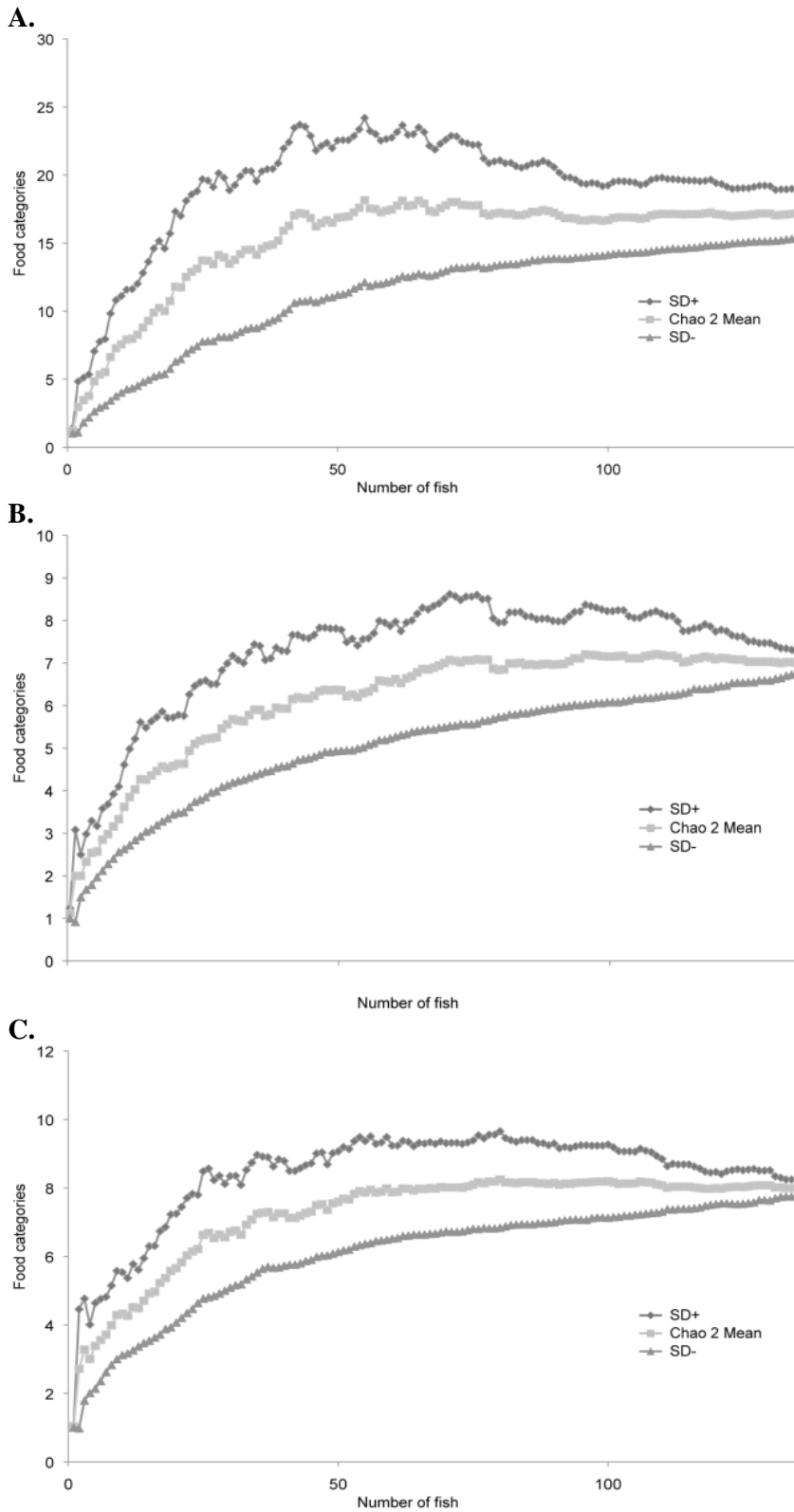


Figure 24. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of basketwork eel from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

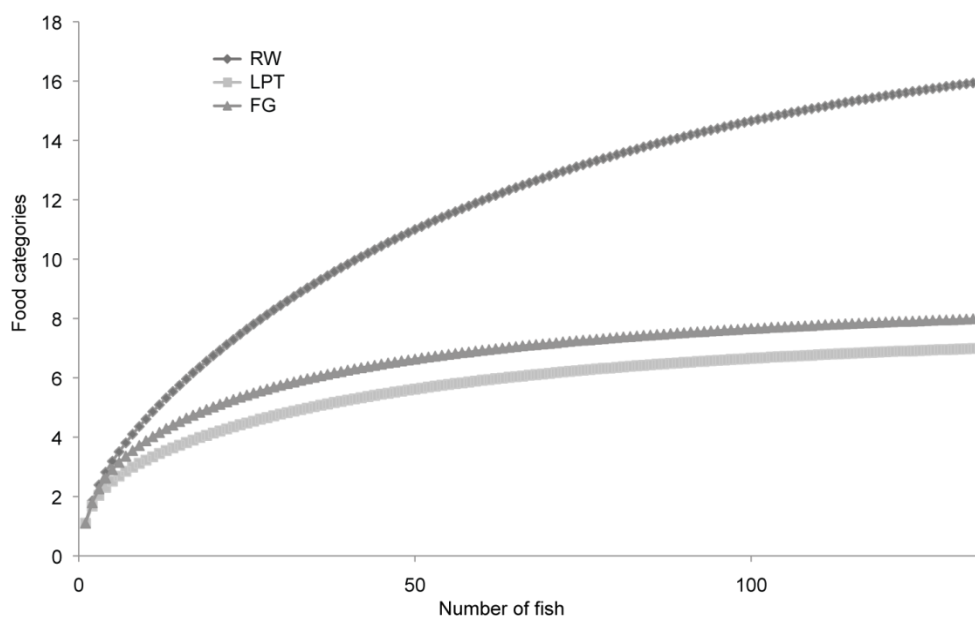


Figure 25. S_{obs} accumulation curves for the stomach contents of basketwork eel for three dietary classifications for basketwork eel from northeastern Chatham Rise, standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 14. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of basketwork eel from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	51	31	27
S_{max} 80%	69	47	42
S_{max} 90%	93	73	68
Min. total	130	122	125
S_t	4	1	1
n	16	7	8

4.1.5. Large-scaled brown slickhead (SBI), *Alepocephalus australis* ($n = 196$)



Figure 26. Big-scaled brown slickhead, (SBI), *Alepocephalus australis*.

Fifteen of the 196 big-scaled brown slickhead examined possessed stomachs containing food (**Fig. 27**), with a further 80 having identifiable material in their intestines. This gave a PES of 92.3 percent, and a PEI of 59.2 percent. Thaliaceans, particularly *Pyrosoma atlanticum* Péron, 1804, were the most important food item (62.2% IRI), with natant decapod prawns (12.1%) and squid (10.2%) less important (**Fig. 28A**). Gammaridean and hyperiidean amphipods, and fish remains, made up about four percent of the diet with the remainder consisting of the mysid *Gnathophausia* sp., gastropods (*Anatoma* sp.), and pelagic ostracods (?*Alacia valdiviae* Müller, 1906). Over the whole sample, the trophic level was 3.20. Pelagic invertebrates and pelagic crustaceans were the two most important functional food-item groups (**Fig. 28B**). There was a significant positive relationship between the weight of food items and the size of the fish, but not for the number of food items (Spearman rank correlation $r_s = 0.532$, $P < 0.021$, and $r_s = -0.152$, $P > 0.294$ respectively). Over the total sample, standardised niche breadth was very low (0.07). Calanoid copepods, thaliaceans, and the remains of fish were the most abundant food items recovered from the intestines (**Fig. 29A, B**). Calanoid copepod remains were recovered from the intestines, but not from stomachs, while squid remains were recovered from the stomachs, but not the intestines.

The dietary variation within the stomach contents of big-scaled brown slickhead was adequately described by two of the dietary classifications (LPT & FG) (**Fig. 30, Fig. 31, Table 15**). The minimum total number of stomachs required to describe the dietary variation ranged between nine and thirteen (LPT & FG respectively), with

between eight and eleven stomachs required for S_{\max} 90% (LPT & FG respectively) (**Table 15**). There were multiple singletons in all dietary classifications.

The dietary variation within the intestinal contents of small-scaled brown slickhead was adequately described by two of the dietary classifications (RW, LPT) (**Fig. 32, Fig. 33, Table 15**). The minimum total number of intestines required to describe the dietary variation within the intestines ranged between 60 and 66 (RW and LPT). The number of intestines for S_{\max} 90% ranged between 40 and 43 (RW & LPT). Singletons were present in the RW, LPT, and FG classifications (**Table 15**).

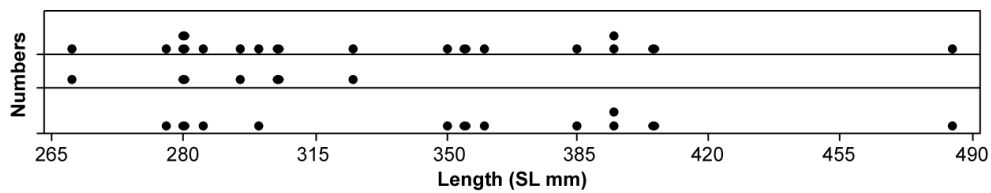
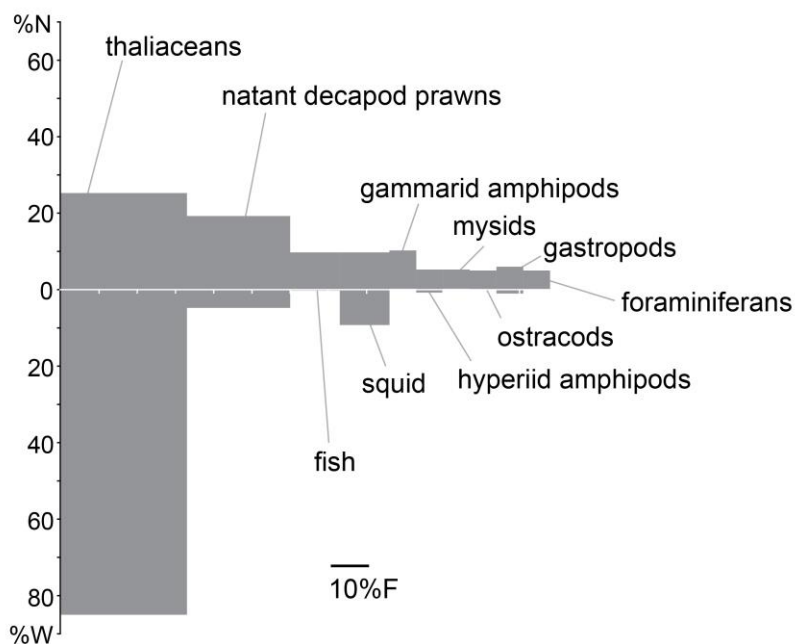


Figure 27. Size-frequency distribution for big-scaled brown slickhead (stomachs containing food) (SL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

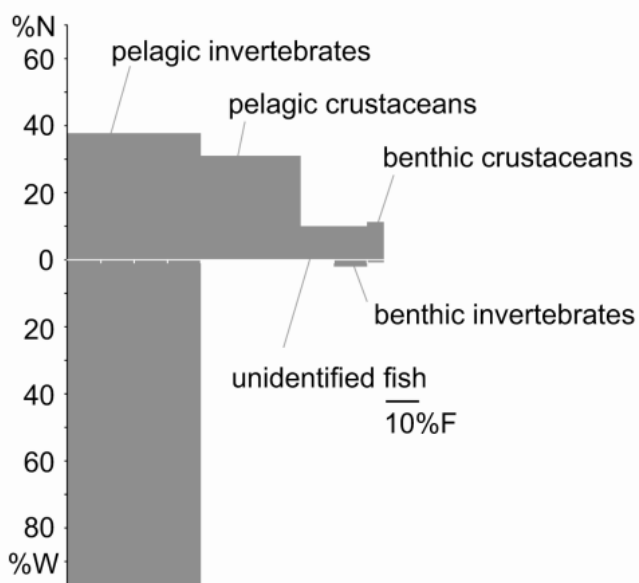
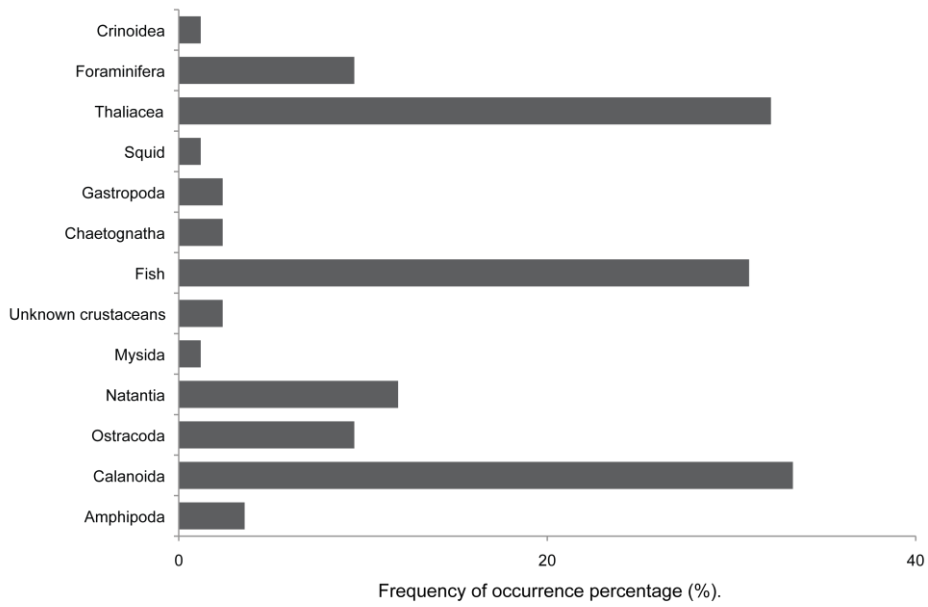


Figure 28. Diet of big-scaled brown slickhead from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 15$). **A.** Lowest practical taxon: other taxa: ostracods, calanoid copepods, and gastropods. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

A.



B.

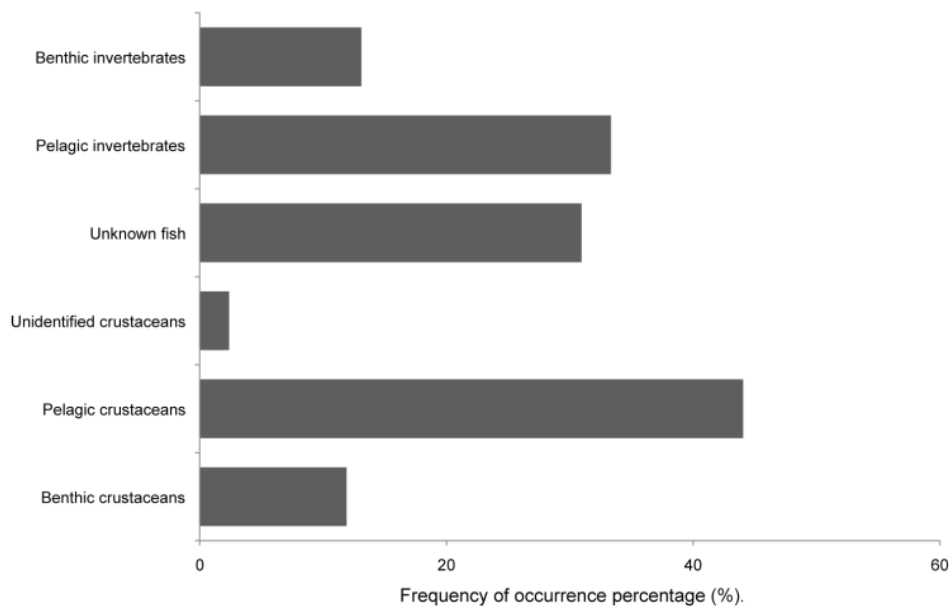


Figure 29. Intestinal contents of big-scaled brown slickhead from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 80$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

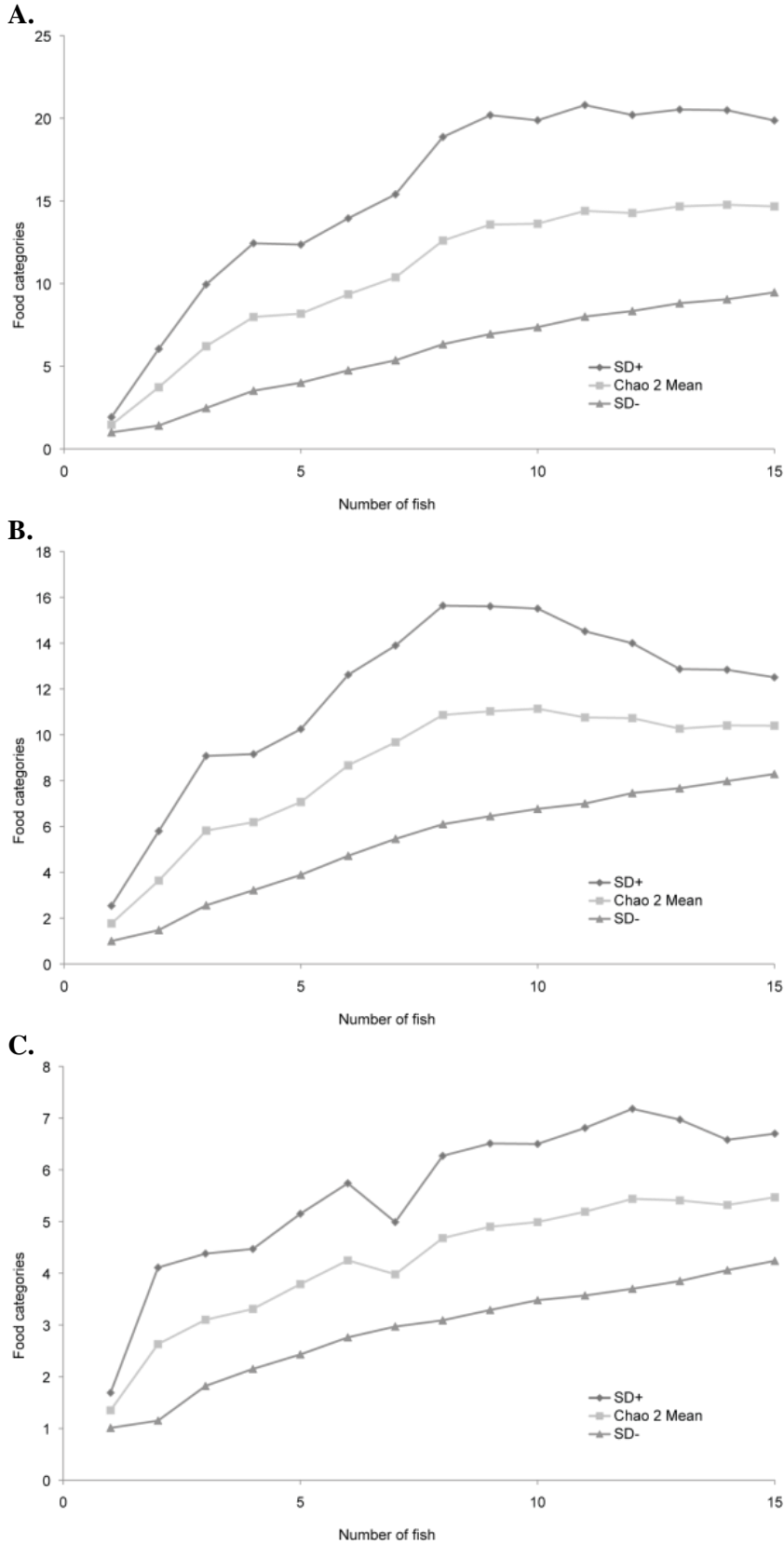


Figure 30. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of big-scaled brown slickhead from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

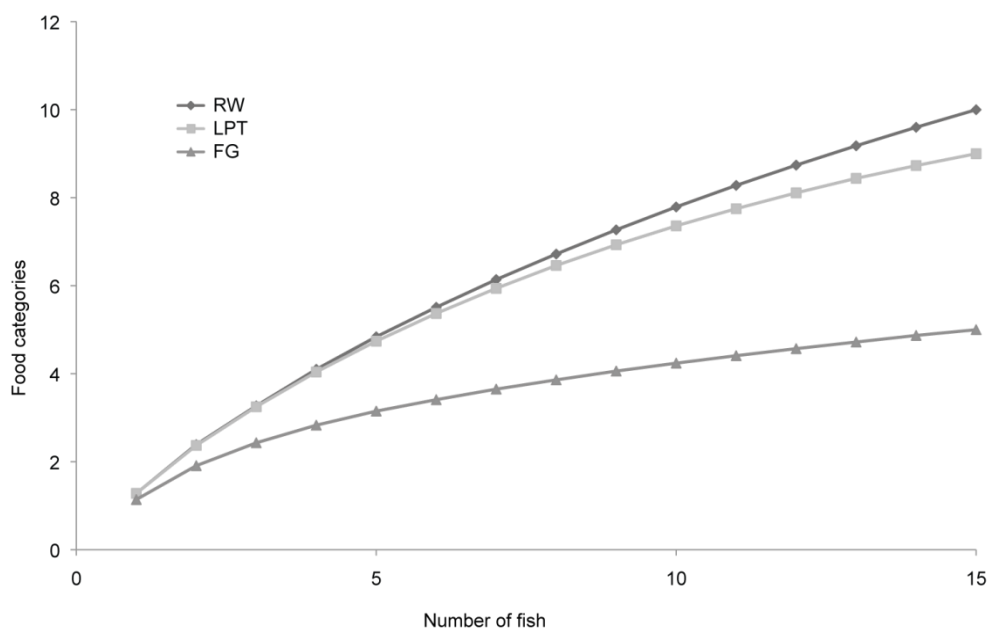


Figure 31. S_{obs} accumulation curves for the stomach contents of big-scaled brown slickhead from northeastern Chatham Rise over three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 15. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of big-scaled brown slickhead from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease; n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%		6	6
S_{max} 80%		7	8
S_{max} 90%		8	11
Min. total	NA	9	13
S_t	6	4	2
n	10	9	5

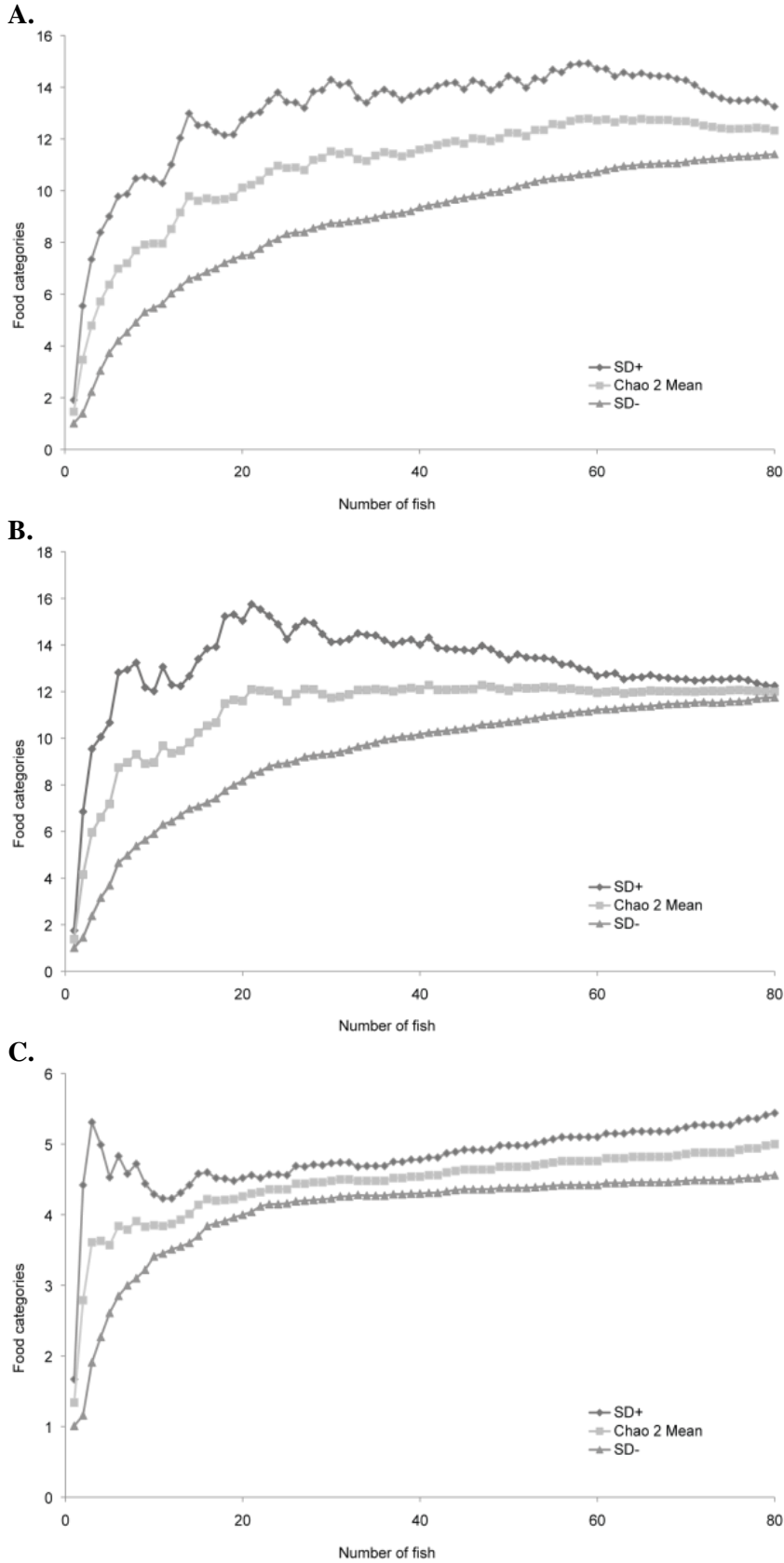


Figure 32. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of big-scaled brown slickhead from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

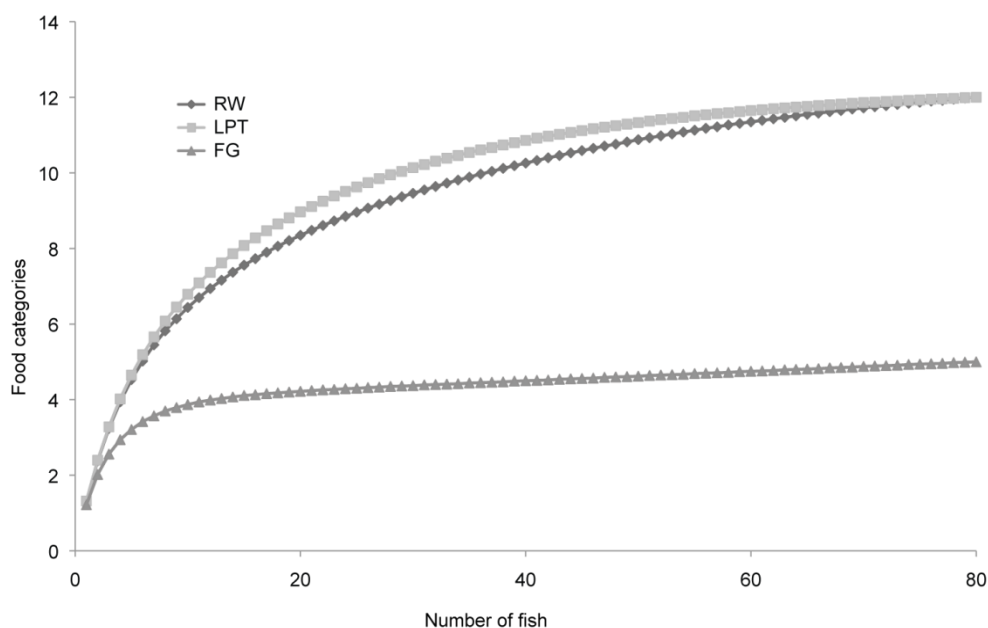


Figure 33. S_{obs} accumulation curves for the intestinal contents of big-scaled brown slickhead from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, FC: lowest practical taxon, FG: functional food groups).

Table 16. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of big-scaled brown slickhead from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease. n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups). NA: no asymptote reached. S_t : total number of singletons in each food category.

INTESTINES	RW	LPT	FG
S_{max} 70%	19	17	
S_{max} 80%	28	29	
S_{max} 90%	43	40	
Min. total	66	60	NA
S_t	2	1	1
n	13	12	5

4.1.6. Small-scaled brown slickhead (SSM), *Alepocephalus antipodius* ($n = 101$)

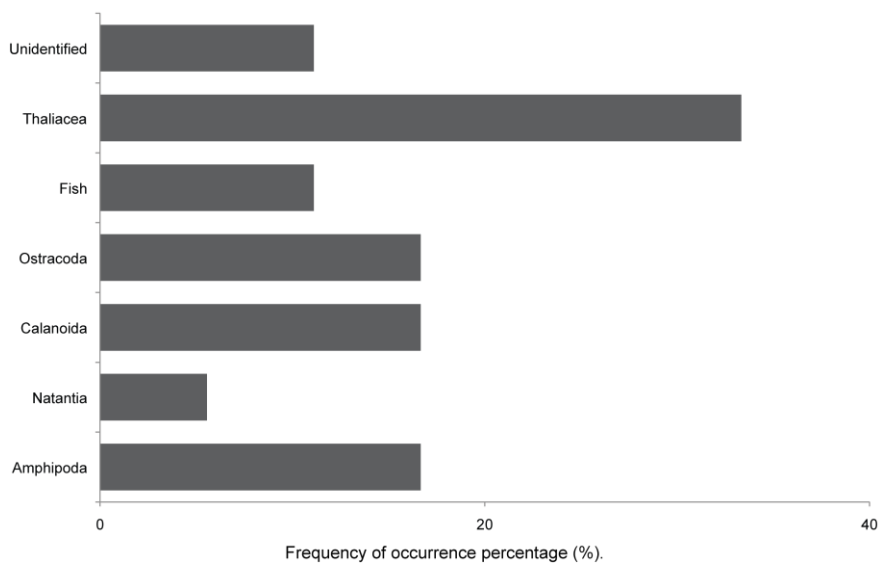


Figure 34. Small-scaled brown slickhead, (SSM), *Alepocephalus antipodius*.

Nine of the 101 small-scaled brown slickhead examined proved to have identifiable stomach contents (**Fig. 35**), and another 18 had material in their intestines. This gave a PES value of 91.1 percent, and a PEI of 82.1 percent. A piece of unidentifiable gelatinous material (possibly Scyphozoa) was the heaviest material found in one of the stomachs, followed by fish remains. The remains of natant decapods, gammaridean and hyperiidean amphipods, squid, and pteropods (*Cavolinia telemus* Linnaeus, 1758), were also recovered. Thaliaceans (*P. atlanticum*) and fish remains were the most frequently occurring material recovered from the stomachs, and their remains also occurred in the intestines. Over the whole sample, the trophic level was 3.77. Ostracods and calanoid copepods were recovered from the intestines but not from the stomachs.

The dietary variation within the intestinal contents of small-scaled brown slickhead was adequately described by two of the dietary classifications (RW & FG) (**Fig. 36, Fig. 37, Table 16**). The minimum total numbers of intestines needed to describe the dietary variation within these were 16 and 17 (RW & FG respectively). There were multiple singletons in each of the dietary classifications (**Table 16**).

A.



B.

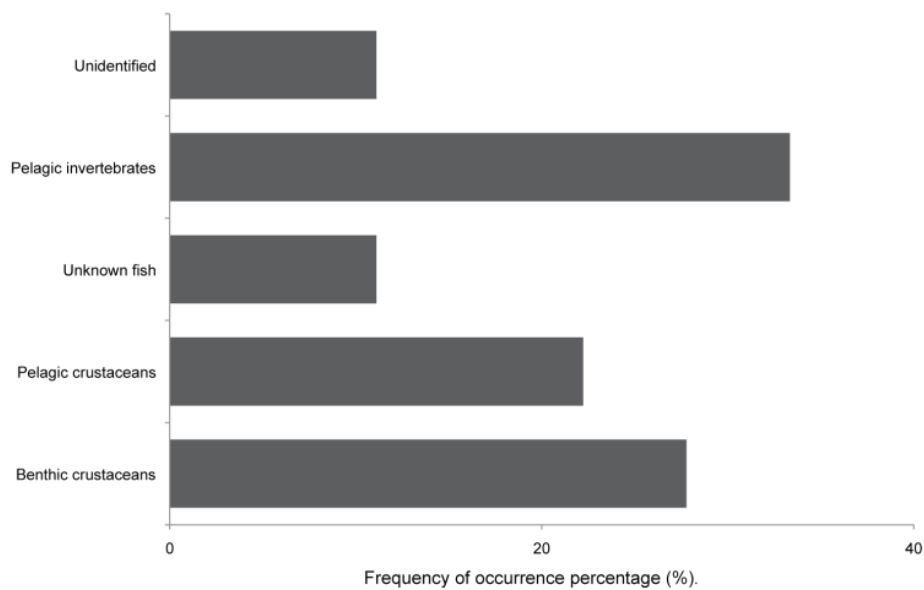


Figure 35. Intestinal contents of small-scaled brown slickhead from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 18$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

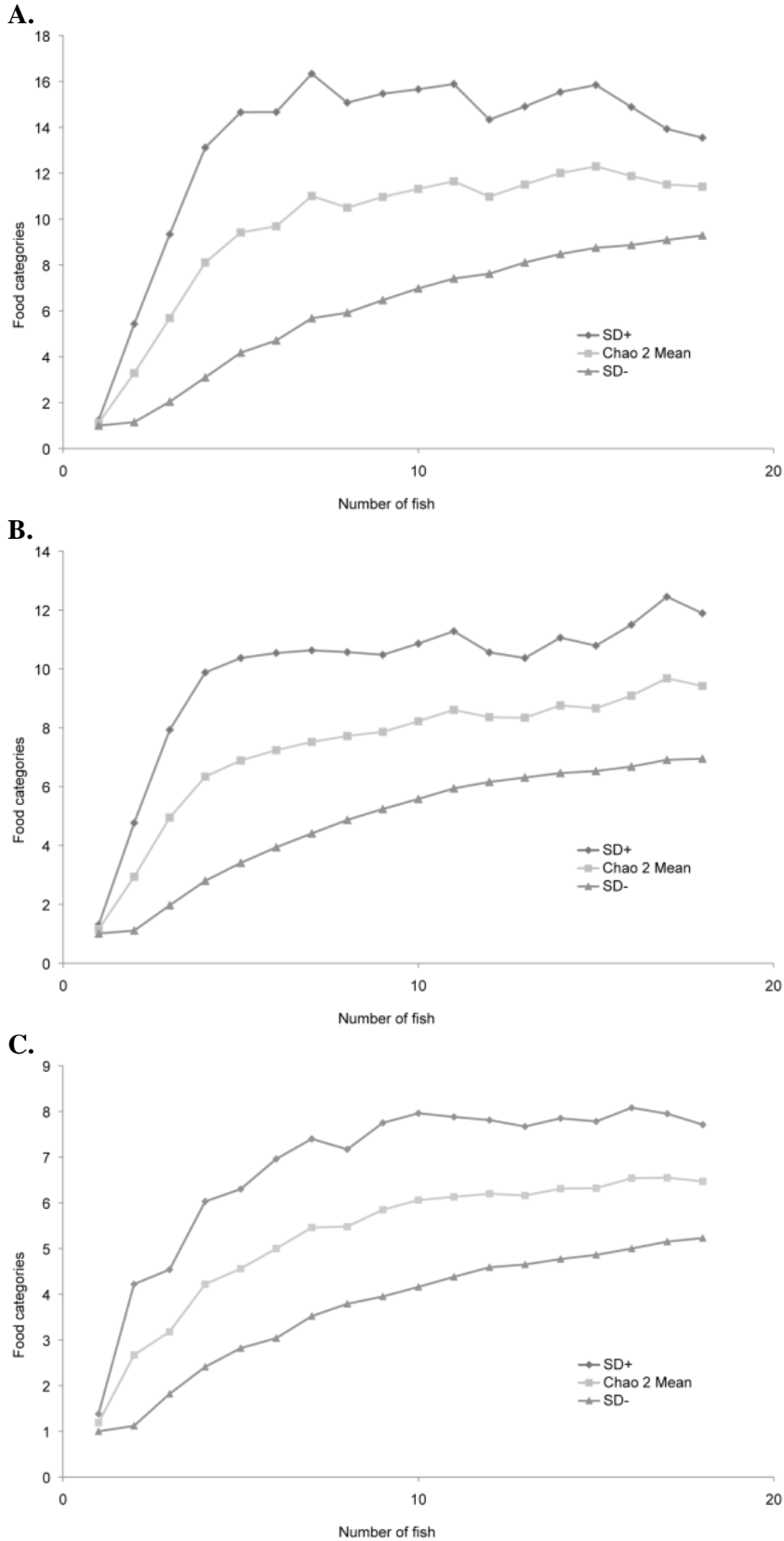


Figure 36. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of small-scaled brown slickhead from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

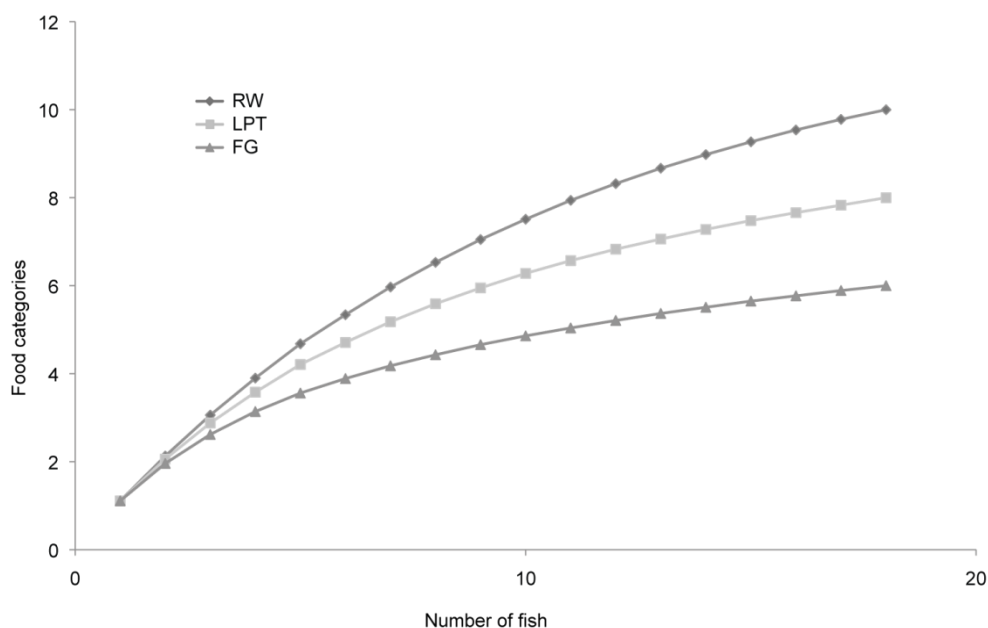


Figure 37. S_{obs} accumulation curves for the intestinal contents of small-scaled brown slickhead from northeastern Chatham Rise for three dietary classifications. Standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 17. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of small-scaled brown slickhead from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

INTESTINES	RW	LPT	FG
S_{max} 70%	9		7
S_{max} 80%	11		10
S_{max} 90%	13		13
Min. total	16	NA	17
S_t	3	3	2
n	10	8	6

4.1.7. Black slickhead (BSL), *Xenodermichthys copei* ($n = 86$)



Figure 38. Black slickhead (BSL), *Xenodermichthys copei*.

Food was recovered from the stomachs of 58 black slickheads (**Fig. 39**), while further food items were recovered from 25 intestines. The PES was 32.6 percent, while the PEI was 70.9 percent. The diet of black slickhead comprised primarily natant decapod prawns (59.3% IRI), calanoid copepods (13.4%), fish (12.2%), gammaridean, and hyperiidean amphipods (5.4%), and to a reduced extent ostracods, unidentified crustacean material, squid, gastropods, thaliaceans, polychaetes and chaetognaths (**Fig. 40A**). Black slickhead ate far fewer thaliaceans than the other slickhead species (**Fig. 40A**). Over the whole sample, the trophic level was 4.10. Pelagic crustaceans and benthic crustaceans were the two most important functional food-item groups (**Fig. 40B**). There was no significant correlation between numbers and/or weight of food with increasing fish size (Spearman rank $r_s = 0.124$, $P > 0.179$ and $r_s = 0.079$, $P > 0.281$ respectively). There was no clear ontogenic trend in the diet (**Fig. 41**), and there were high levels of dietary overlap between the 238–289 and 310+ mm SL size classes (**Table 18**). Standardised niche breadth was low for the three size classes and over the total sample (0.20) (**Fig. 41**).

The dietary variation within the stomach contents of black slickhead was not adequately described by any of the dietary classifications (**Fig. 42**, **Fig. 43**), and singletons were present in all dietary classifications. The RW and LPT intestinal contents datasets were identical, so were treated as one. The intestinal contents of black slickhead were mainly made up of natant decapods, amphipods, and calanoid copepods (**Fig. 44**). The dietary variation within the intestinal contents of black slickhead was adequately described by all three dietary classifications (**Fig. 45**, **Fig. 46**, **Table 19**). The minimum total number of intestines required to describe the variation in the diet of black slickhead ranged between five and 23 (FG and RW & LPT respectively). The number of intestines required to describe 90 percent of the dietary variation ranged

between seven (RW & LPT), and ten (FG), and singletons were present in the RW and LPT classifications (**Table 19**).

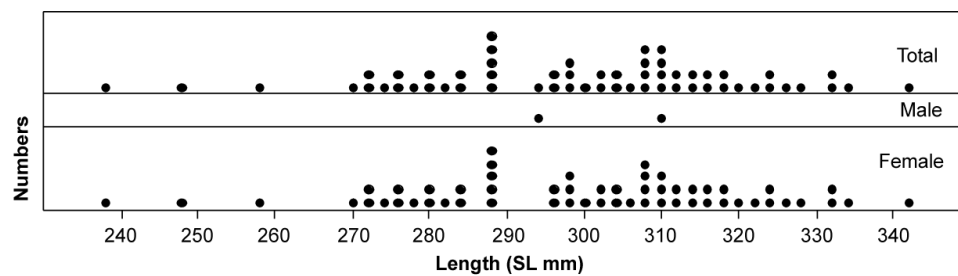
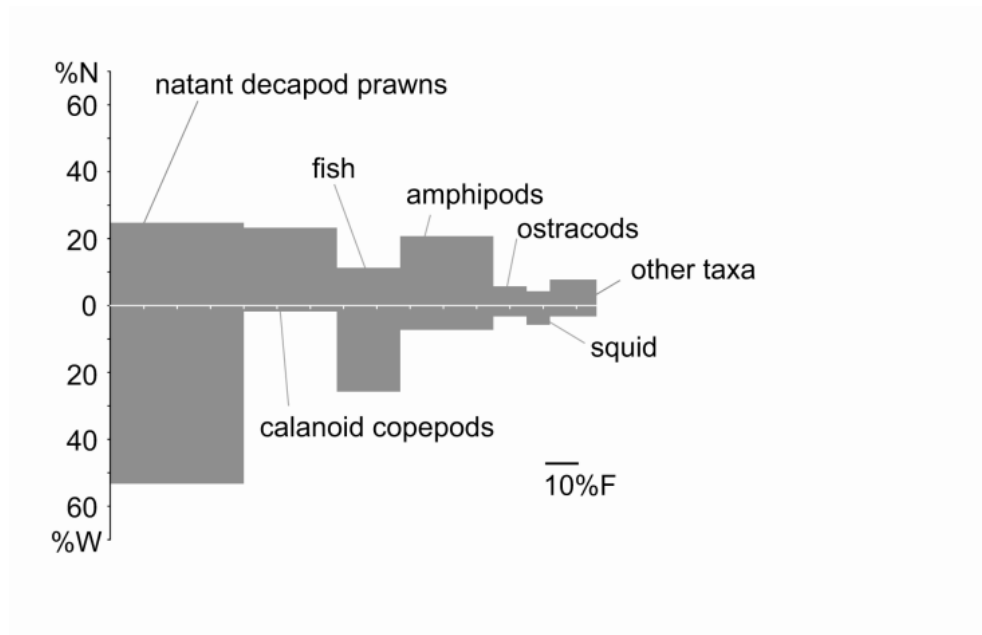


Figure 39. Size-frequency distribution for black slickhead (stomachs containing food) (SL mm).

A.



B.

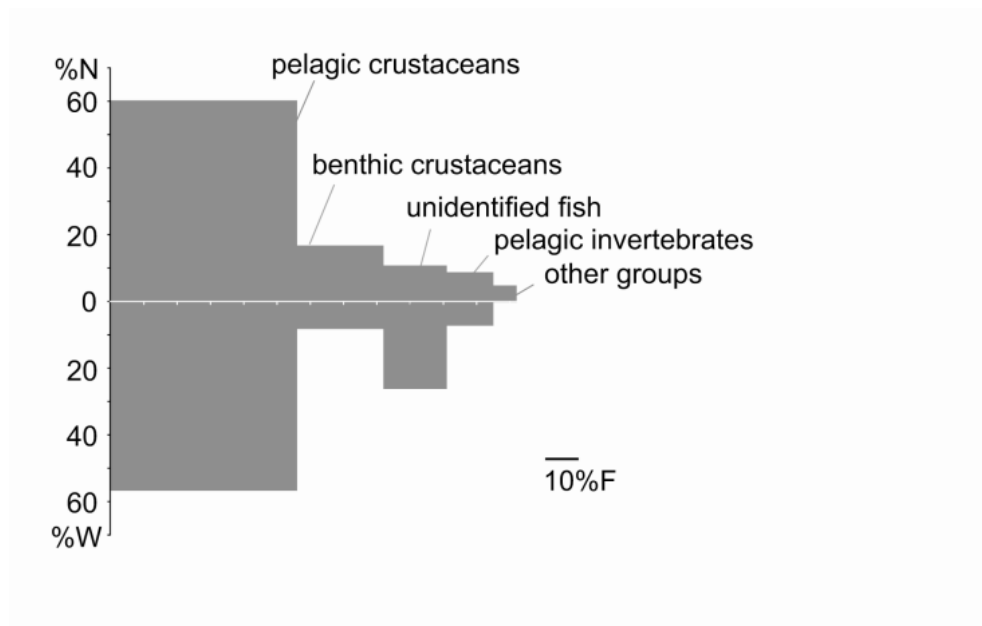


Figure 40. Diet of black slickhead from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 58$). **A.** Lowest practical taxon: other taxa; gastropods, polychaetes, thaliaceans, chaetognaths, and unidentified crustaceans. **B.** Functional food-item groups: other groups; unidentified crustaceans and polychaetes. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

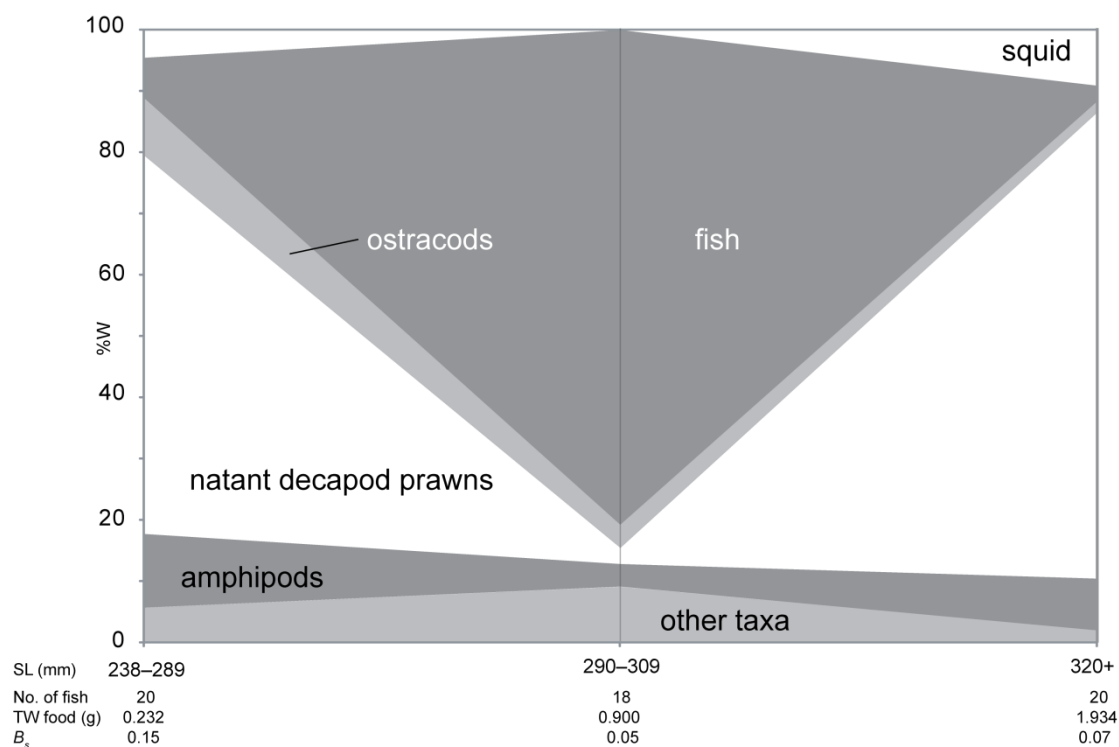


Figure 41. Diet of black slickhead from northeastern Chatham Rise over three size classes ($n = 58$, SL mm) (%W); number of fish in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon. Other taxa: gastropods, squids, polychaetes, thaliaceans, chaetognaths, and unidentified crustacean material.

Table 18. Dietary overlap values (%W) for black slickhead from northeastern Chatham Rise over three size classes ($n = 58$, SL mm). Food categories are based on lowest practical taxon. Dark grey rectangles indicate biologically significant dietary overlaps >60%. Calculations are based on %W.

Length (SL mm)	238–289 ($n = 20$)	290–319 ($n = 18$)	320+ ($n = 20$)
238–289		0.2	0.8
290–319			0.1
320+			

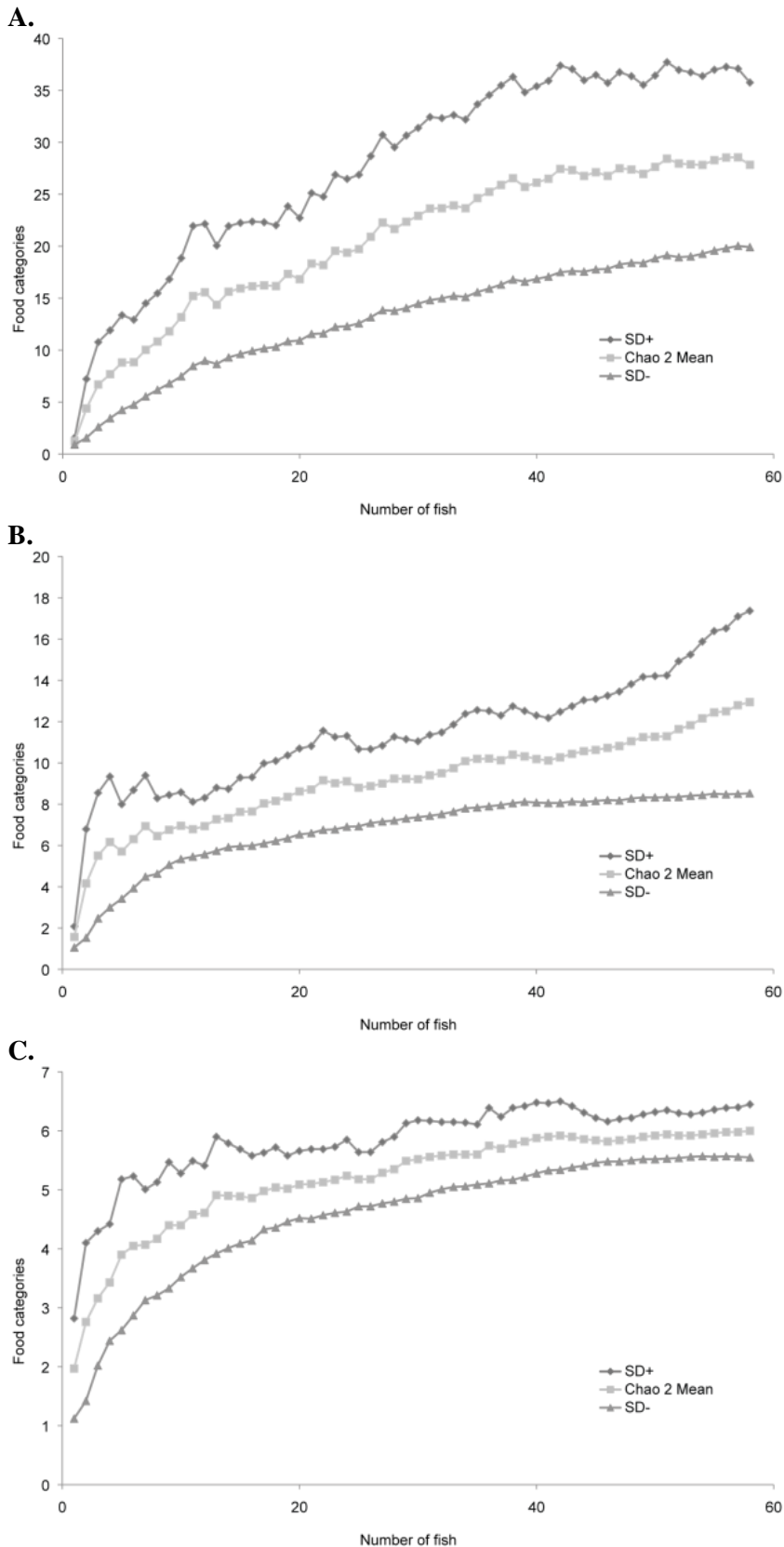


Figure 42. Mean Chao 2 estimation curves (plus and minus one standard deviation) for three dietary classifications for the stomach contents of black slickhead from northeastern Chatham Rise. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis). **A.** Raw data (10, 3). **B.** Lowest practical taxon (8, 3). **C.** Functional food groups (6, 3).

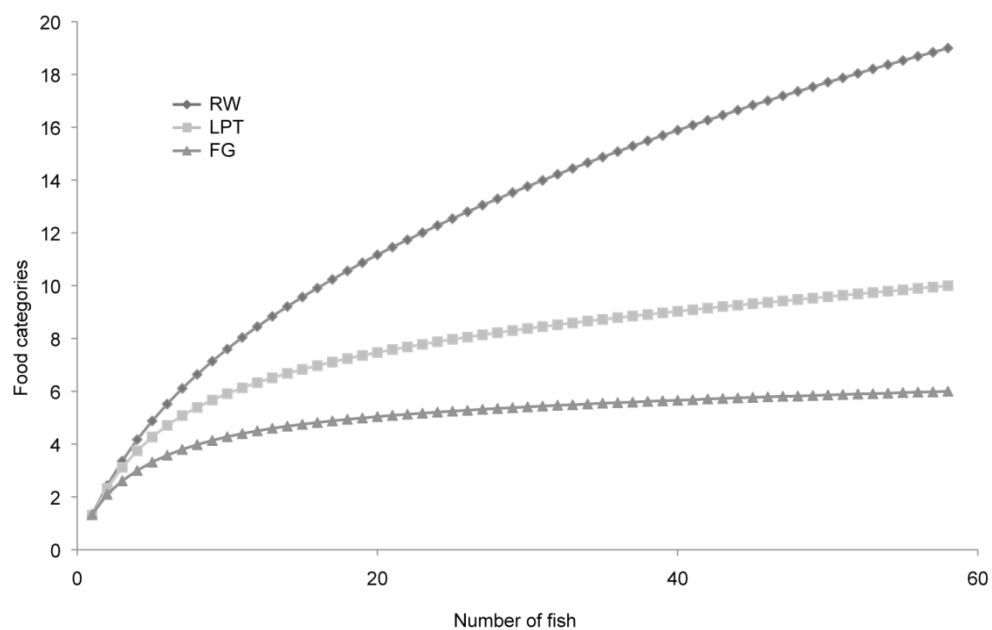
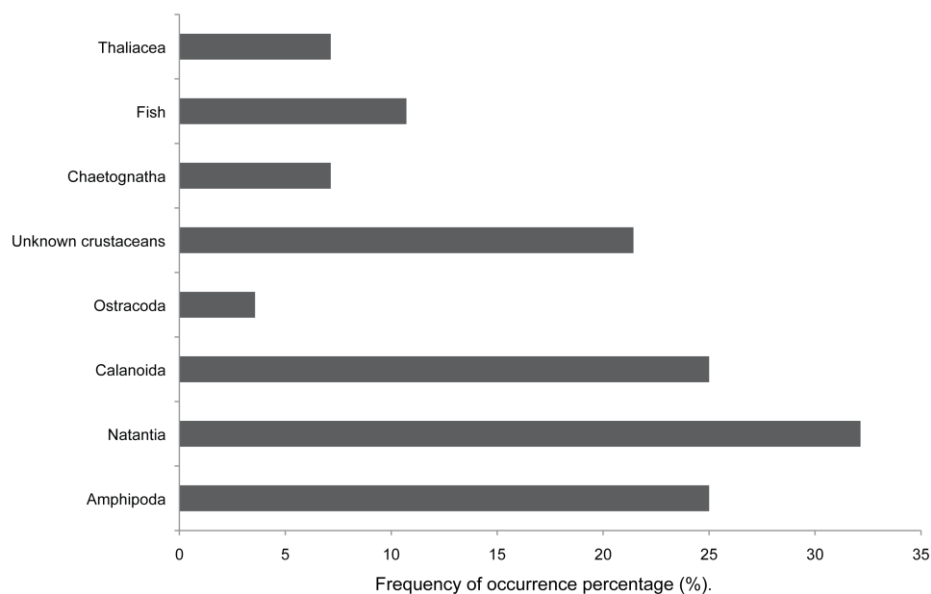


Figure 43. S_{obs} accumulation curves for the stomach contents of black slickhead from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

A.



B.

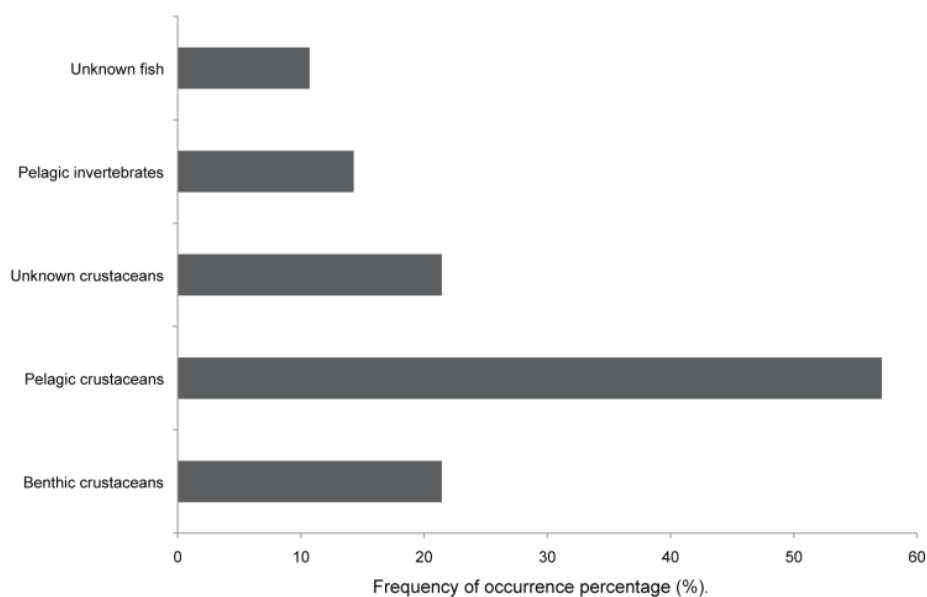


Figure 44. Intestinal contents of black slickhead from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 25$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

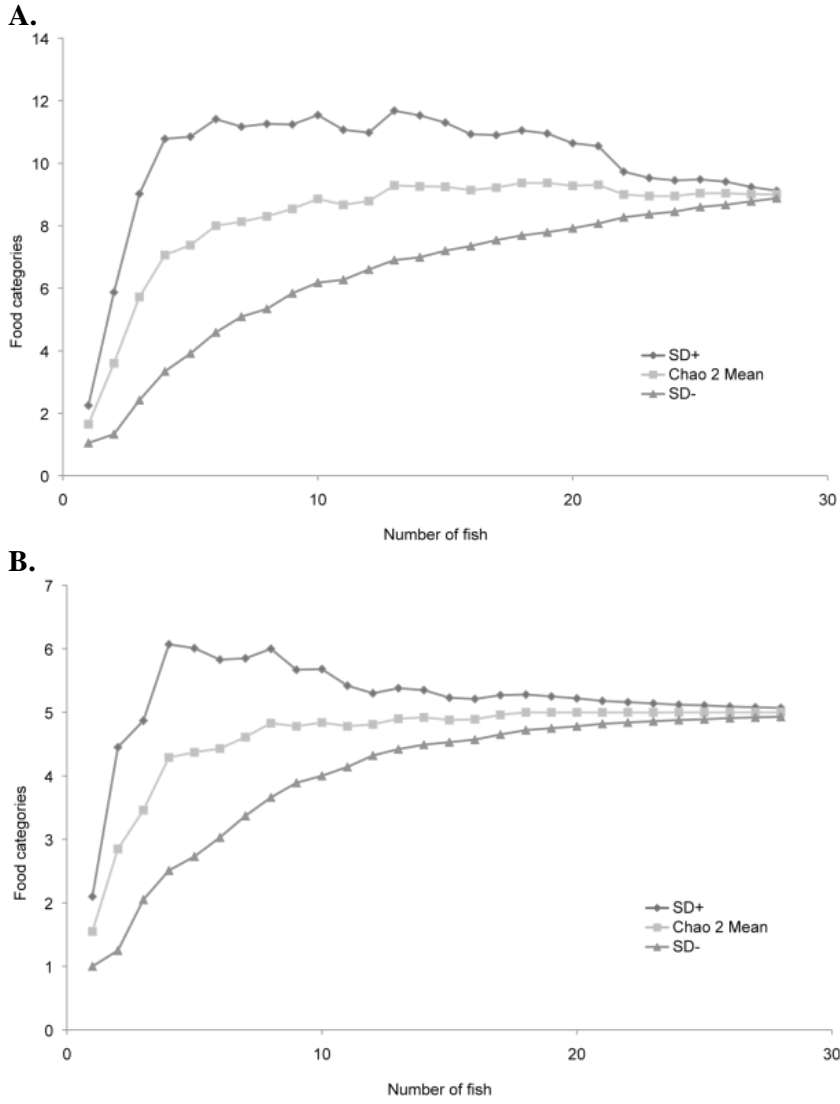


Figure 45. Mean Chao 2 estimation curves (plus and minus one standard deviation) for three dietary classifications for the intestinal contents of black slickhead from northeastern Chatham Rise. **A.** Raw data, and Lowest practical taxon. **B.** Functional food groups.

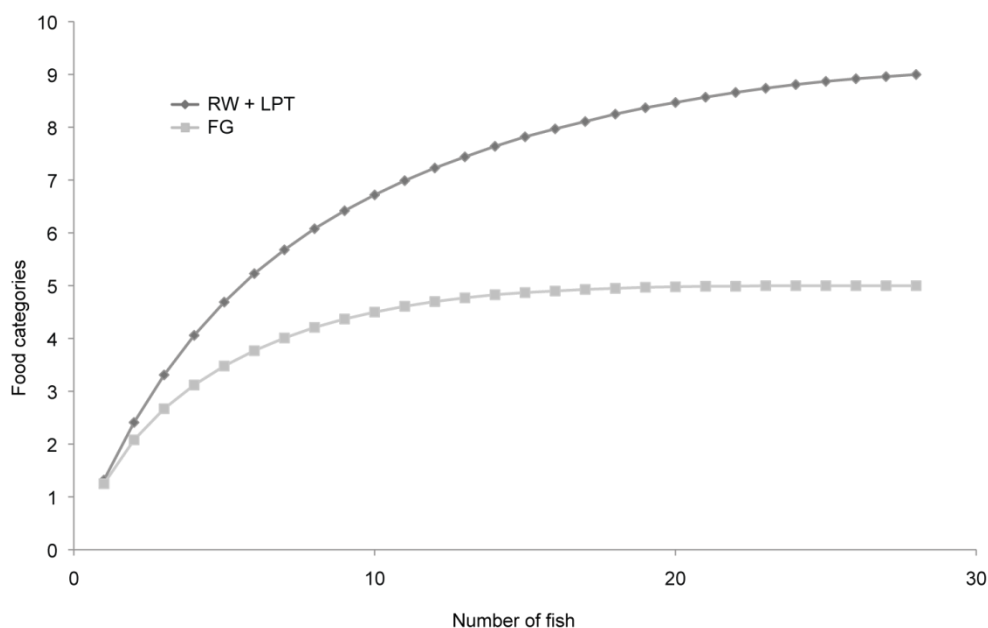


Figure 46. S_{obs} accumulation curves for the intestinal contents of black slickhead from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 19. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of black slickhead from northeastern Chatham Rise over three dietary classifications based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	7	3
S_{max} 80%	9	4
S_{max} 90%	11	5
Min. total	14	5
S_t	1	0
n	9	5

4.1.8. Johnson’s cod (HJO), *Halargyreus johnsonii* (n = 41)

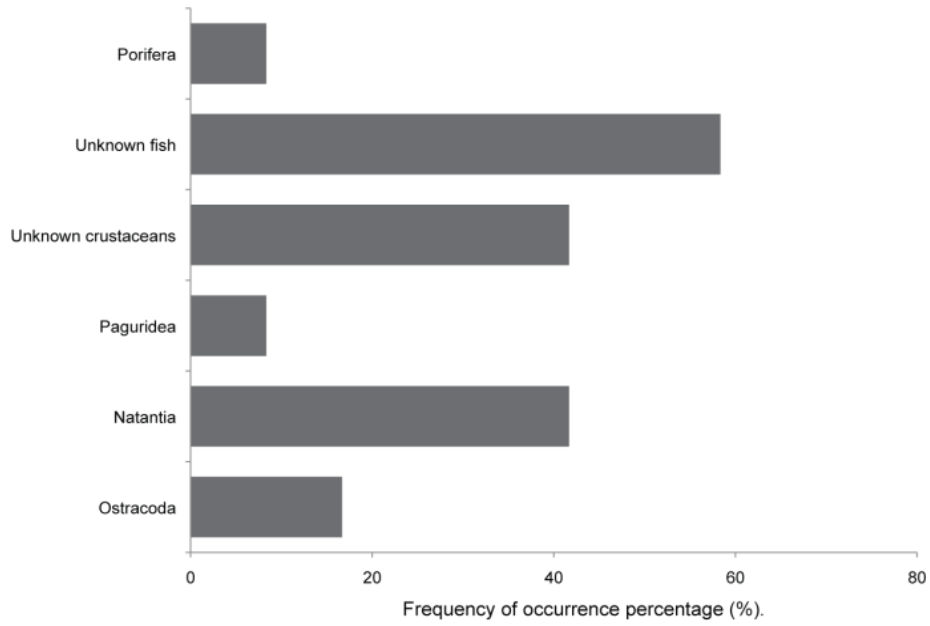


Figure 47. Johnson’s cod, (HJO), *Halargyreus johnsonii*.

All but one of the 41 Johnson’s cod had everted stomachs (this stomach was empty). Material was recovered from the intestines of 11 fish, and this gave a PEI of 73.2 percent. This intestinal material consisted of the remains of natant decapod prawns, myodocopid ostracods, and fish (bones and eye lenses) (**Fig. 48**). Over the whole sample the trophic level was 4.29.

The RW and LPT datasets were identical, so both were treated collectively. The dietary variation within the intestinal contents of Johnson’s cod from northeastern Chatham Rise was not adequately described by any of the dietary classifications (**Fig. 49**, **Fig. 50**), as there were singletons in all dietary classifications.

A.



B.

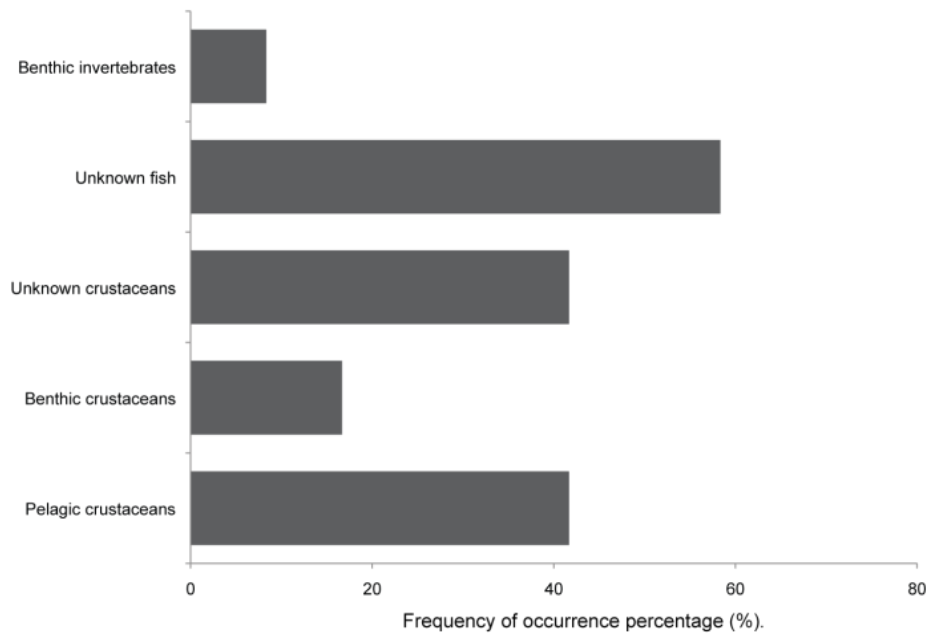


Figure 48. Intestinal contents of Johnson's cod from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 11$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

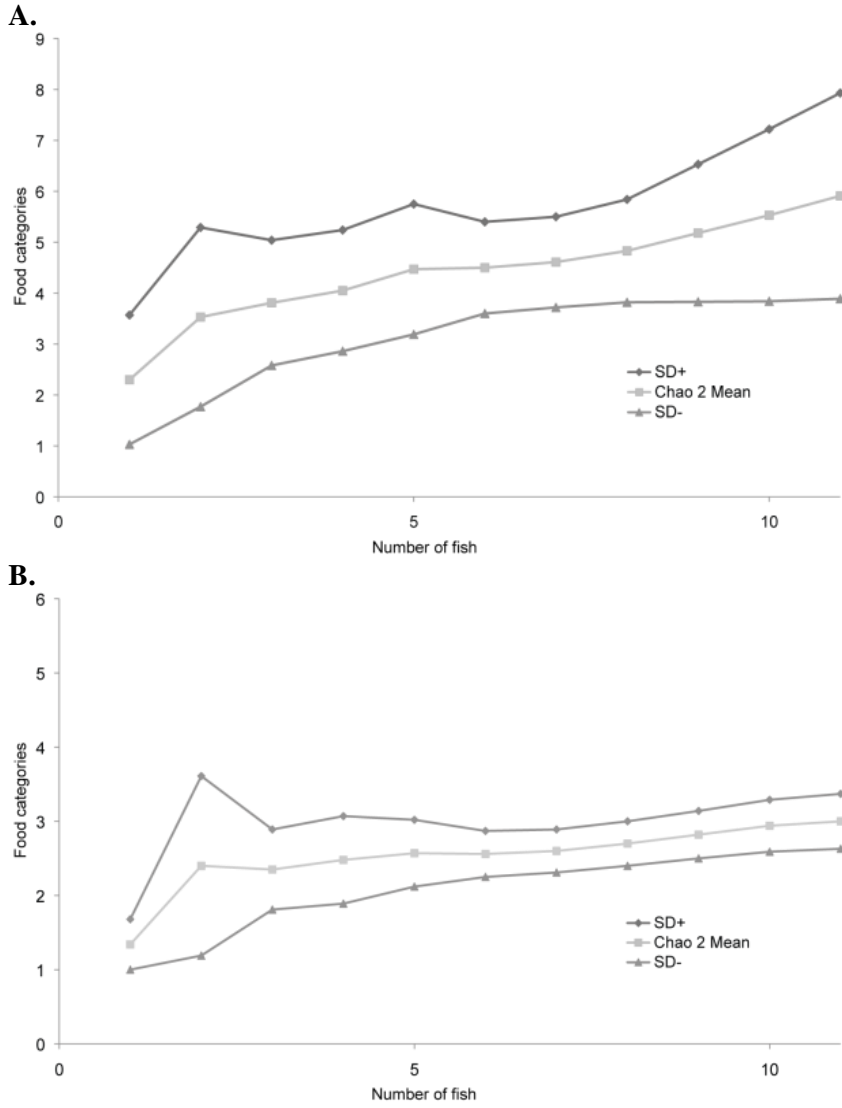


Figure 49. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of Johnson’s cod from northeastern Chatham Rise. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis. **A.** Raw data, lowest practical taxon (5, 2). **B.** Functional food groups (3, 1).

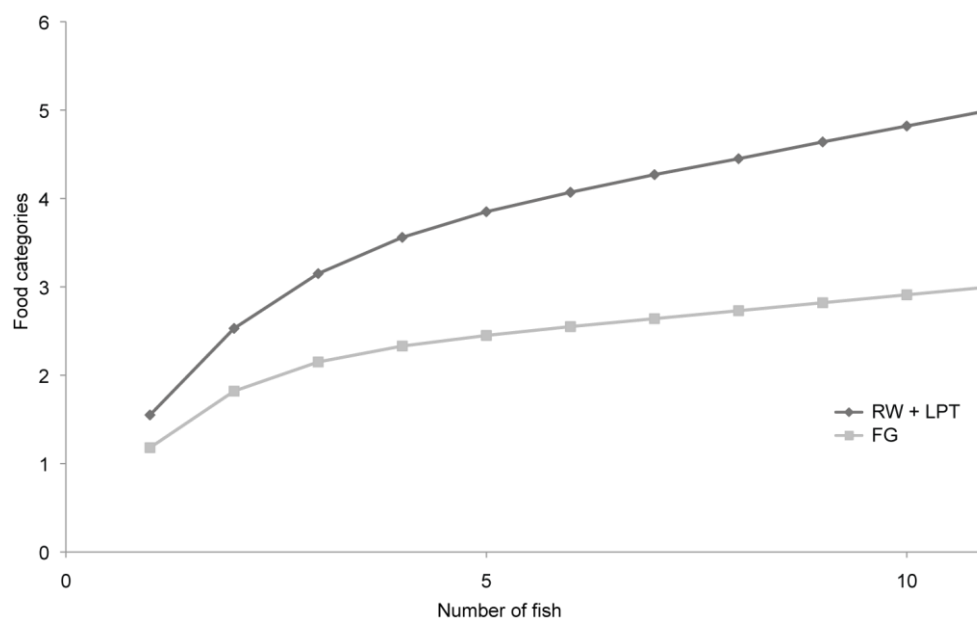


Figure 50. S_{obs} accumulation curves for the intestinal contents of Johnson's cod from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

4.1.9. Small-headed cod (SMC), *Lepidion microcephalus* (n = 21)

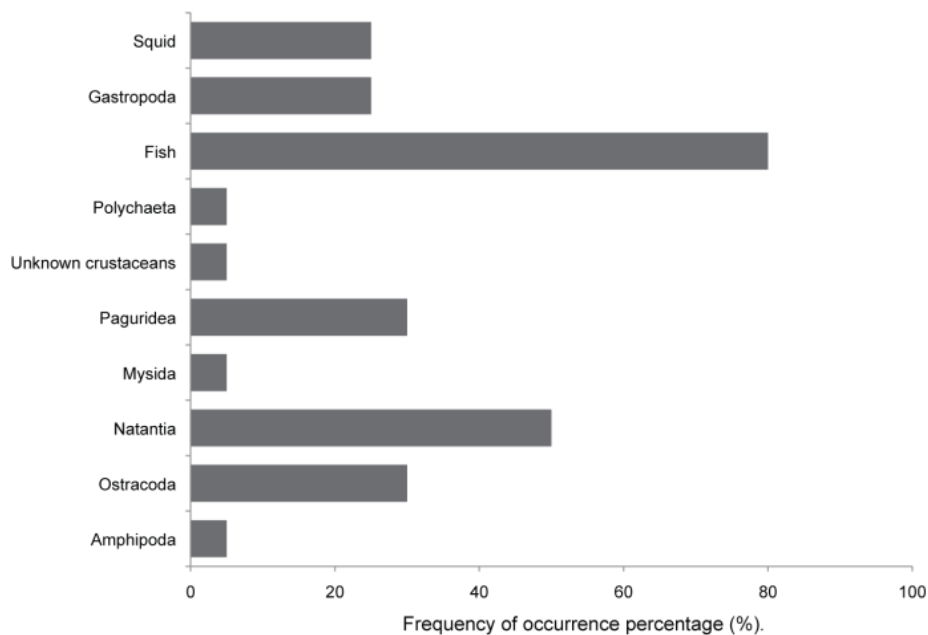


Figure 51. Small-headed cod (SMC), *Lepidion microcephalus*.

Six of the 21 small-headed cod had stomachs that contained food items; the rest had everted stomachs. Natant decapod and mysid prawns (*Gnathophausia* sp.), hermit crabs (Paguridea), squid and fish remains occurred in more than one stomach. Nineteen intestines contained food items, giving a PEI of 9.5 percent. This intestinal material comprised amphipods, myodocopid ostracods (*Bathyvargula* sp.), gastropods (*Nassarius ephamillus* (Watson, 1882)), and fragments of pteropods (**Fig. 52**). Over the whole sample the trophic level was 4.07.

The dietary variation of the intestinal contents of small-headed cod was not adequately described by any of the three dietary classifications. There were multiple singletons in all but one (FG) of the dietary classifications (**Fig. 53, Fig. 54**).

A.



B.

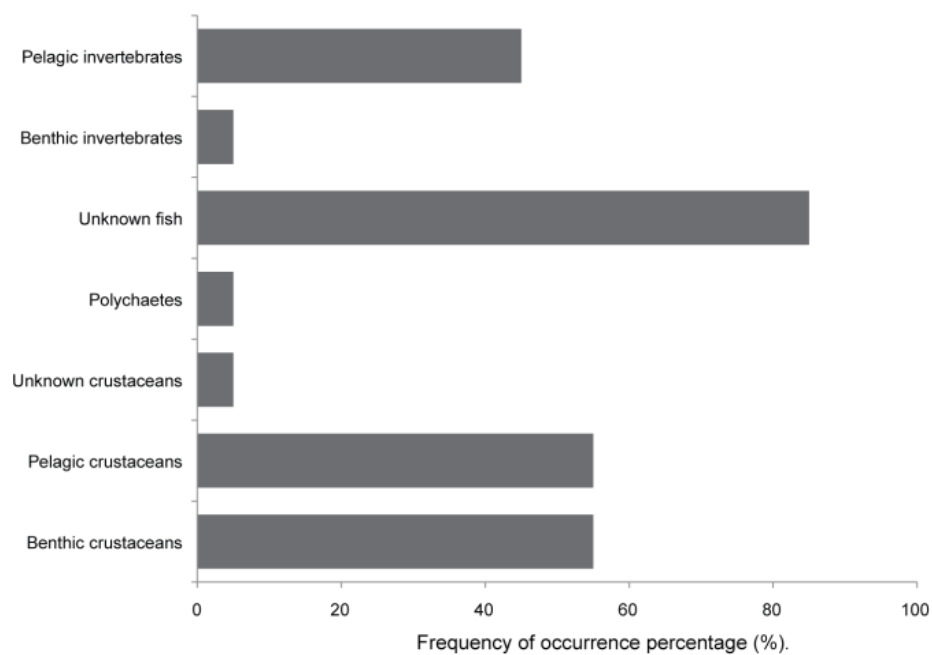


Figure 52. Intestinal contents of small-headed cod from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 19$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

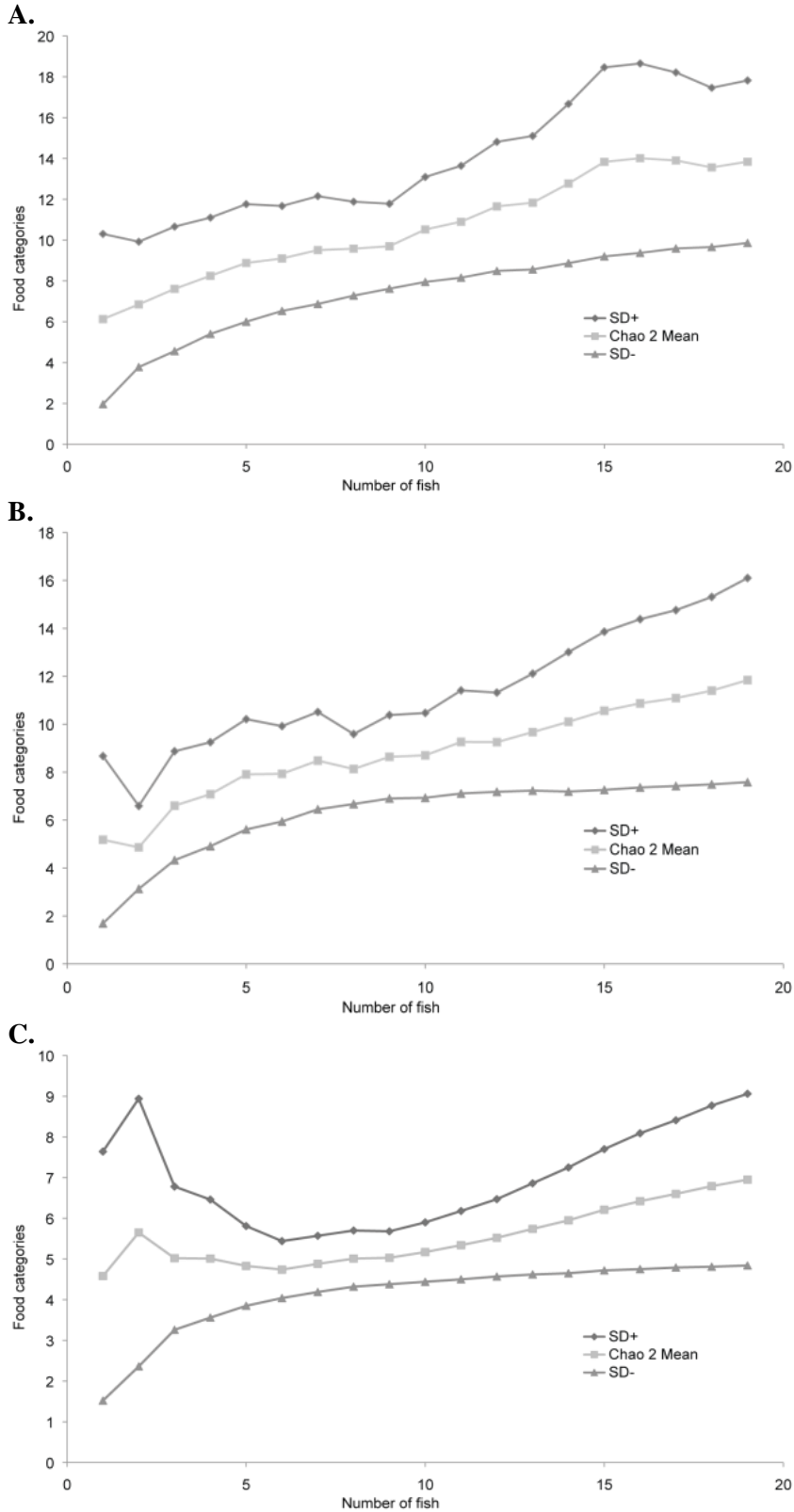


Figure 53. Mean Chao 2 estimation curves (plus and minus one standard deviation: SD) for the intestinal contents small-headed cod from northeastern Chatham Rise. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis. **A.** Raw data (11, 2). **B.** Lowest practical taxon (8, 2). **C.** Functional food groups (7, 1).

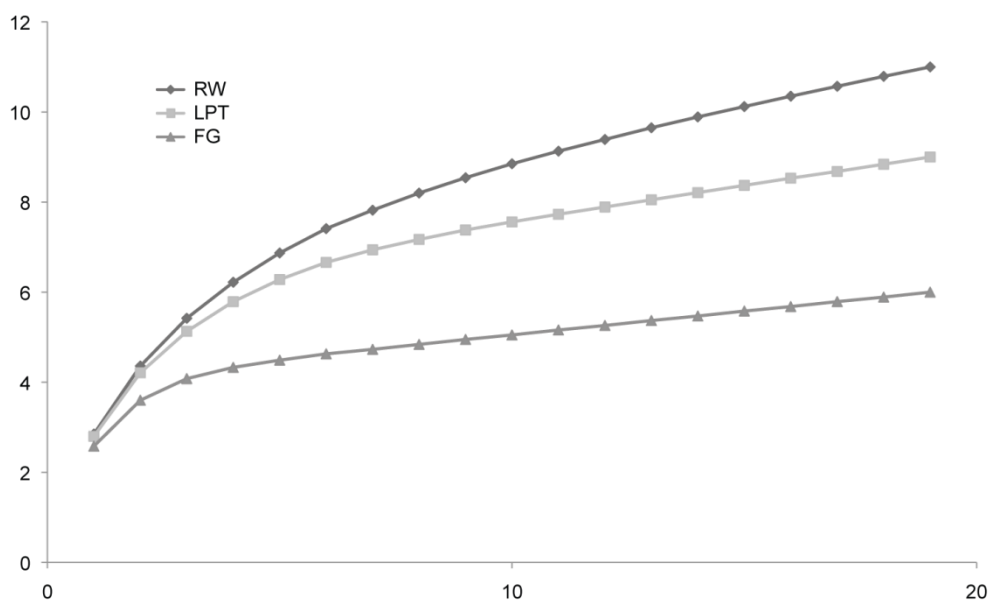


Figure 54. S_{obs} accumulation curves for the intestinal contents of small-headed cod from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

4.1.10. Surgeon rattail (CTH), *Coelorinchus acanthiger* (n = 22)

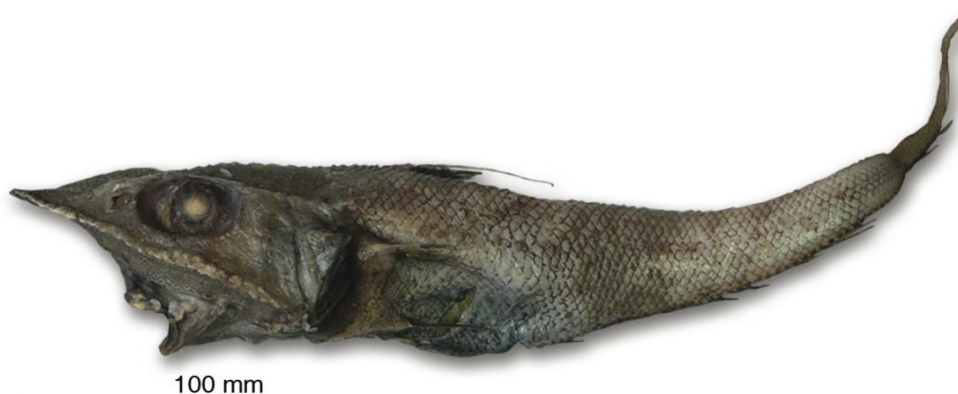
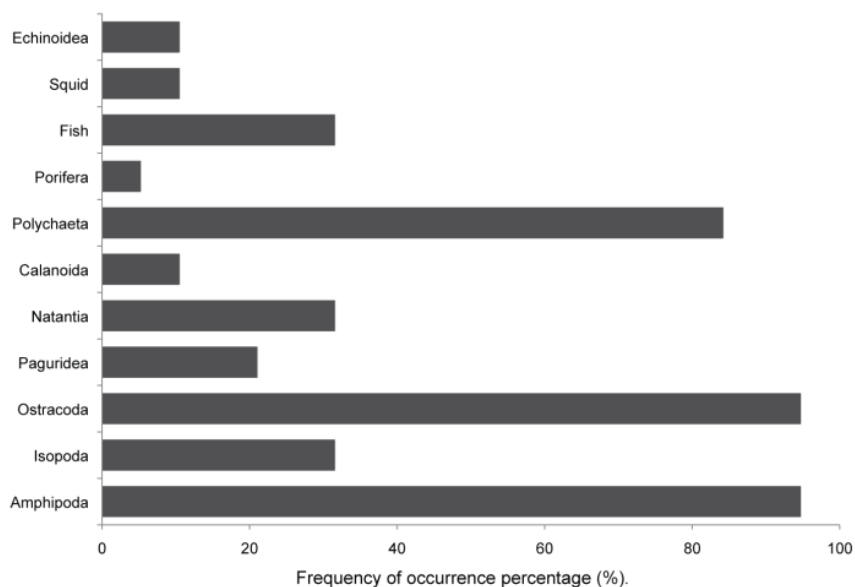


Figure 55. Surgeon rattail, (CTH), *Coelorinchus acanthiger*.

All but two surgeon rattail had everted stomachs; the two non-everted stomachs contained gammaridean amphipods, myodocopid ostracods (*Bathyvargula* sp.), and fish remains in one, while the other (from a much larger individual, HL = 127 mm) had eaten a small fish which was too digested to identify further. Analysis of 19 intact intestines revealed that myodocopid ostracods (*Bathyvargula* sp., *Vargula* sp., *Metavargula bradfordae* Kornicker, 1979), gammaridean and caprellidean amphipods, isopods (*Natanolana* sp., Cryptoniscidae, Serolidae, and Gnathiidae), polychaetes (Glyceridae) and foraminiferans had been eaten (**Fig. 56**). Over the whole sample, the trophic level was 3.69.

The dietary variation within the intestinal contents of surgeon rattail was adequately described by two dietary classifications (LPT & FG) (**Fig. 57, Fig. 58, Table 20**). The minimum total number of fish required to describe the dietary variation within the intestines ranged between five and 13 (LPT & FG respectively) (**Table 20**). Between four and nine intestines described 90 percent of the S_{\max} values (LPT & FG respectively). There were multiple singletons in the RW classification (**Table 20**).

A.



B.

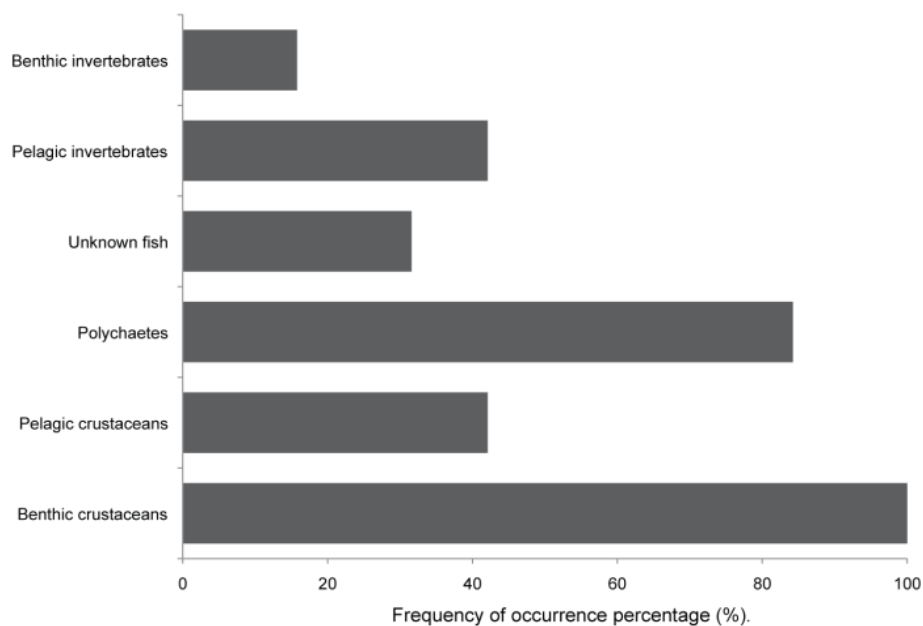


Figure 56. Intestinal contents of surgeon rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 19$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

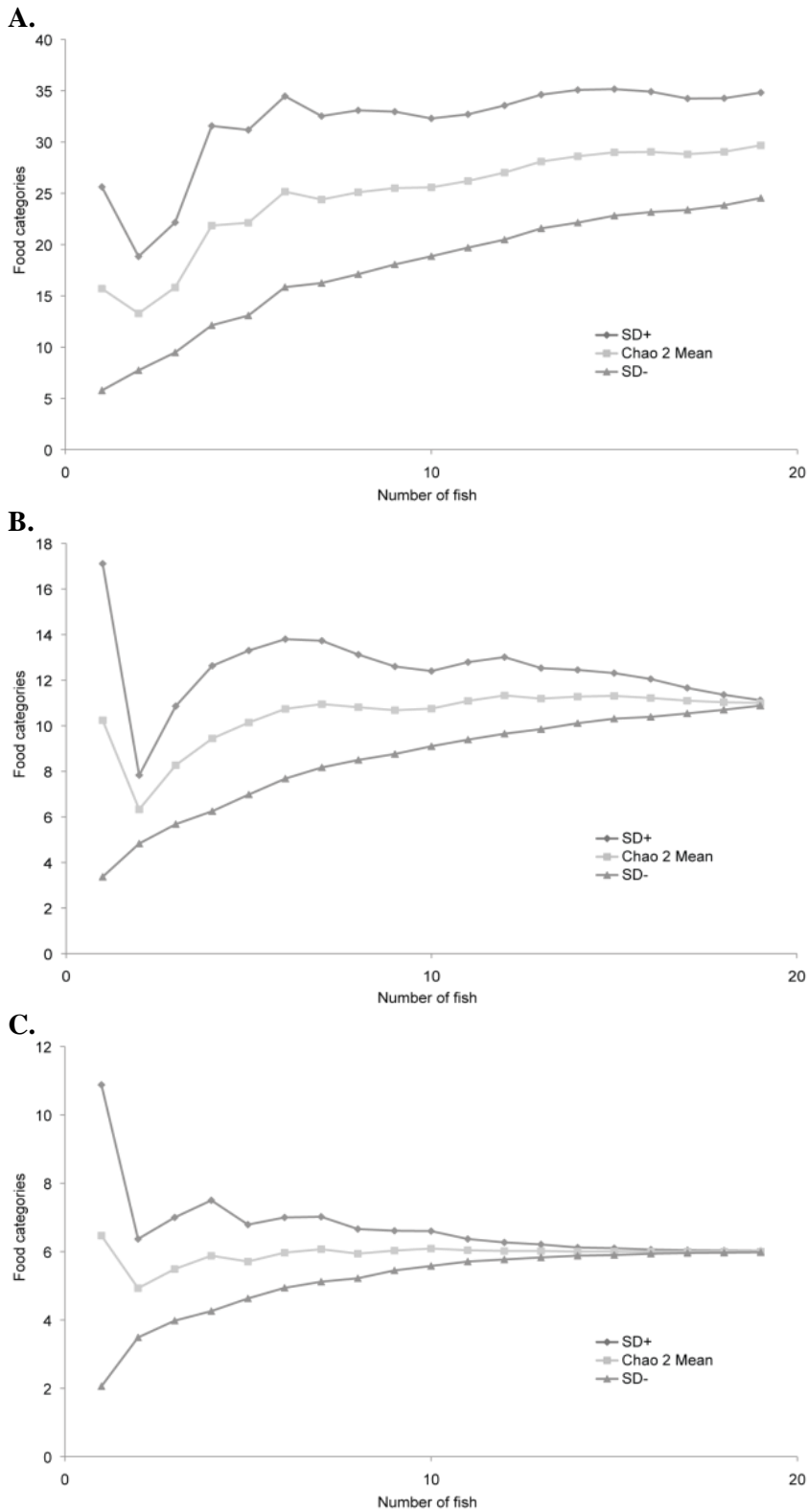


Figure 57. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of surgeon rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

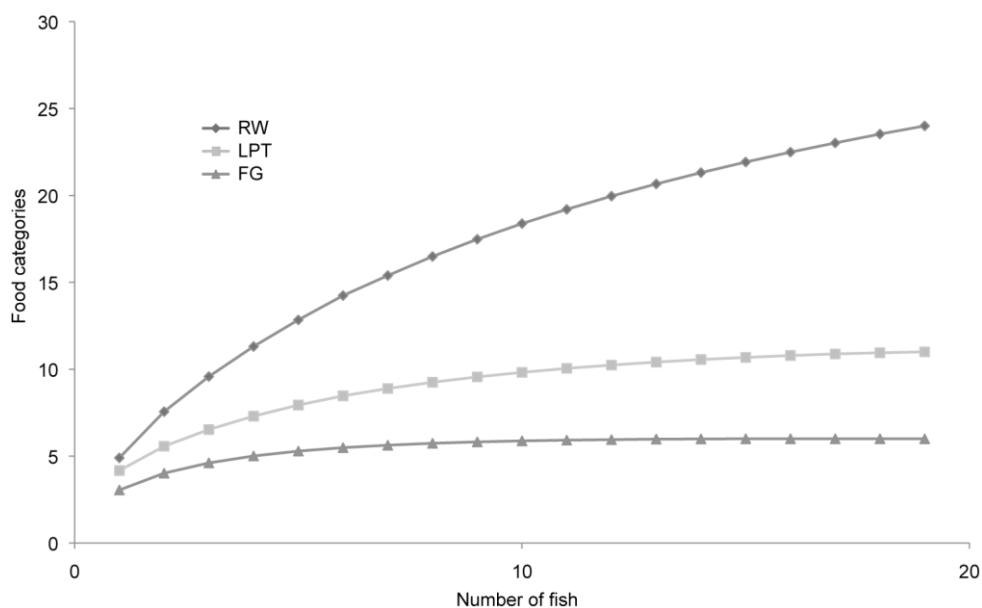


Figure 58. S_{obs} accumulation curves for the intestinal contents of surgeon rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 20. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents surgeon rattail from northeastern Chatham Rise over three dietary classifications based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups, S_t : total number of singletons in each food category).

INTESTINES	RW	LPT	FG
S_{max} 70%		4	2
S_{max} 80%		6	3
S_{max} 90%		9	4
Min. total	NA	13	5
S_t	9	1	0
n	24	12	6

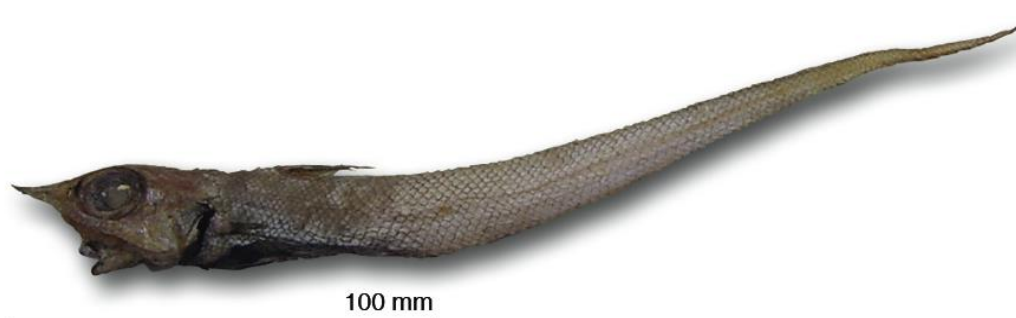
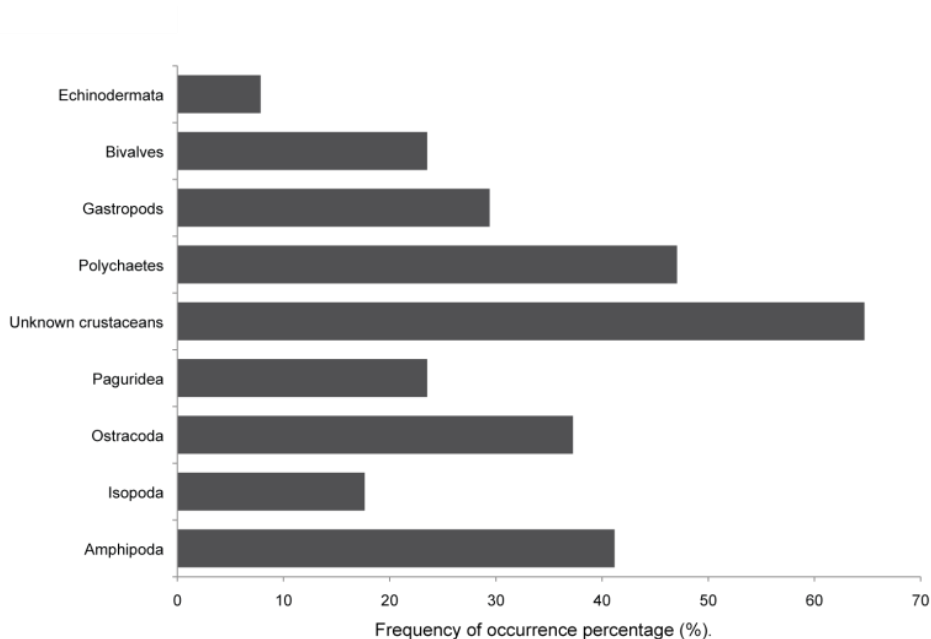
4.1.11. Notable rattail (CIN), *Coelorinchus innotabilis* ($n = 74$)

Figure 59. Notable rattail, (CIN), *Coelorinchus innotabilis*.

All but one notable rattail had an everted stomach, and this non-everted stomach was empty. Identifiable material was recovered from 51 intestines, which gave a PEI of 31.4 percent (**Fig. 60**). Intestinal material composed polychaetes, unidentified crustaceans, gammaridean (Lysianassidae and Stegocephalidae) and caprellidean amphipods, myodocopid ostracods (*Vargula* sp., *Metavargula* sp.), hermit crabs, gastropods (two undescribed species of *Benthonella*; *Brookula benthicola* Dell, 1956; *Zetela variabilis* Dell, 1956; *Archiminolia meridiana* Dell, 1953; *Fusitriton magellanicus* (protoconchs) (Röding, 1798); *Globisinum* sp.; *Amalda benthicola* (Dell, 1956); Marginellidae; *N. ephamillus* and Turridae, *Ringicula* sp., *Crenelabium* sp., *Retusa* sp., and *Volvulella truncata* Newton, 1891), and bivalves (three undescribed species of *Deminucula*, *Pseudotindaria flemingi* (Dell, 1956), and *Bathyarca cybaea* Hedley, 1906). Sediment was present in most intestines. Over the whole sample, the trophic level was 3.68.

Two of the dietary classifications adequately described the variation within the intestinal contents of notable rattail (LPT & FG) (**Fig. 61, Fig. 62, Table 21**). In these, the minimum total number of fish needed to describe the dietary variation ranged between three and 23 (FG & LPT respectively). Between three and eight intestines described 90 percent of the dietary variation (FG & LPT respectively). The food classification with multiple singletons (RW) was also the only food classification that failed to describe the variation within the intestinal contents (**Table 21**).

A.



B.

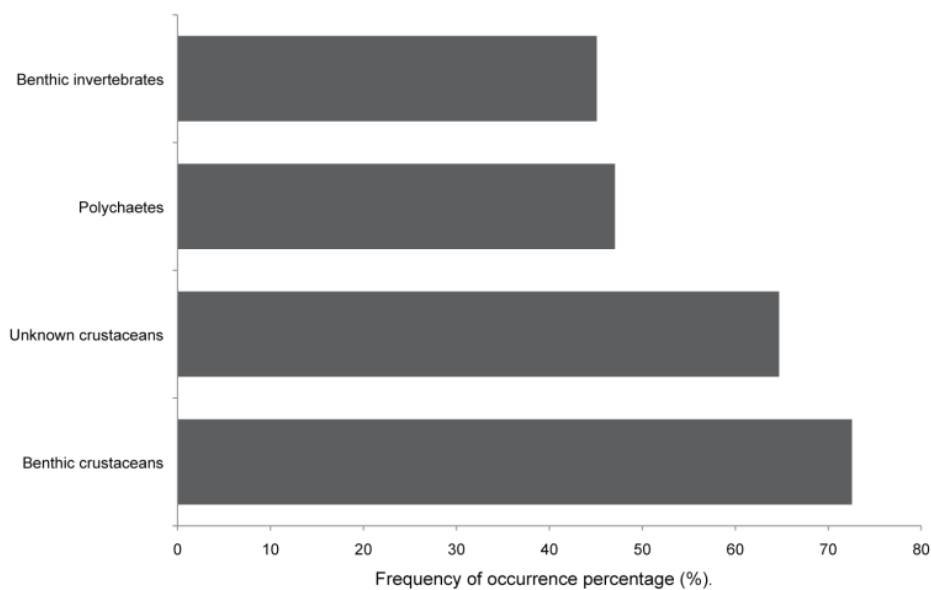


Figure 60. Intestinal contents of notable rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 53$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

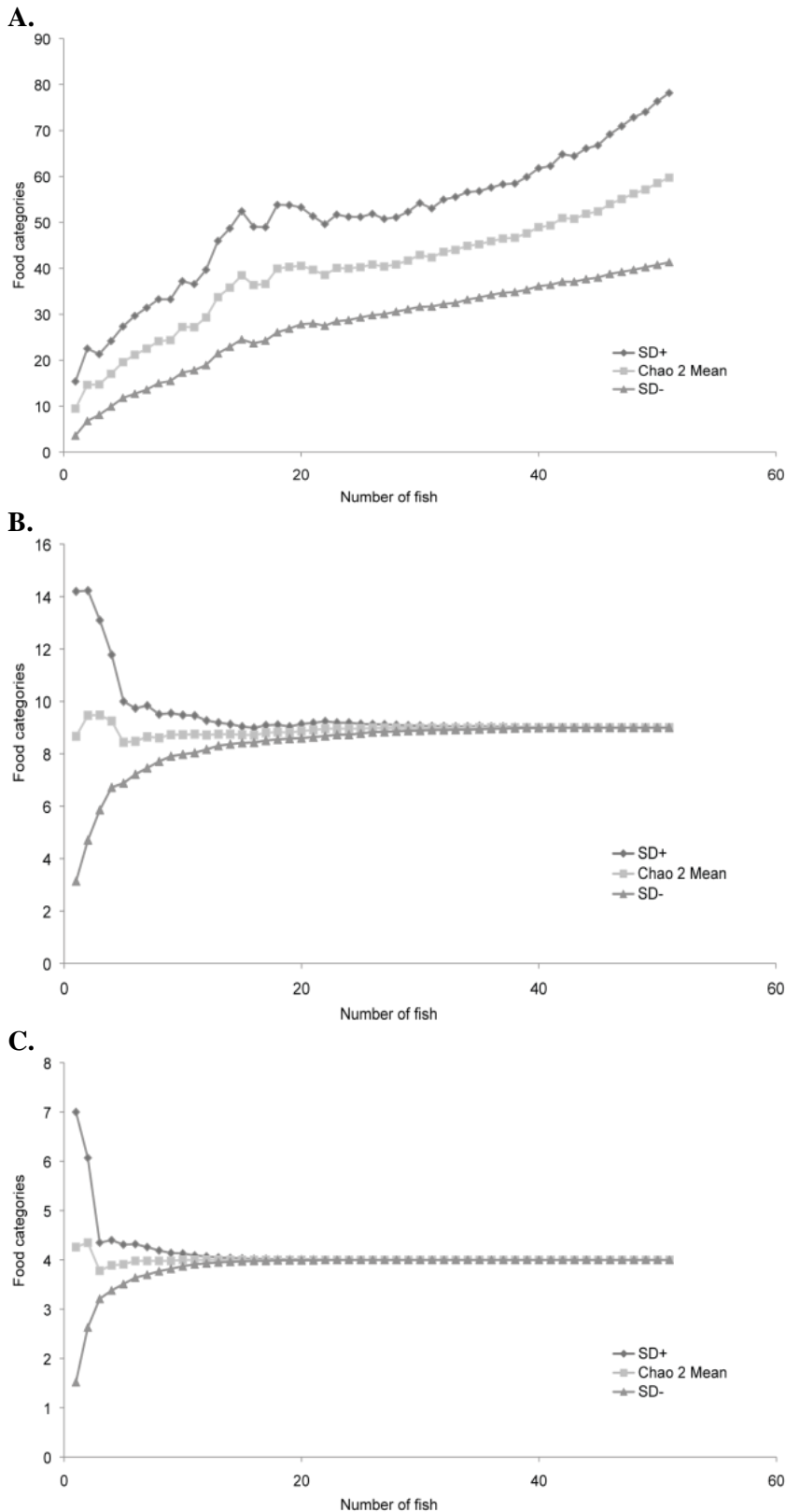


Figure 61. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of notable rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

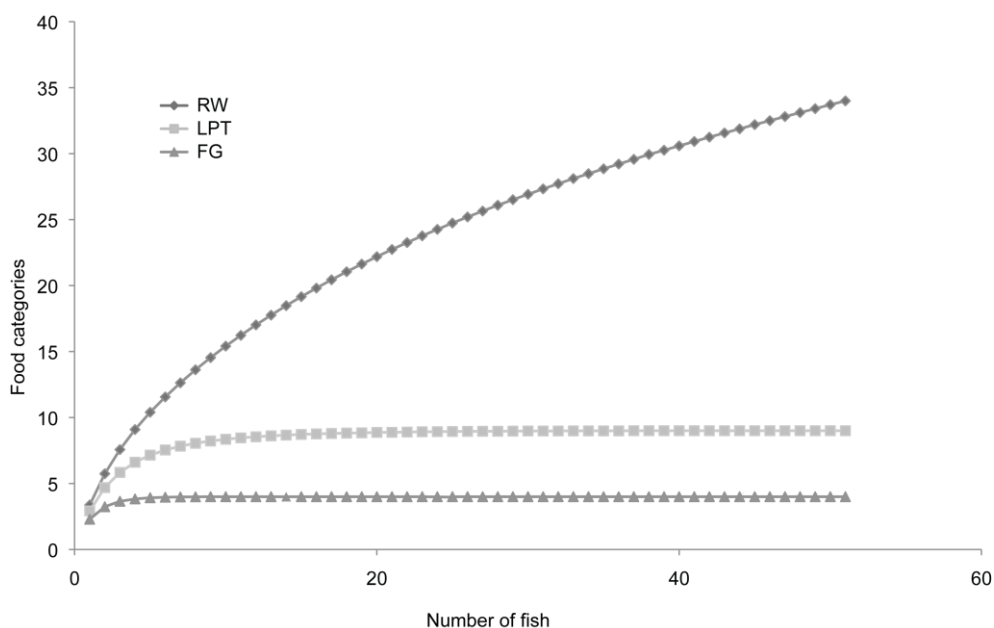


Figure 62. S_{obs} accumulation curves for the intestinal contents of notable rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 21. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of notable rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups, S_t : total number of singletons in each food category).

INTESTINES	RW	LPT	FG
S_{max} 70%		4	2
S_{max} 80%		5	2
S_{max} 90%		8	3
Min. total	NA	23	3
S_t	15	0	0
n	34	9	4

4.1.12. Rough-headed rattail (CHY), *Coelorinchus trachycarus* ($n = 17$)

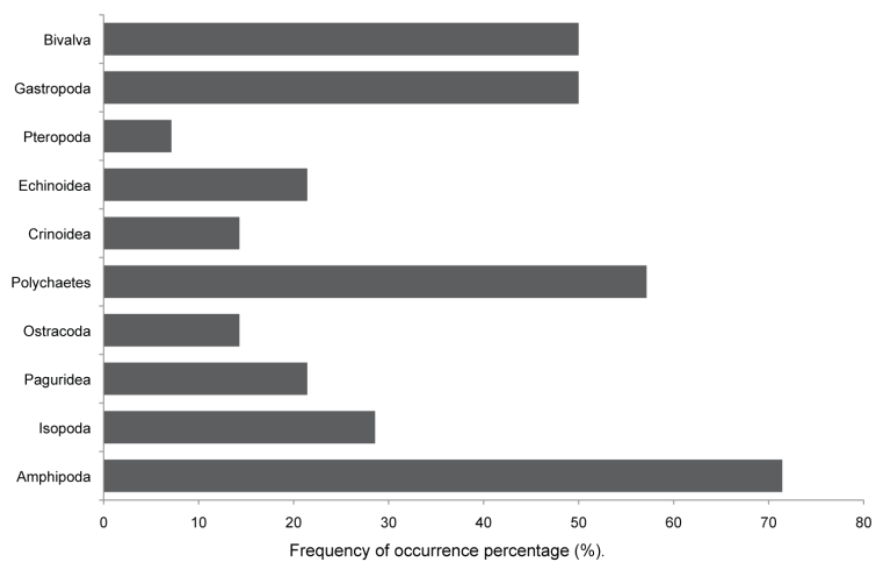


Figure 63. Rough-headed rattail, (CHY), *Coelorinchus trachycarus*.

All 17 rough-headed rattail had everted stomachs, and 13 intestines contained food items giving a PEI of 23.5 percent. This intestinal material consisted of caprellidean and gammaridean amphipods; hermit crabs; asellote and serolid isopods; myodocopid ostracods (*Vargula* sp., *Metavargula* sp.); polychaetes, including ?*Hyalinoecia* sp.; gastropods (*Anatoma* sp.; *Archiminolia meridiana* (Dell, 1953); *Globisinum* sp.; *Amalda benthicola*; *Antiguraleus* sp.; *Cylichna bulloides* Dell, 1956; *Retusa* sp.); bivalves (*Parvamussium maorium* Dell, 1956; *Pseudotindaria flemingi* and *Yoldiella* sp.); crinoid remains; and foraminiferans (**Fig. 64**). Sediment was present in most intestines. Over the whole sample, the trophic level was 3.67.

Two of the dietary classifications adequately described the variation within the intestinal contents of rough-headed rattail (LPT & FG) (**Fig. 65, Fig. 66, Table 22**). Two intestines were needed to describe the minimum number of fish and S_{\max} 90% of the dietary variation for all dietary classifications. The food classification with multiple singletons (RW) was also the only food classification that failed to describe the variation within the intestinal contents (**Table 22**).

A.



B.

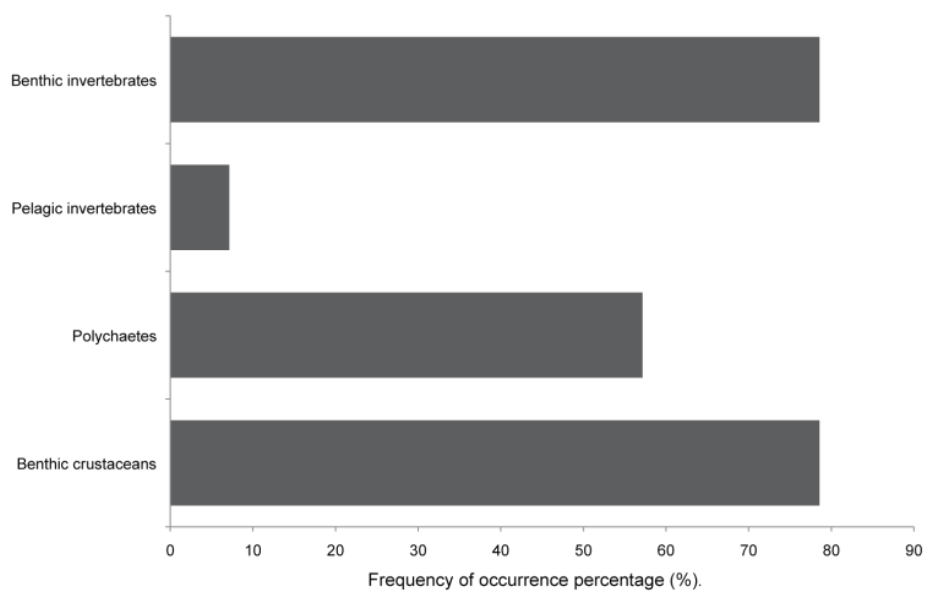


Figure 64. Intestinal contents of rough-headed rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 13$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

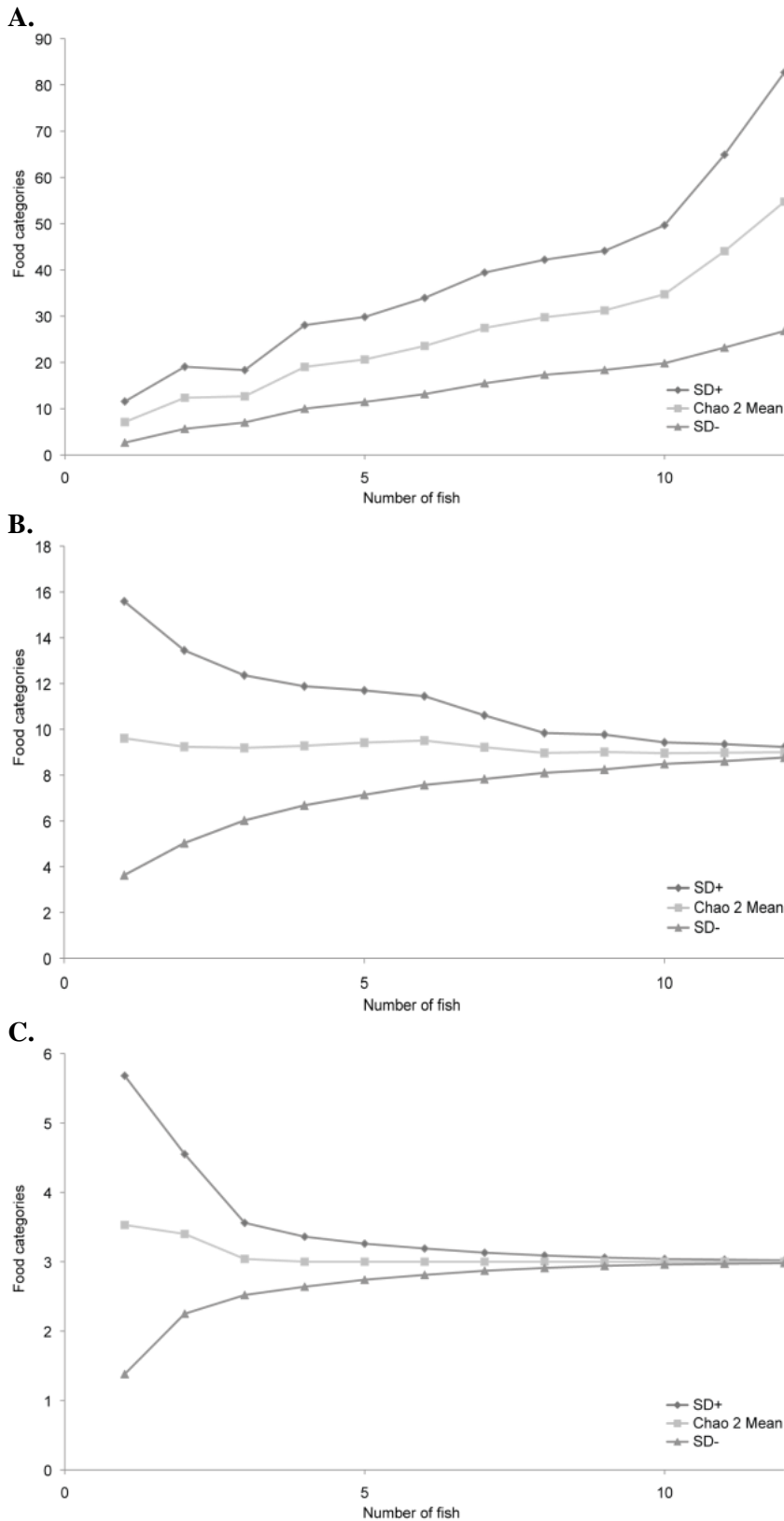


Figure 65. Mean Chao 2 estimation curves (plus and minus one standard deviation: SD) for the intestinal contents of rough-headed rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

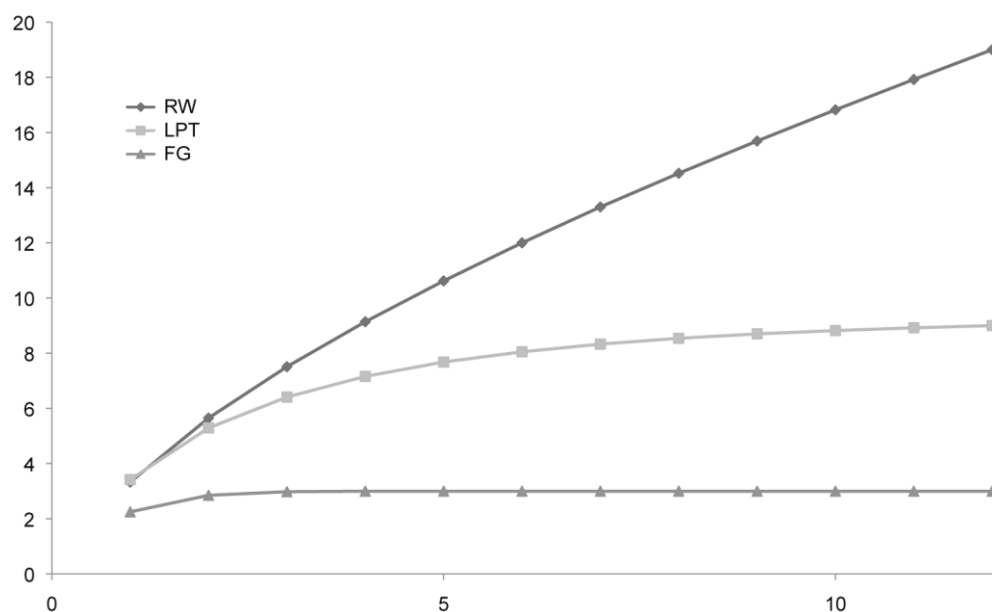


Figure 66. S_{obs} accumulation curves for the intestinal contents of rough-headed rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 22. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of rough-headed rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW	LPT	FG
S_{max} 70%		2	1
S_{max} 80%		2	2
S_{max} 90%		2	2
Min. total	NA	2	2
S_t	13	1	0
n	19	9	3

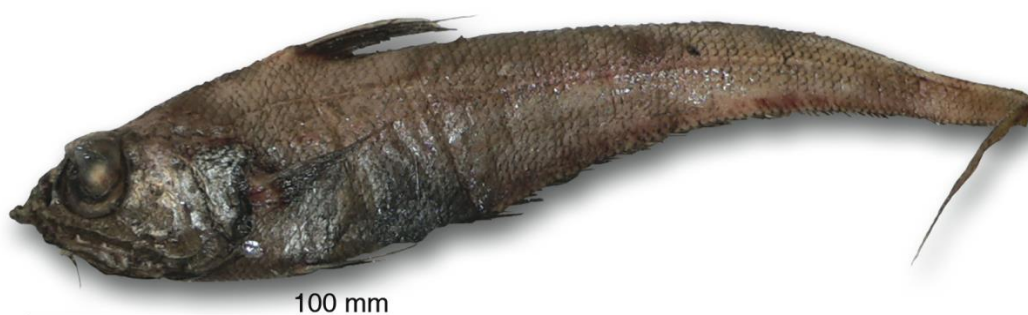
4.1.13. Serrulate rattail (CSE), *Coryphaenoides serrulatus* ($n = 102$).

Figure 67. Serrulate rattail, (CSE), *Coryphaenoides serrulatus*.

Sixty eight of the 102 serrulate rattail examined had non-everted stomachs containing food (**Fig. 68**), giving a PES of 56.6 percent. Natant decapod prawns (27.0% IRI), and gammaridean and caprellidean amphipods (24.6%) (*Unciolella* sp.; *Tetradeion* cf. *quattro* Berge & Vader, 2000; *Eurythenes* sp.; Phtisicidae) were the most important food items (**Fig. 69A**). The remainder of the diet consisted of polychaetes, calanoid copepods (*Bradydium* spp.), squid (comprising spermatophores, eye lenses and beaks, occasionally with adhering flesh), unidentified crustaceans, myodocopid ostracods (*Vargula* sp.; *M. bradfordae*; *Bathyvargula ?walfordi* Baird, 1850; *Bathyvargula* sp.; *Cypridinoides* cf. *reticulata* Poulsen, 1962), isopods (Gnathiidae; Munnopsidae; *Natatolana* sp.; *Cymodopsis ?impudica* Hurley & Jansen, 1977; *Acutiserolis* sp.), fish (remains, not whole), hermit crabs, gastropods (*Antiguraleus* sp.), bivalves (*Deminucula* spp.), sponge, gorgonians, and ophiuroids (all <7%). Over the whole sample, the trophic level was 4.17. Benthic crustaceans and pelagic crustaceans were the two most important functional food-item groups (**Fig. 69B**).

There was a significant correlation with the weight of food items increasing with the size of the fish (Spearman rank correlation $r_s = 0.331$, $P < 0.003$). There was also a significant negative correlation with the numbers of food items decreasing with increasing fish size ($r_s = -0.405$, $P < 0.000$). Small-bodied organisms such as calanoid copepods, isopods and amphipods were replaced in the diets of larger fish by fewer, larger-bodied items: natant decapod prawns, fish and squid (**Fig. 70**). In general terms, dietary overlaps between size classes were low, with only one high level of overlap between the 50–69 and 70–77 mm HL classes (**Table 23**). Standardised niche breadths were low amongst the five size classes (**Fig. 70**), and over the total sample (0.21).

A further 102 intestines were examined, of which 87 contained food remains, giving a PEI of 14.7 percent. Polychaete and crustacean remains were the most frequently occurring items in the intestines (**Fig 71**).

Two of the dietary classifications adequately described the variation within the stomach contents of serrulate rattail (LPT & FG) (**Fig. 72, Fig. 73, Table 33**).

The minimum total number of stomachs required to describe the variation in the diet of serrulate rattail ranged between 23 and 67 (FG & LPT respectively). This was reflected in the S_{\max} values with between five and 32 stomachs describing 90 percent of the dietary variation (FG & LPT respectively) (**Table 24**). As the number of food categories decreased across the dietary classifications, the data were more able to describe the variation within the sample (**Table 24**). The food classification with multiple singletons (RW) was also the only food classification that failed to describe the variation within the stomach contents.

The intestinal contents datasets for RW and LPT were identical, so were treated as one. All of the dietary classifications adequately described the variation within the intestinal contents of serrulate rattail (**Fig 74, Fig 75, Table 25**). The minimum total number of intestines ranged between 80 and 83 (RW & LPT, and FG respectively), and S_{\max} values reflected this (**Table 25**). A singleton was present on each of the dietary classifications.

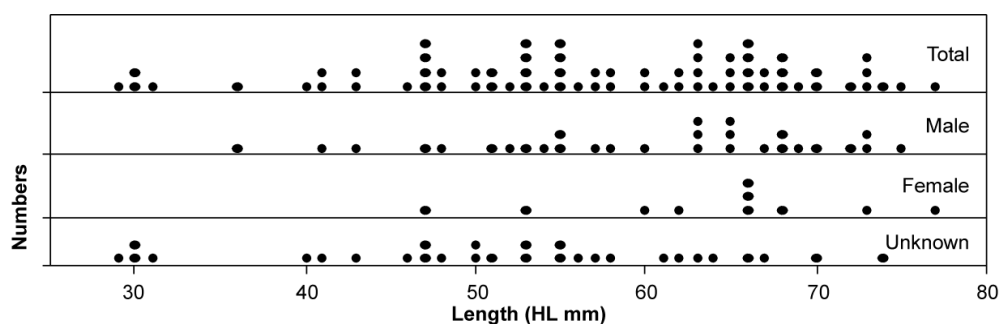
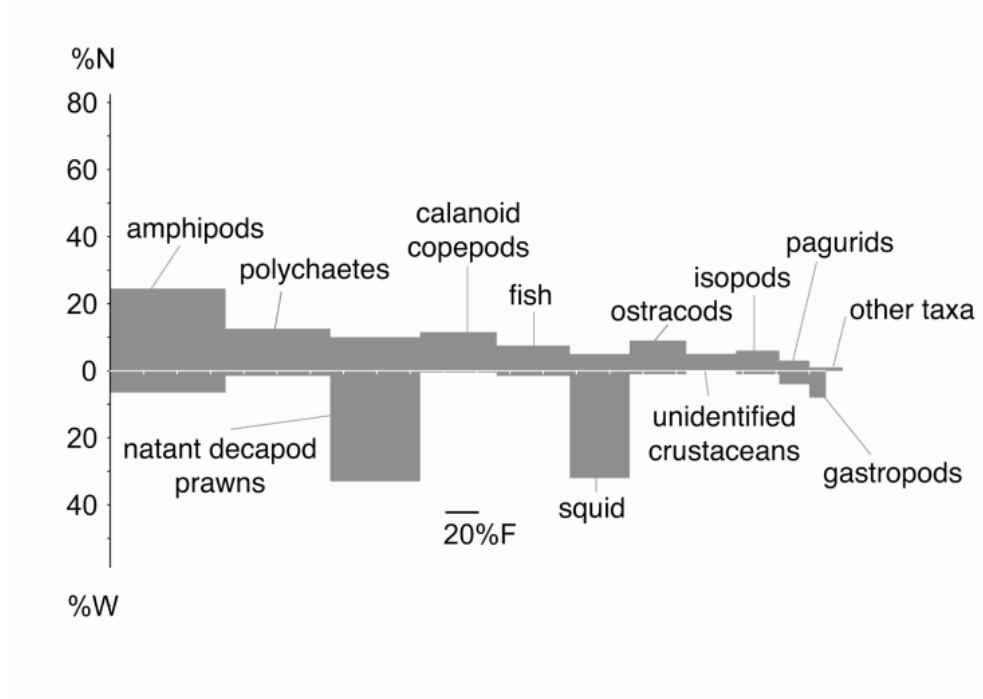


Figure 68. Size-frequency distribution for serrulate rattail (stomachs containing food) ($n = 68$, HL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

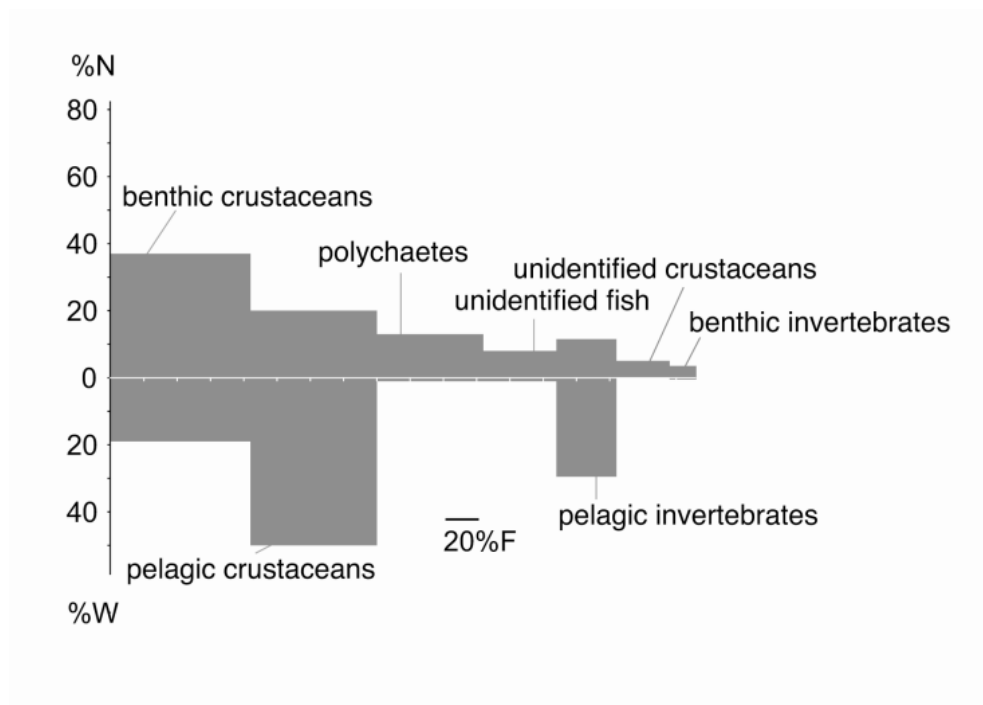


Figure 69. Diet of serrulate rattail from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 68$). **A.** Lowest practical taxon: other taxa: sponges, bivalves, and ophiuroids. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

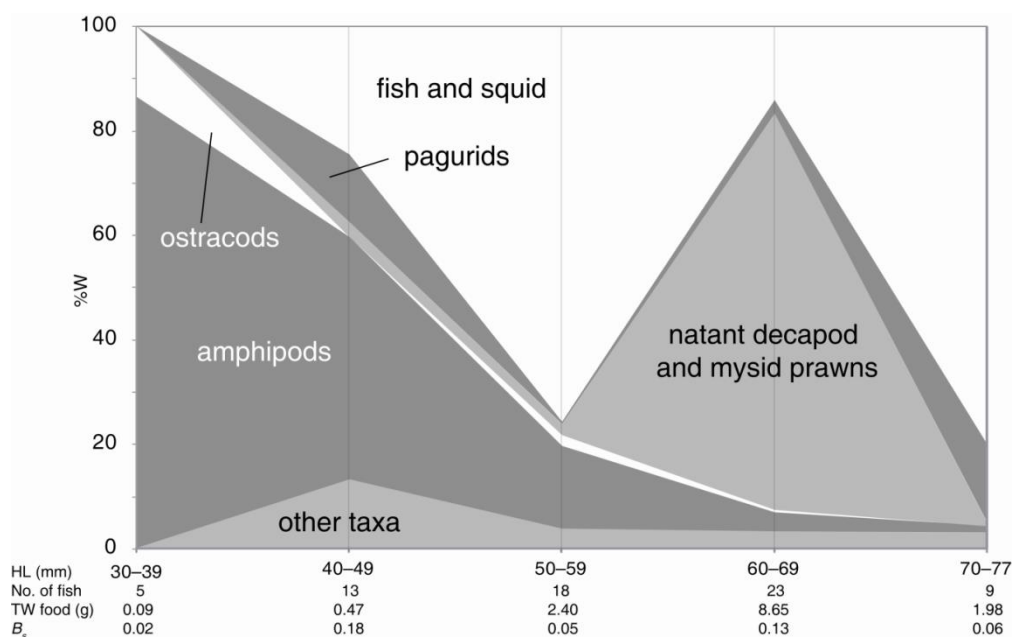


Figure 70. Diet of serrulate rattail from northeastern Chatham Rise over five size classes ($n = 68$, HL mm) (%W); number of fish (No.) in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon. Other taxa: calanoid copepods, isopods, gastropods, bivalves, ophiuroids, sponges, and gorgonians.

Table 23. Dietary overlap values for serrulate rattail from northeastern Chatham Rise over five size classes ($n = 68$, HL mm). Food categories are based on lowest practical taxon. Dark grey rectangles indicate biologically significant dietary overlaps $>60\%$. Calculations are based on %W.

Length (HL mm)	30-39 ($n = 5$)	40-49 ($n = 13$)	50-59 ($n = 18$)	60-69 ($n = 23$)	70-77 ($n = 9$)
30-39		0.5	0.1	0.0	0.0
40-49			0.5	0.3	0.4
50-59				0.2	0.8
60-69					0.2
70-77					

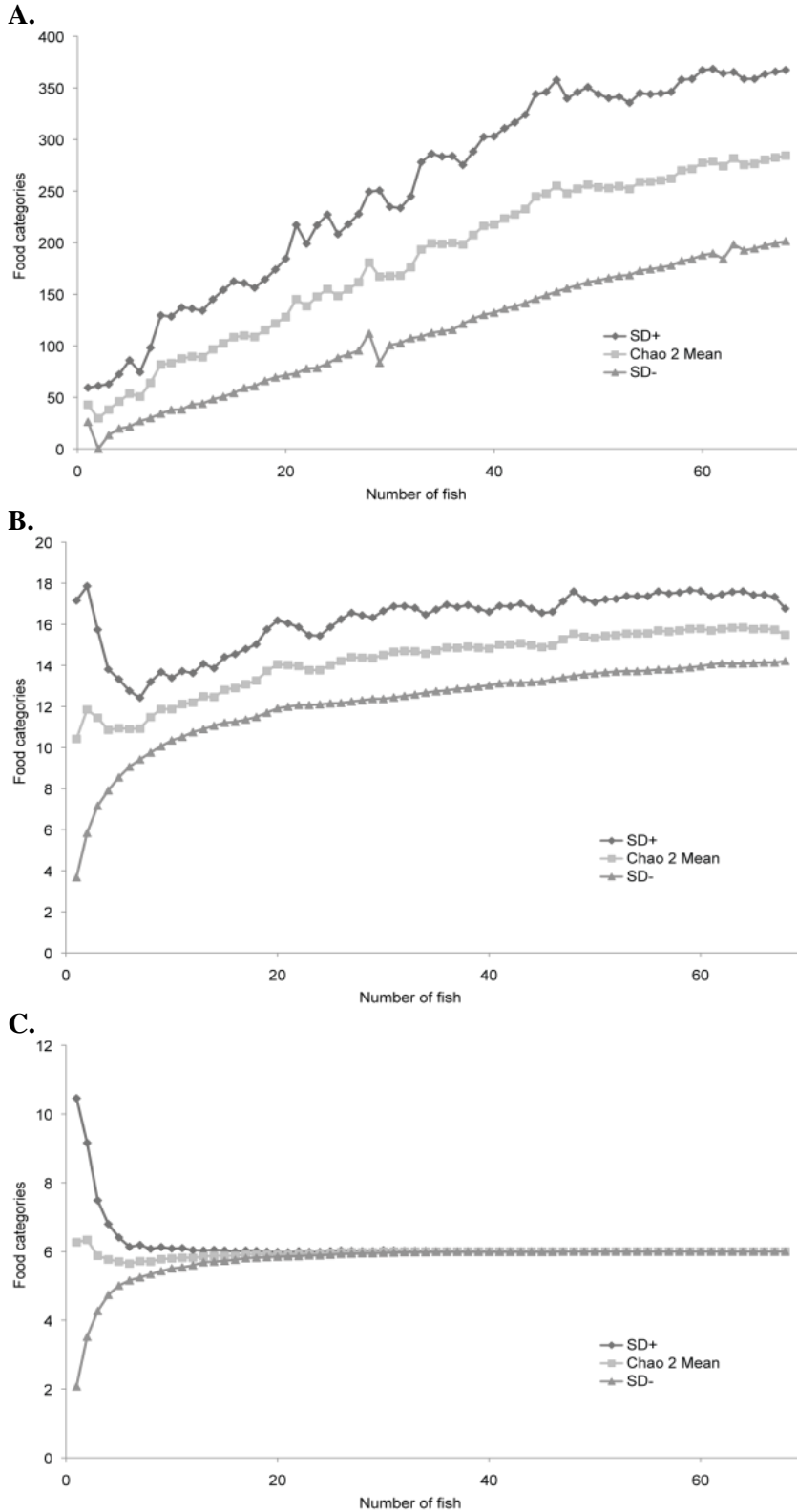


Figure 71. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of serrulate rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

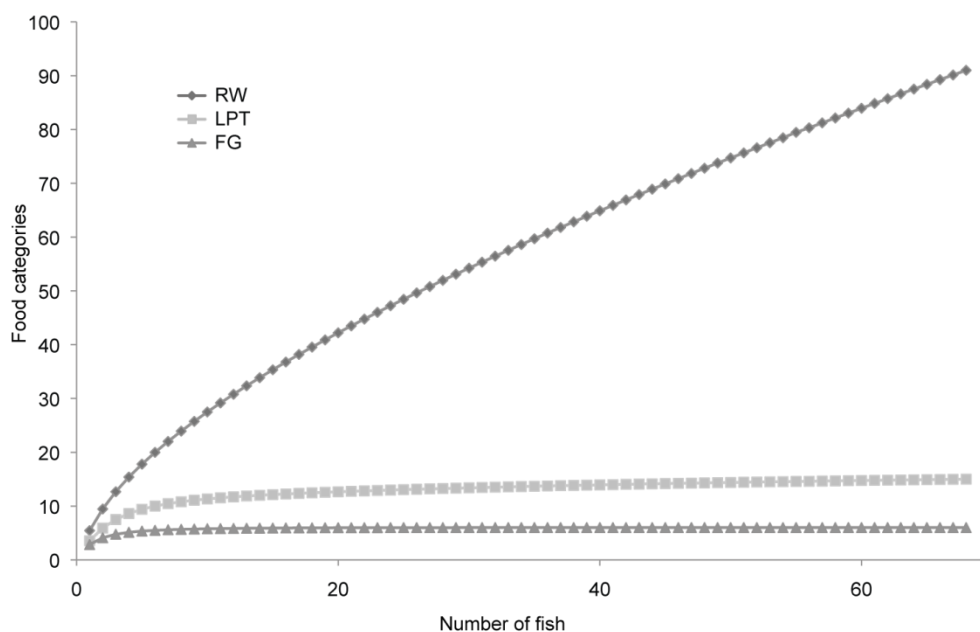
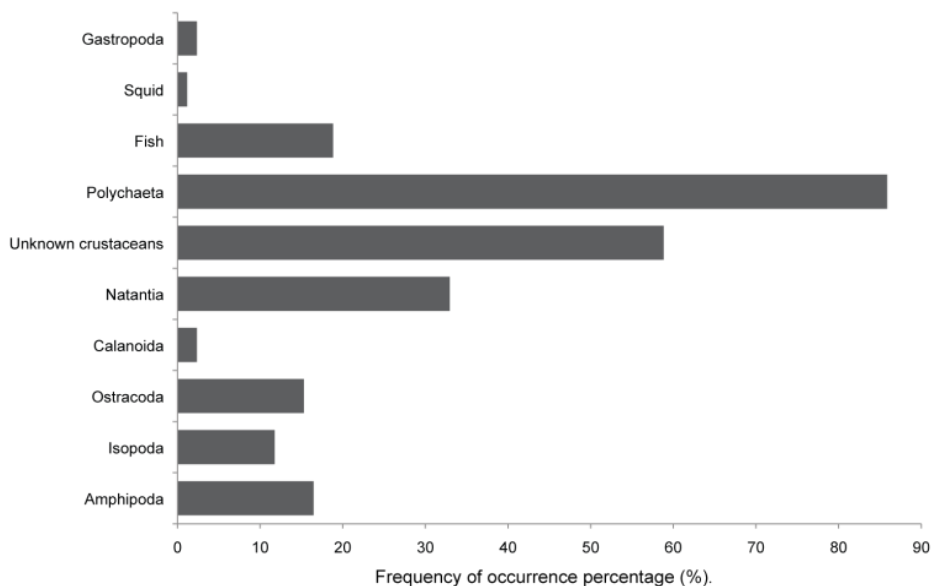


Figure 72. S_{obs} accumulation curves for the stomach contents of serrulate rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 24. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of serrulate rattail from northeastern Chatham Rise over three dietary classifications based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_i : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%		8	3
S_{max} 80%		14	4
S_{max} 90%		32	5
Min. total	NA	67	23
S_t	59	2	0
n	91	15	6

A.



B.

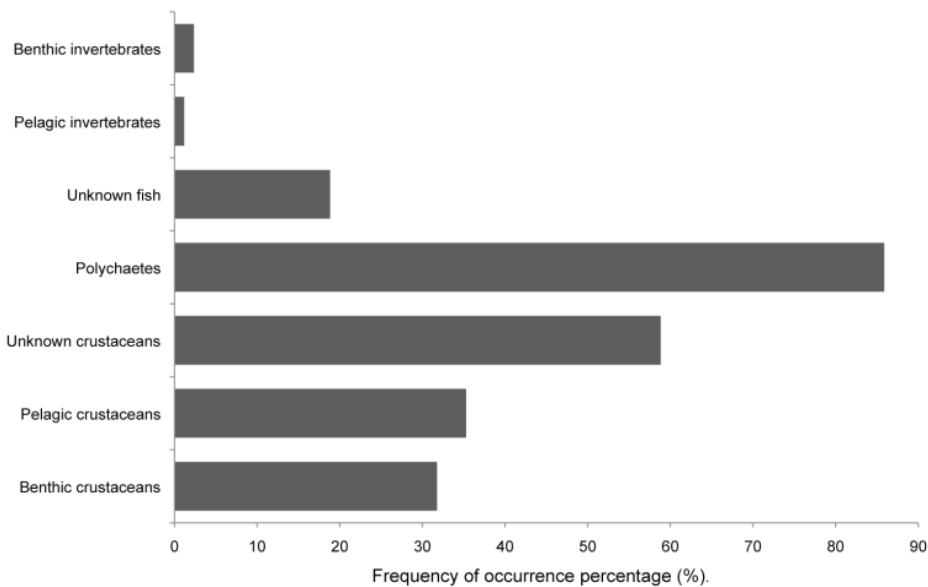


Figure 73. Intestinal contents of serrulate rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 87$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

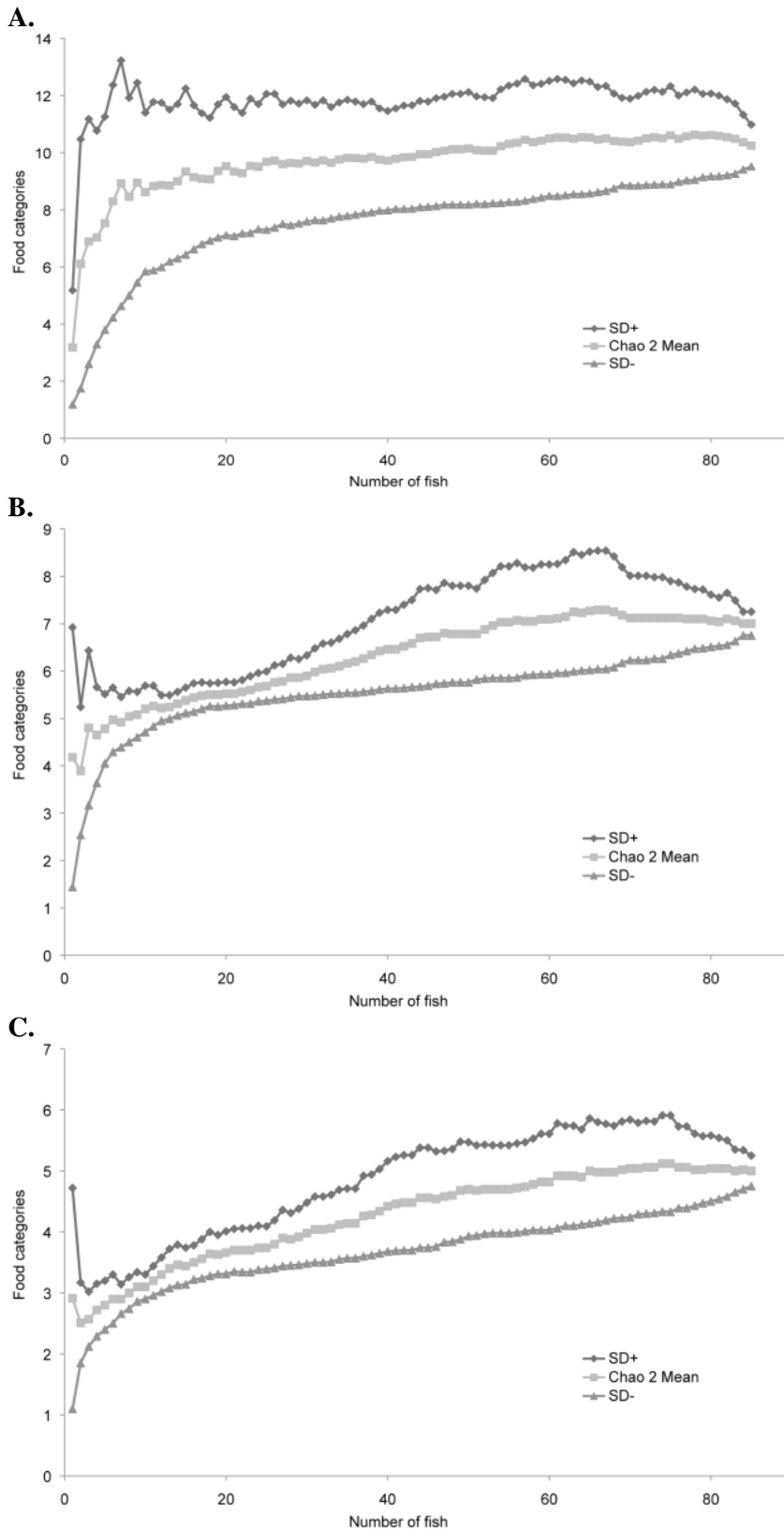


Figure 74. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of serrulate rattail from northeastern Chatham Rise. **A.** Raw data, lowest practical taxon. **C.** Functional food groups.

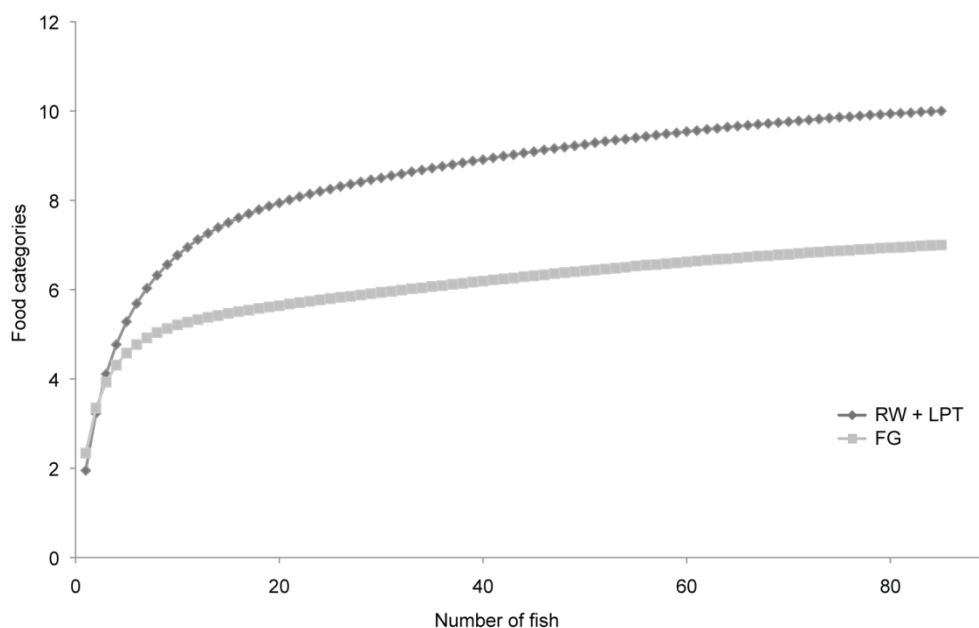


Figure 75. S_{obs} accumulation curves for the intestinal contents of serrulate rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 25. Number of fish estimated to describe 70–90% of S_{max} of the intestinal contents of serrulate rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	12	7
S_{max} 80%	21	18
S_{max} 90%	42	45
Min. total	80	83
S_t	1	1
n	10	7

4.1.14. Four-rayed rattail (CSU), *Coryphaenoides subserrulatus* ($n = 469$).

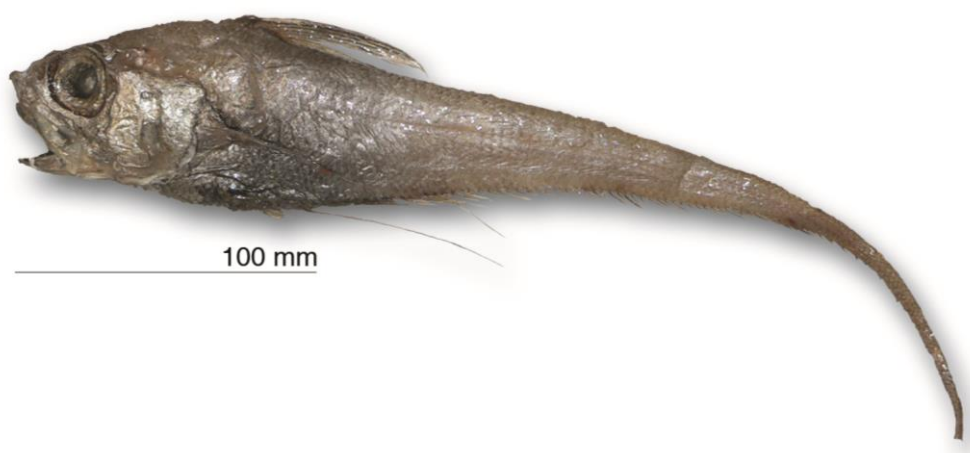


Figure 76. Four-rayed rattail, (CSU), *Coryphaenoides subserrulatus*.

Four hundred and sixty nine four-rayed rattail were examined and out of 107 non-everted stomachs, 97 contained food (**Fig. 77**). This gave a PES value of 9.3 percent. Calanoid copepods were the most important food-item for four-rayed rattail (84.2% IRI), particularly species from the family Aetideidae (*Bradyidius* spp., *Pseudoeuchaeta* sp., *?Uneuchaeta* sp.) and to a lesser extent those of the family Metridinidae (*Pleuromamma abdominalis* Lubbock, 1856; *P. quadrungulata* Dahl, 1893). The remainder of the diet consisted of gammaridean amphipods, polychaetes, natant decapod prawns, chaetognaths, fish, squid, ostracods, mysid prawns and isopods. Over the whole sample, the trophic level was 4.00. The most important functional food-item group was pelagic crustaceans (**Fig. 78A**). There was a significant correlation with the weight of food items increasing with the size of the fish, but not the number of food items (Spearman rank correlation $r_s = 0.172$, $P < 0.046$, $r_s = -0.026$, $P > 0.399$ respectively). Dietary overlap values were high for all size class comparisons (**Table 26**). Standardised niche breadth values were low for the four size classes (**Fig. 79**), and low overall (0.12).

Two of the dietary classifications adequately described the variation within the stomach contents of four-rayed rattail (LPT, FG) (**Fig. 80**, **Fig. 81**, **Table 27**). The minimum total number of stomachs required to describe the variation in the diet of four-rayed rattail ranged between four and 53 (FG & LPT) (**Table 27**). This was also reflected in the S_{\max} values (**Table 27**), with between three and 23 stomachs required to describe 90 percent of the dietary variation (FG and LPT respectively). Multiple singletons were present in RW (**Table 27**).

Material was also recovered from 210 intestines, and this was mostly calanoid copepod, polychaete and chaetognath remains (Fig. 82). The RW and LPT intestinal contents datasets were identical so were treated as one. The dietary variation within the intestines of four-rayed rattail was adequately described by all dietary classifications (Fig 83, Fig 84, Table 28). The minimum total number of intestines required to describe the dietary variation of four-rayed rattail ranged between 78 (FG), and 138 (RW & LPT) (Table 28).

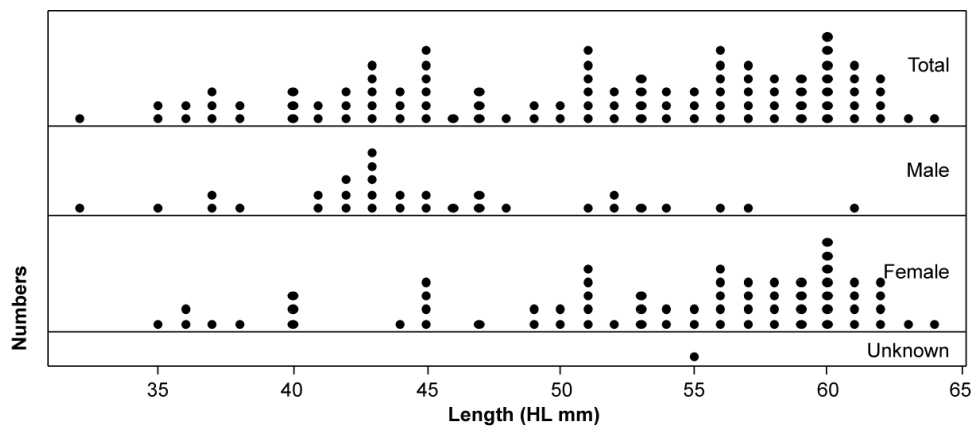
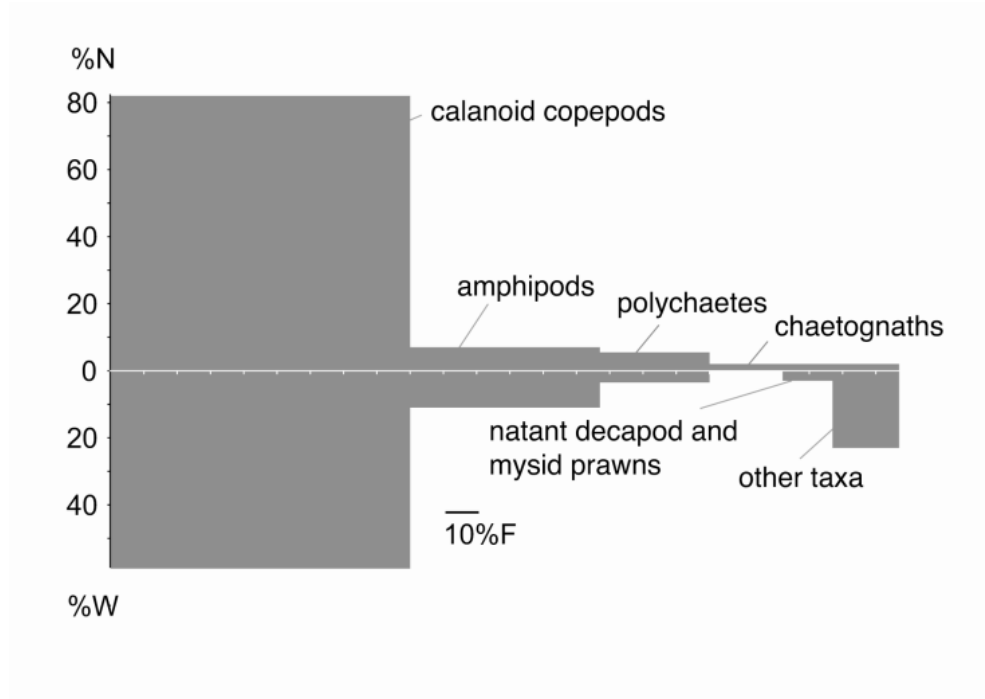


Figure 77. Size-frequency distribution for four-rayed rattail (stomachs containing food), ($n = 97$, HL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

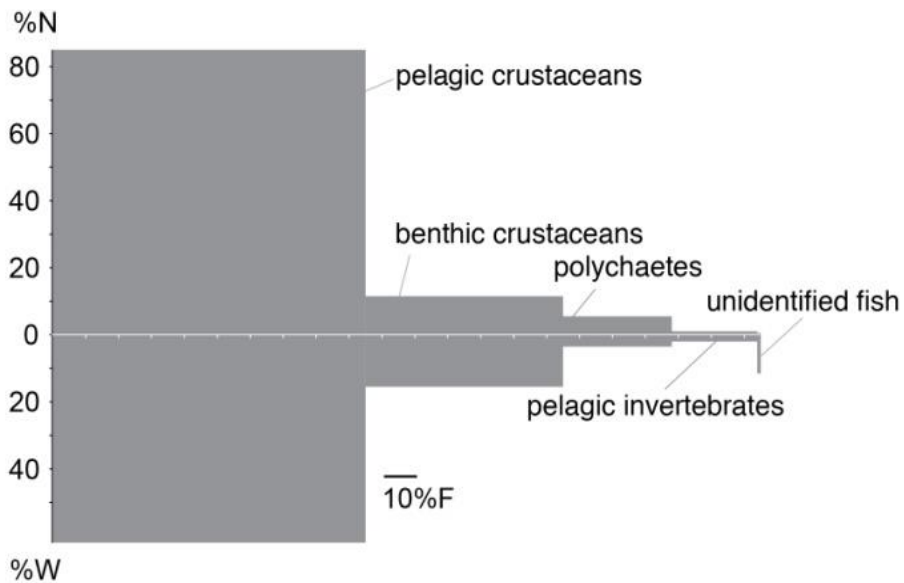


Figure 78. The diet of four-rayed rattail from northeastern Chatham Rise expressed as percentage IRI area charts. **A.** Lowest practical taxon: other taxa; ostracods, isopods. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

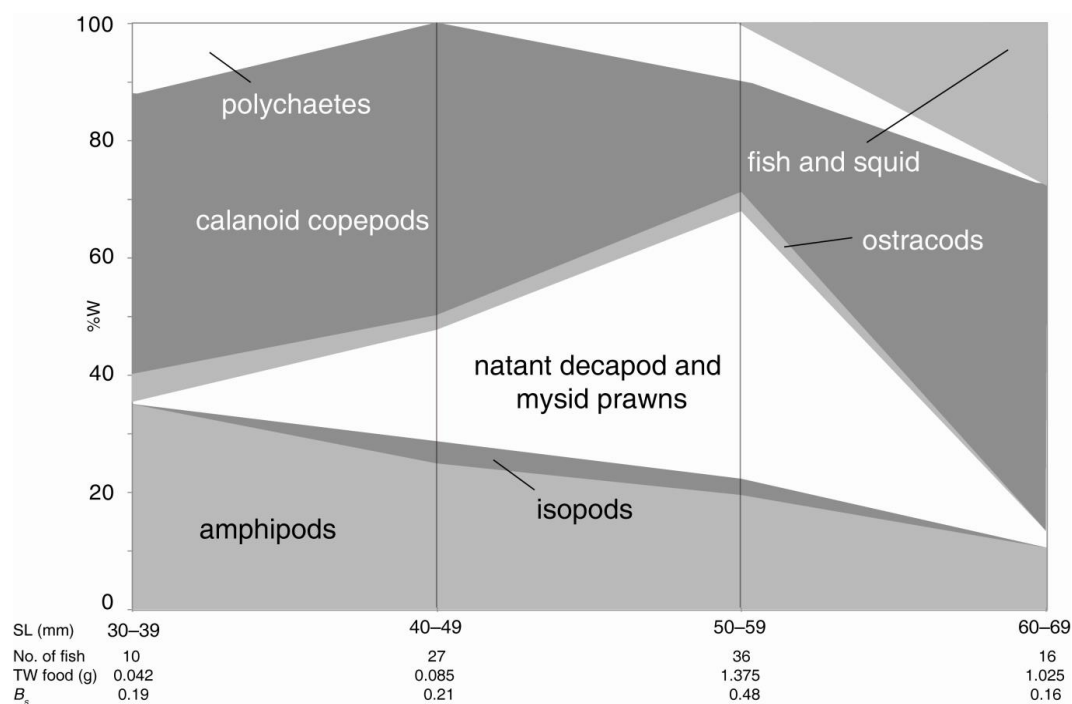


Figure 79. Diet of four-rayed rattail from northeastern Chatham Rise over four size classes ($n = 97$, HL mm) (%W); number of fish (No.) in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon.

Table 26. Dietary overlap values (%W) for four-rayed rattail from northeastern Chatham Rise for four size classes ($n = 97$, HL mm). Food categories are based on the lowest practical taxon. Dark grey rectangles indicate biologically significant dietary overlaps >60%. Calculations are based on %W.

Length (HL mm)	30-39 ($n = 10$)	40-49 ($n = 27$)	50-59 ($n = 36$)	60-69 ($n = 16$)
30-39		0.8	0.6	0.7
40-49			0.6	0.8
50-59				0.7
60-69				

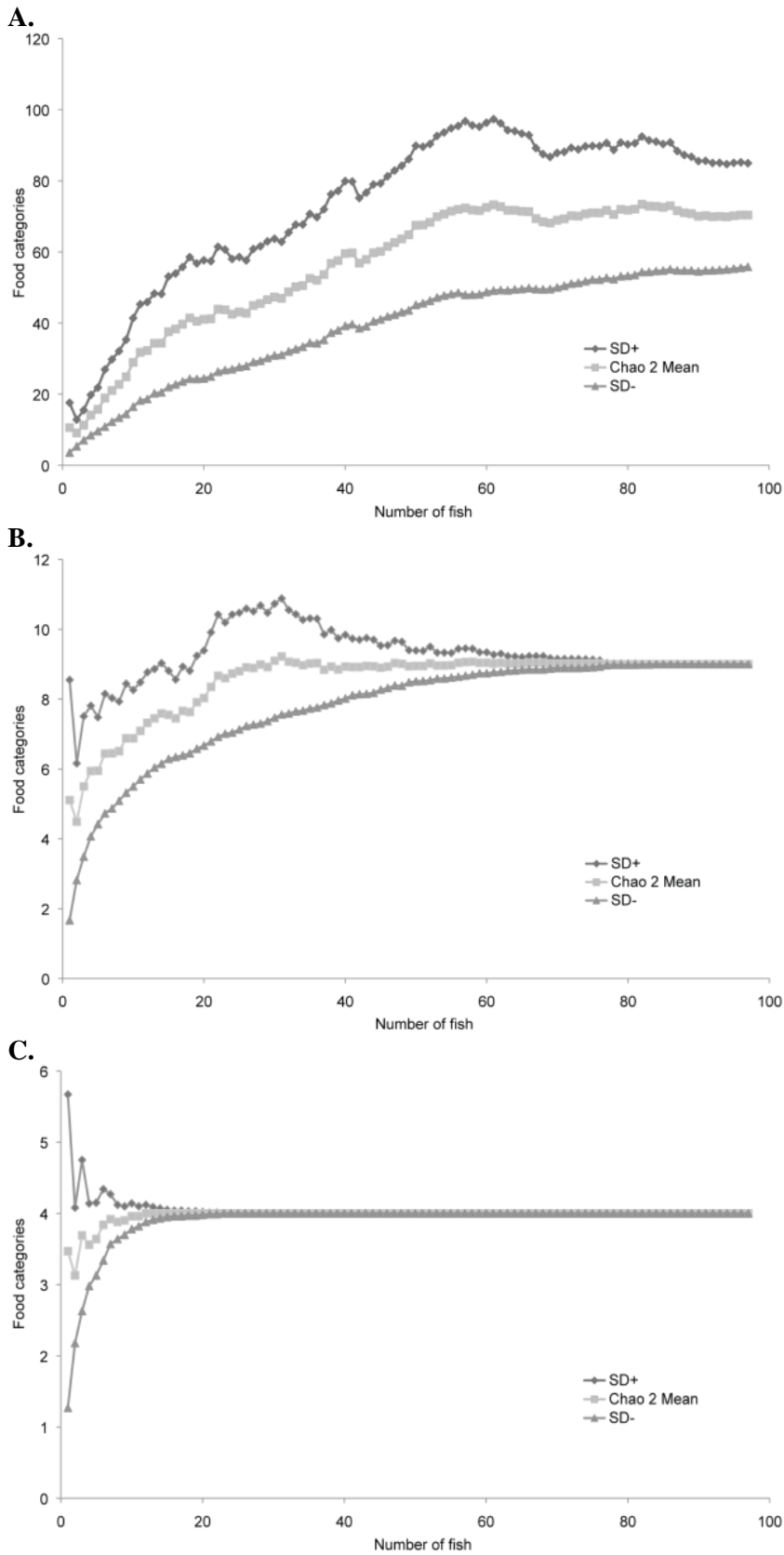


Figure 80. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of four-rayed rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

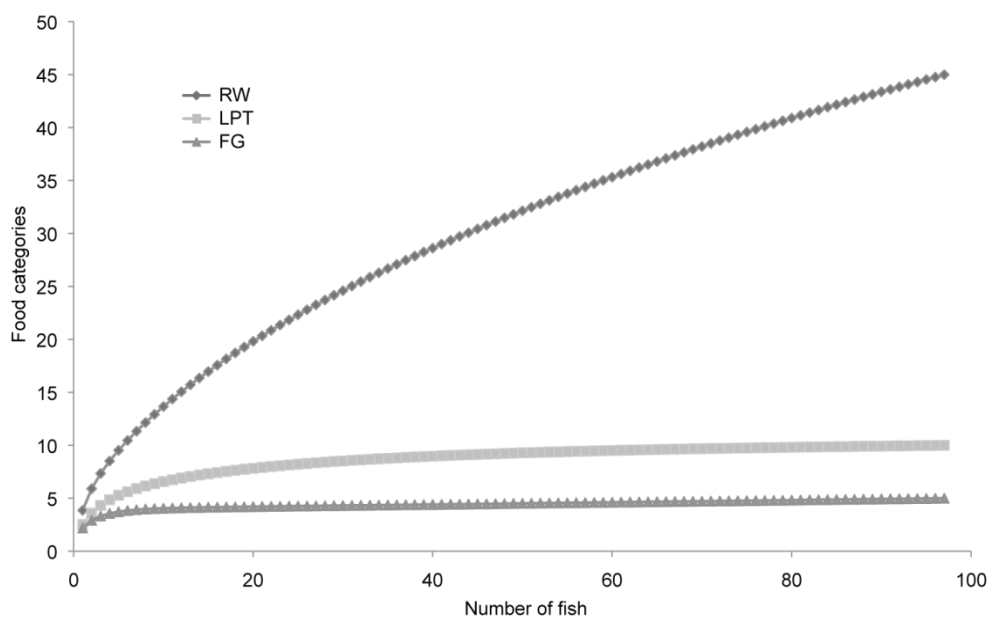
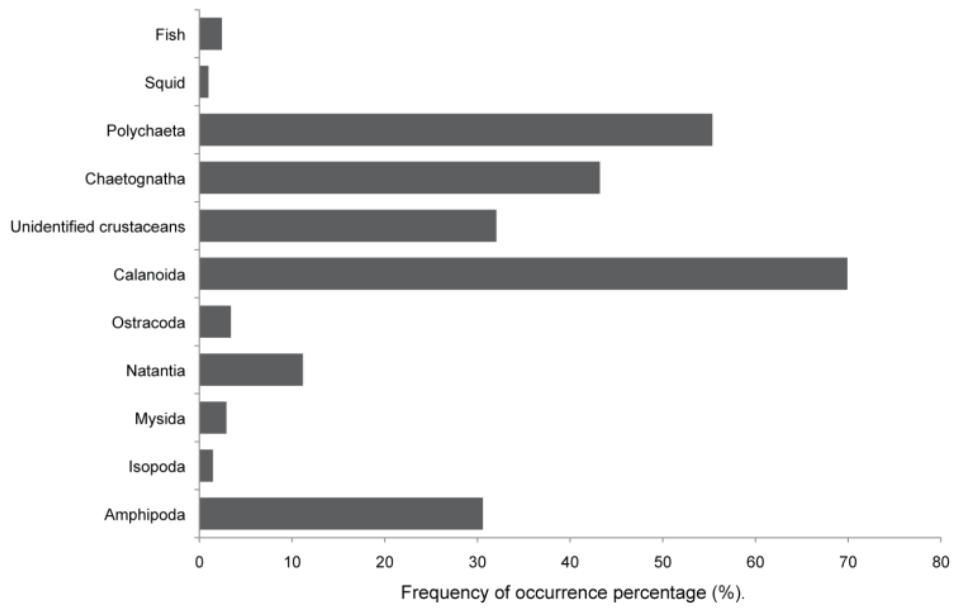


Figure 81. S_{obs} accumulation curves for the stomach contents of four-rayed rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 27. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of four-rayed rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%		9	2
S_{max} 80%		14	2
S_{max} 90%		20	3
Min. total	NA	53	4
S_t	22	1	0
n	45	9	4

A.



B.

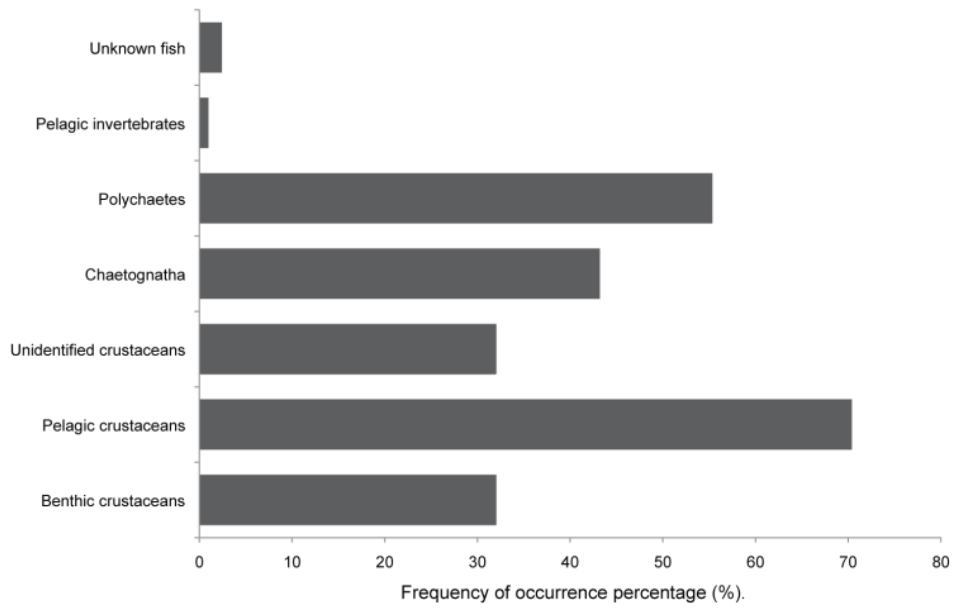


Figure 82. Intestinal contents of four-rayed rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 101$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

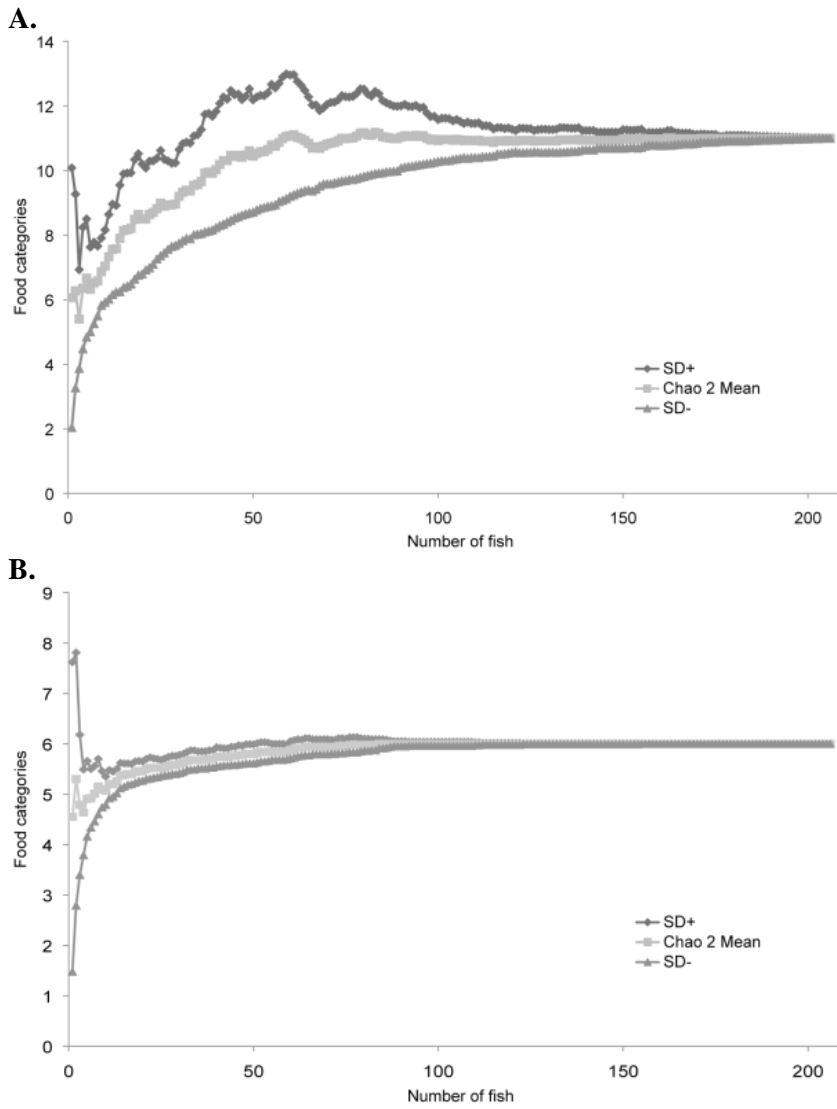


Figure 83. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of four-rayed rattail from northeastern Chatham Rise. **A.** Raw data, lowest practical taxon. **B.** Functional food groups.

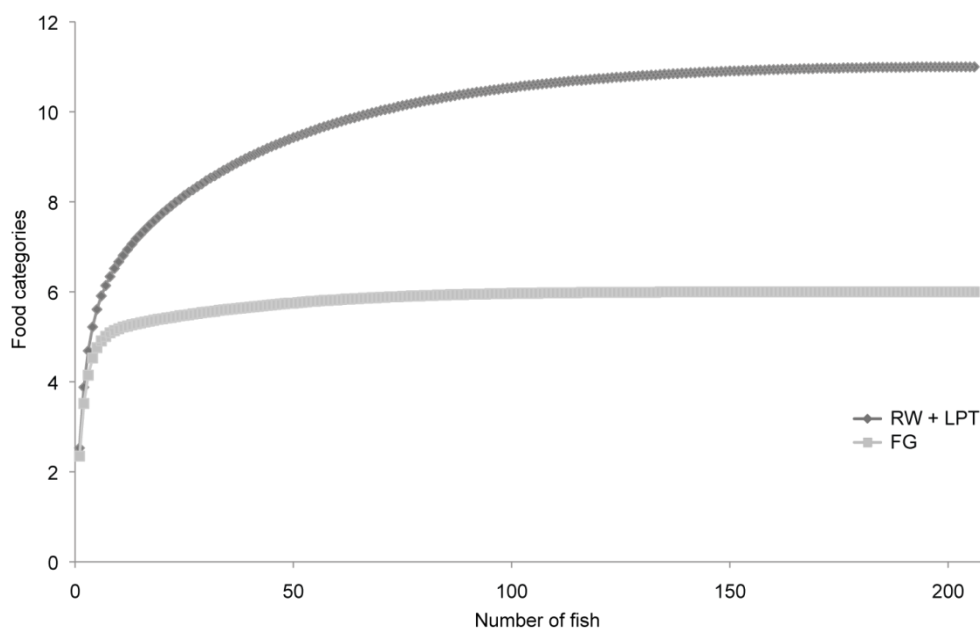


Figure 84. S_{obs} accumulation curves for the intestinal contents of four-rayed rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 28. Number of fish estimated to describe 70–90% of S_{max} of four-rayed rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	20	4
S_{max} 80%	33	6
S_{max} 90%	66	20
Min. total	138	78
S_t	0	0
n	11	6

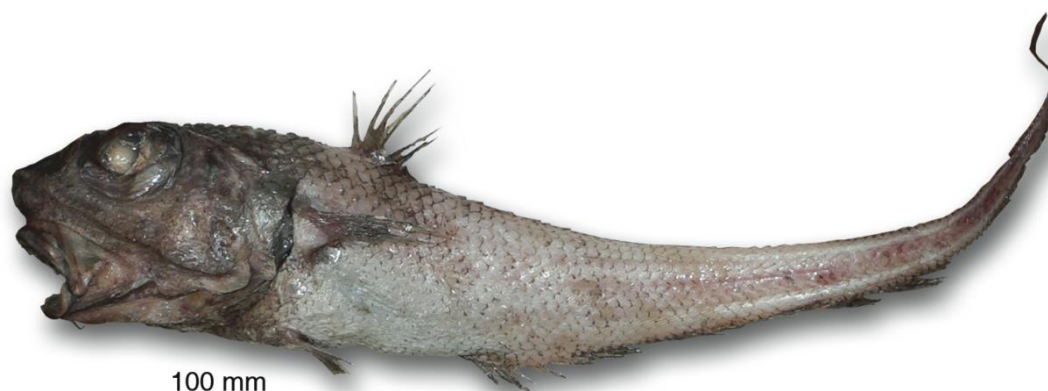
4.1.15. Ridge-scaled rattail (MCA), *Macrourus carinatus* ($n = 40$)

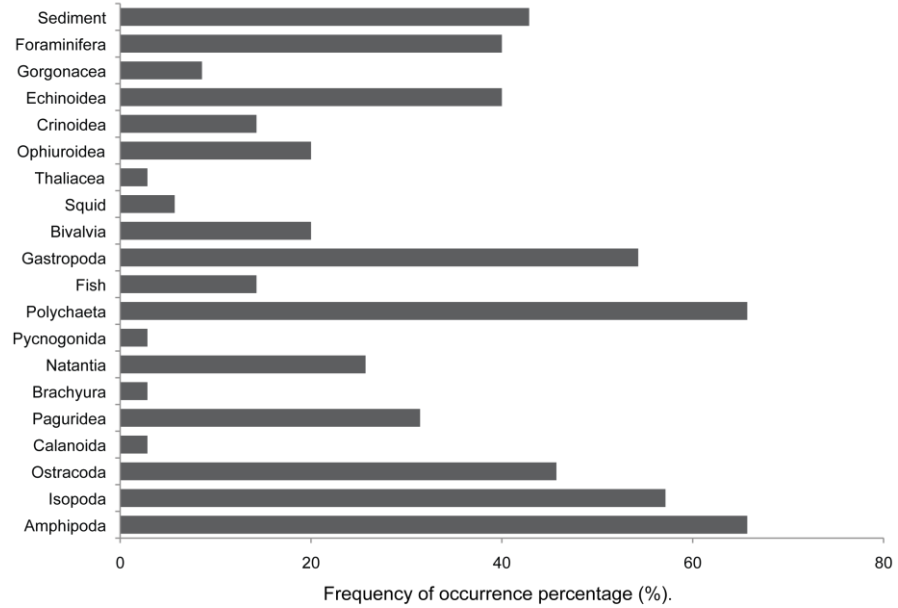
Figure 85. Ridge-scaled rattail, (MCA), *Macrourus carinatus*.

Forty ridge-scaled rattail were examined and only six stomachs contained food; all others were everted. These six non-everted stomachs were from a wide range of fish sizes; of these only the largest individuals (>100 mm HL) had eaten fish (?Myctophidae); smaller fish were found to have consumed gammaridean amphipods (including *Eurythenes thurstoni*, Stoddart & Lowry 2004), polychaetes, ophiuroids, natant decapod prawns, myodocopid ostracods (*Bathyvargula* sp.), isopods (Sphaeromatidae, Gnathiidae), and hermit crabs. Over the whole sample, the trophic level was 3.62.

The intestines of 35 ridge-scaled rattail contained a wide variety of food items (**Fig. 86**): amphipods (Eurytheneidae, Stegocephalidae), polychaetes (including *Hyalinoecia* sp.); gastropods (*A. meridiana*; *Falsilunatia* sp.; *Globisinum* sp.; *N. ephamillus*; *Paracomitas* cf. *gypsata* Watson, 1881; ?*Leucosyrinx* sp.; *Philine* sp.), bivalves (*Parvamussium maorium*, *Psuedotindaria flemingi*, *Dacrydium* sp., *Cuspidaria* sp.), isopods (*Acutiserolis* sp., *Natatolana* sp., *C. ?impudica*), and myodocopid ostracods (*Bathyvargula* sp.; *M. bradfordae*; *Cyprinoides ?reticulata*). One fish had eaten a sea spider (*Colossendeis* sp.), and another had 12 *P. maorium* in its intestine. Sediment was present in most intestines. The PEI was 12.5 percent.

The dietary variation within the intestines of ridge-scaled rattail was adequately described by all dietary classifications (**Fig 87, Fig 88, Table 29**). The minimum total number of intestines needed to describe the variation in the diet ranged between 21 (FG) and 32 (RW) (**Table 29**). This was reflected in the S_{\max} values, with fewer intestines required to describe the dietary variation with the reduction of food categories (**Table 29**).

A.



B.

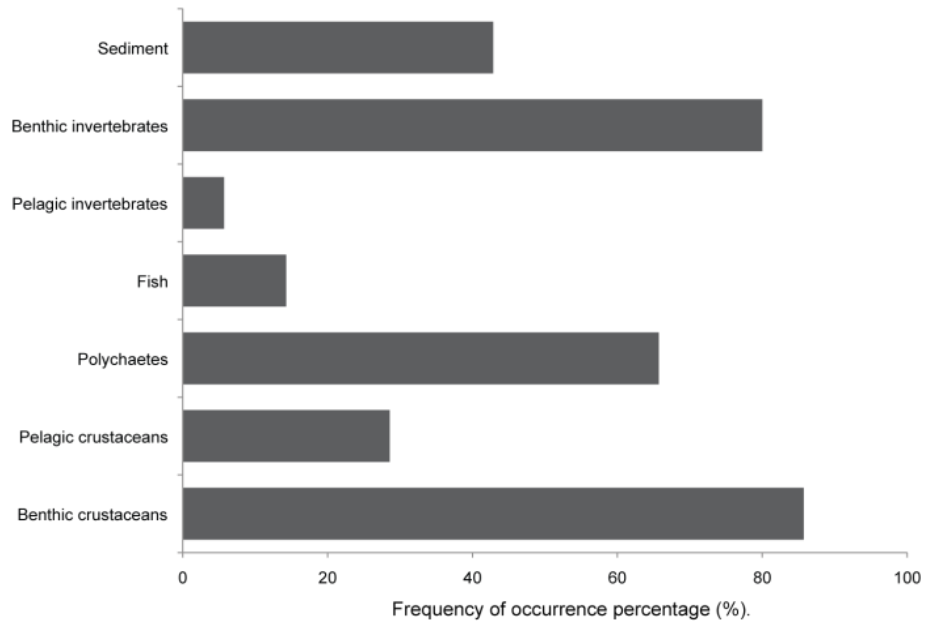


Figure 86. Intestinal contents of ridge-scaled rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 35$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

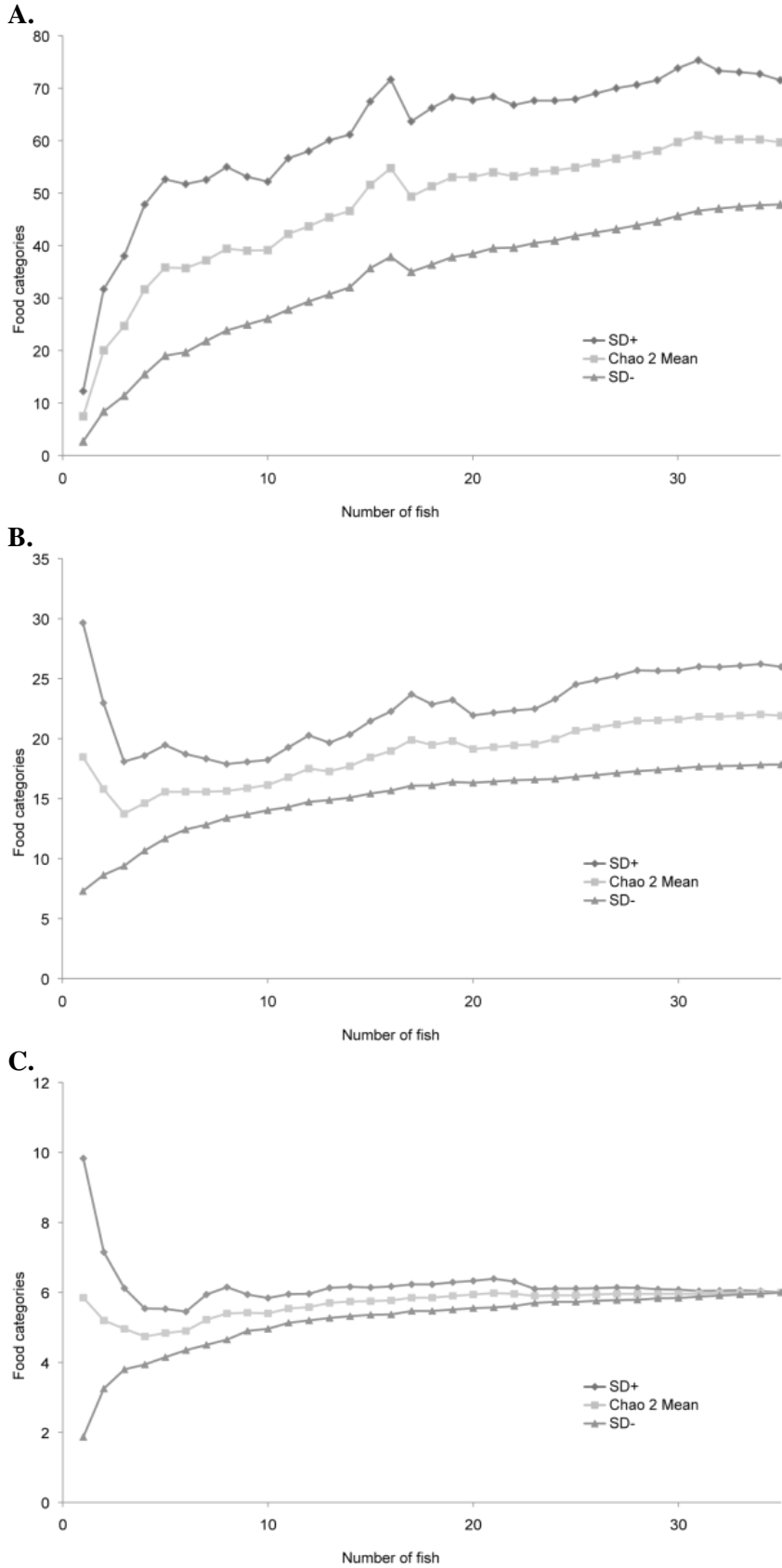


Figure 87. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of ridge-scaled rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

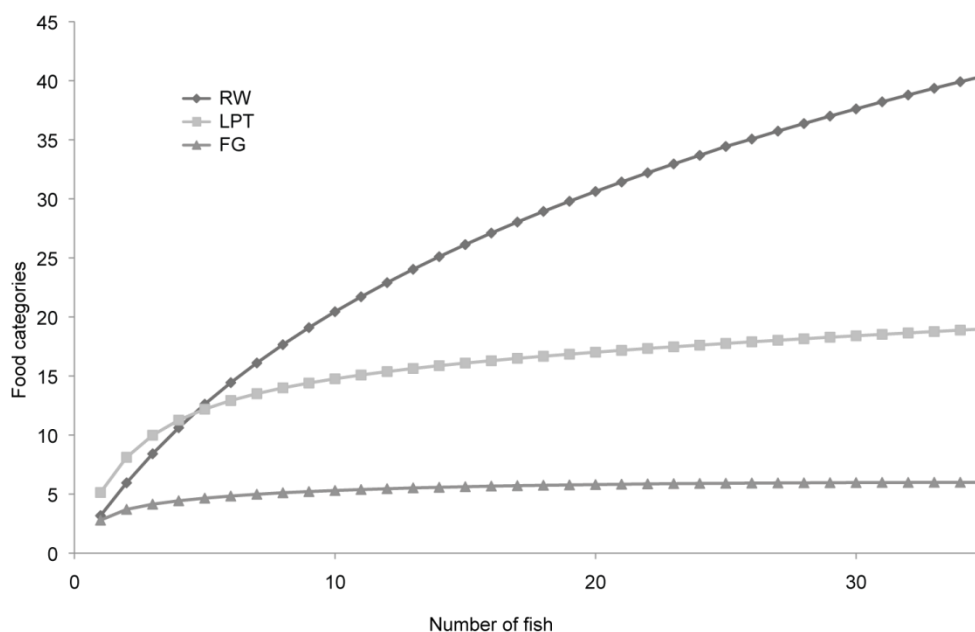


Figure 88. S_{obs} accumulation curves for the intestinal contents of ridge-scaled rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 29. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of ridge-scaled rattail from northeastern Chatham Rise over four dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

INTESTINES	RW	LPT	FG
S_{max} 70%	17	7	4
S_{max} 80%	21	12	6
S_{max} 90%	26	21	12
Min. total	32	26	21
S_t	19	4	0
n	42	19	6

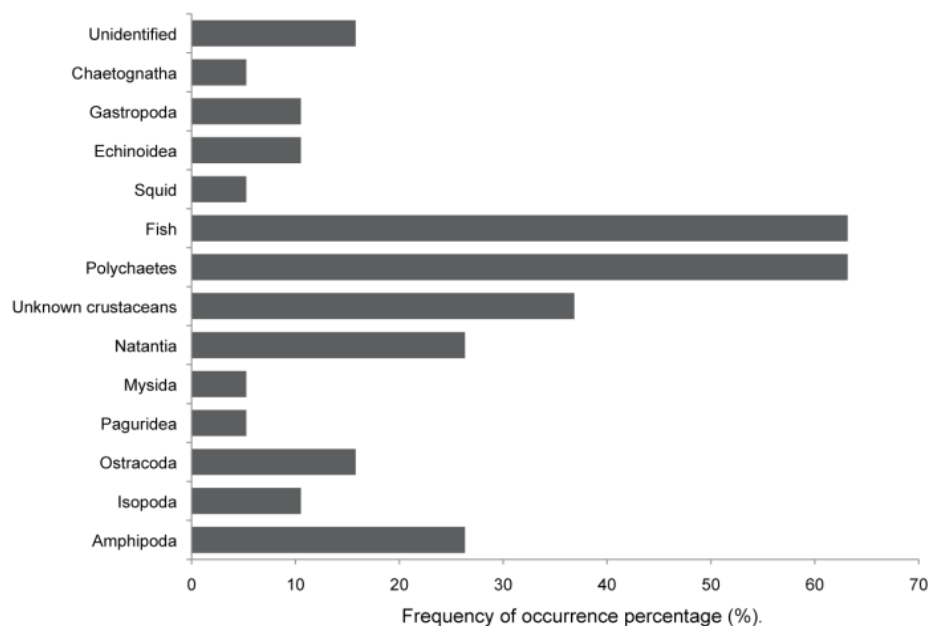
4.1.16. White rattail (WHX), *Trachyrincus aphoydes* ($n = 19$)



Figure 89. White rattail, (WHX), *Trachyrincus aphoydes*.

All 19 white rattail examined had everted stomachs and all intestines contained food items (**Fig. 90**), the latter comprising polychaetes, fish, amphipods (Stegocephalidae), gastropods (?*Mesoginella* sp.), natant decapod and mysid prawns (*Gnathophausia* sp.), and myodocopid ostracods (*Bathyvargula* sp.). Sediment also was present in most intestines. Over the whole sample, the trophic level was 3.67. The dietary variation within the stomachs of white rattail was adequately described by all dietary classifications (**Fig. 91, Fig. 92, Table 30**). The minimum total number of intestines needed to describe the variation in the diet ranged between 10 (FG) and 16 (LPT) (**Table 30**). This was reflected in the S_{\max} values, with fewer intestines required to describe the dietary variation with the reduction of food categories (**Table 30**).

A.



B.

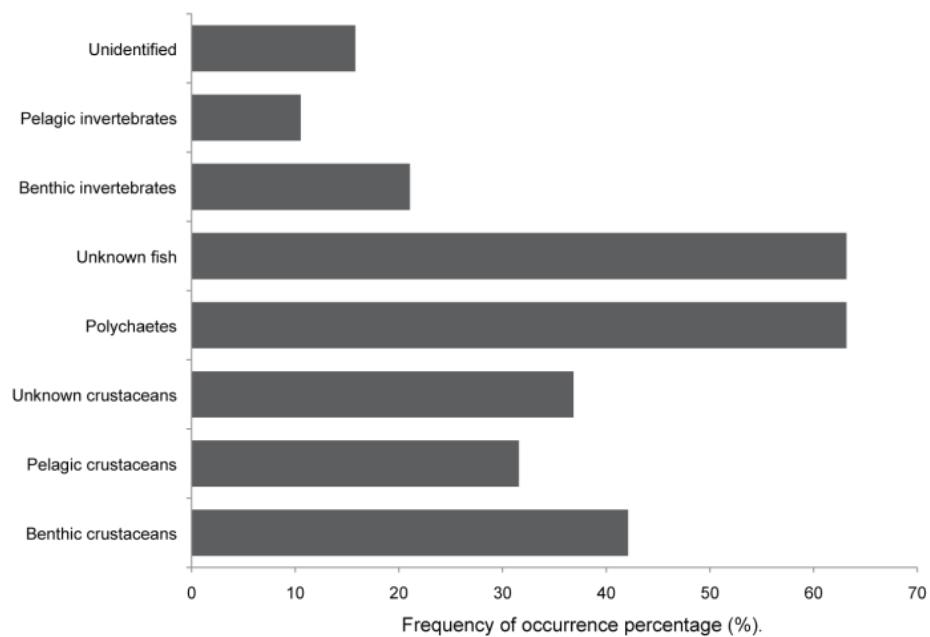


Figure 90. Intestinal contents of white rattail from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 19$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

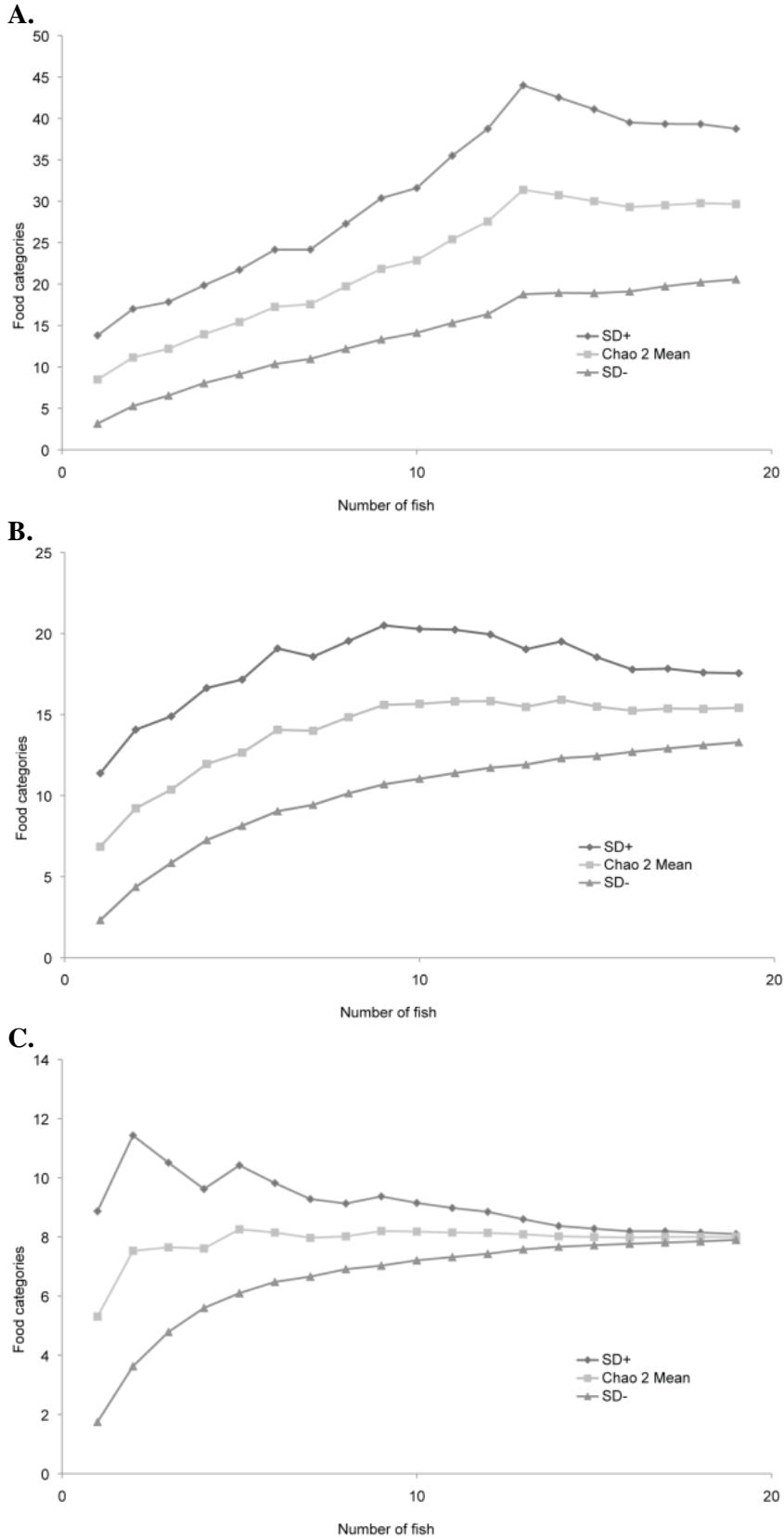


Figure 91. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of white rattail from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

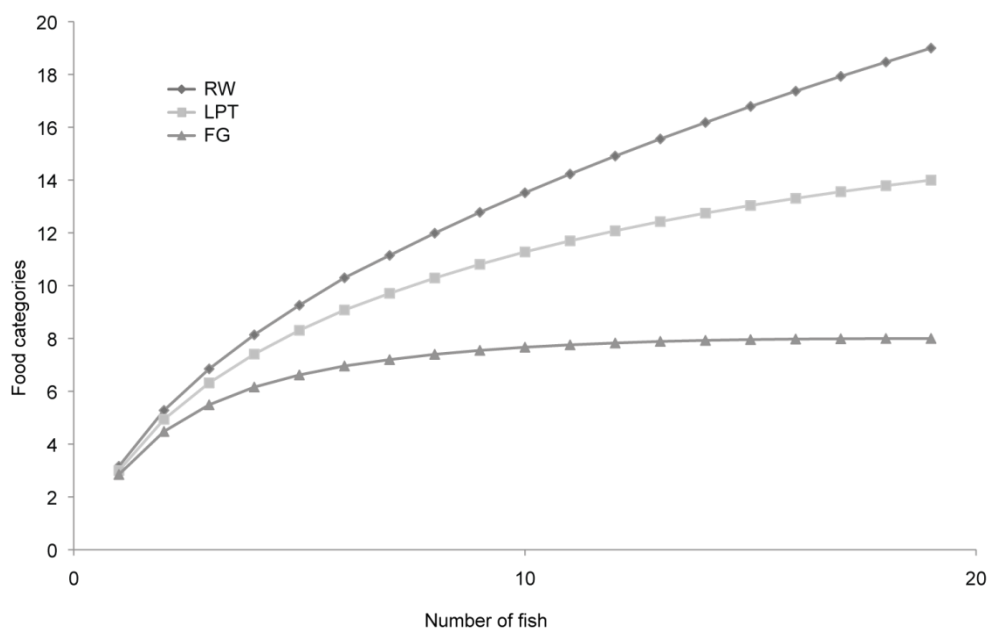


Figure 92. S_{obs} accumulation curves for the intestinal contents of white rattail from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 30. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of white rattail from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

INTESTINES	RW	LPT	FG
S_{max} 70%	8	6	3
S_{max} 80%	10	10	4
S_{max} 90%	12	14	6
Min. total	14	16	10
S_t	10	4	0
n	19	14	8

4.1.17. Warty oreo (WOE), *Allocyttus verrucosus* ($n = 29$)

Figure 93. Warty oreo (WOE), *Allocyttus verrucosus*.

Thirteen warty oreo had stomachs containing food; all other stomachs were everted (**Fig. 94**), giving a PES of 55.2 percent. Fish (whole and remains) dominated the diet of warty oreo (61.1% IRI) (**Fig. 95A**), followed by calanoid copepods (including *Paraeuchaeta sarsi* Farran, 1908) (29.3% IRI). Natant decapod (Crangonidae, Sergestidae and Nematocarcinidae) and mysid prawns (*Gnathophausia* sp.), chaetognaths, squids (Cranchiidae and *H. atlantica*) and thaliaceans (remains) were also consumed (each <3%). Over the whole sample, the trophic level was 4.88. Pelagic crustaceans and unidentified fish were the two most important functional food-item groups (**Fig. 95B**). There was a significant correlation between the weight of food items and increasing fish size (Spearman rank $r_s = 0.626$, $P < 0.011$), but not the number of food items per stomach (Spearman rank $r_s = 0.188$, $P > 0.269$). Overall standardised niche breadth was low (0.11). Eleven warty oreo had intestines containing food, and this comprised mainly fish and calanoid copepod remains (**Fig 97**).

The dietary variation in the stomachs of warty oreo was adequately described by one of the dietary classifications (LPT) (**Fig. 97, Fig. 98, Table 31**). The minimum number of stomachs required to describe the dietary variation for LPT was ten (**Table 31**), with eight required to describe S_{\max} 90%. There were multiple singletons in each dietary classification (**Table 31**).

The RW and LPT intestinal contents datasets were identical, so were treated as one, and adequately described the dietary variation, while FG did not (**Fig. 99, Fig. 100, Table 32**). The minimum number of intestines needed to describe the dietary

variation in warty oreo was eight, with 90 percent of the dietary variation being described by seven intestines (**Table 32**).

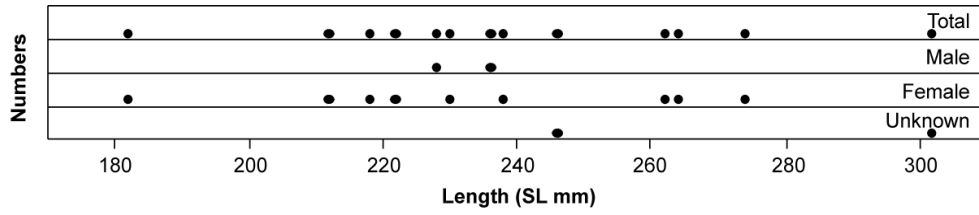
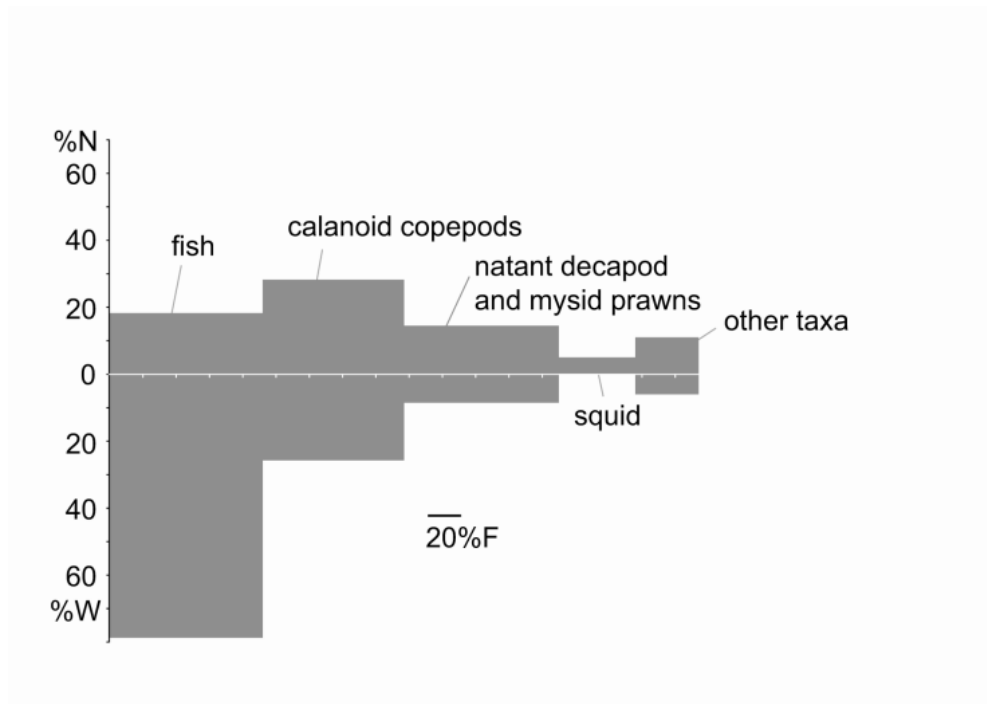


Figure 94. Size-frequency distribution for warty oreo (stomachs containing food) ($n = 13$, SL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

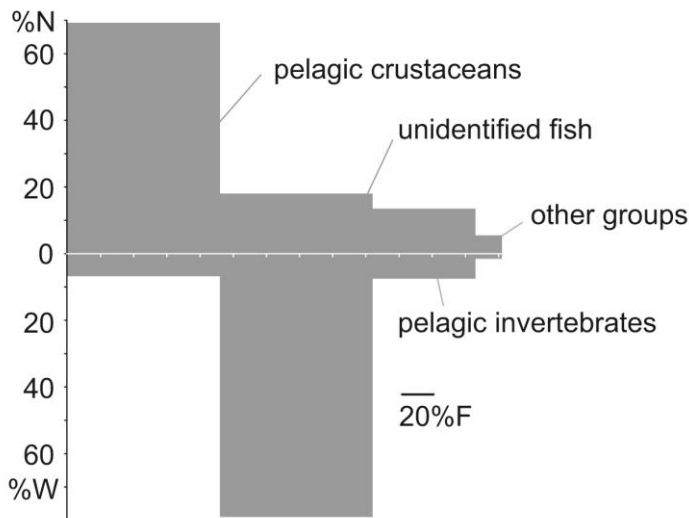


Figure 95. Diet of wary oreo from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 13$). **A.** Lowest practical taxon: other taxa; thaliaceans, ostracods, chaetognaths, and unidentified material. **B.** Functional food-item groups: other groups, benthopelagic crustaceans and unidentified. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

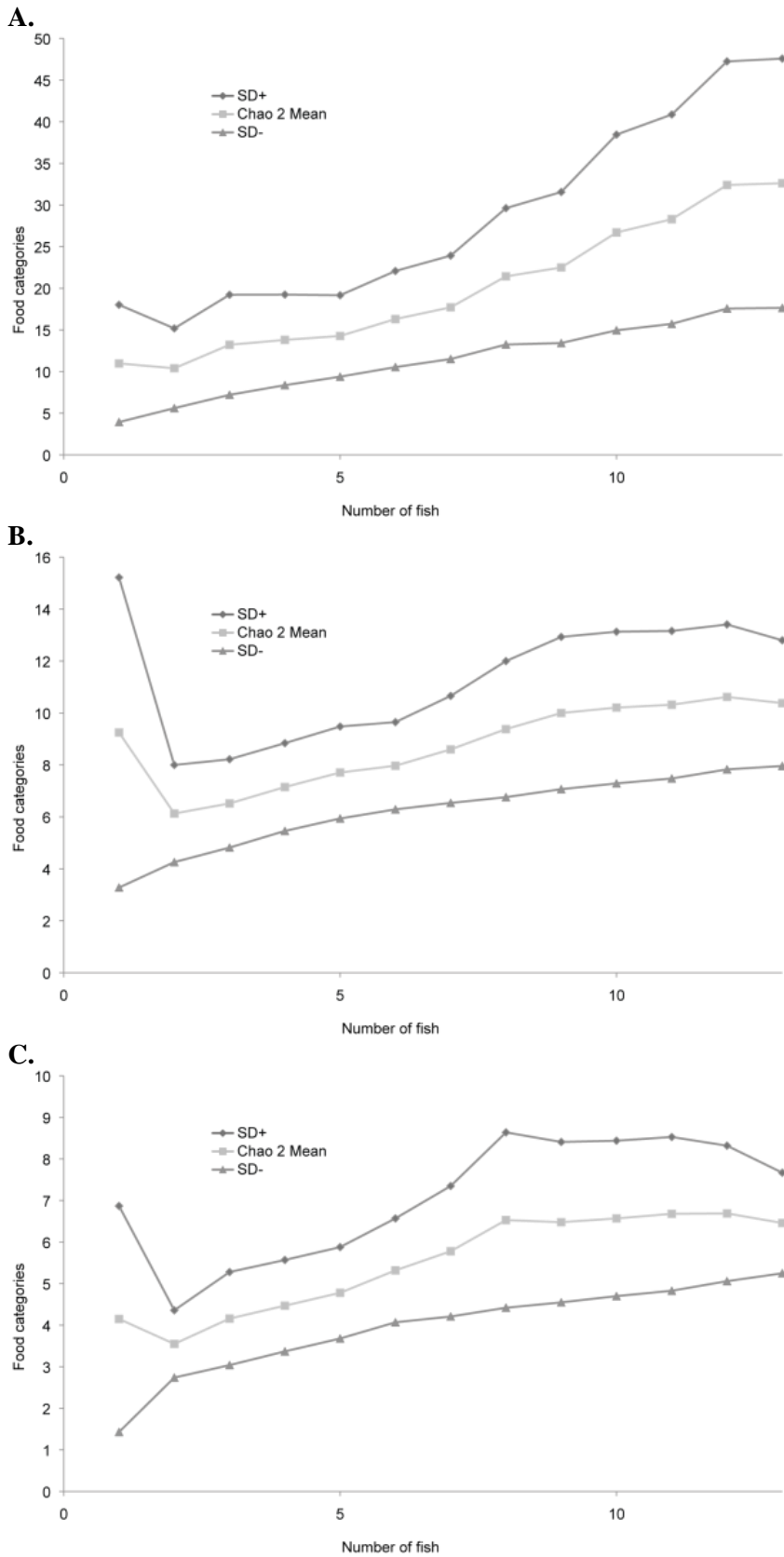


Figure 96. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of wary oreo from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

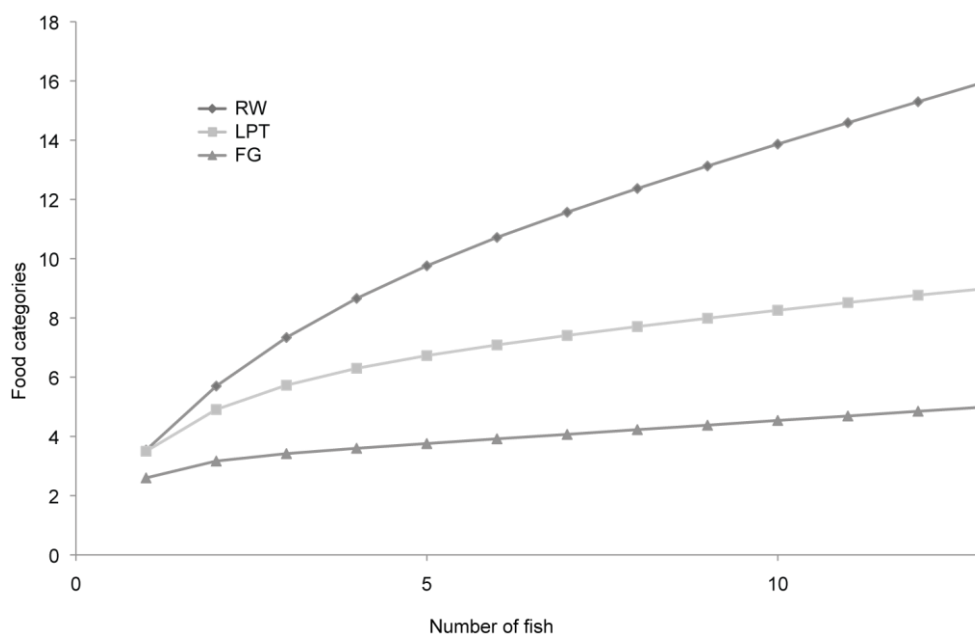
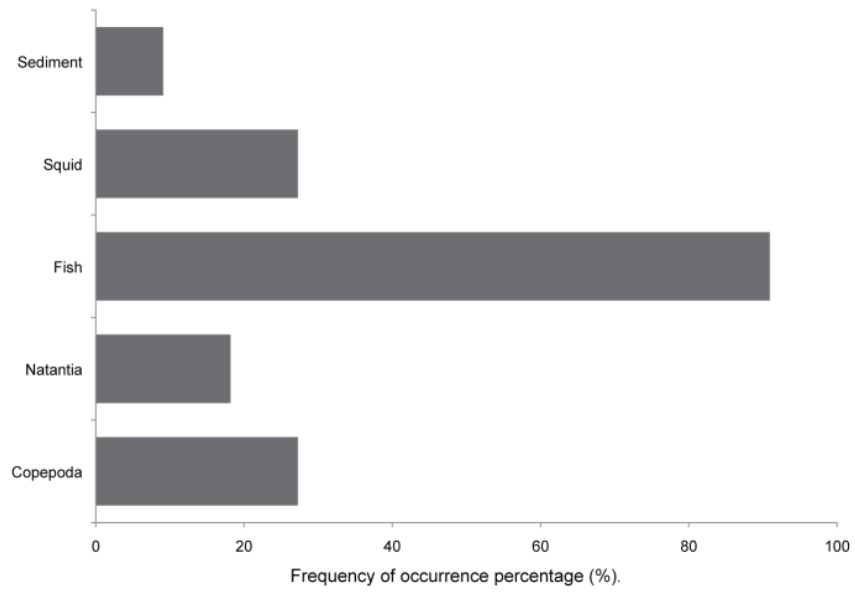


Figure 97. S_{obs} accumulation curves for the stomach contents of warty oreo from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 31. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of warty oreo from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification, S_t : total number of singletons in each food category (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

STOMACHS	RW	LPT	FG
S_{max} 70%		4	
S_{max} 80%		5	
S_{max} 90%		8	
Min. total	NA	10	NA
S_t	9	3	2
n	11	11	7

A.



B.

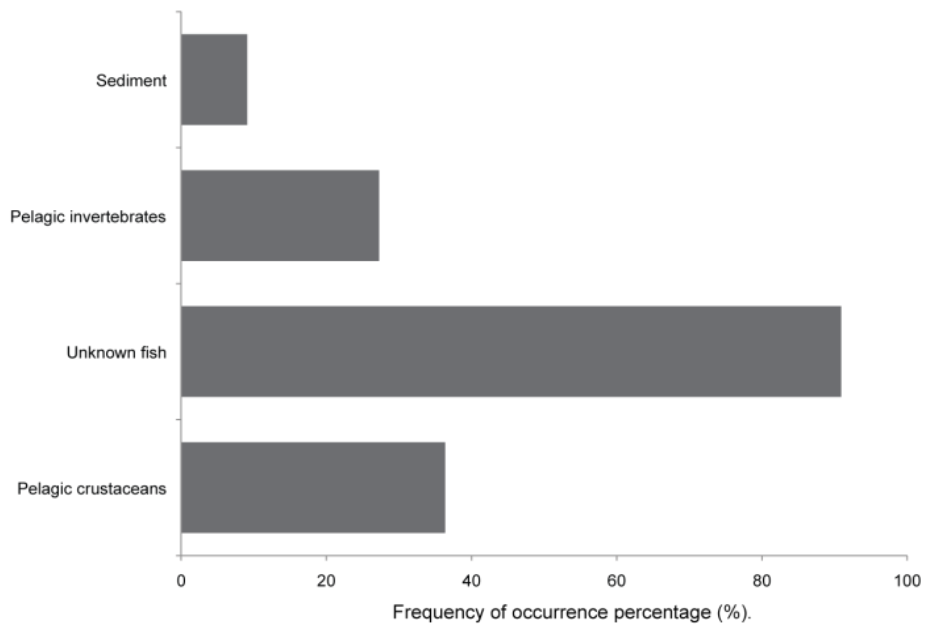


Figure 98. Intestinal contents of warty oreo from northeastern Chatham Rise expressed as percentage frequency of occurrence ($n = 12$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

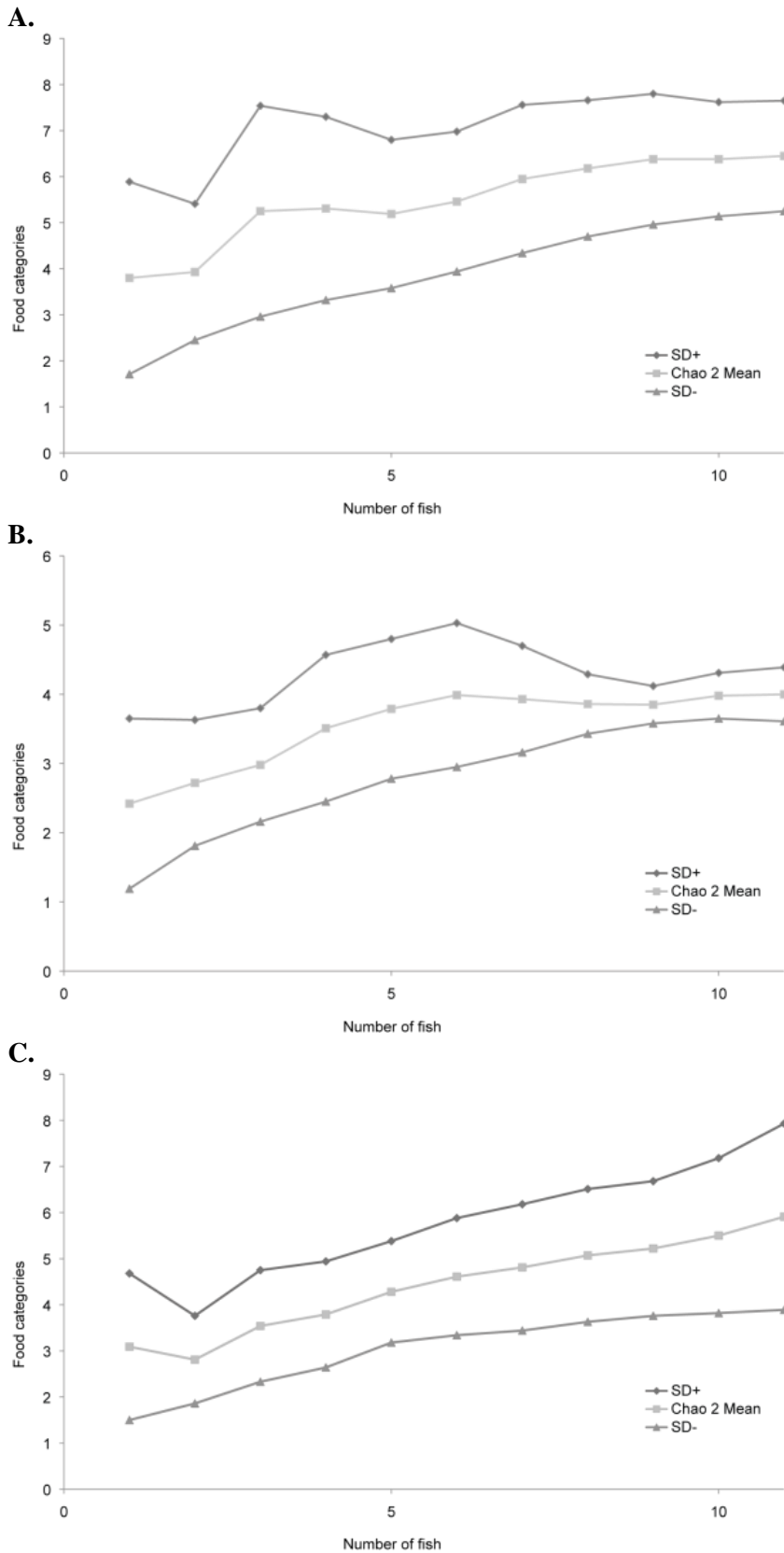


Figure 99. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents of warty oreo from northeastern Chatham Rise. **A.** Raw data, lowest practical taxon. **B.** Functional food groups.

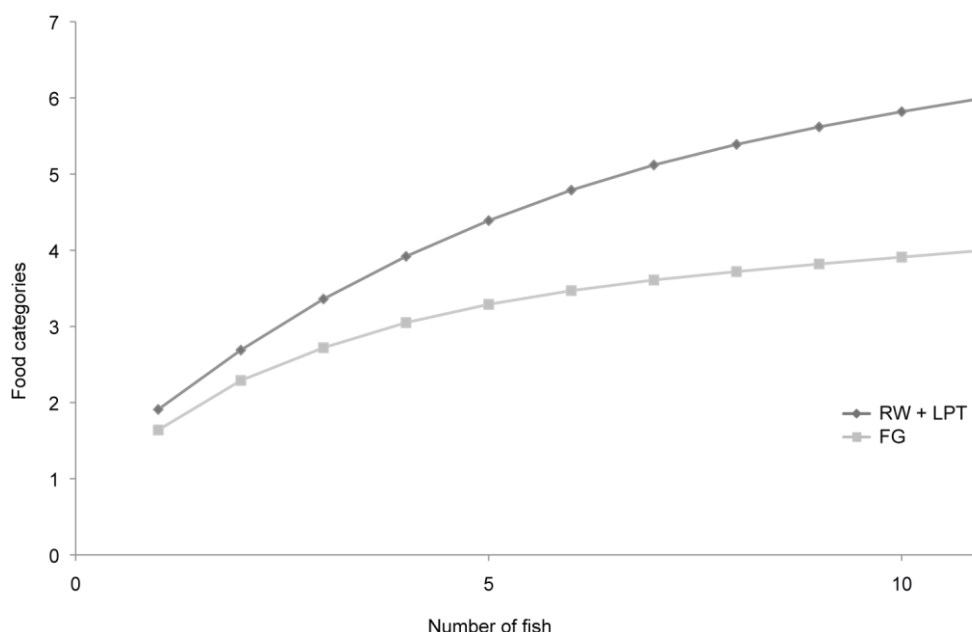


Figure 100. S_{obs} accumulation curves for the intestinal contents of warty oreo from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 32. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of warty oreo from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	3	
S_{max} 80%	5	
S_{max} 90%	7	
Min. total	8	NA
S_t	2	1
n	6	4

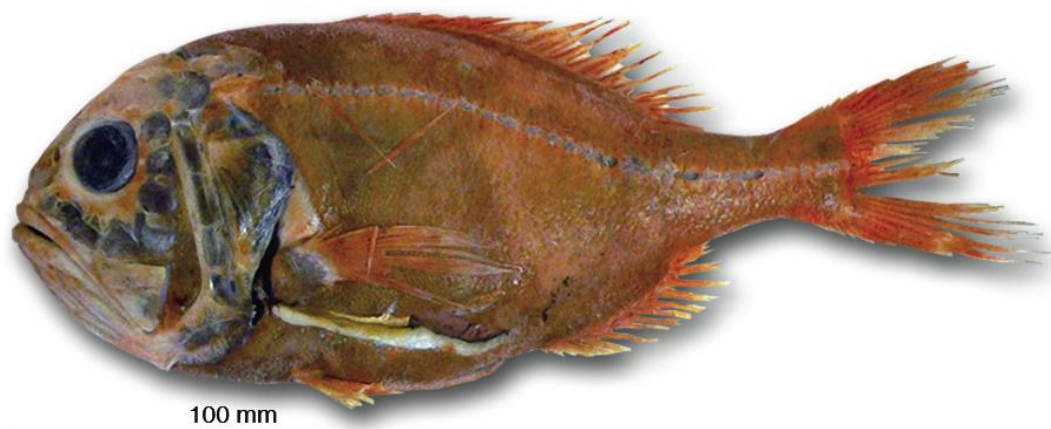
4.1.18. Orange roughy (ORH), *Hoplostethus atlanticus* ($n = 96$)

Figure 101. Orange roughy, (ORH), *Hoplostethus atlanticus*.

Forty-four orange roughy had stomachs that contained food items (**Fig. 102**), giving a PES of 54.2 percent. Fish were the principal food of orange roughy (79% IRI) (**Fig. 103A**), followed by natant decapod prawns (18%), particularly *AcanthePHYra pelagica* Risso, 1816; *Sergestes* sp.; and an unidentified species of *Nematocarcinus*. The rest of the diet was made up of gammaridean amphipods (particularly *Eurythenes gryllus* Lichtenstein, 1822), the mysid *Gnathophausia* sp., and the squid *H. atlantica* (each <5%). Over the whole sample, the trophic level was 4.84. Unidentified fish and pelagic crustaceans were the two most important functional food-item groups (**Fig. 103B**). There was a significant positive correlation between the weight of food items and the increasing size of the fish (Spearman rank correlation, $r_s = 0.261$, $P < 0.038$), but not for the number of food items per fish ($r_s = 0.080$, $P > 0.297$). Standardised niche breadth was low (0.12), and no material was recovered from the intestines. The dietary variation within the stomach contents of orange roughy was adequately described by one dietary classification (FG) (**Fig. 104, Fig. 105, Table 33**). The minimum total number of stomachs required to describe the dietary variation was 28, and S_{\max} values indicated that 90 percent of the dietary variation was described by 20 stomachs (**Table 33**).

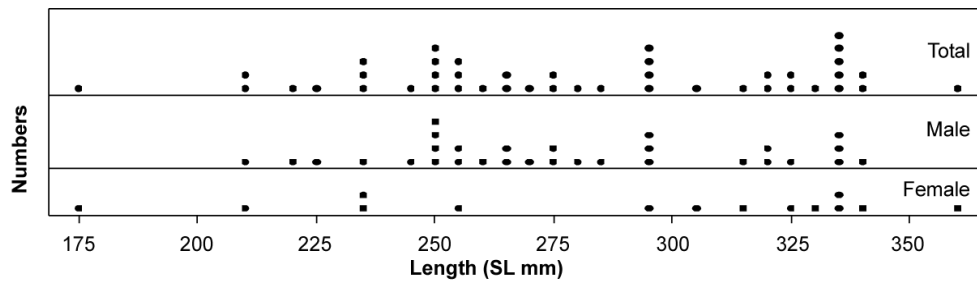
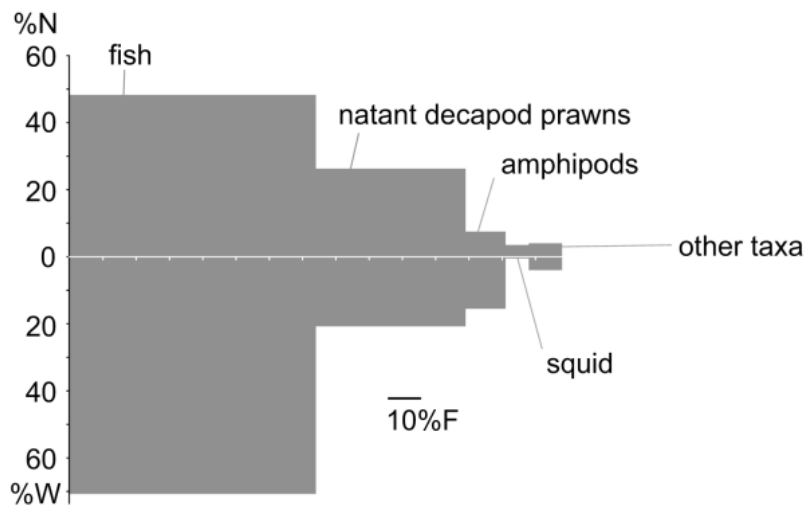


Figure 102. Size-frequency distribution for orange roughy from northeastern Chatham Rise (stomachs containing food), ($n = 44$, SL mm).

A.



B.

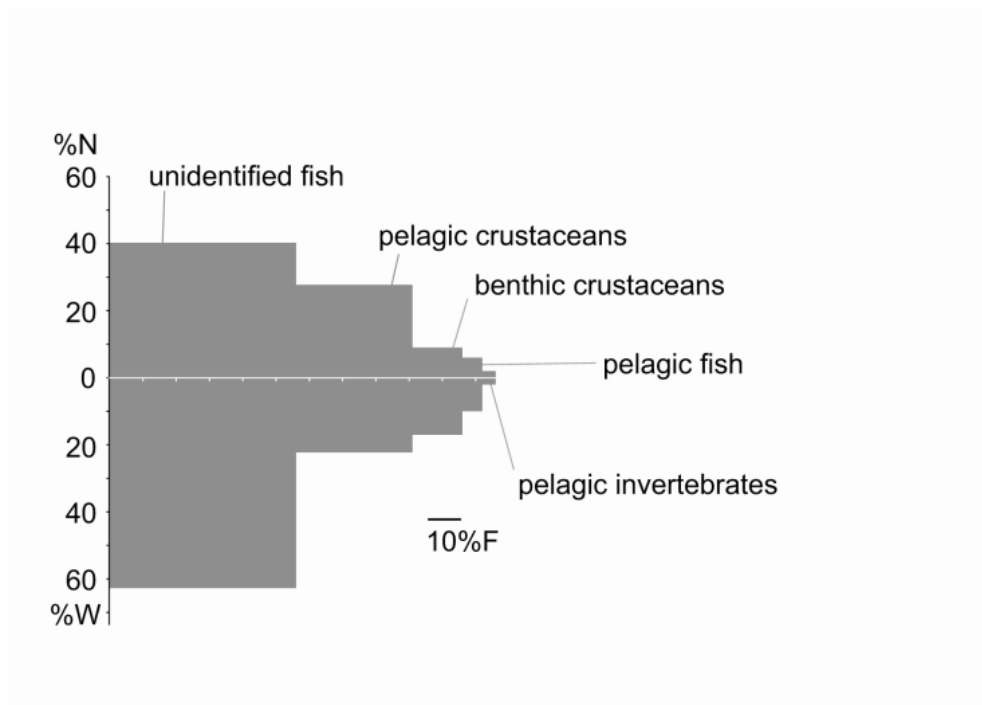
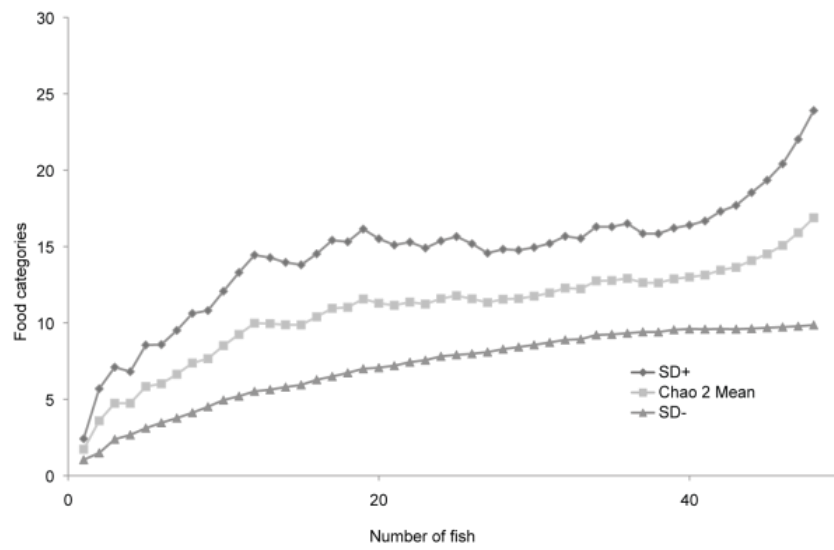
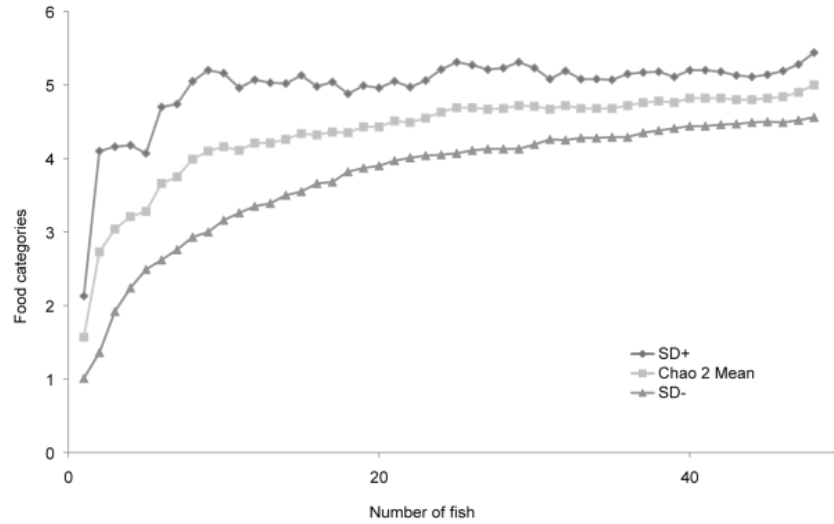


Figure 103. Diet of orange roughy from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 44$). **A.** Lowest practical taxon: other taxa, mysids and unidentified. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

A.



B.



C.

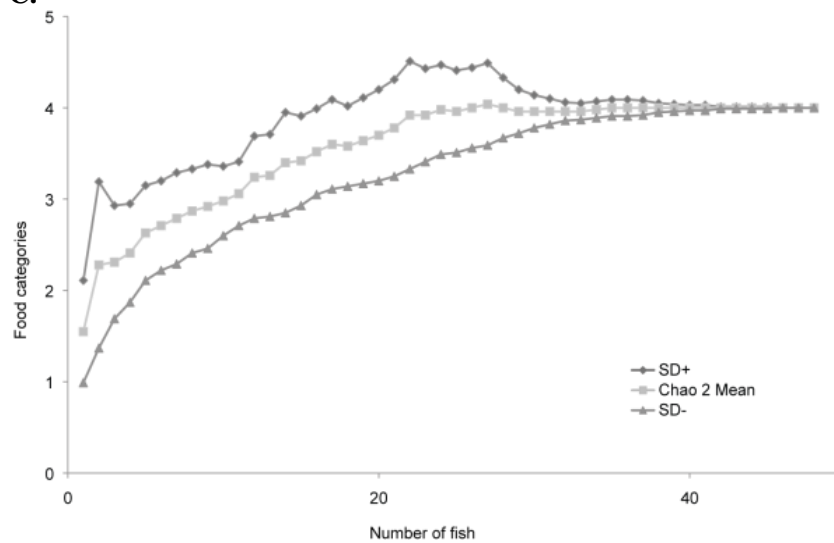


Figure 104. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of orange roughy from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

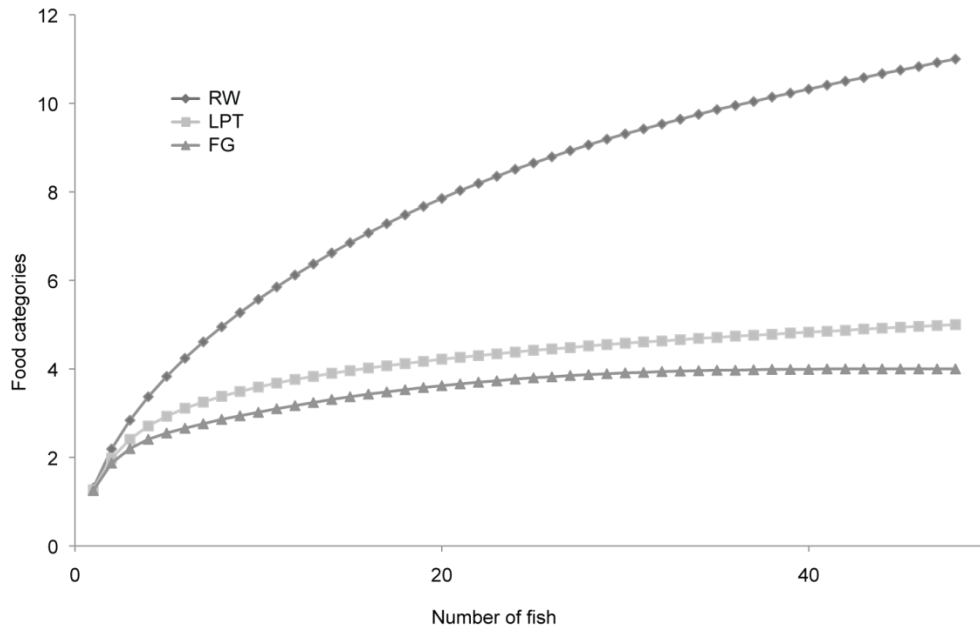


Figure 105. S_{obs} accumulation curves for the stomach contents of orange roughy from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 33. Number of fish estimated to describe 70–90% of S_{max} of the stomach contents of orange roughy from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%			7
S_{max} 80%			11
S_{max} 90%			20
Min. total	NA	NA	28
S_t	4	1	0
n	8	5	5

4.1.19. Robust cardinal fish (EPR), *Epigonus robustus* ($n = 188$)

Figure 106. Robust cardinal fish, (EPR), *Epigonus robustus*.

Thirty-two of the 188 fish examined contained food items in their stomachs (**Fig. 107**); this gave a PES of 82.9 percent. The diet was mainly calanoid copepods (69.8% IRI) (including *P. abdominalis*; *P. quadrangulata*; and *Lucicutia bicornuta* Wolfenden, 1905); chaetognaths (27.1%), unidentified crustacean remains and thaliaceans (1%) made up the remainder of the diet (**Fig. 108A**). Over the whole sample, the trophic level was 3.85. Pelagic crustacean and pelagic invertebrates were the two most important functional food-item groups (**Fig. 108B**). The numbers and weight of food items did not change significantly with fish size (Spearman rank $r_s = 0.028$, $P > 0.440$ and $r_s = 0.067$, $P > 0.357$ respectively). Standardised niche breadth was high (0.64). No material was recovered from the intestines.

The dietary variation within the stomach contents of robust cardinal fish was adequately described by all three dietary classifications (**Fig. 109**, **Fig. 110**, **Table 33**). The minimum total number of stomachs required to describe the dietary variation ranged from 18 (FG) and 29 (RW), and generally decreased with the number of food categories in each dietary classification (**Table 34**). The S_{\max} values indicated that 90 percent of the dietary variation was described by between 23 (RW), and six (FG) stomachs (**Table 34**).

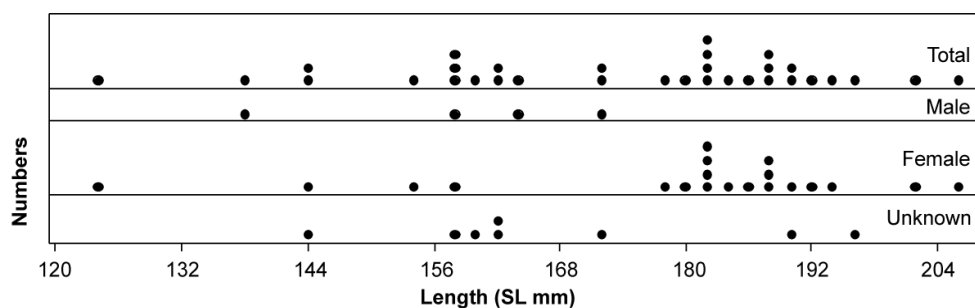
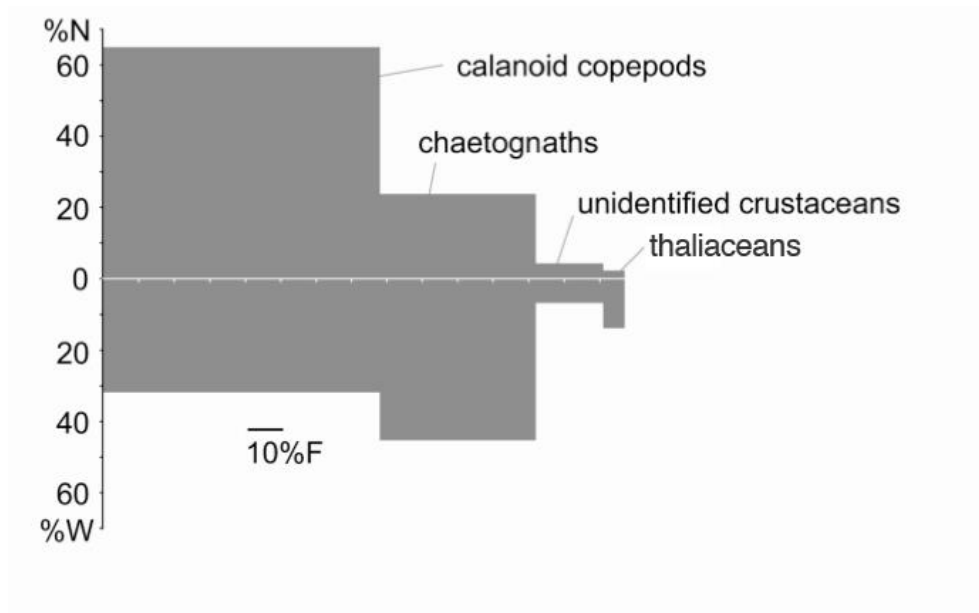


Figure 107. Size-frequency distribution for robust cardinal fish from Chatham Rise (stomachs containing food), ($n = 32$, SL mm).

A.



B.

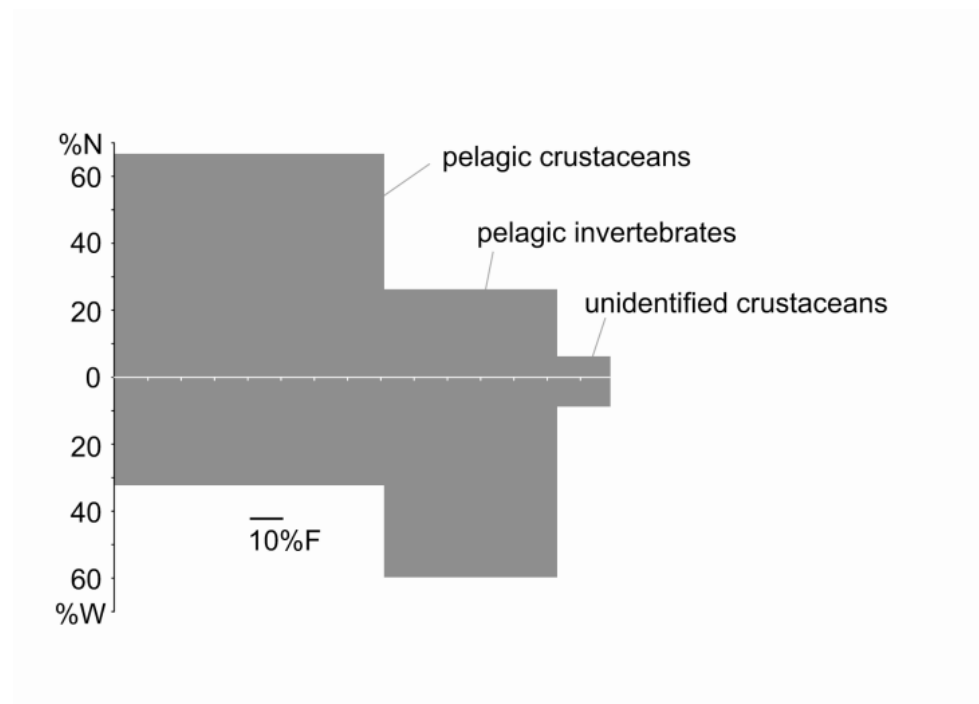


Figure 108. Diet of robust cardinal fish from northeastern Chatham Rise expressed as percentage IRI area charts ($n = 32$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

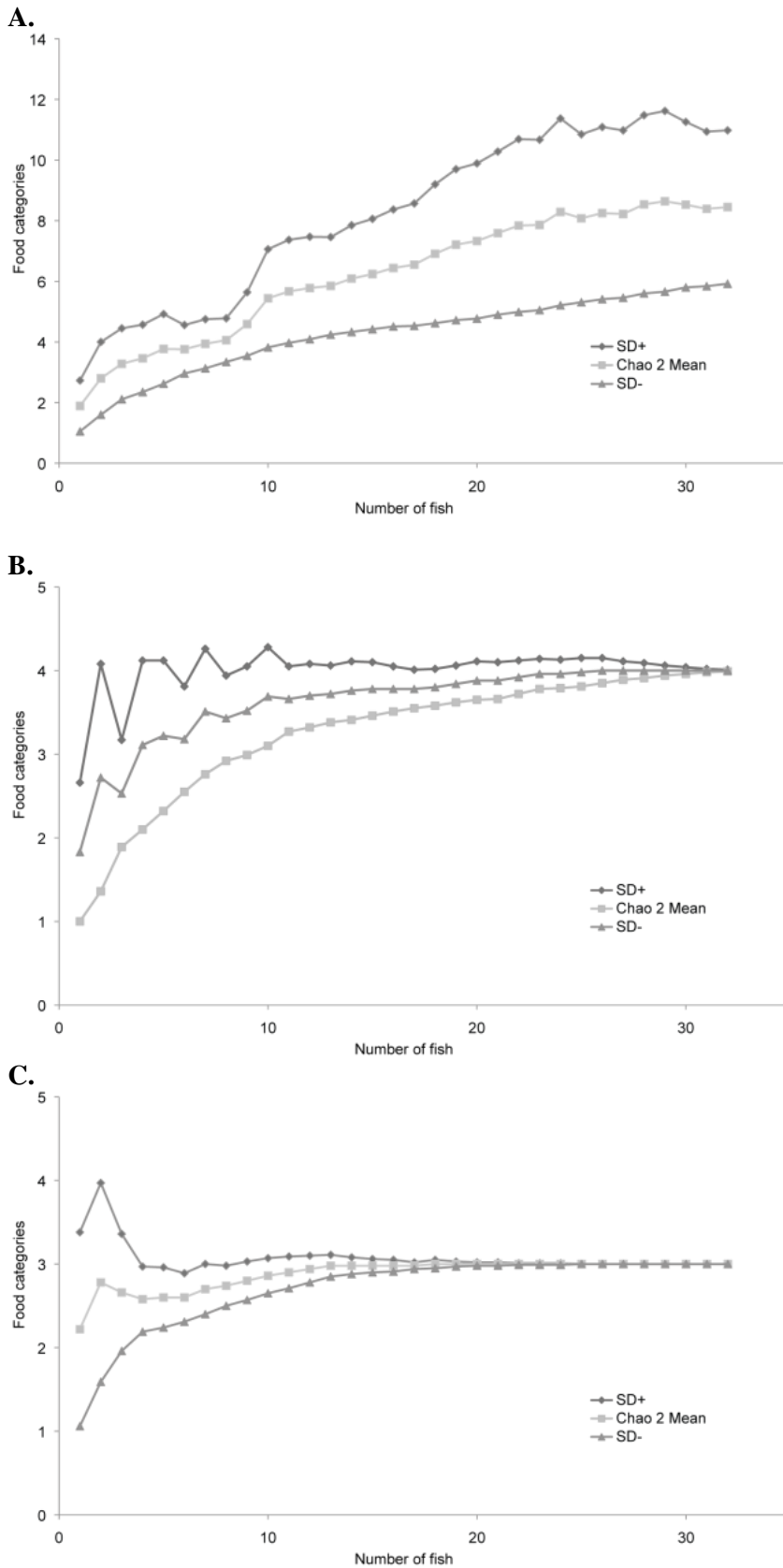


Figure 109. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of robust cardinal fish from northeastern Chatham Rise. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

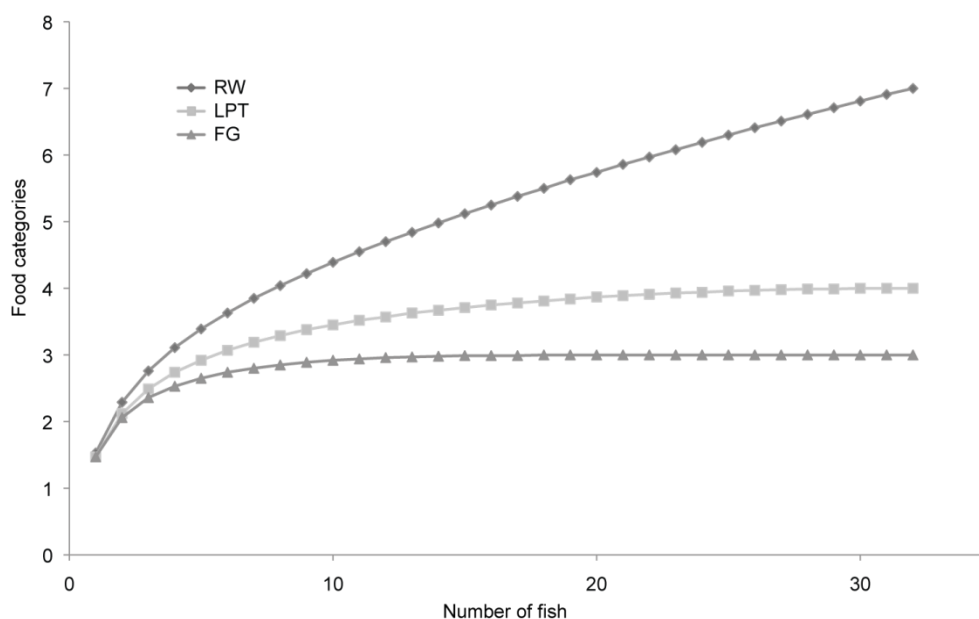


Figure 110. S_{obs} accumulation curves for the diet of robust cardinal fish from northeastern Chatham Rise for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 34. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of robust cardinal fish from northeastern Chatham Rise over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	12	2	3
S_{max} 80%	17	5	4
S_{max} 90%	23	9	6
Min. total	29	21	18
S_t	3	0	0
n	7	4	3

4.2. Principal food items of other fish species from northeastern Chatham Rise

The diets of 21 additional species of fish represented in bycatch by <10 stomach or intestinal samples are described here, and unless otherwise stated, are obtained from stomach contents. Their mean lengths, weights and gender (where known) are described in **Table 35**.

Three *Chimaera* sp. ?C had consumed a variety of small invertebrates: gammaridean amphipods, asellote and cirolanid isopods, ostracods (*Bathyvargula* sp.), mysids, pagurids, polychaetes, gastropods (*A. meridiana* and *Falsilunatia* sp.), a limid bivalve (?*Escalima regularis* Powell 1955), squid spermatophores, and echinoid remains.

Three long-nosed deep-sea skate *Bathyraja shuntovi* had eaten a blind lobster (Polychelidae: *Polycheles* cf. *suhmi* Bate, 1978), natant decapods, and serolid isopods (*Acutiserolis* sp.) respectively.

A single *Rhinochimaera pacifica* had eaten a fish, but its remains were too digested for precise identification.

The stomachs of all nine spine-back eels, *Notocanthus sexispinus*, were empty, but a small amount of material (prawn remains, fish bones and foraminiferans) was recovered from three of the intestines.

Two female hairy conger eels, *Bassanago hirsutus*, had consumed crabs (*Pycnoplax* sp.); one also had eaten a crangonid prawn (*Pontophilus acutirostratus*). Crab remains were also found in the intestines of both eels.

There were five tubeshoulders, *Perspasia kopua*, with identifiable stomach contents, and each had eaten calanoid copepods (including *Gaetanus pileatus* Farran, 1903), and natant decapod remains.

One of the three lighthouse fishes, *P. argenteus*, had fish scales in its stomach; the stomachs of the two other fishes were empty.

All four female violet cod, *Antimora rostrata*, had everted stomachs; unidentified green spicules were found in the intestines of three fish, whereas the fourth contained unidentifiable, amorphous green material.

There were four deep-sea smelt, *Bathylagus ?bericoides*, of which one had eaten a calanoid copepod (Aetideidae: *Undeuchaeta major* Giesbrecht, 1888); unidentified crustacean material was recovered from the intestine of another; the stomachs and intestines of the two other individuals were empty.

Two of three giant hatchet fish, *Argyropelecus gigas*, retained trace crustacean material in their intestines, while a calanoid copepod (*G. pilatus*) was recovered from the stomach of the other.

Two of three hoki, *Macruronus novaezelandiae*, had fish remains (?Myctophidae) in their stomachs, while the third fish stomach was empty.

One banded rattail, *Coelorinchus fasciatus*, had an everted stomach, but its intestine contained a large number of bivalves (*B. cybaea*; *Deminucula* spp.; *Yoldiella ?finlayi* (Powell, 1935); *Pseudotindaria flemingi*; *Pseudotindaria* sp.), and gastropods (*Philine* sp.; *Benthonella* sp.; *Globisinum* sp.; *Volvulella truncata* Dell, 1956; and a marginellid gastropod (?*Mesoginella* sp.), serolid and asellote isopods (*Acutiserolis* sp.) and crinoid remains, in addition to foraminiferans, and sediment.

Two Mahia rattails, *C. matamua*, were examined, and both had everted stomachs. One intestine contained the ostracod *Vargula* sp. and prawn remains, plus chaetognath jaw hooks; the other contained polychaete jaws and unidentifiable crustacean material.

Of five humpback rattails, *Coryphaenoides dossenus*, examined, three had stomachs containing food, and two had everted stomachs. The three stomachs contained the natant decapod prawn *Nematocarcinus* sp. and serolid isopods (*Acutiserolis* sp.); one fish had also eaten a hermit crab; crustacean remains and polychaete jaws were recovered from the intestines of all five fish.

One male filamentous rattail, *Gadomus aoteanus*, had eaten two crangonid prawns (*Pontophilus* sp.), and a calanoid copepod; its intestine also contained prawn remains.

A female javelin fish, *Lepidorhynchus denticulatus*, stomach contained natant decapod remains, an upper squid beak, and fish remains; fish remains were also recovered from its intestine.

Of nine squashed-face rattails, *Nezumia namatahi*, four stomachs contained food comprising gammaridean amphipods (*Oediceroides* cf. *rostrata* (Barnard, 1961), lysianassids, stegocephalids, and a caprellidean), isopods (*Natatolana* sp., antarcturids, ?*Ischnomesidae*, munnopsids, gnathiids, and epicarideans), and myodocopid ostracods (*Bathyvargula* sp., *Vargula* sp., *Cypridinoides ?reticulata*). Munnopsid isopods, gammaridean amphipods, and myodocopid ostracods (*M. ?bradfordae*, *Vargula* sp.), were obtained from nine intestines.

All eight unicorn rattails, *T. longirostris*, had everted stomachs; the remains of amphipods, natant decapod prawns and fish were found in six intestines that contained

food items, although this material was highly digested and could not be reliably identified further.

Two black oreo, *Pseudocyttus maculatus*, stomachs contained food items; one had eaten a gammaridean amphipod and the other a thaliacean.

A single cape scorpionfish, *Trachyscorpia capensis*, had natant decapod prawn remains in both its stomach and intestine. A blobfish, *Psychrolutes microporos*, had eaten a hermit crab (within a *N. ephamillus*), a crangonid prawn, and brown seaweed.

Table 35. Mean length (mm) and weight (g) (male and female) of 21 fish species from NECH, with <10 stomach or intestinal samples containing food items. Length measurements: snout-vent length, SV; total length, TL; head length, HL and SL standard length; values are also given for the co-efficient of variation (CV).

Species Code	Gender	Number	Mean length (SV) (TL ¹) (HL ²) (SL ³) (mm)	CV	Mean weight (g)	CV
<i>Chimaera</i> sp. ?C CHC	Male	0				
	Female	3	235	4.3	864	4.3
	Unknown	0				
<i>Bathyraja shuntovi</i> PSK	Male	2	523 ¹	26.3		
	Female	1	670 ¹			
	Unknown	0				
<i>Rhinochimarea pacifica</i> RCH?	Male	0				
	Female	1	675 ¹		3912	
	Unknown	0				
<i>Notocanthus sexispinus</i> SBK	Male	3	602	10.3	179.2	26.3
	Female	6	732	7.1	271.6	31.6
	Unknown	0				
<i>Bassanago hirsutus</i> HCO	Male	0				
	Female	2	593 ¹	4.9	399.2	84.3
	Unknown	0				
<i>Persparsia kopua</i> PKO*	Male	3	130 ³	4.2	17.7	21.4
	Female	3	134 ³	22.3	22.3	9.6
	Unknown	0				
<i>Phosichthys argenteus</i> PAR*	Male	0				
	Female	0				
	Unknown	3	216 ³	29.2	47.5	94.4
<i>Antimora rostrata</i> VCO	Male	0				
	Female	4	481 ³	3.7	662.4	26.4
	Unknown	0				
<i>Bathylagus bercoides</i> BBE*	Male	2	190 ³	0.7	45.7	0.7
	Female	2	193 ³	14.9	40.45	32.1
	Unknown	0				
<i>Agyropelecus gigas</i> AGI*	Male	1	85 ³		12	
	Female	1	95 ³		19.2	
	Unknown	1	71 ³		6.9	

Table 35. (continued).

Species Code	Gender	Number	Mean length (SV) (TL ¹) (HL ²) (SL ³) (mm)	CV	Mean weight (g)	CV
<i>Macruronus novaezelandiae</i> HOK	Male	0				
	Female	3	250 ³	39.4	820.4	102.7
	Unknown	1				
<i>Coelorinchus fasciatus</i> CFA	Male	0				
	Female	1	72 ²		108.3	
	Unknown	0				
<i>C. matamua</i> CMA	Male	0		29	51.9	71.5
	Female	0				
	Unknown	2	62 ²			
<i>Coryphaenoides dossenus</i> CBA	Male	2	59 ²		72.0	
	Female	3	101 ²	25	432.7	53
	Unknown	0				
<i>Gadomus aoteanus</i> GAO	Male	1	103 ²		92.9	
	Female	0				
	Unknown	0				
<i>Lepidorhynchus denticulatus</i> JAV	Male	0				
	Female	1	122 ²		319.7	
	Unknown	0				
<i>Nezumia namatahi</i> NNA*	Male	1	45 ²		46.5	
	Female	4	46 ²	11.5	54.36	30.4
	Unknown	0				
<i>Trachyrincus longirostris</i> WHR	Male	2	114 ²	5.6	260.9	9.7
	Female	6	133 ²	4.6	296.5	9.5
	Unknown	0				
<i>Pseudocyttus maculatus</i> SBL	Male	3	218 ³	58.3	295	71.4
	Female	2	194 ³	24.5	232	28.7
	Unknown	8				
<i>Trachyscorpia capensis</i> TRS	Male	1	303 ³		1038.2	
	Female	0				
	Unknown	0				
<i>Psychrolutes microporos</i> PSY	Male	1	156 ³		120	
	Female	0				
	Unknown	0				

*Non NZ Ministry of Fisheries species code.

4.3. Aspects of the biology and principal food items of fish from Puysegur Bank (PUY), southern New Zealand, from 1020–1072 m, for those fish with >10 stomach or intestinal samples containing food items

Overall, 205 fish attributed to 13 species (**Table 36, 41**) were retained from Puysegur Bank (PUY). Baxter’s dogfish, Johnson’s cod and four-rayed rattail had >10 stomach or intestinal samples containing food, and for these three species, females were significantly larger and heavier than males (**Table 36**).

Table 36. Mean length and weight of male and female Baxter’s dogfish, Johnson’s cod, and four-rayed rattail from Puysegur Bank. Acronyms: pre-caudal fin length, PCL; standard length, SL; pre-anal fin length, PAL; co-efficient of variation (CV). Statistical tests for lengths and weights verses sex for each species: one way ANOVA (F), and Kruskal-Wallis ANOVA (H). Significant differences are in bold.

Species	Gender	Number	Mean length (PCL) (SL ¹) (PAL ²) (mm)	CV	Weight (g)	CV
<i>E. baxteri</i> ETBp	Male	30	410	22.3	733	55.3
	Female	20	484	17.0	1233.9	57.0
	Unknown	0				
			$H = 7.69, P < 0.006$	$F = 10.44, P < 0.002$		
<i>H. johnsonii</i> HJOp	Male	11	3641	10.9	325.4	33.4
	Female	12	4081	4.5	496.6	17.3
	Unknown	0				
			$F = 18.52, P < 0.000$	$H = 9.09, P < 0.003$		
<i>C. subserrulatus</i> CSUp	Male	40	682	11.5	43.7	28.0
	Female	83	782	12.2	55.4	23.5
	Unknown	9				
			$H = 27.44, P < 0.000$	$H = 25.84, P < 0.000$		

4.3.1. Baxter’s dogfish (ETBp), *Etmopterus baxteri* ($n = 50$)

Twenty-five Baxter’s dogfish had stomachs containing food (**Fig. 111**), which gave a PES of 50 percent. Baxter’s dogfish fed mainly on fish (55% IRI) (including whole four-rayed rattail, sections of orange roughy), and squid (44.5%) (often warty squid, *Onykia ingens*), (**Fig. 112A**). Diet was supplemented by the mysid *Gnathophausia* sp. and natant decapod prawns. Over the whole sample, the trophic level was 5.01. Unidentified fish and pelagic invertebrates were the two more important functional food-item groups (**Fig. 112B**). There was no apparent trend in the weight or number of food items with increasing fish size (Spearman rank correlation, $r_s = 0.213$,

$P > 0.405$ and $r_s = 0.063$, $P > 0.383$ respectively). Standardised niche breadth was low (0.27).

The dietary variation within the stomach contents of Baxter's dogfish from Puysegur Bank was adequately described by one dietary classification (FG) (**Fig. 113, Fig. 114, Table 37**). The minimum total number of stomachs required to describe the dietary variation within the stomachs was 23 (FG), with between 13 stomachs required for S_{\max} 90% (FG respectively). There were multiple singletons in two of the dietary classifications (RW & LPT), and these two classifications failed to adequately describe the dietary variation (**Table 37**).

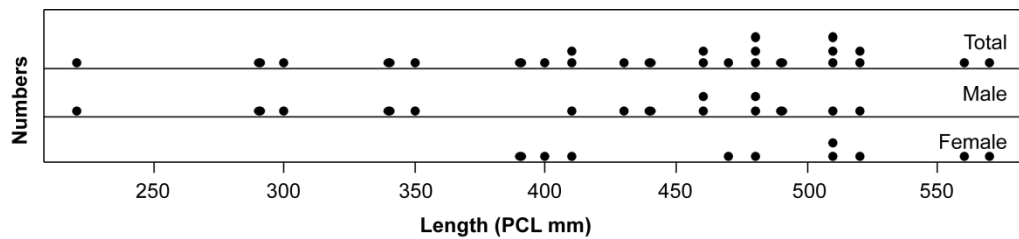
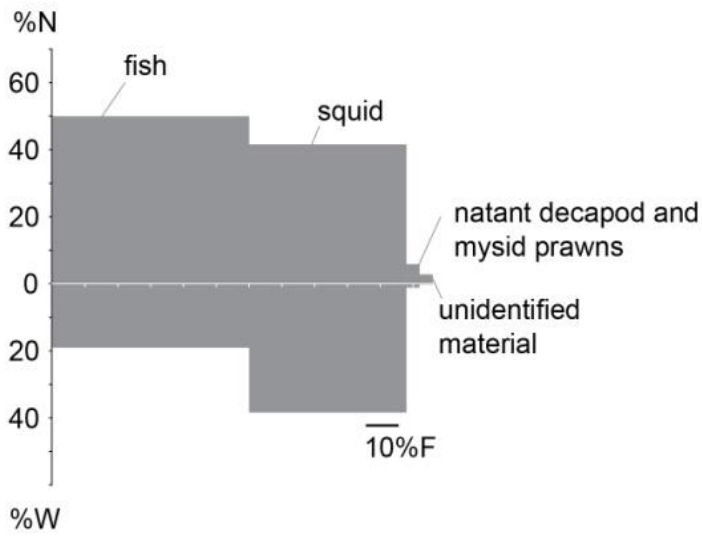


Figure 111. Size-frequency distribution for Baxter's dogfish from Puysegur Bank (stomachs containing food), ($n = 25$, PCL mm).

A.



B.

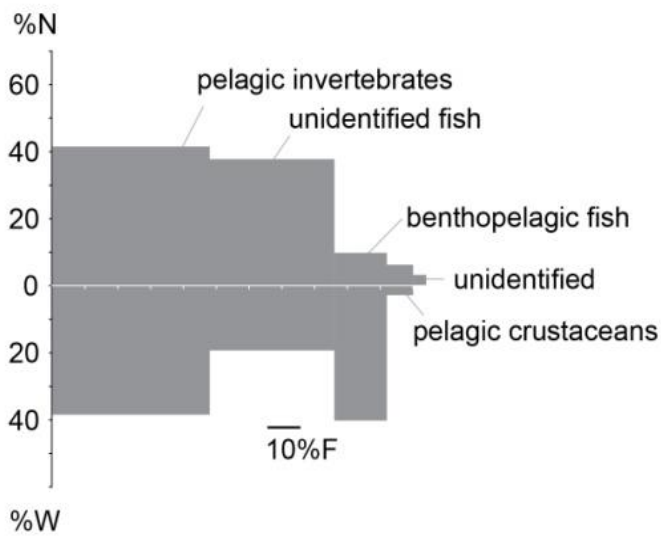


Figure 112. Diet of Baxter's dogfish from Puysegur Bank expressed as percentage IRI area charts. ($n = 25$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

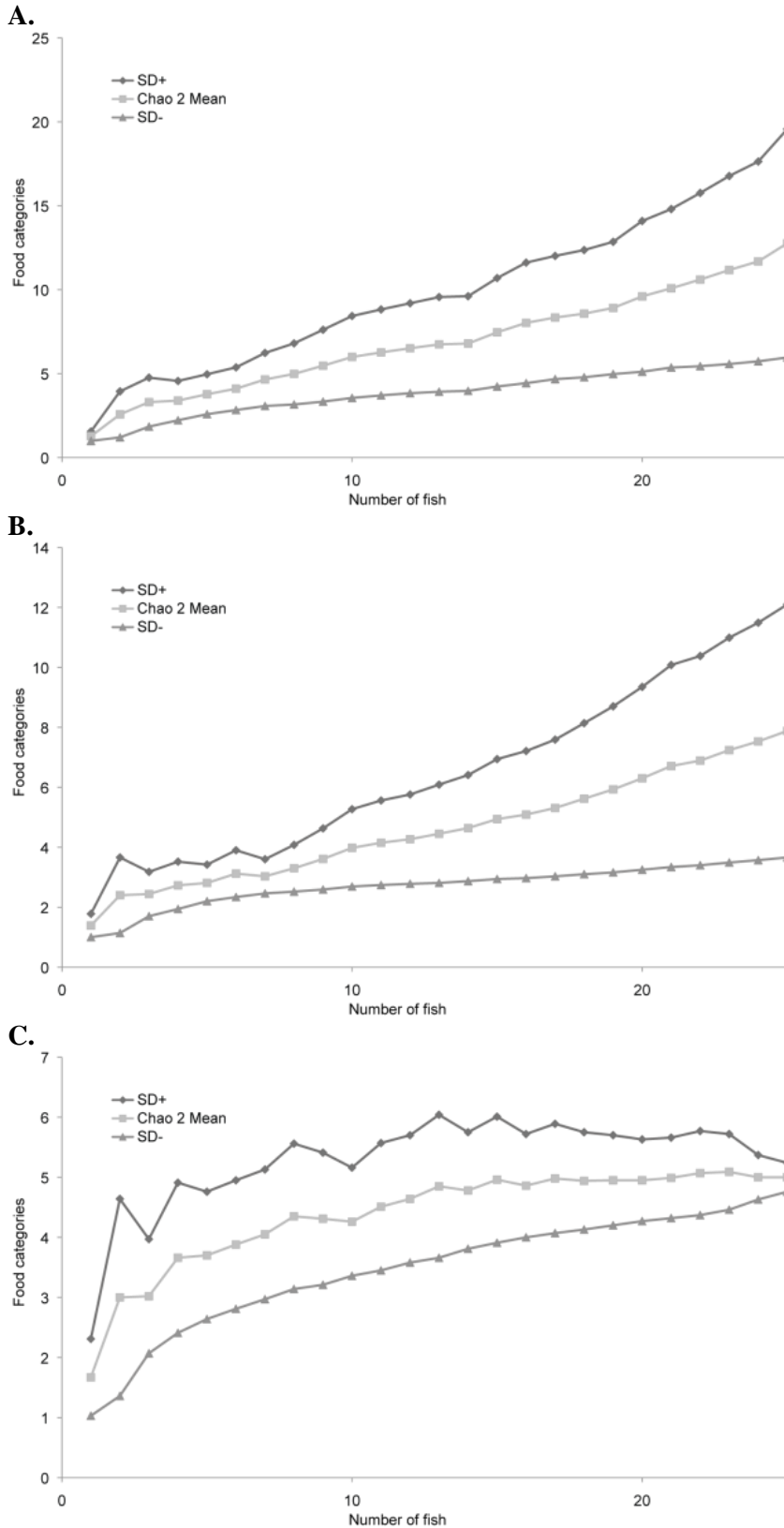


Figure 113. Mean Chao 2 estimation curves (plus and minus one standard deviation) for three dietary classifications for the stomach contents of Baxter’s dogfish from Puysegur Bank. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

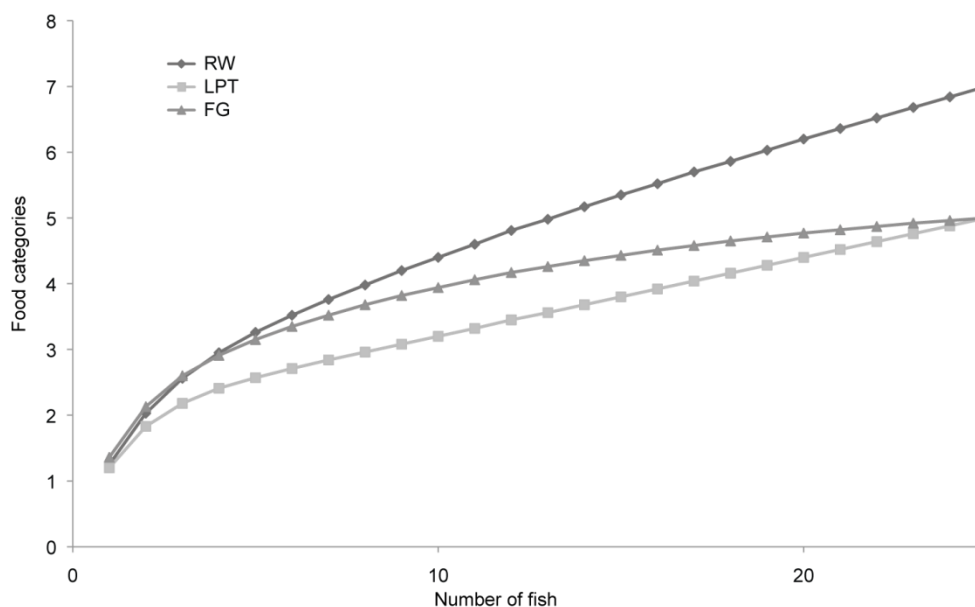


Figure 114. S_{obs} accumulation curves for the stomach contents of Baxter's dogfish from Puysegur Bank for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 37. Number of fish estimated to describe 70–90% of S_{max} of the stomach contents of Baxter's dogfish from Puysegur Bank over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

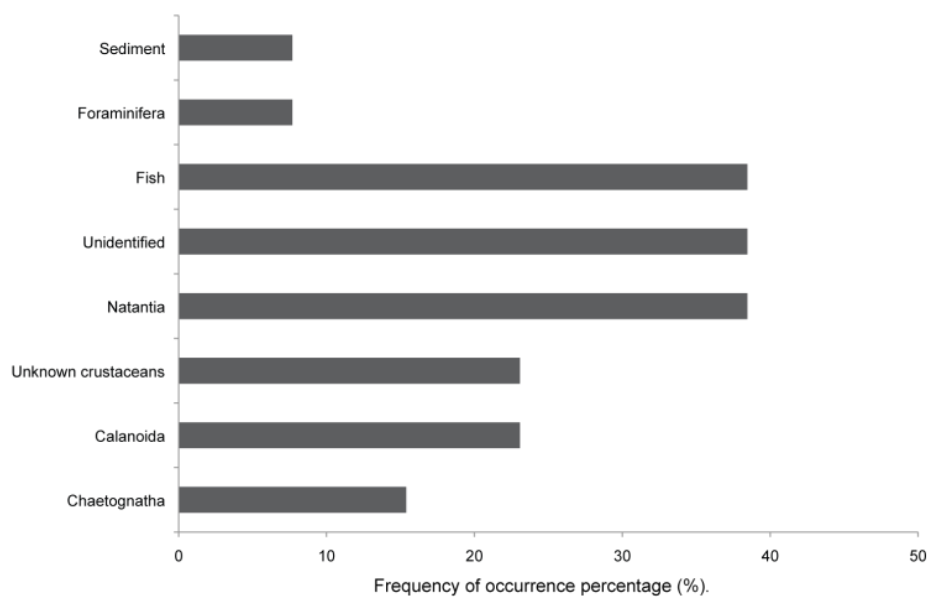
STOMACHS	RW	LPT	FG
S_{max} 70%			6
S_{max} 80%			9
S_{max} 90%			13
Min. total	NA	NA	23
S_t	4	3	1
n	7	5	5

4.3.2. Johnson's cod (HJO), *Halargyreus johnsonii* ($n = 23$)

All Johnson's cod had everted stomachs, but material was recovered from the intestines of 12 of them, giving a PEI of 47.7 percent. This consisted of unidentifiable red crustacean material (probably natant decapod or mysid prawn remains), fish remains (bones, scales, and otoliths), calanoid copepods, chaetognath jaw hooks, and other unidentified crustacean material (distinct from 'red' material) (**Fig. 115**). Over the whole sample, the trophic level was 4.24.

The RW and LPT datasets were identical, so were treated as one. The dietary variation within the intestinal contents of Johnson's cod from Puysegur Bank was adequately described by all three dietary classifications (**Fig. 116, Fig. 117, Table 38**). The minimum total number of intestines required to describe the dietary variation was 12 for all three dietary classifications, and between eight and nine intestines described 90 percent of the dietary variation (RW & LPT, and FG respectively). There were multiple singletons in all but one (FG) of the dietary classifications (**Table 38**).

A.



B.

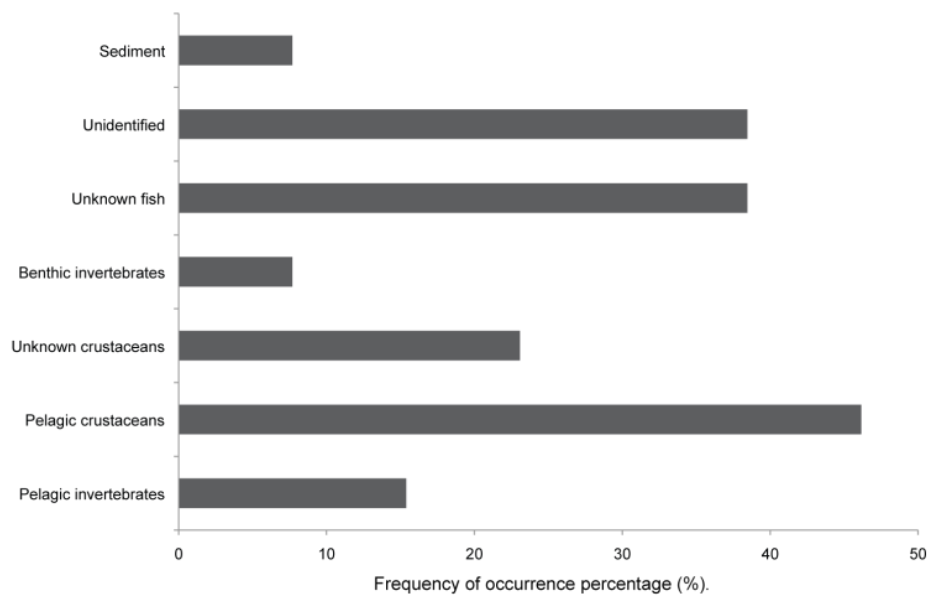


Figure 115. Intestinal contents of Johnson's cod from Puysegur Bank expressed as percentage frequency of occurrence ($n = 12$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

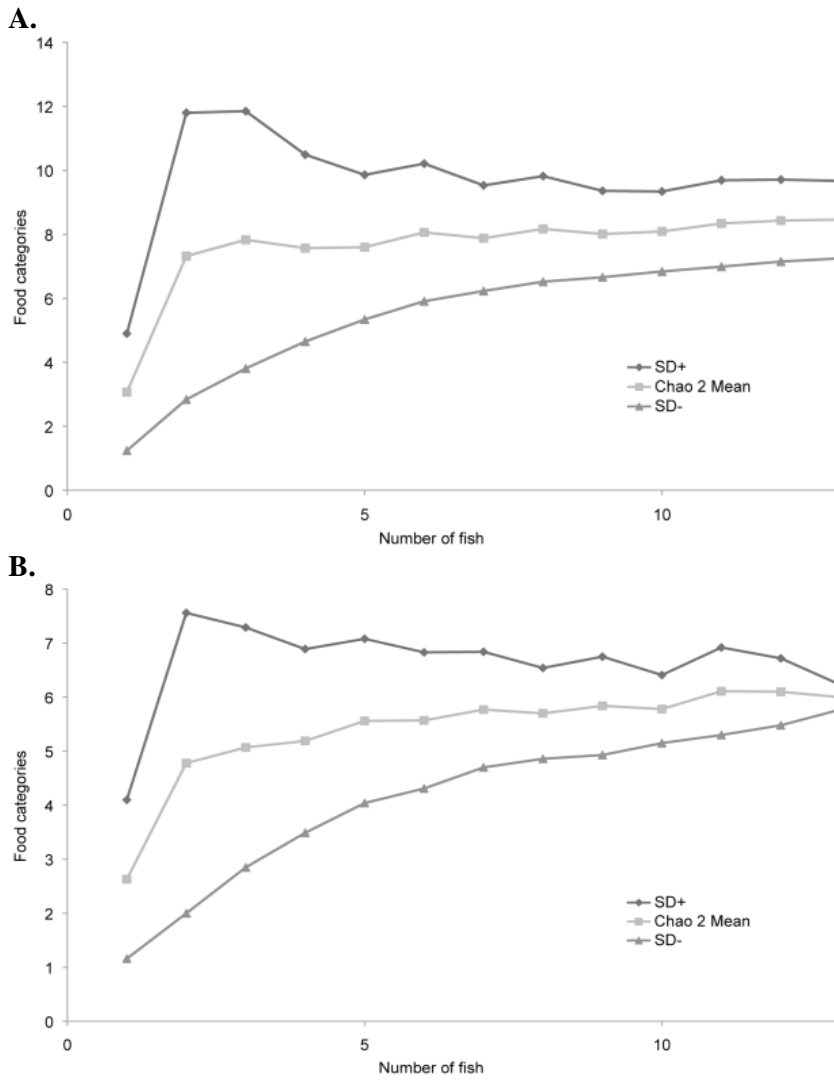


Figure 116. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents Johnson’s cod from Puysegur Bank. **A.** Raw data, and lowest practical taxon. **B.** Functional food groups.

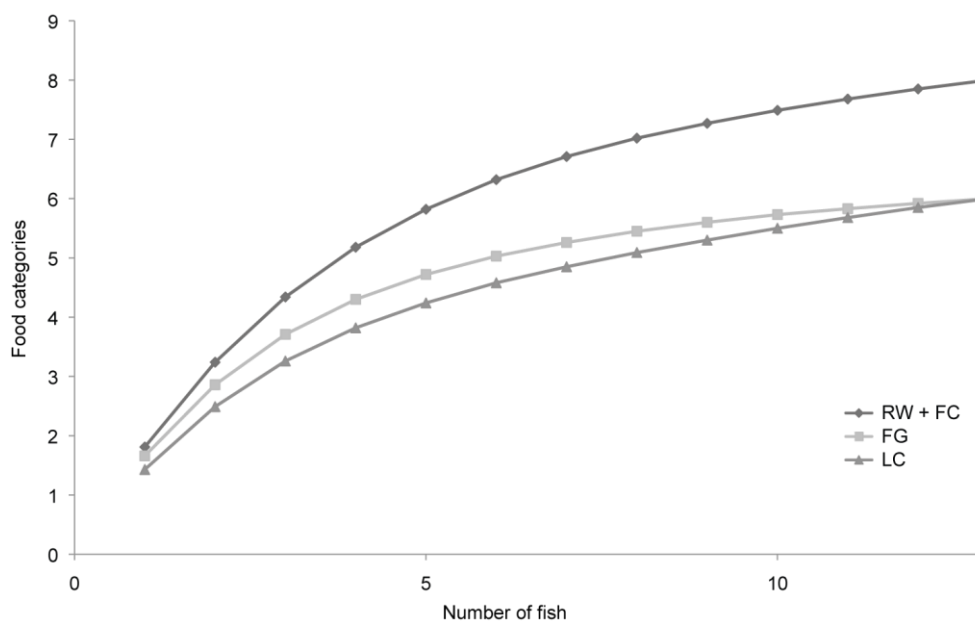


Figure 117. S_{obs} accumulation curves for the intestinal contents of Johnson's cod from Puysegur Bank for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups, LC: lowest common taxon).

Table 38. Number of fish estimated to describe 70–90% of S_{max} for the intestinal contents of Johnson's cod from Puysegur Bank over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	5	4
S_{max} 80%	6	6
S_{max} 90%	9	8
Min. total	12	12
S_t	2	1
n	8	6

4.4.3. Four-rayed rattail (CSUp), *Coryphaenoides subserrulatus* ($n = 132$)

Fifty three four-rayed rattail had stomachs containing food, giving a PES of 59.8 percent (**Fig. 119**). Four-rayed rattail consumed mainly calanoid copepods (79.8% IRI) (**Fig. 120A**) (including *Chiridius pacificus* Brodsky, 1950; *Aetideopsis tumorosa* Bradford, 1969, and *Neocalanus tonsus* (Brady, 1883)), and chaetognaths (19.3%). Over the whole sample, the trophic level was 4.00. Pelagic crustaceans and pelagic invertebrates were the two most important functional food-item groups (**Fig. 120B**). Overall, there was a significant positive correlation between the weight and number of food items, and the size of the fish (Spearman rank correlation $r_s = 0.439$, $P < 0.000$, and $r_s = 0.228$, $P < 0.050$ respectively). There was a high level of dietary overlap between the two size classes examined (0.7) (**Fig. 121**). Overall, the standardised niche breadth was moderate (0.31), but low for the two size classes (0.03) for each.

The dietary variation within the stomachs of four-rayed rattail was adequately described by all dietary classifications (**Fig. 122, Fig. 123, Table 39**). The minimum total number of stomachs required describing the dietary variation ranged between 15 (FG), and 49 (RW) (**Table 39**). Ninety percent of the dietary variation was described by between 10 and 38 stomachs (FG & RW). There were generally fewer stomachs required to describe the dietary variation when there were fewer food categories (**Table 39**), and multiple singletons were only present in RW.

A further 34 four-rayed rattail had identifiable material in their intestines, consisting of the remains of calanoid copepods and other unidentified crustacean material, and also the jaw hooks of chaetognaths (**Fig. 124**). Both the RW and LPT intestinal contents datasets were identical, so were treated as one (**Fig. 126**). The dietary variation within the intestines of four-rayed rattail was adequately described by all dietary classifications (**Fig. 125, Fig. 126, Table 40**). The minimum total number of intestines needed to describe the diet of four-rayed rattail ranged between 37 (FG), and 102 (RW & LPT). This was reflected in the S_{\max} 90% values (18 and 28 respectively, **Table 40**), and there were no singletons in any of the dietary classifications.

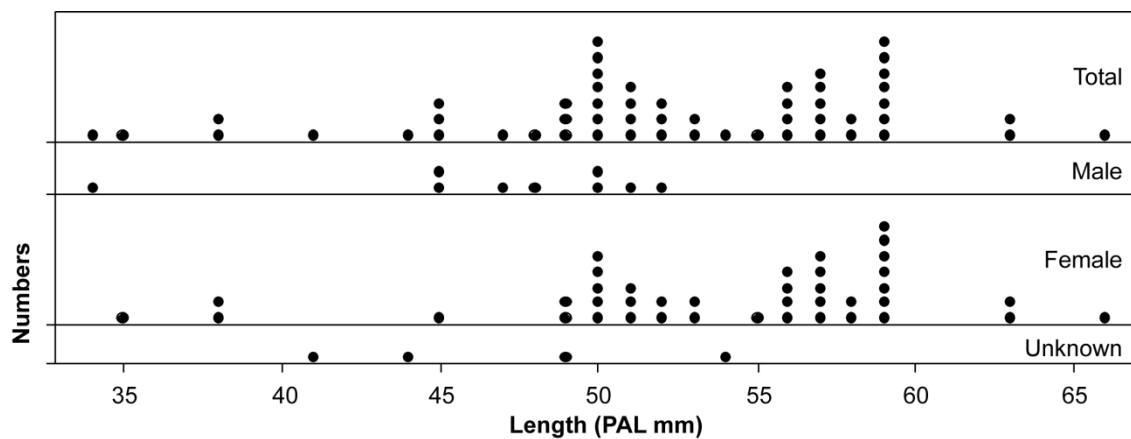
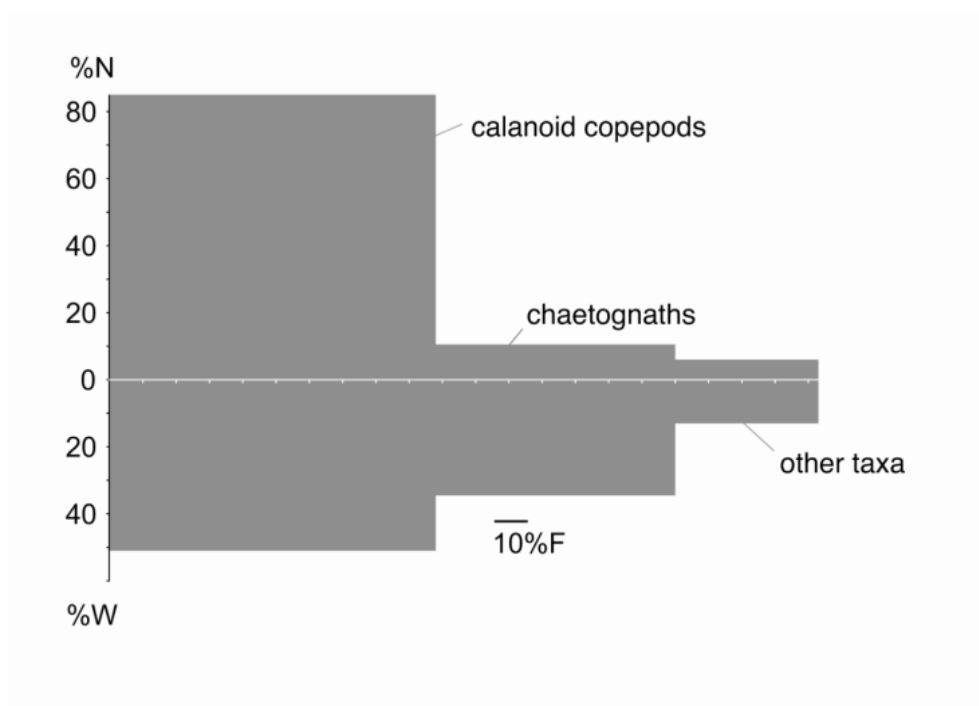


Figure 119. Size-frequency distribution for four-rayed rattail from Puysegur Bank (stomachs containing food) ($n = 53$, PAL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

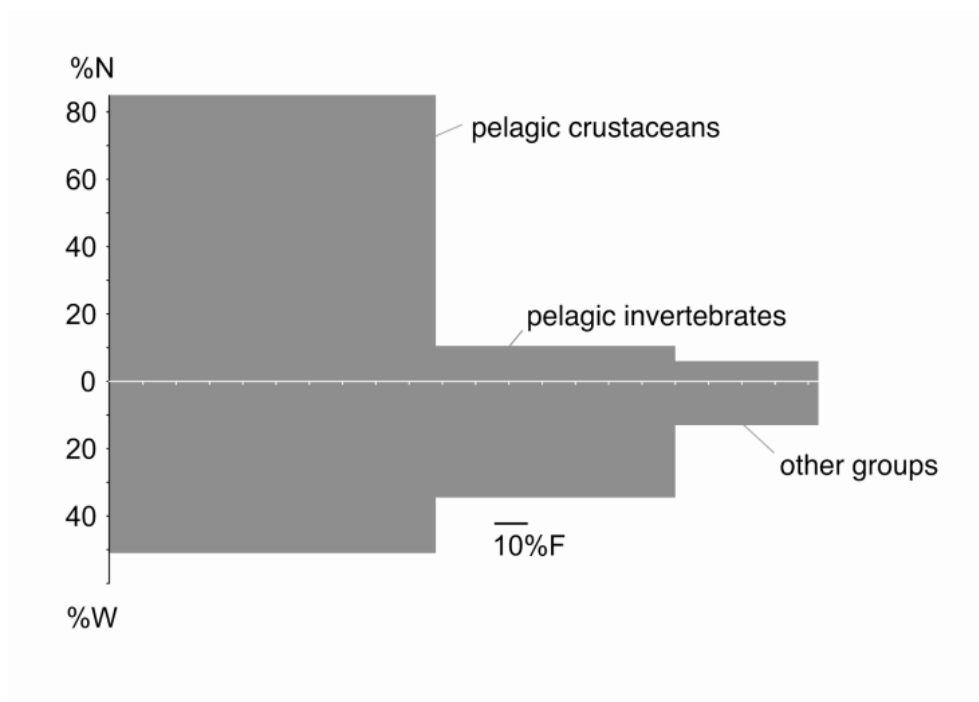


Figure 120. Diet of four-rayed rattail from Puysegur Bank expressed as percentage IRI area charts ($n = 53$). **A.** Lowest practical taxon: other taxa: fish, euphausiid and natant decapod prawns, amphipods, and unidentified. **B.** Functional food-item groups: other groups: benthic crustaceans, unidentified fish, and unidentified. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

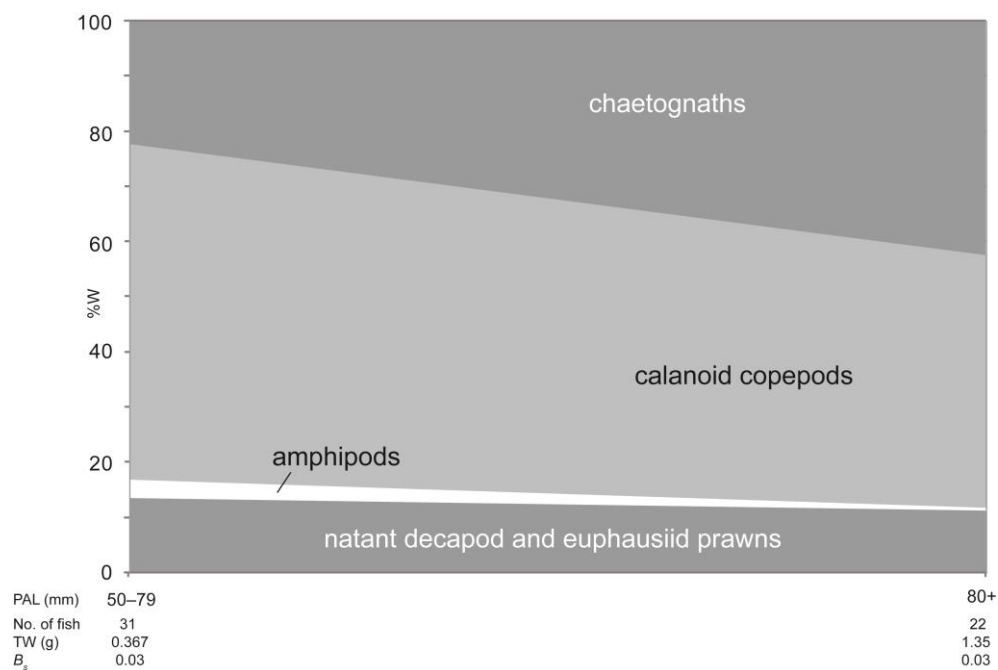


Figure 121. Diet of four-rayed rattail from Puysegur Bank over two size classes ($n = 53$, PAL mm) (%W); number of fish (No.) in each size class, the total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon.

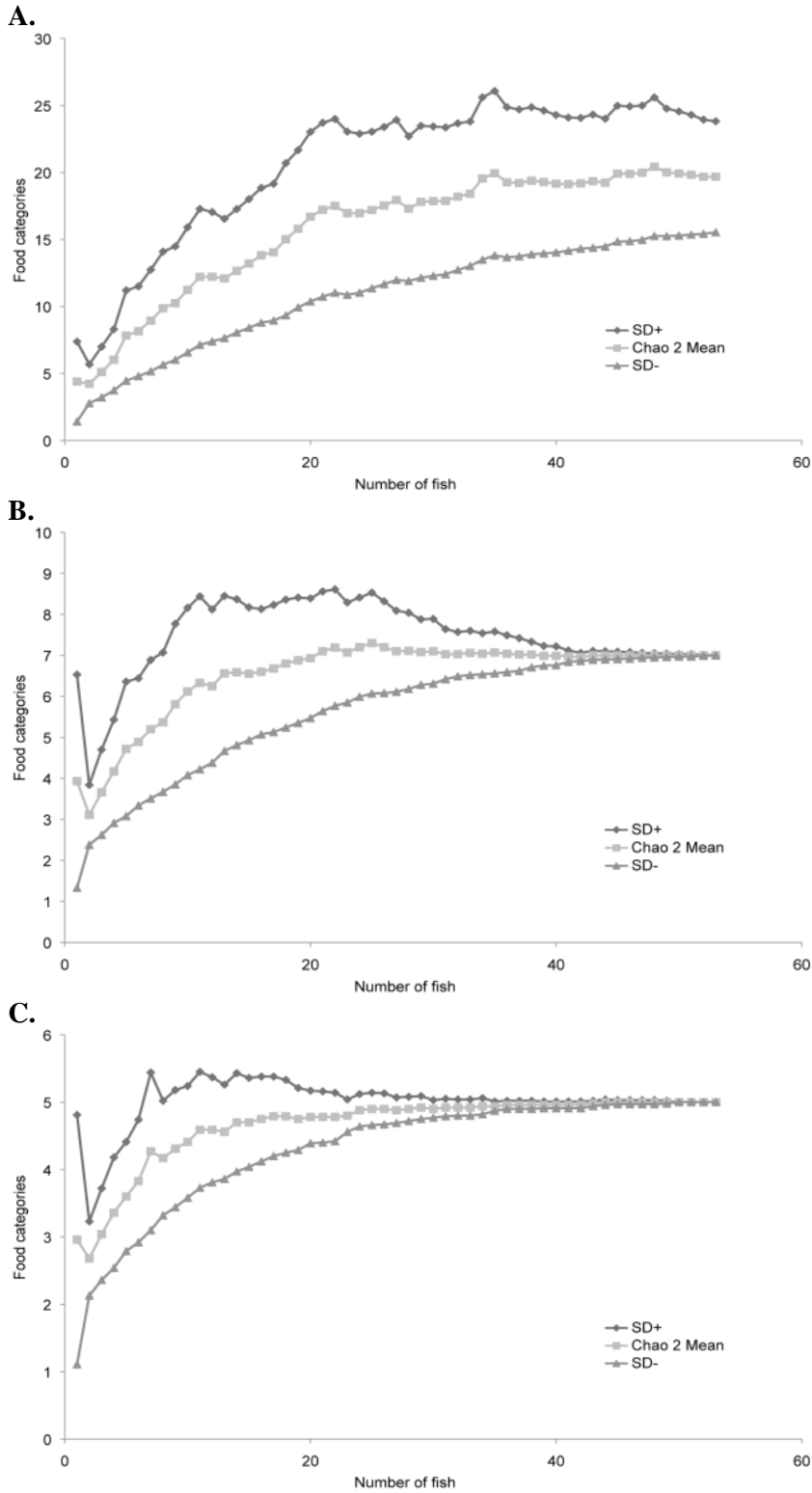


Figure 122. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of four-rayed rattail from Puysegur Bank. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

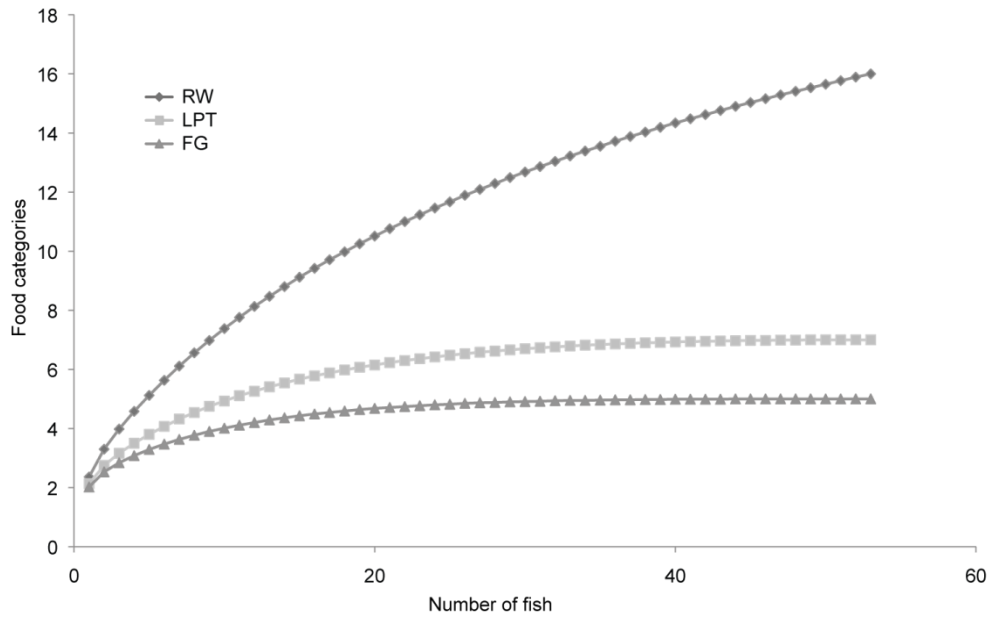
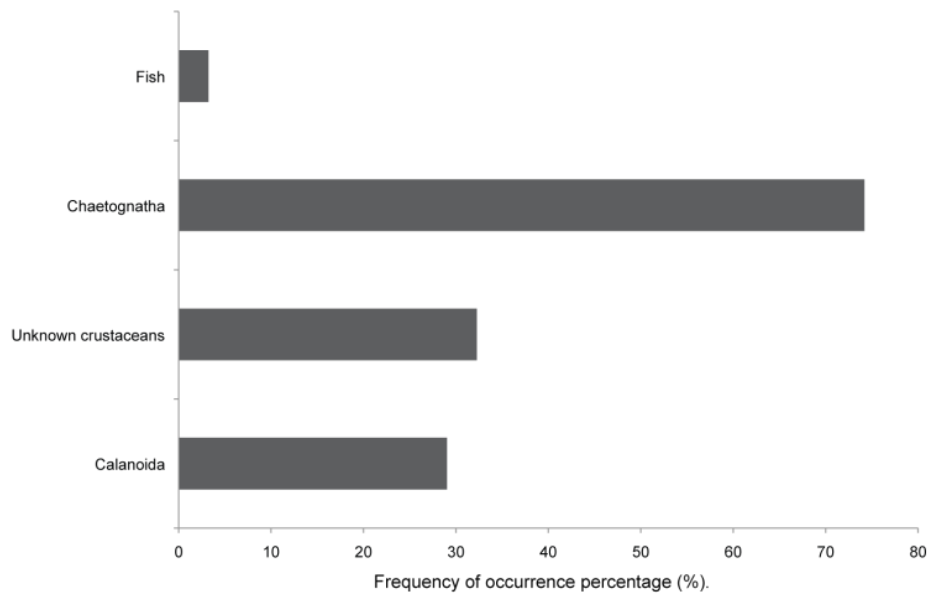


Figure 123. S_{obs} accumulation curves for the stomach contents of four-rayed rattail from Puysegur Bank for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 39. Number of fish estimated to describe 70–90% of S_{max} of the stomach contents of four-rayed rattail from Puysegur Bank over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	22	10	5
S_{max} 80%	29	14	7
S_{max} 90%	38	21	10
Min. total	49	44	15
S_t	6	0	0
n	16	7	5

A.



B.

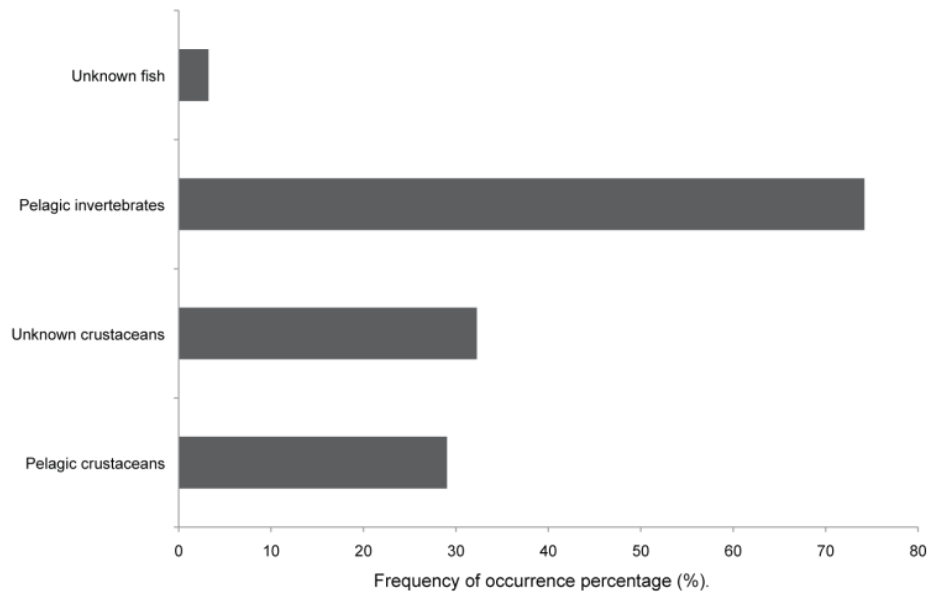


Figure 124. Intestinal contents of four-rayed rattail from Puysegur Bank expressed as percentage frequency of occurrence ($n = 34$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

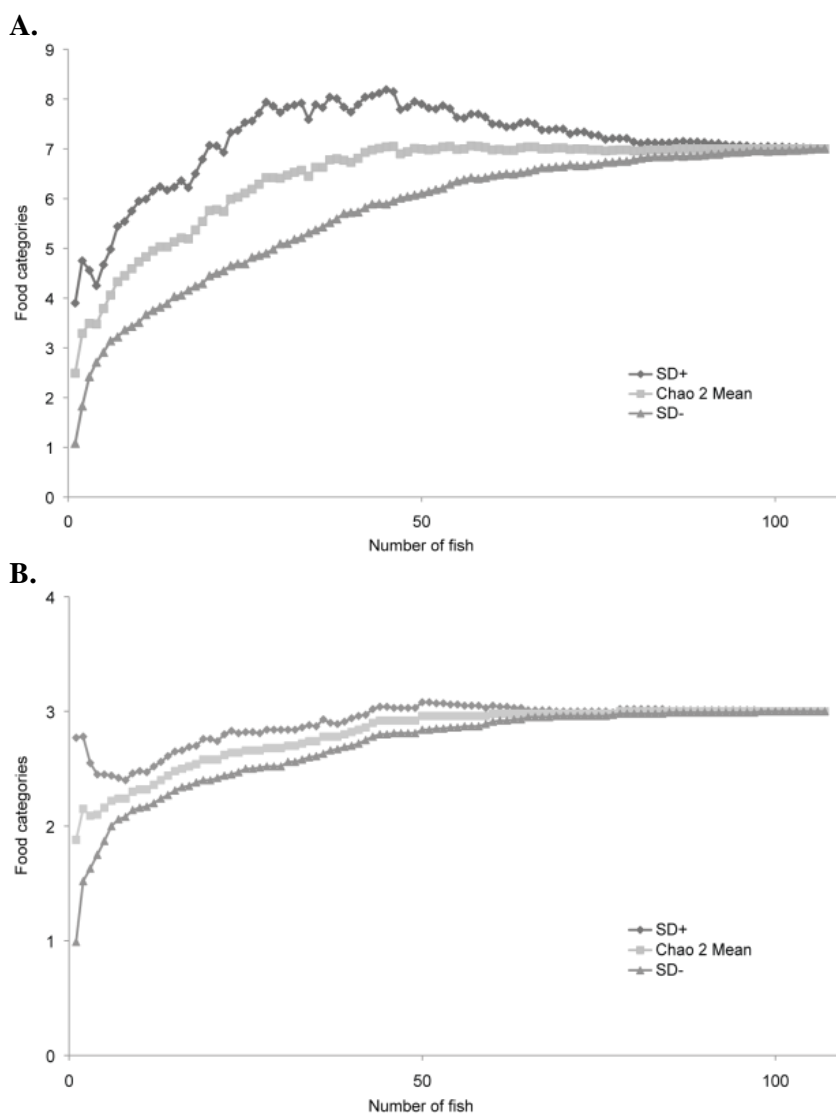


Figure 125. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the intestinal contents four-rayed rattail from Puysegur Bank. **A.** Raw data and lowest practical taxon. **B.** Functional food groups.

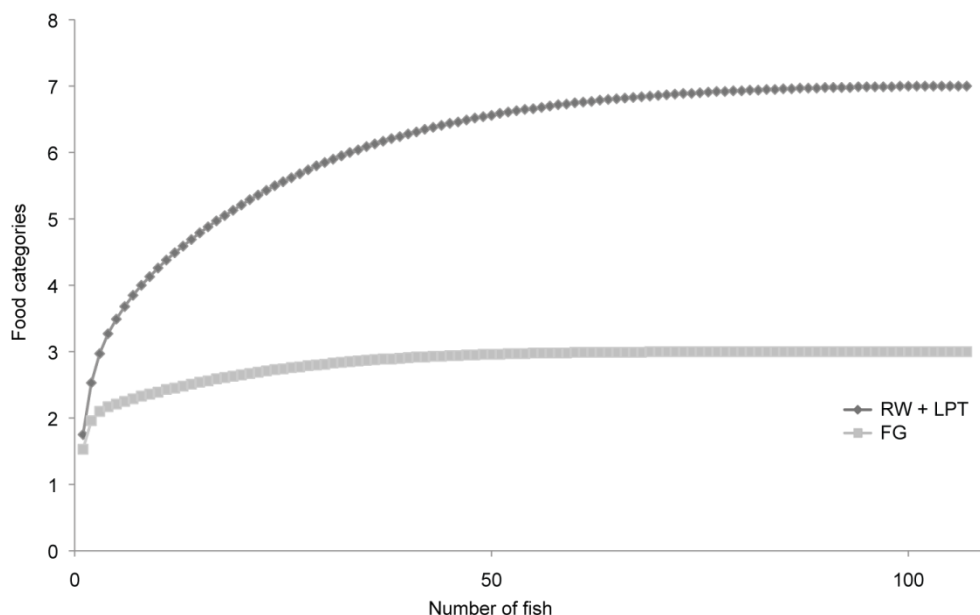


Figure 126. S_{obs} accumulation curves for the intestinal contents of four-rayed rattail from Puysegur Bank for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 40. Number of fish estimated to describe 70–90% of S_{max} of the intestinal contents of four-rayed rattail from Puysegur Bank over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

INTESTINES	RW & LPT	FG
S_{max} 70%	12	3
S_{max} 80%	20	8
S_{max} 90%	28	18
Min. total	102	37
S_t	0	0
n	7	3

4.5. Principal food items of other fish species from Puysegur Bank

An additional 11 fish species were retained from the Puysegur Bank trawls with <10 stomach or intestinal samples containing food items (**Table 41**). Unless otherwise stated, food items were recovered from fish stomachs.

Six long-nosed velvet dogfish had stomachs containing food comprised of fish and squid spermatophores; both were too digested for precise identification. Three of four Owston's dogfish, *Centroscymnus owstoni*, had also eaten squid spermatophores.

One catshark, *Apristurus* sp. A, had eaten a fish, possibly from the family Myctophidae. Another two species of catshark, *Apristurus* sp. B, and *Apristurus exsanguis*, had each stomachs containing unidentifiable fish remains.

Two basketwork eels were examined. One eel had eaten a severed orange roughy head, the other, unidentifiable fish remains.

Five small-headed cod were examined. Two fish had stomachs containing food comprising the remains of natant decapod prawns, squid, and fish. The other three fish had everted stomachs; their intestines contained fish and unidentifiable crustacean remains.

Three Kaiyomaru rattail, *Coelorinchus kaiyomaru*, were examined; two fish had stomachs containing food: gammaridean amphipods; cirolanid, sphaeromatid and valviferan isopods; naticid and marginellid gastropods (?*Mesoginella* sp.); and calanoid copepods.

Five of seven serrulate rattail had stomachs containing food comprising natant decapod remains, gammaridean amphipods, galatheids (*Munida isos* Ahyong & Poore, 2004), isopods, ostracods, calanoid and parasitic copepods, polychaetes, and squid and fish remains. The intestines of five fish contained amphipod, prawn, ostracod, fish, polychaete remains, and sediment.

Four of eight javelin fish, *L. denticulatus*, had stomachs containing food, comprising natant decapod prawn remains and chaetognath jaw hooks. One intestine contained unidentifiable crustacean material; the rest were empty.

The two largest ridge-scaled rattail had intact stomachs and had eaten four-rayed rattail—one had eaten three, and the other, one. The other stomach came from a much smaller ridge-scaled rattail (131 mm PAL), and contained a cirolanid isopod, galatheid (*M. isos*), and the remains of a eunicid polychaete. Identifiable material was recovered from the intestines of all seven fish, comprising gammaridean amphipods, isopods (Cirolanidae, Sphaeromatidae), galatheids (*M. isos*), hermit crabs (Parapaguridae),

ostracods, gastropods, bivalves, polychaetes (Eunicidae), crinoids, and squid and fish remains.

Table 41. Mean length (mm) and weight (g) of male and female fish of 11 species from Puysegur Bank; fish with <10 stomach or intestinal samples containing food items. Length measurements: Pre-caudal fin length, PCL; snout-vent, SV; standard length, SL; pre-anal fin length, PAL; co-efficient of variation (CV).

Species Code	Gender	Number	Mean length (PCL), (SV ¹), (SL ²) (PAL ³), (mm).	CV	Weight (g)	CV
<i>Centroselachus crepidater</i> CYP	Male	7	519	15.4	1122	33.4
	Female	2	350	38.6	420.2	109.0
	Unknown	0				
<i>Centroscyrmus owstoni</i> CYO	Male	1	400		587.8	
	Female	3	371	7.8	415.6	10.9
	Unknown	0				
<i>Apristurus</i> sp. A APA*	Male	0				
	Female	1	549		1030.0	
	Unknown	0				
<i>Apristurus</i> sp. B APB*	Male	1	515		978.9	
	Female	0				
	Unknown	0				
<i>A. exsanguis</i> AEX*	Male	1	527		900.3	
	Female	0				
	Unknown	0				
<i>Diastobranchus capensis</i> BEE	Male	0				
	Female	2	204 ¹	0.8	1085.2	18.3
	Unknown	0				
<i>Lepidion microcephalus</i> SMC	Male	4	342 ²	6.2	336.0	13.2
	Female	1	351 ²		393.0	
	Unknown	0				
<i>Coelorinchus kaiyomaru</i> CKA	Male	1	131 ³		133.2	
	Female	2	114 ³	3.5	85.2	11.3
	Unknown	0				
<i>Coryphaenoides serrulatus</i> CSE	Male	4	104 ³	40.8	191.7	18.6
	Female	2	128 ³	8.1	262.9	3.7
	Unknown	0				
<i>Lepidorhynchus denticulatus</i> JAV	Male	3	115 ³	9.4	269.3	15.6
	Female	5	115 ³	7.5	232.6	23.7
	Unknown	0				
<i>Macrourus carinatus</i> MCA	Male	3	225 ³	19.8	1271.2	56.2
	Female	4	206 ²	30.2	1133.2	80.6
	Unknown	0				

4.6. Aspects of the biology and principal food items of fish from off the Wairarapa coast with >10 stomach or intestinal samples containing food items

Overall, 636 fish attributed to 27 species were examined (**Table 42, 51**).

Eight species were represented by >10 individuals with stomach samples containing food items (**Table 42**). Most fish were immature, so gender-based analyses were not attempted. Cumulative food-item plots for the eight species indicated that the diets of silver roughy, javelin fish, capro dory and sea perch were likely to be adequately represented by samples, whereas those of silverside, two-banded, Bollons' and Oliver's rattail were not.

Table 42. Mean length (mm) and weight (g) of eight fish species (male and female) from off the Wairarapa coast; fish with >10 stomach or intestinal samples containing food items. Acronyms: standard length, SL; pre-anal fin length, PAL; co-efficient of variation (CV).

Species Code	Gender	Number	Mean length (SL) (PAL ¹) (mm)	CV	Weight (g)	CV
<i>Argentina elongata</i> SSI	Male	0				
	Female	0				
	Unknown	21	155.8	12.8	31.3	35
<i>Coelorinchus biclinozonalis</i> CBI	Male	5	110.2 ¹	4.9	81.0	18
	Female	6	115.7 ¹	25.4	246.3	107.5
	Unknown	0				
<i>C. bollonsi</i> CBO	Male	1	99 ¹		125	
	Female	6	133 ¹	28.8	393.6	82.1
	Unknown	51	58 ¹	10.4	20.9	29
<i>C. oliverianus</i> COL	Male	12	82.2 ¹	14.8	57.7	40.7
	Female	9	87 ¹	14.3	76.6	28.3
	Unknown	27	74.8 ¹	11.9	42.7	42.1
<i>Lepidorhynchus denticulatus</i> JAV	Male	11	81 ¹	21	94.6	63.5
	Female	16	92.3 ¹	13.8	135.2	38.7
	Unknown	94	60.7 ¹	36.1	52.2	100.2
<i>Hoplostethus mediterraneus</i> SRO	Male	0				
	Female	0				
	Unknown	82	76.6	21.3	15.5	77
<i>Capromimus abbreviatus</i> CAP	Male	0				
	Female	0				
	Unknown	71	72.9	10	13.9	28.9
<i>Helicolenus percoides</i> PER	Male	6	173.3	41.1	238.2	156.3
	Female	13	172	28.6	181.5	93.8
	Unknown	105	130.7	23.4	69.1	78

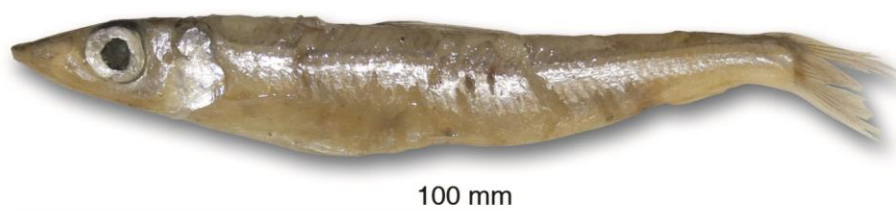
4.6.1. Silverside (SSI), *Argentina elongata* ($n = 22$)

Figure 127. Silverside, (SSI), *Argentina elongata*.

Of the 22 fish examined, 13 had food in their stomachs (**Fig. 128**), but none had food remains in their intestines, giving a PES of 40.9 percent. Silverside had fed upon polychaetes (at least three species) (46.3% IRI), ophiuroids (19.6%), gastropods (*Ringicula delecta* Murdoch & Suter, 1906; ?*Antiguraleus* sp.; and ?*Odostomia* sp.) (9.6%), and foraminiferans (5%) (**Fig. 129A**). Over the whole sample, the trophic level was 3.27. Benthic invertebrates, polychaetes and benthic crustaceans were the most important functional food-item groups (**Fig. 129B**). There was a significant positive correlation between both the weight and number of food items and increasing fish size (Spearman rank correlation $r_s = 0.802$, $P < 0.000$; $r_s = 0.715$, $P < 0.003$). The standardised niche breadth was moderate (0.49).

None of the three dietary classifications adequately described the variation within the stomach contents of silverside (**Fig. 130**, **Fig 131**). There were multiple singletons in all dietary classifications.

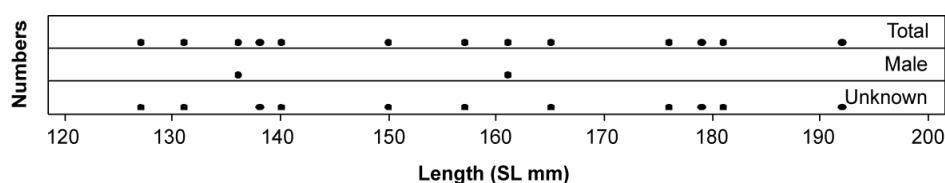
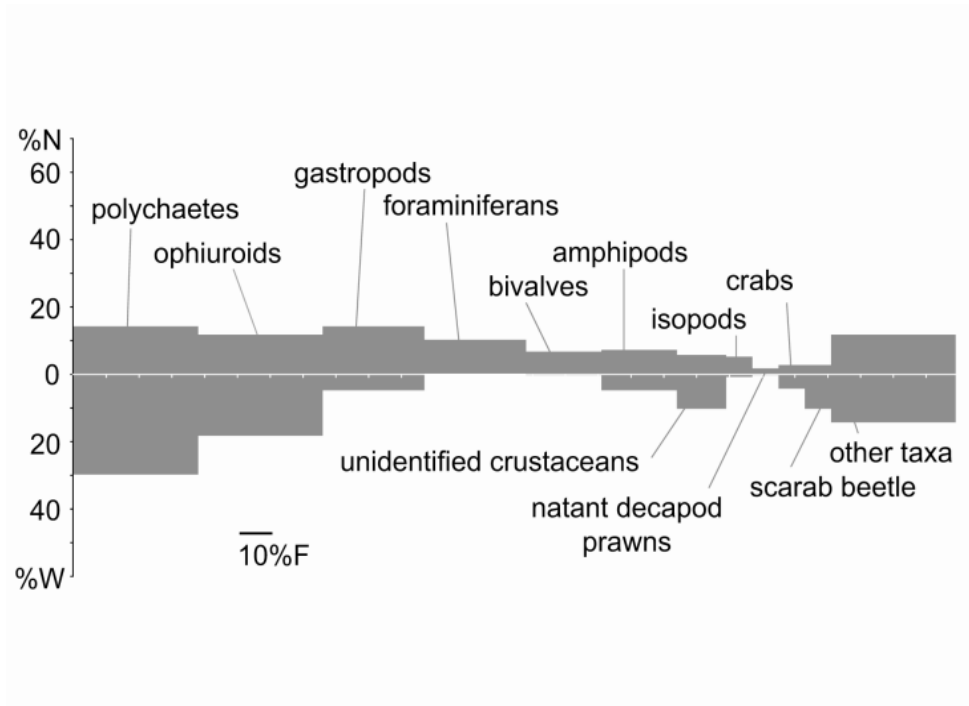


Figure 128. Size-frequency distribution for silverside from off the Wairarapa coast (stomachs containing food) ($n = 13$, SL mm).

A.



B.

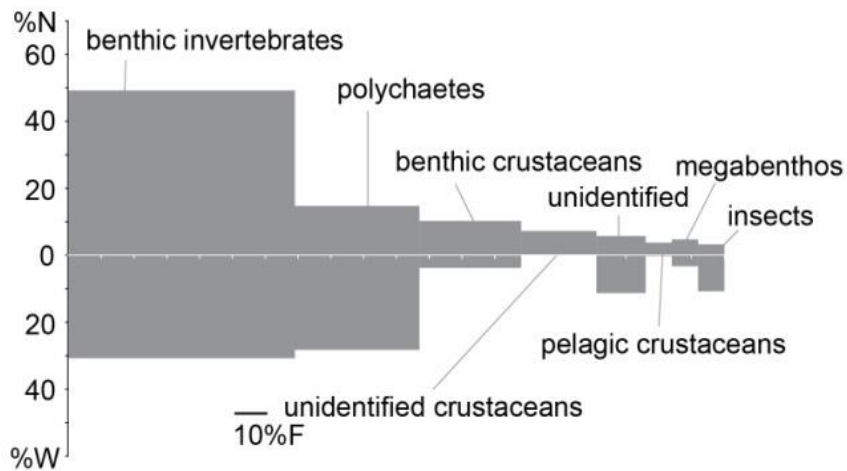


Figure 129. Diet of silverside from off the Wairarapa coast expressed as percentage IRI area charts ($n = 13$). **A.** Lowest practical taxon: other taxa; sponge, and unidentified material. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

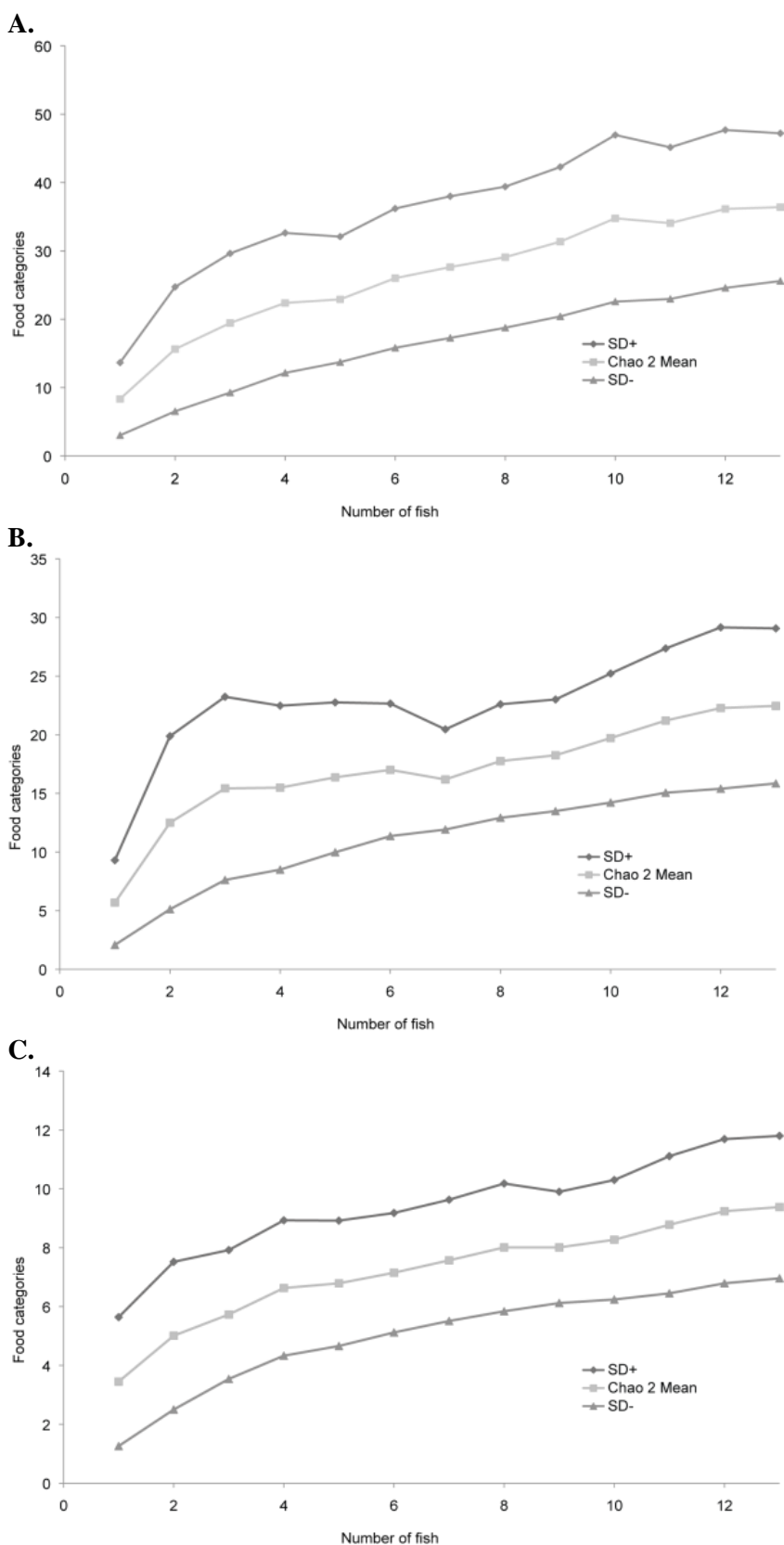


Figure 130. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of silverside from off the Wairarapa coast. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis. **A.** Raw data (23, 13). **B.** Lowest practical taxon (16, 7). **C.** Functional food groups (13, 3).

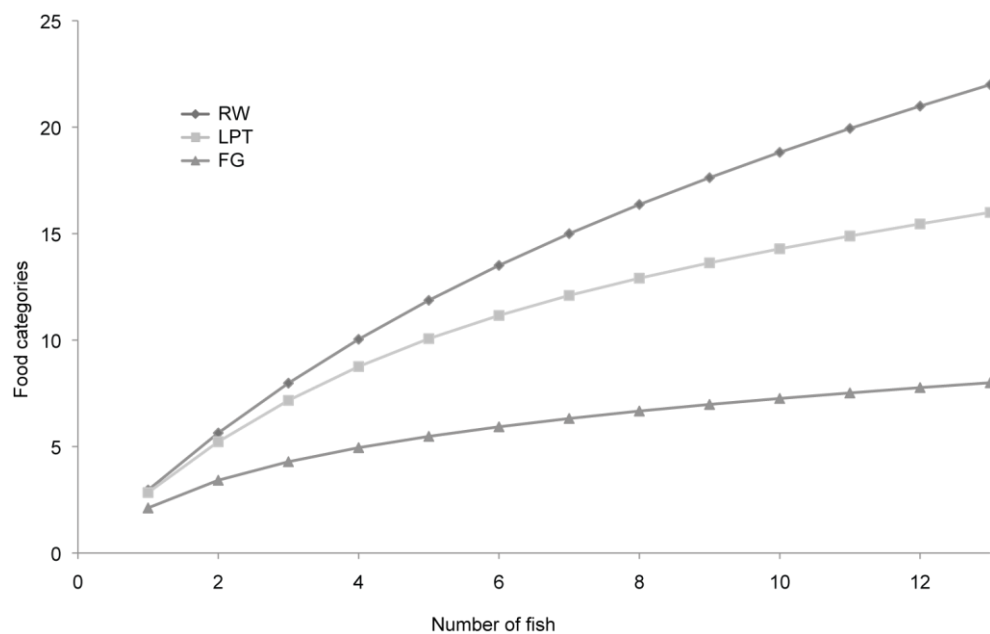


Figure 131. S_{obs} accumulation curves for the stomach contents of silverside from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

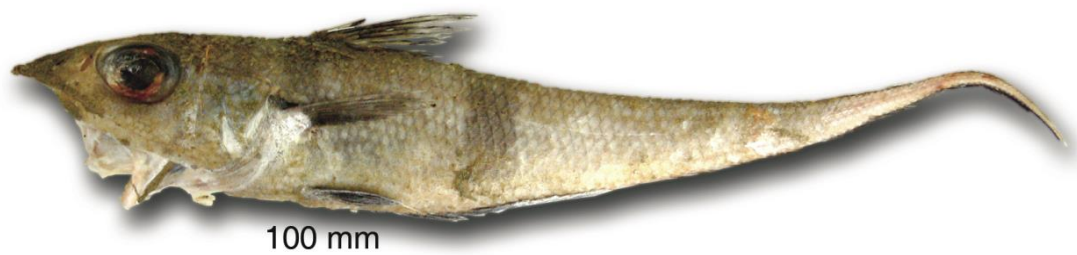
4.6.2. Two-banded rattail (CBI), *Coelorinchus biclinozonalis* ($n = 11$)

Figure 132. Two-banded rattail, (CBI), *Coelorinchus biclinozonalis*.

Ten of the 11 two-banded rattail examined had non-everted stomachs (**Fig. 133**) that contained food material, giving a PES value of 9.1 percent. Natant decapod prawns (*P. acutirostratus* and *N. magnoculus*) (29.4% IRI), the squat lobster (*Munida gracilis* Henderson, 1885) (27.1% IRI), polychaetes (16.8%), and the crab *Pycnoplax* (*Carcinoplax*) *victoriensis* Rathbun, 1923, were the most important food items (**Fig. 135A**). Over the whole sample, the trophic level was 3.57. Megabenthos, polychaetes and benthic crustaceans were the most important functional food-item groups (**Fig. 135B**). There were no significant trends with either the weight or number of food items and the size of the fish (Spearman rank correlation $r_s = 0.255$, $P > 0.238$, $r_s = 0.176$, $P > 0.314$), and the standardised niche breadth was moderate (0.40). None of the dietary categories adequately described the variation in the diet of two-banded rattail (**Fig. 136**, **Fig. 137**). Material was also recovered from eight intestines, and was mostly crabs and other benthic crustaceans (**Fig. 138**).

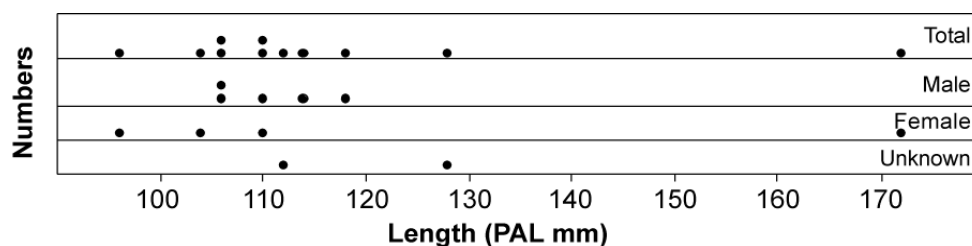
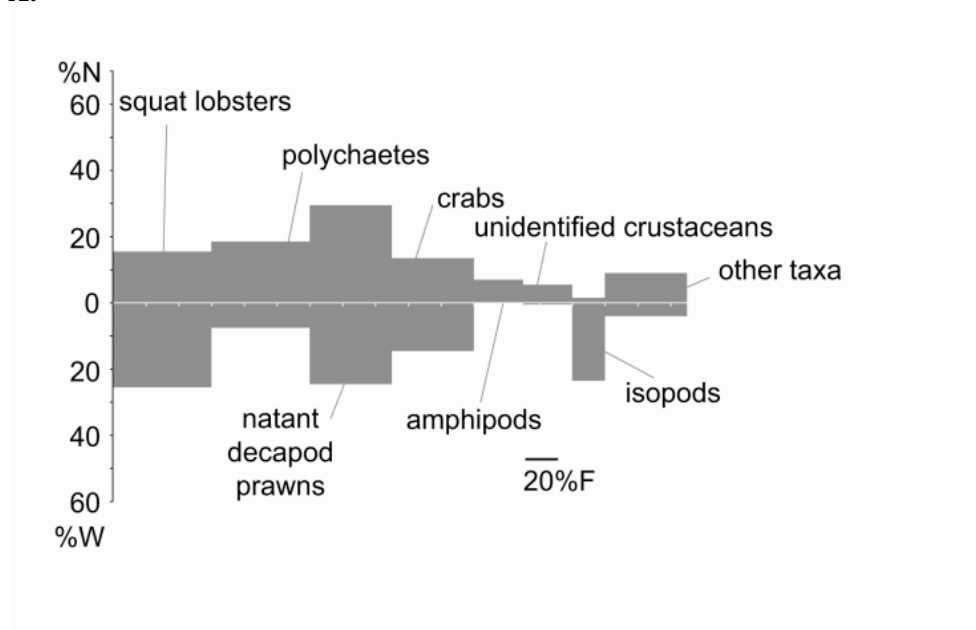


Figure 133. Size-frequency distribution for two banded rattail from off the Wairarapa coast (stomachs containing food) ($n = 10$, PAL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

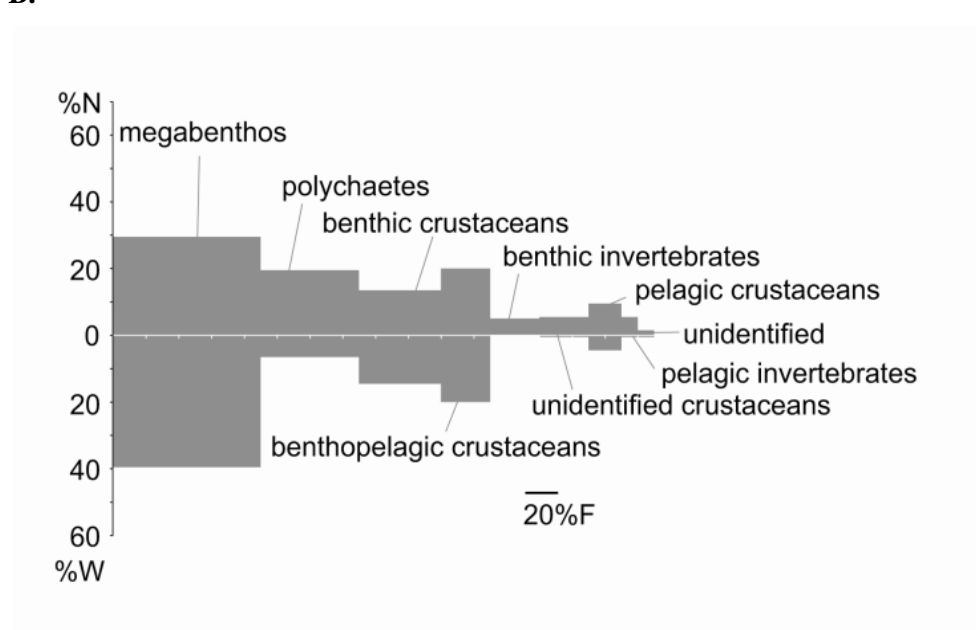


Figure 134. Diet of two-banded rattail from off the Wairarapa coast expressed as percentage IRI area charts ($n = 10$). **A.** Lowest practical taxon: other taxa; gastropods, squid, ophiuroids, and unidentified material. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

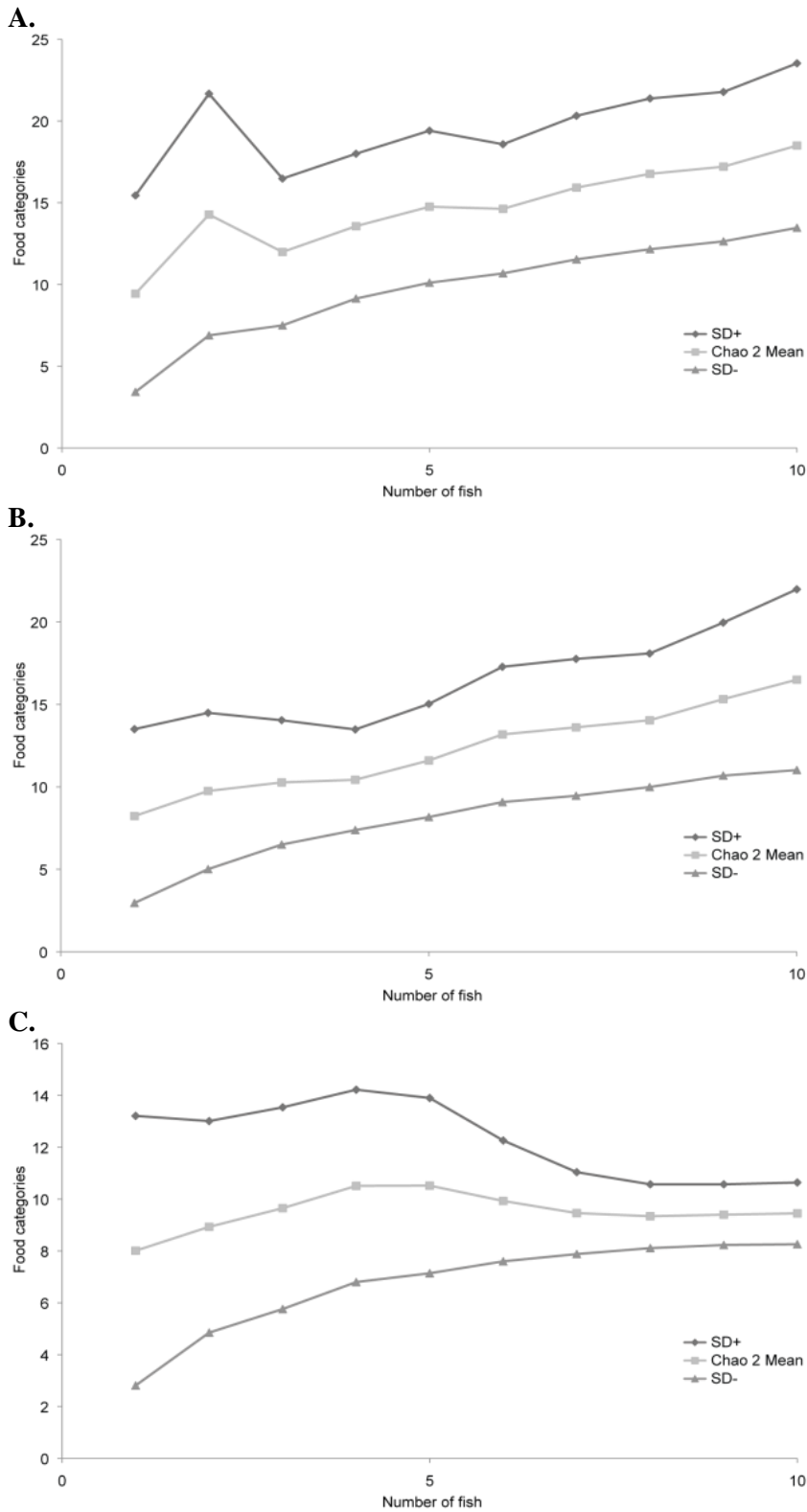


Figure 135. Mean Chao 2 estimation curves (plus and minus one standard deviation) for three dietary classifications for two-banded rattail from off the Wairarapa coast. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

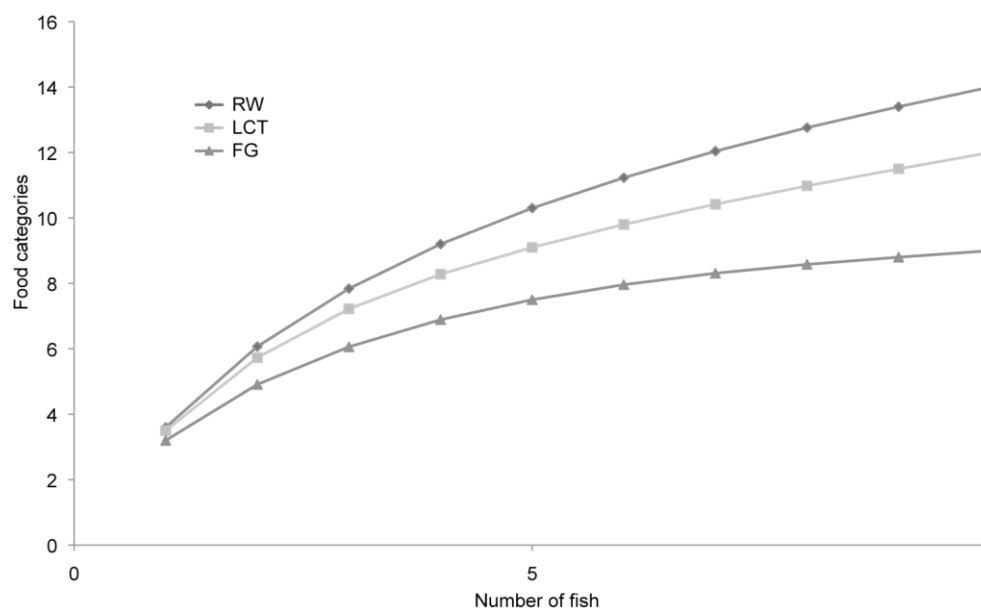
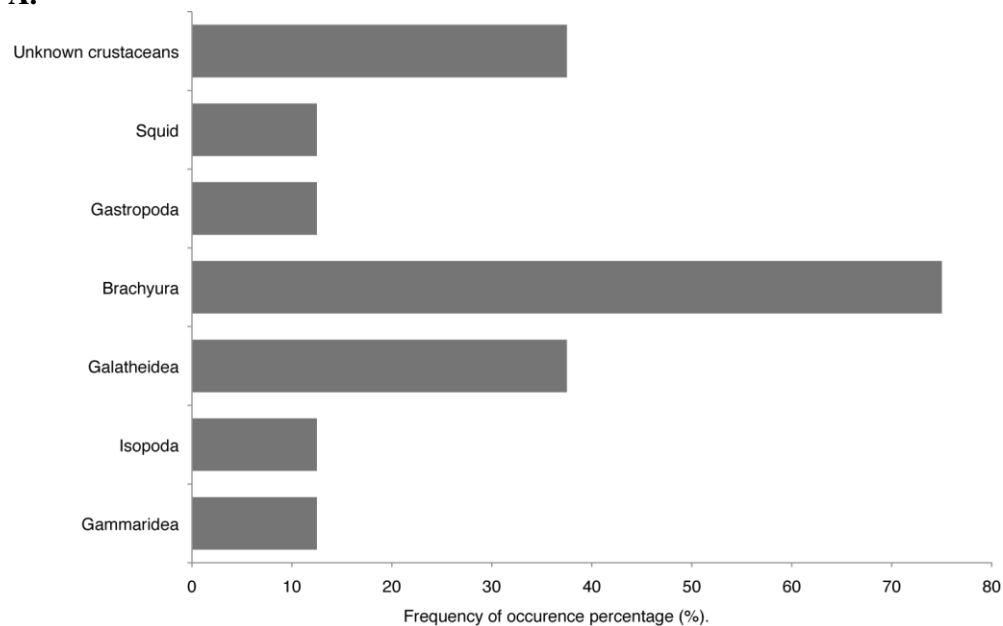


Figure 136. S_{obs} accumulation curves for the stomach contents of two-banded rattail from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

A.



B.

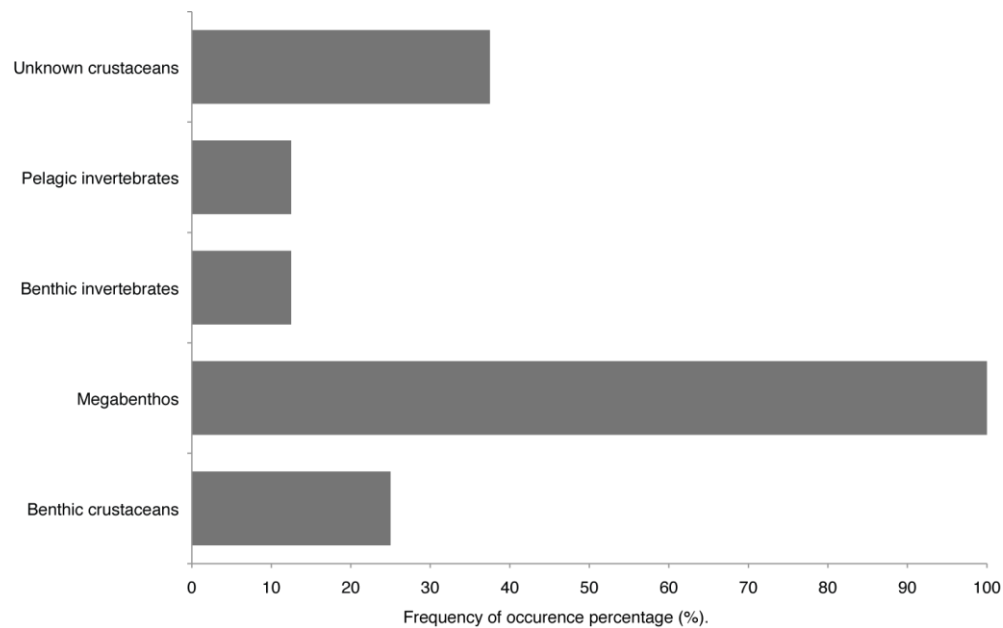


Figure 137. Intestinal contents of two-banded rattail from off the Wairarapa coast expressed as percentage frequency of occurrence ($n = 8$). **A.** Lowest practical taxon. **B.** Functional food-item group.

4.6.3. Bollons' rattail (CBO), *Coelorinchus bollonsi* (n = 58)



Figure 138. Bollons' rattail, (CBO), *Coelorinchus bollonsi*.

Fifty-eight Bollons' rattail were examined and 39 possessed non-everted stomachs that contained food (**Fig. 139**), giving a PES of 32.9 percent. Crabs (*P. (C.) victoriensis*) (62% IRI), and at least four species of polychaetes (26%) were the most important food items (**Fig. 140A**). Megabenthos and polychaetes were the most important functional food-item groups (**Fig. 140B**). Over the whole sample, the trophic level was 4.12. There was a significant positive correlation between both the weight and number of food items per fish, and increasing fish size (Spearman rank correlation $r_s = 0.280$, $P < 0.033$ and $r_s = 0.418$, $P < 0.004$). The standardised niche breadth was low (0.08).

Three of the dietary classifications adequately described the variation within the stomach contents of Bollons' rattail (RW, LPT, & FG) (**Fig. 141**, **Fig. 142**, **Table 43**). In these, the minimum total number of fish needed to describe the dietary variation ranged between 31 and 37 (FG & RW respectively), and this was reflected in the S_{\max} values (**Table 43**). There were multiple singletons in two of the dietary classifications (RW & LPT).

Material was recovered from the intestines of 53 fish (giving a PEI of 8.6%), and this consisted mostly of crab and unidentified polychaete and crustacean remains (**Fig. 143**). The RW and LPT intestinal contents datasets were identical and were treated as one. None of the dietary classifications adequately described the dietary variation within the intestinal contents of Bollons' rattail (**Fig. 144**, **Fig. 145**), as there were multiple singletons in each of the dietary classifications.

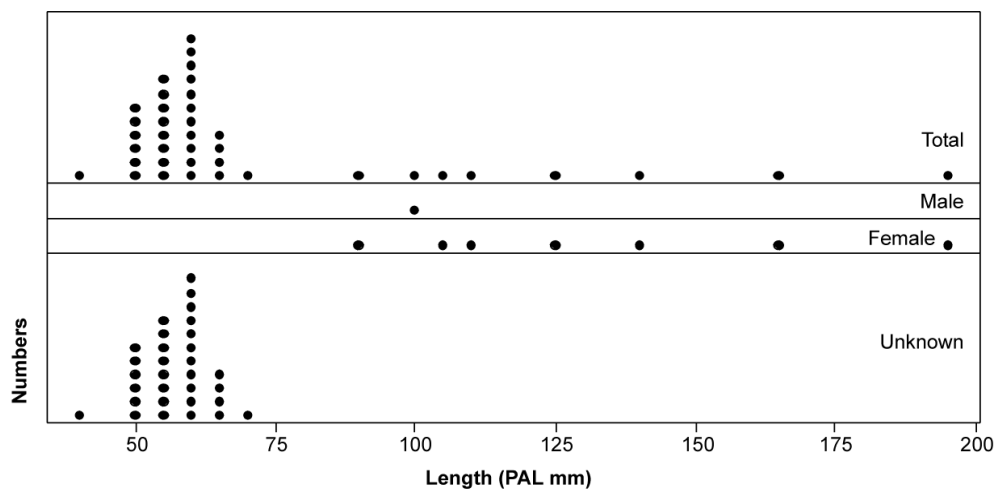
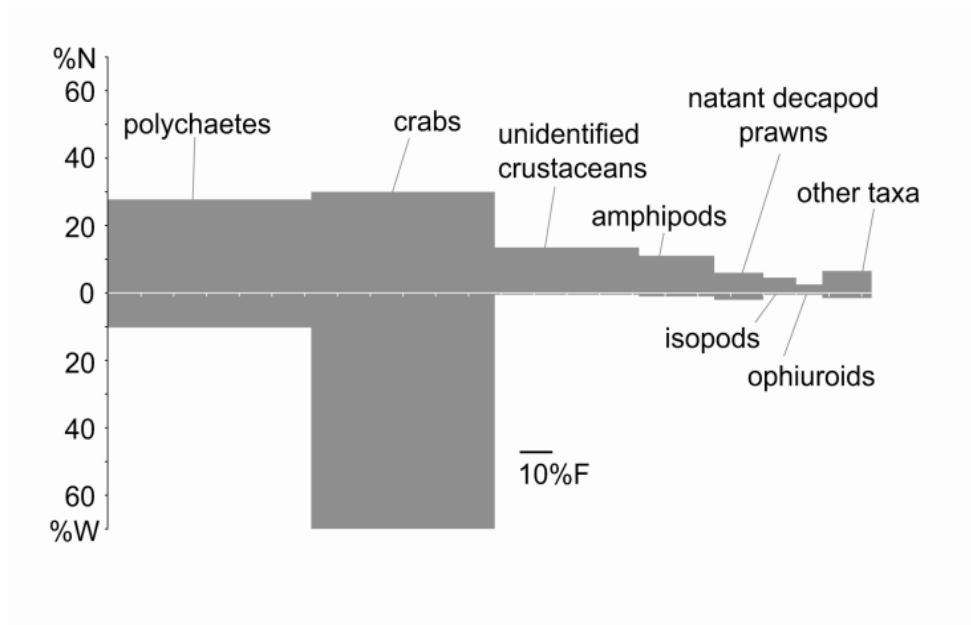


Figure 139. Size-frequency distribution for Bollons' rattail from off the Wairarapa coast (stomachs containing food) ($n = 39$, PAL mm). The Unknown category includes damaged and/or immature fish.

A.



B.

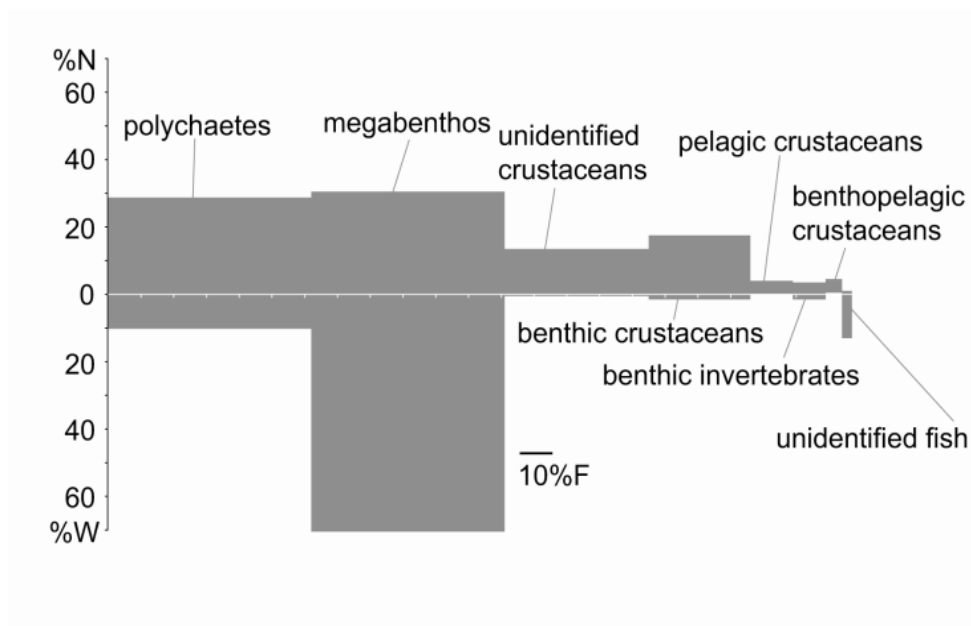


Figure 140. Diet of Bollons' rattail from off the Wairarapa coast expressed as percentage IRI area charts ($n = 39$). **A.** Lowest practical taxon: other taxa; fish, squid, natant decapod prawns, squat lobsters, gastropods, and calanoid copepods. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

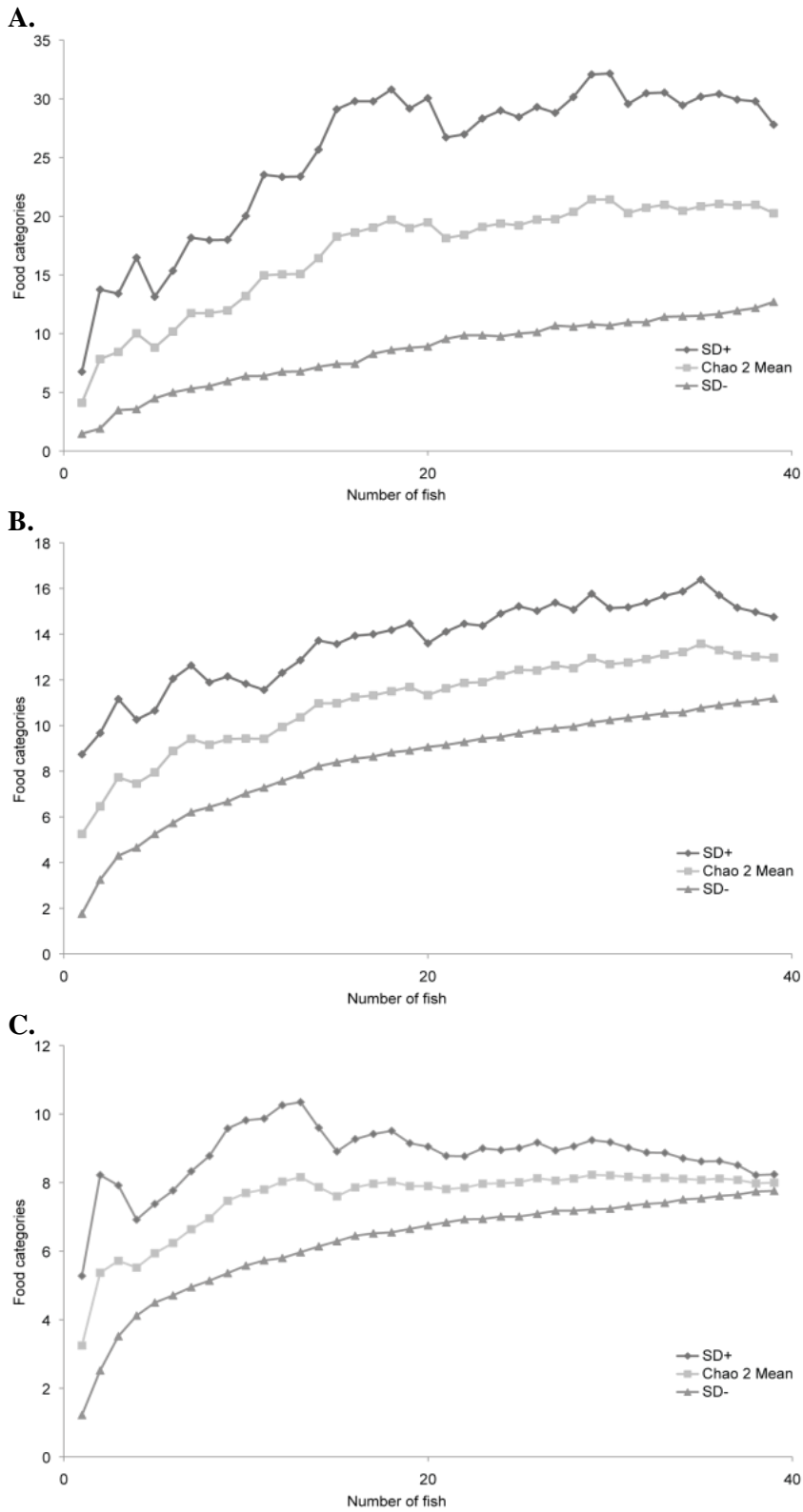


Figure 141. Mean Chao 2 estimation curves (plus and minus one standard deviation SD) for the stomach contents of Bollons' rattail from off the Wairarapa coast. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

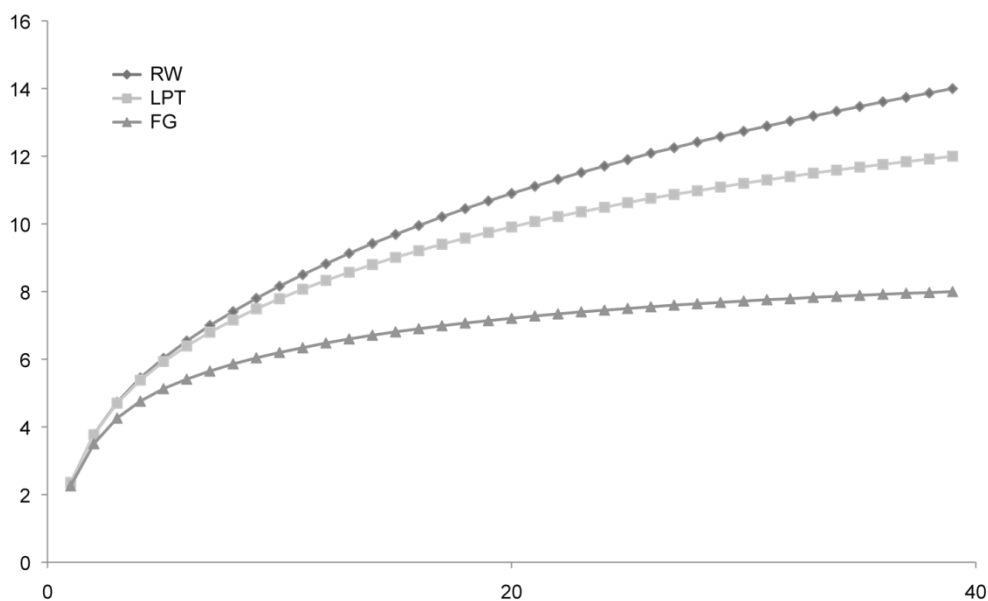
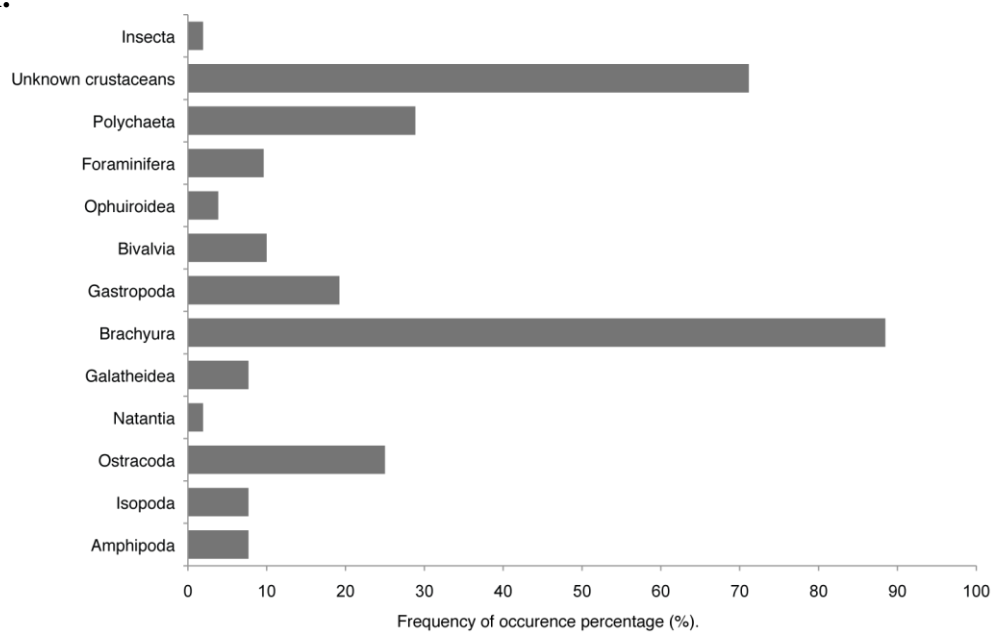


Figure 142. S_{obs} accumulation curves for the stomach contents of Bollons’ rattail from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 43. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of Bollons’ rattail from off the Wairarapa coast over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups,). S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	15	12	6
S_{max} 80%	21	18	10
S_{max} 90%	28	25	17
Min. total	37	36	31
S_t	5	3	1
n	14	12	8

A.



B.

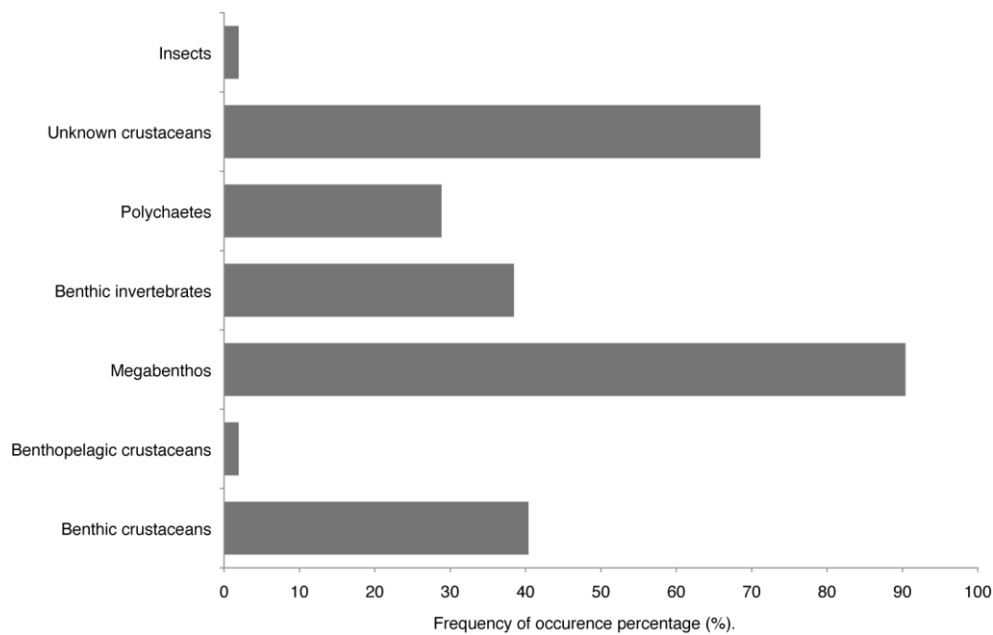


Figure 143. Intestinal contents of Bollons' rattail from off the Wairarapa coast expressed as percentage frequency of occurrence ($n = 53$). **A.** Lowest practical taxon. **B.** Functional food-item groups.

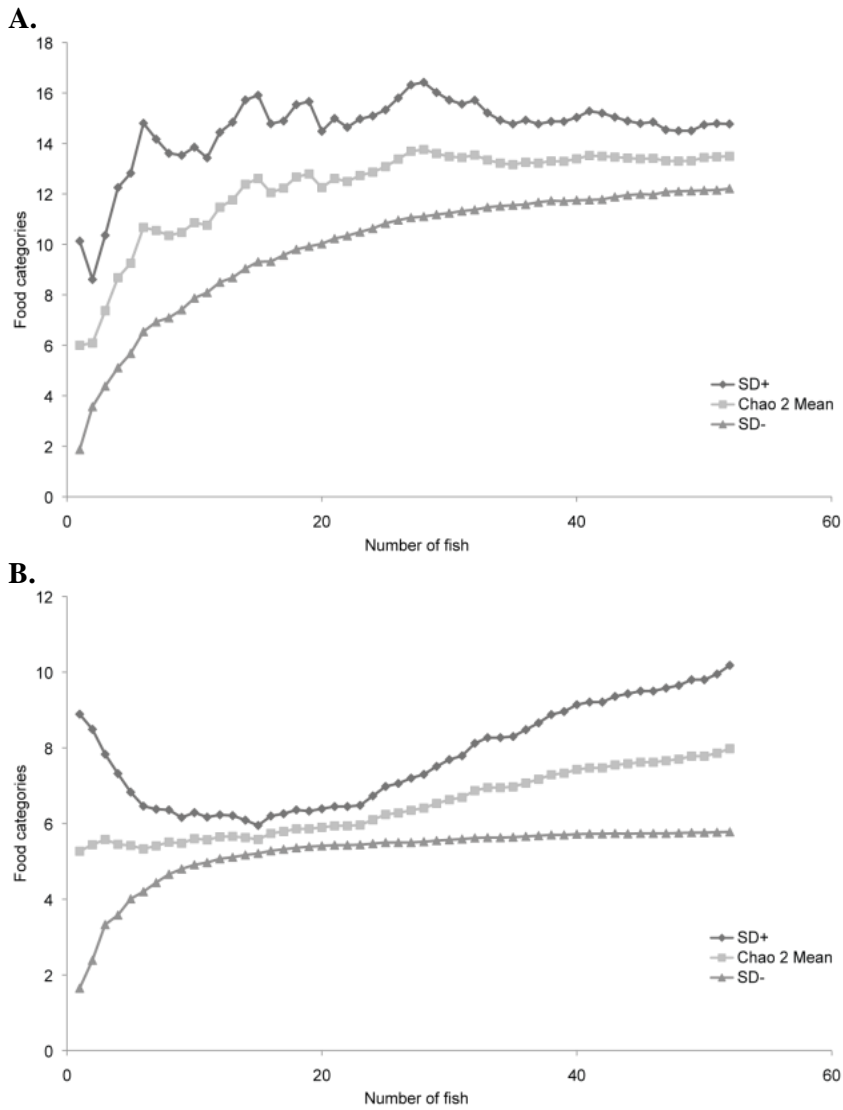


Figure 144. Mean Chao 2 estimation curves (plus and minus one standard deviation) for three dietary classifications for the intestinal contents of Bollons' rattail from off the Wairarapa coast. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis. **A.** Raw data, and Lowest practical taxon (13, 2). **B.** Functional food groups (7, 2).

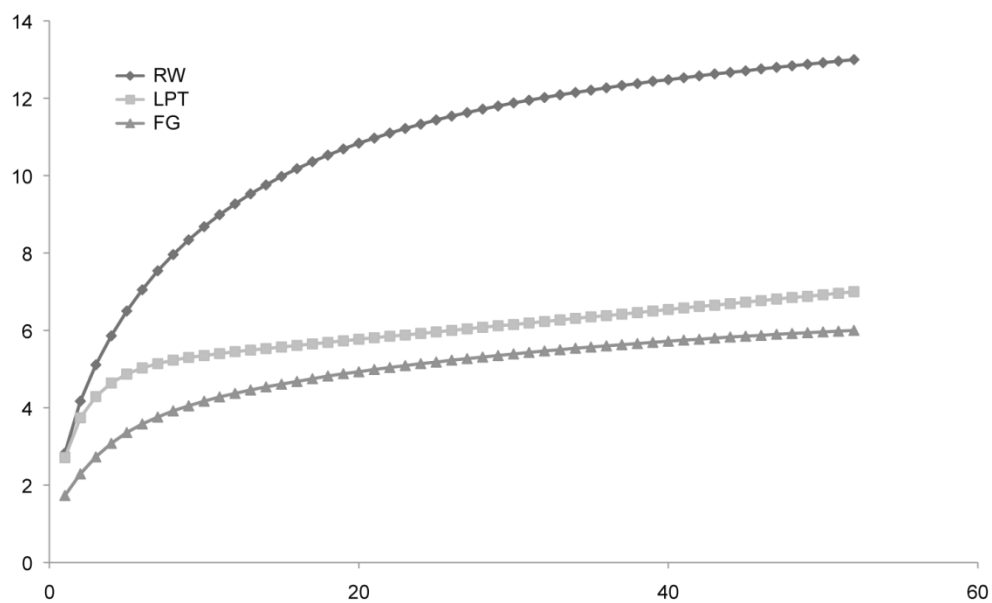


Figure 145. S_{obs} accumulation curves for the intestinal contents of Bollons' rattail from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

4.6.4. Oliver's rattail (COL), *Coelorinchus oliverianus* ($n = 48$)

Figure 146. Oliver's rattail, (COL), *Coelorinchus oliverianus*.

Thirty-seven of the 48 Oliver's rattail examined had stomachs containing food, (Fig. 147) giving a PES of 22.9 percent. Natant decapod prawns and prawn remains (either natant decapod, mysid, or euphausiid prawn remains, but too digested to be reliably identified) were the most important food for Oliver's rattail (57.4% IRI), followed by the crab *P. victoriensis* (19.9%), and unidentified crustaceans (10.2%) (Fig. 148A). Over the whole sample, the trophic level was 4.04. Pelagic crustaceans, megabenthos, and benthopelagic crustaceans were the most important functional food-item groups (Fig. 148B). There was no significant correlation between the weight and numbers of food items and increasing fish size (Spearman rank correlation $r_s = 0.265$, $P > 0.057$ and $r_s = 0.169$, $P > 0.159$). No material was recovered from the intestines. Standardised niche breadth was low (0.15). None of the three dietary classifications adequately described the dietary variation within the stomach contents of Oliver's rattail (Fig. 149, Fig. 150). There were multiple singletons in each food classification.

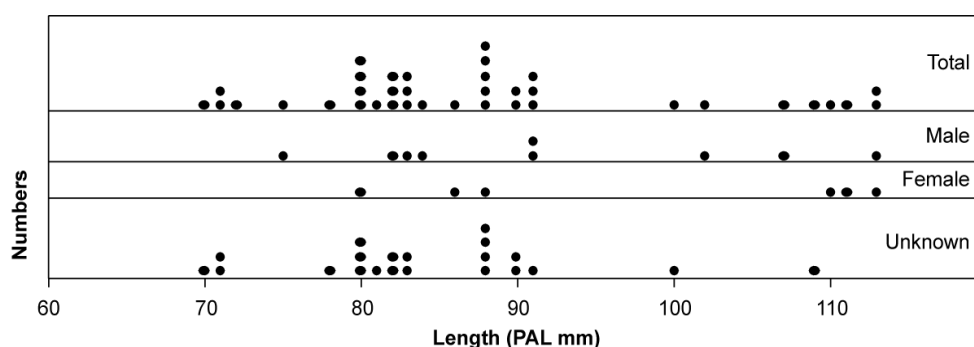
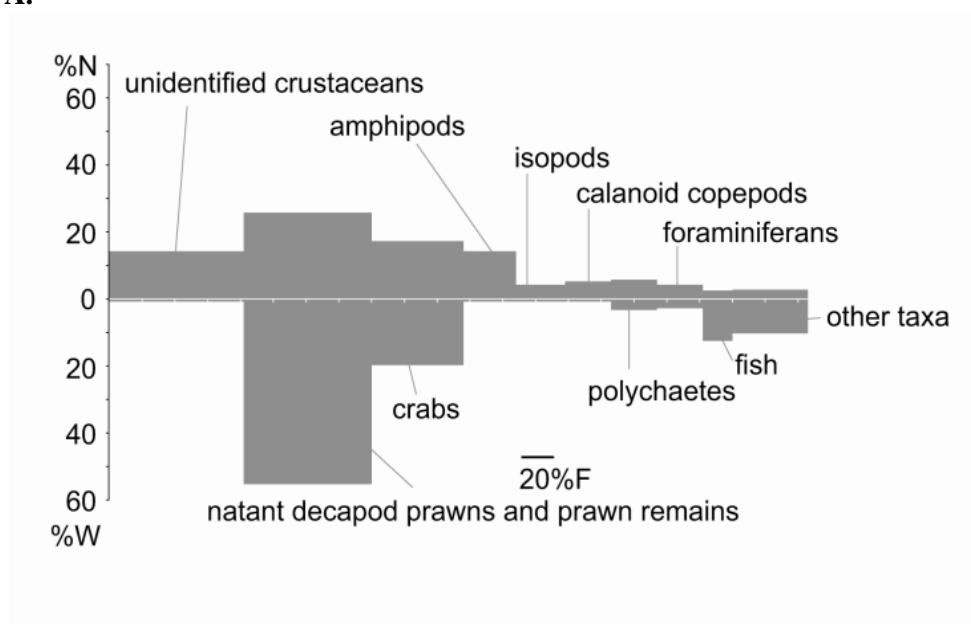


Figure 147. Size-frequency distribution for Oliver's rattail from off the Wairarapa coast (stomachs containing food) ($n = 37$, PAL mm). Fish of unknown gender include those damaged and/or immature.

A.



B.

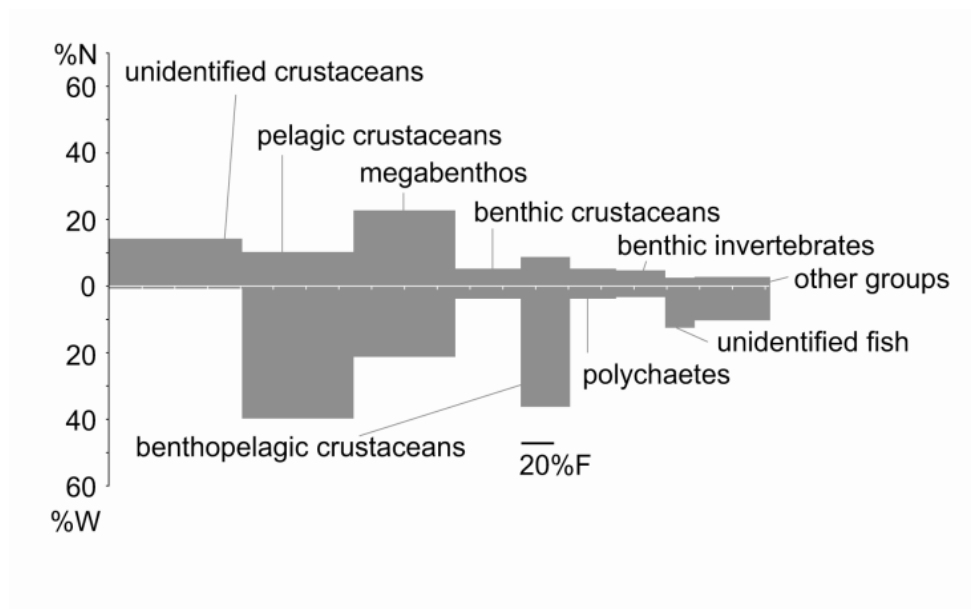


Figure 148. Diet of Oliver's rattail from off the Wairarapa coast expressed as percentage IRI area charts ($n = 37$). **A.** Lowest practical taxon: other taxa; fish, euphausiids, squid, squat lobsters, ophiuroids, and an insect. **B.** Functional food-item groups: other groups; pelagic invertebrates, seaweed, unidentified material, and an insect. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

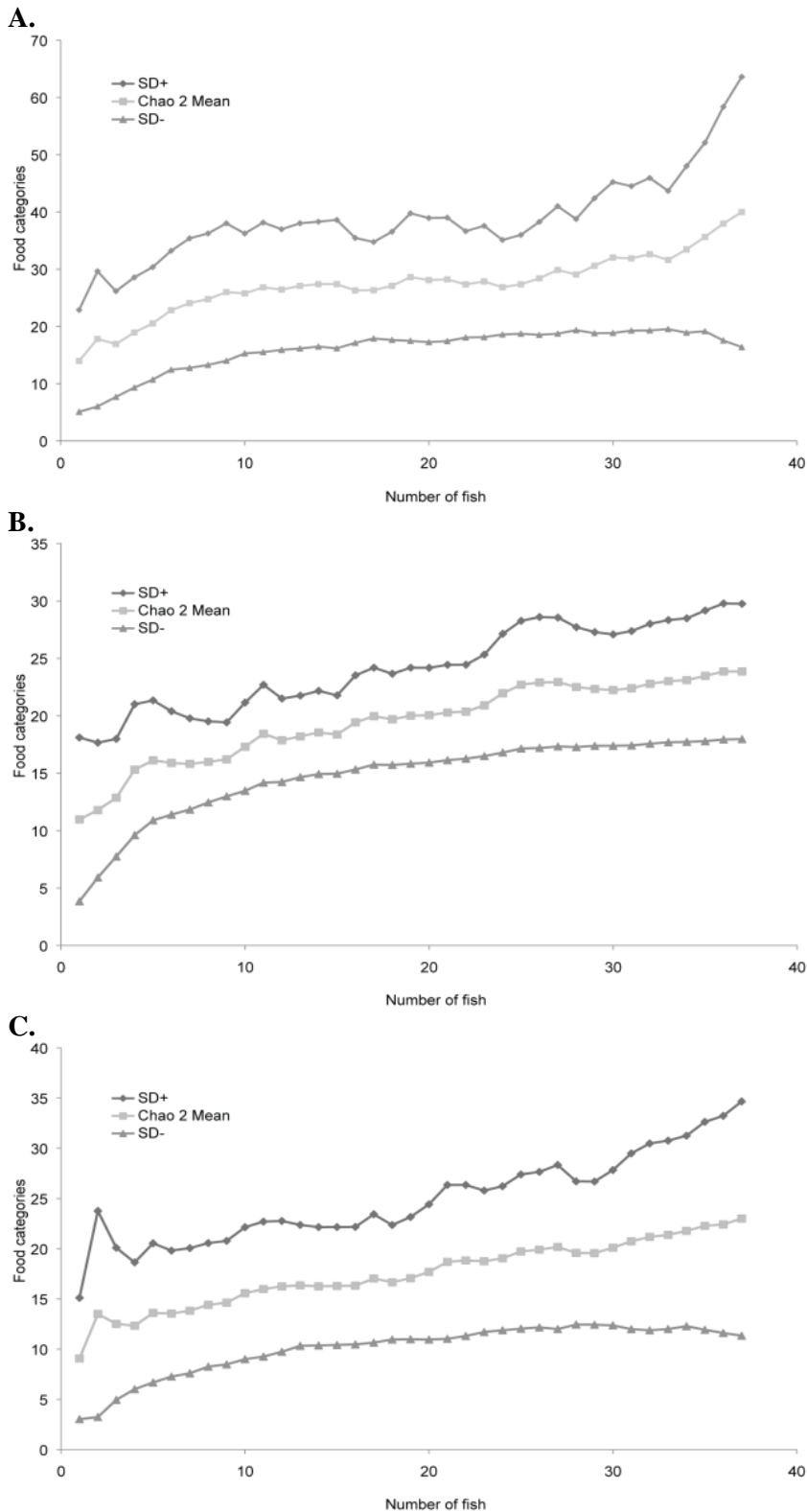


Figure 149. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of Oliver’s rattail from off the Wairarapa coast. The numbers of food categories per dietary classification, followed by the number of singletons in each classification, are in parenthesis. **A.** Raw data (22, 6). **B.** Lowest practical taxon (19, 5). **C.** Functional food groups (15, 4).

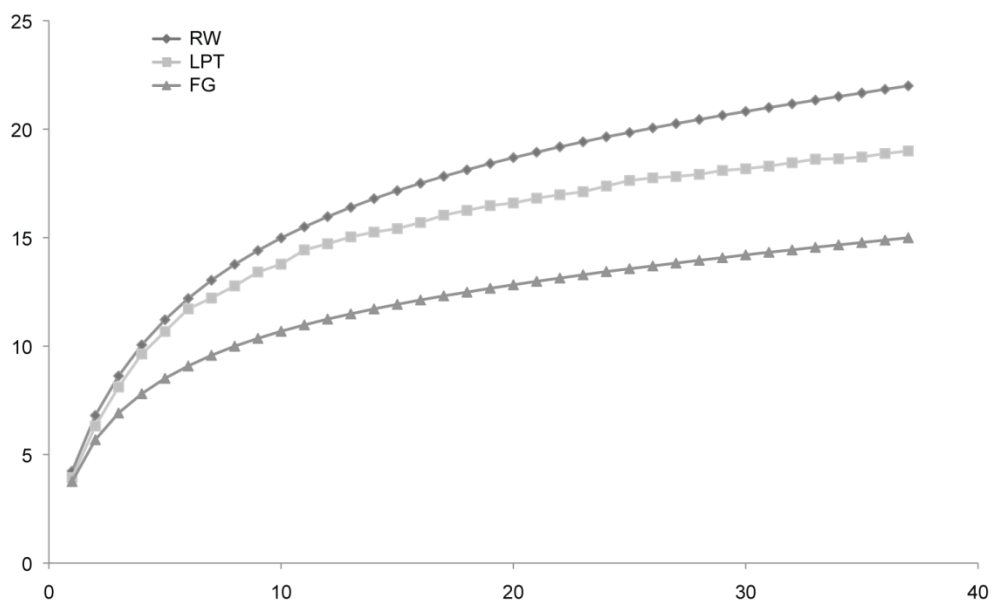


Figure 150. S_{obs} accumulation curves for the stomach contents of Oliver’s rattail from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

4.6.5. Javelin fish (JAV), *Lepidorhynchus denticulatus* (n = 121)



Figure 151. Javelin fish, (JAV), *Lepidorhynchus denticulatus*.

Eighty-five of the 121 javelin fish examined had stomachs containing food items (**Fig. 152**) which gave a PES of 29.8 percent. Natant decapod prawns were the most important dietary item (23% IRI) (**Fig. 153A**), particularly *Notopandalus magnoculus* and *Pasiphaea* aff. *sivado*. Over the whole sample, the trophic level was 4.01. Pelagic crustaceans and pelagic invertebrates were the two most important functional food-item groups (**Fig. 153B**). There was a significant positive correlation between both the weight and numbers of food items increasing with increasing fish size (Spearman rank correlation $r_s = 0.605$, $P < 0.000$ and $r_s = 0.599$, $P < 0.000$), and *N. magnoculus* and *P. aff. sivado*, became more important in the diets of larger fish (**Fig. 54**). There was one high level of dietary overlap between the two smallest classes (26–39 and 40–69 mm PAL) (**Table 44**). Standardised niche breadth values were low for all size classes (**Fig. 154**) and low over the whole sample (0.05).

The dietary variation within the stomachs of javelin fish was adequately described by two of the dietary classifications (RW & LPT) (**Fig. 155, Fig. 156, Table 45**). The minimum total number of stomachs required to describe the variation in stomach contents of javelin fish ranged between 77 and 83 (LPT & RW respectively) (**Table 45**). This was also reflected in the S_{\max} values, with 58 stomachs necessary to describe 90 percent of the dietary variation for LPT and RW (**Table 45**). There were multiple singletons in all dietary classifications.

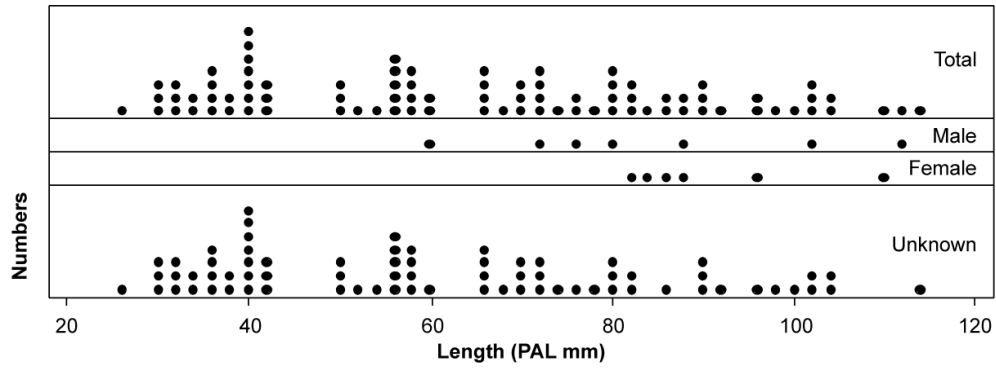
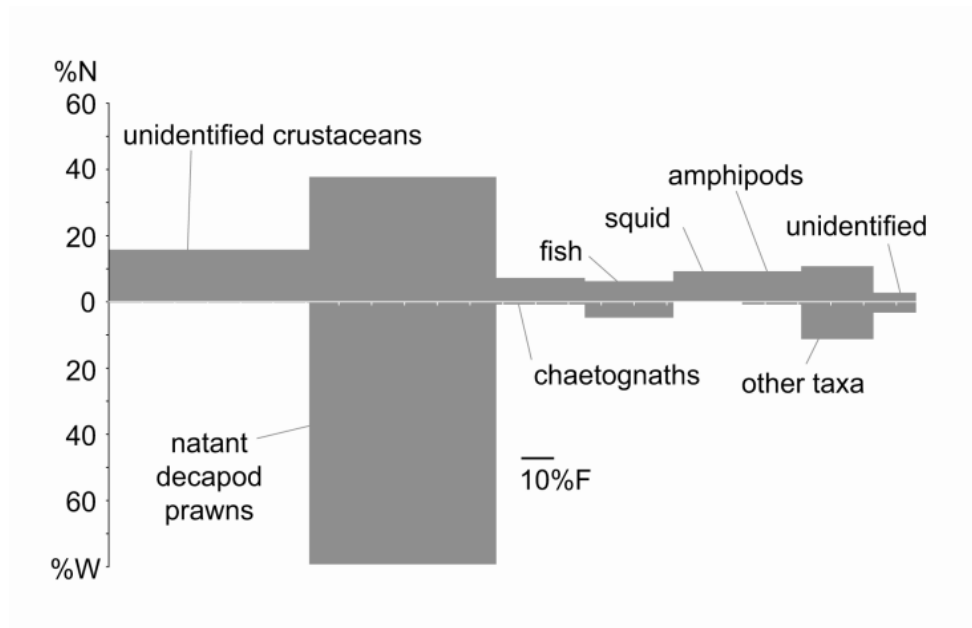


Figure 152. Size-frequency distribution for javelin fish from off the Wairarapa coast (stomachs containing food) ($n = 85$, PAL mm). Fish of unknown gender include those damaged and/or immature.

A.



B.

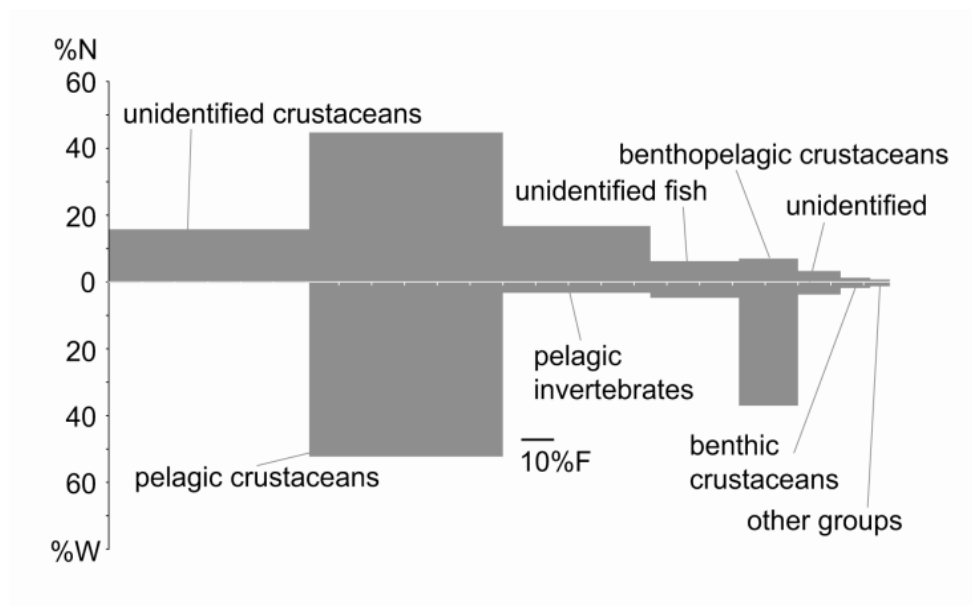


Figure 153. Diet of javelin fish from off the Wairarapa coast expressed as percentage IRI area charts ($n = 85$). **A.** Lowest practical taxon: other taxa: euphausiid prawns, calanoid copepods, ostracods, crabs, an unidentified phyllosoma, pelagic gastropods, thaliaceans, foraminiferans, seaweed, and a weevil. **B.** Functional food-item groups: other groups; megabenthos, benthic invertebrates, an insect, and seaweed. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

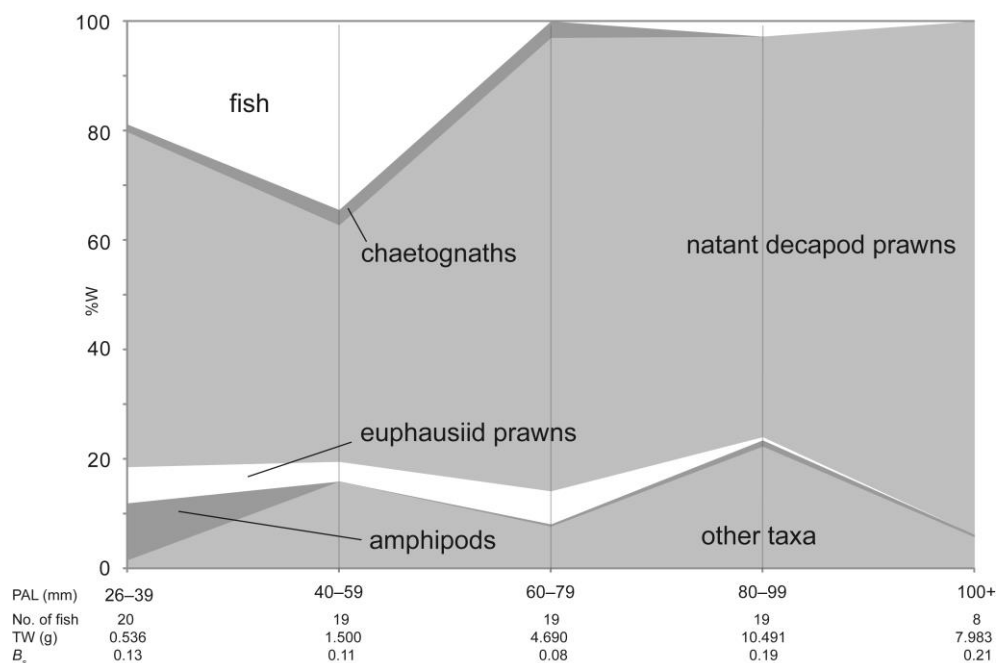


Figure 154. Diet (%W) of javelin fish from off the Wairarapa coast over five size classes ($n = 85$, PAL mm), number of fish (No.) in each size class, the total weight of food (TW) and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon. Other taxa: calanoid copepods, ostracods, crabs, an unidentified phyllosoma, gastropods, thaliaceans, foraminiferans, seaweed, and a weevil.

Table 44. Dietary overlap values for javelin fish from off the Wairarapa coast over five size categories ($n = 85$, PAL mm). Food categories are based on the lowest practical taxon. Food categories are based on the lowest practical taxon. Dark grey rectangles indicate biologically significant dietary overlaps >60%. Calculations are based on %W.

Length (PAL mm)	26–39 ($n = 20$)	40–59 ($n = 19$)	60–79 ($n = 19$)	80–99 ($n = 19$)	100+ ($n = 9$)
26–39		0.7	0.7	0.7	0.6
40–59			0.6	0.5	0.5
60–79				0.8	0.9
80–99					0.8
100+					

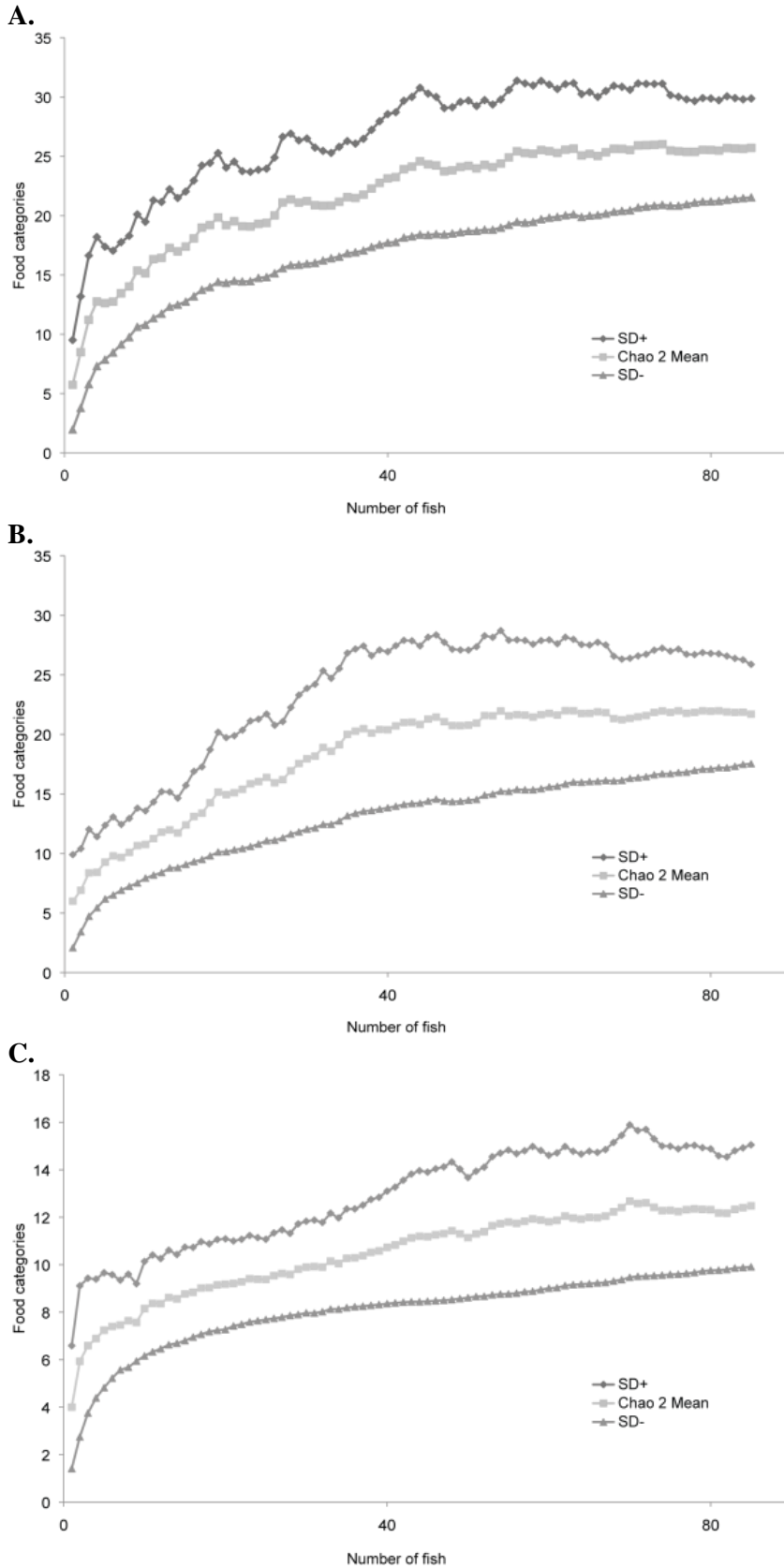


Figure 155. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of javelin fish from off the Wairarapa coast. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

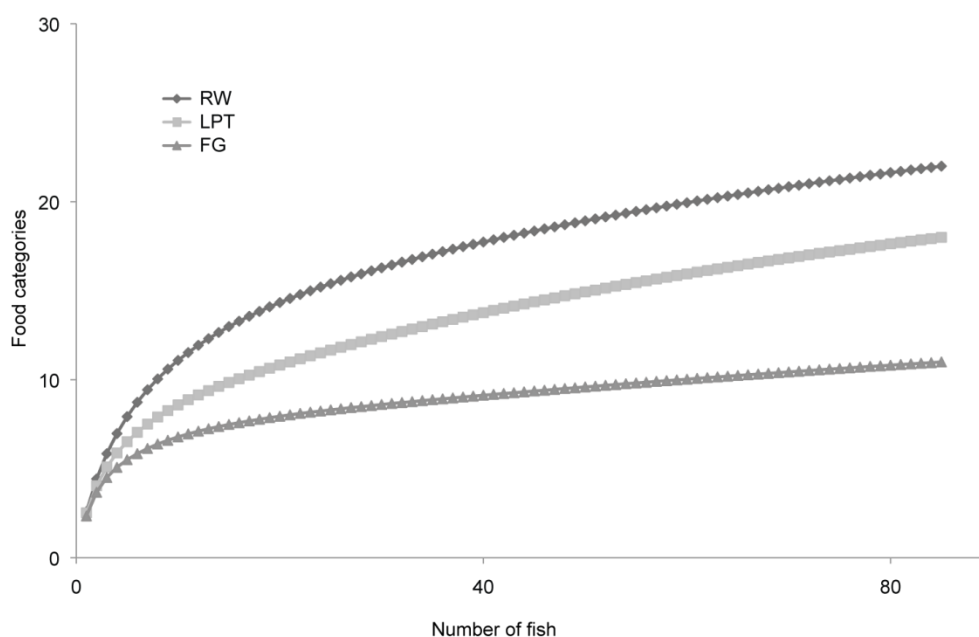


Figure 156. S_{obs} accumulation curves for the stomach contents of javelin fish from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 45. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of javelin fish from off the Wairarapa coast over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_i : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	25	29	
S_{max} 80%	37	42	
S_{max} 90%	58	58	
Min. total	83	77	NA
S_t	6	6	3
n	22	18	11

4.6.6. Silver roughy (SRO), *Hoplostethus mediterraneus* ($n = 82$)

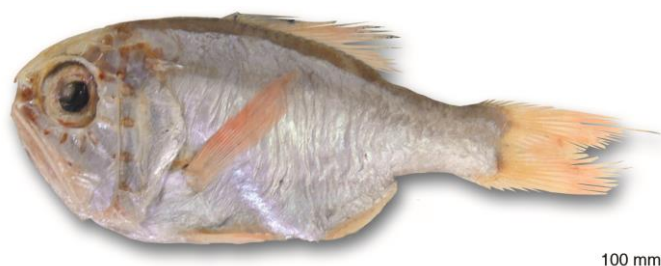


Figure 157. Silver roughy, (SRO), *Hoplostethus mediterraneus*.

Seventy-two of the 82 silver roughy examined had food in their stomachs (none were everted) (**Fig. 158**), giving a PES of 12.2 percent. Their food was mostly natant decapod prawns (99% IRI), most of which were highly digested and too difficult to reliably identify; *N. magnoculus* was one of the few species that was (**Fig. 159A**). Over the whole sample, the trophic level was 4.22. Pelagic and benthopelagic crustaceans were the two most important functional food-item groups (**Fig. 159B**). There was a significant positive correlation between the weight of food items increasing with fish size (Spearman rank correlation $r_s = 0.300$, $P < 0.005$), but not with the number of food items per fish ($r_s = 0.025$, $P > 0.418$). There was a small ontogenic shift in diet, with fish becoming more important in the diets of larger fish (SL >90 mm) (**Fig. 160**). Dietary overlap values were high, with high levels of overlap between all size classes (**Table 46**). The standardised niche breadth values were low for all size classes (**Fig. 160**), and over the whole sample (0.17). No material was recovered from the intestines.

The dietary variation within the stomachs of silver roughy was adequately described by all dietary classifications except FG (**Fig. 161**, **Fig. 162**, **Table 47**). The minimum total number of stomachs needed to describe the dietary variation ranged between 55 and 65 (LPT & RW respectively), and this was reflected in the S_{\max} 90% values (**Table 47**), which ranged between 20 and 45 respectively.

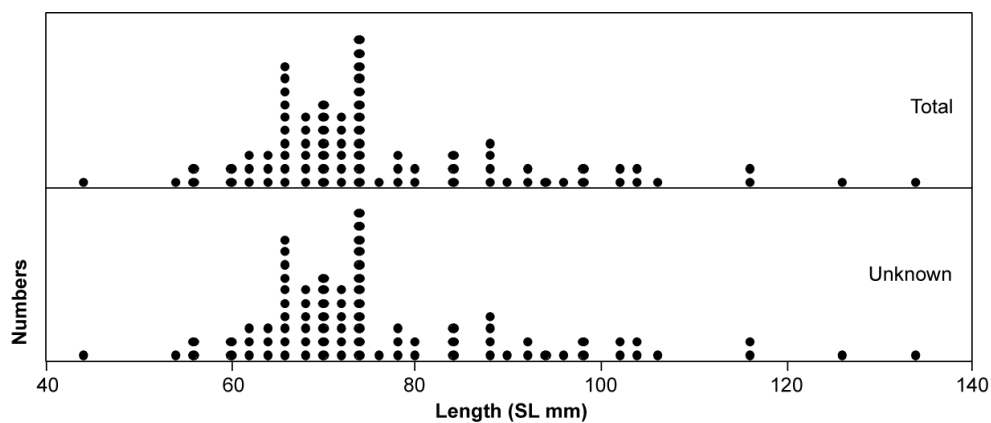
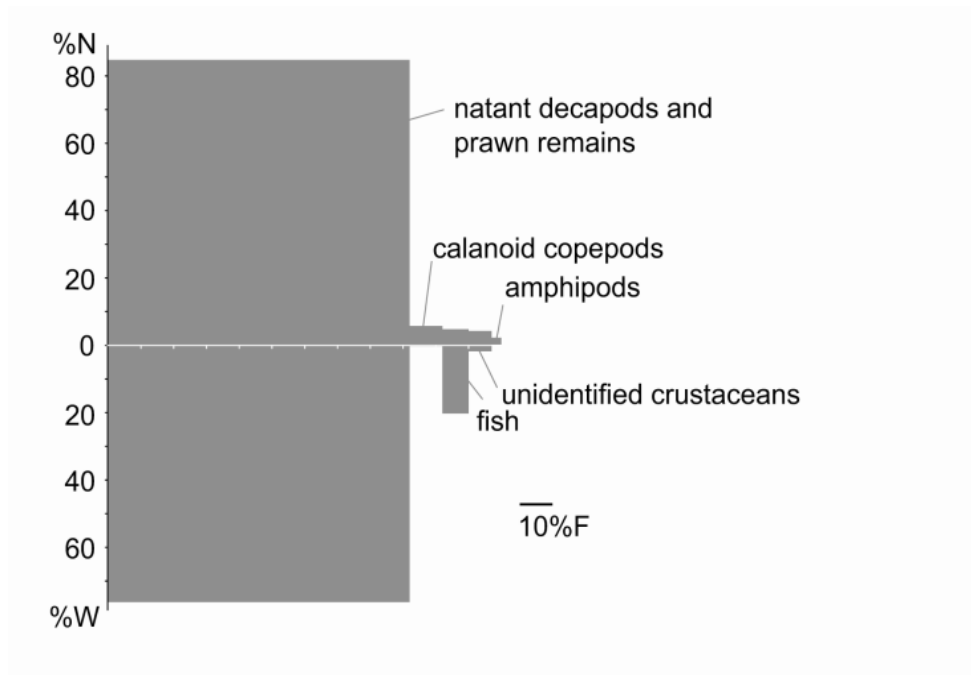


Figure 158. Size-frequency distribution for silver roughy from off the Wairarapa coast (stomachs containing food) ($n = 72$, SL mm). Fish of unknown gender include those damaged and/or immature.

A.



B.

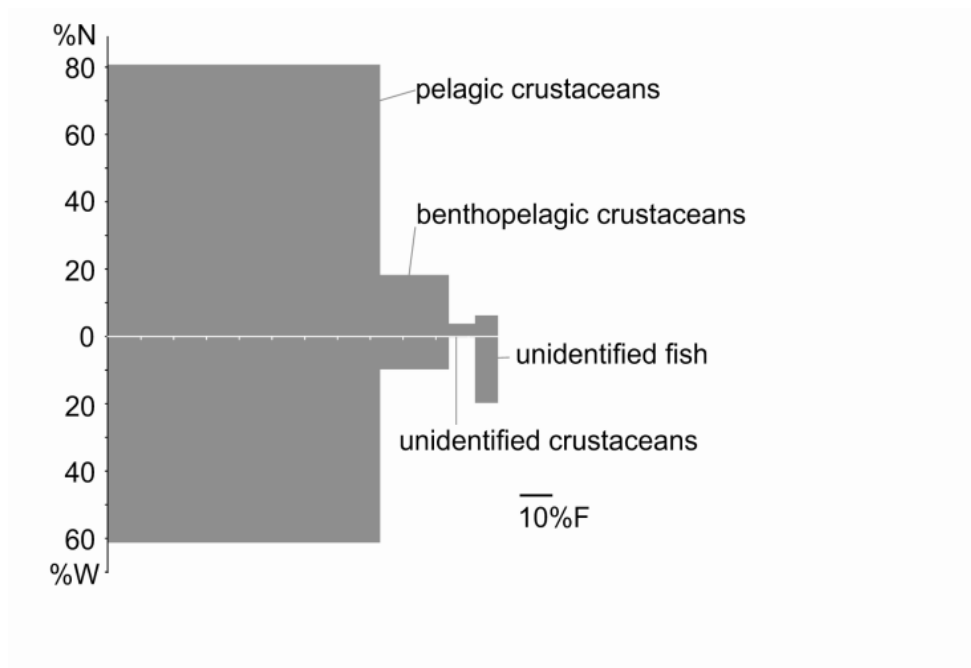


Figure 159. Diet of silver roughy from off the Wairarapa coast expressed as percentage IRI area charts ($n = 72$). **A.** Lowest practical taxon. **B.** Functional food-item groups. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

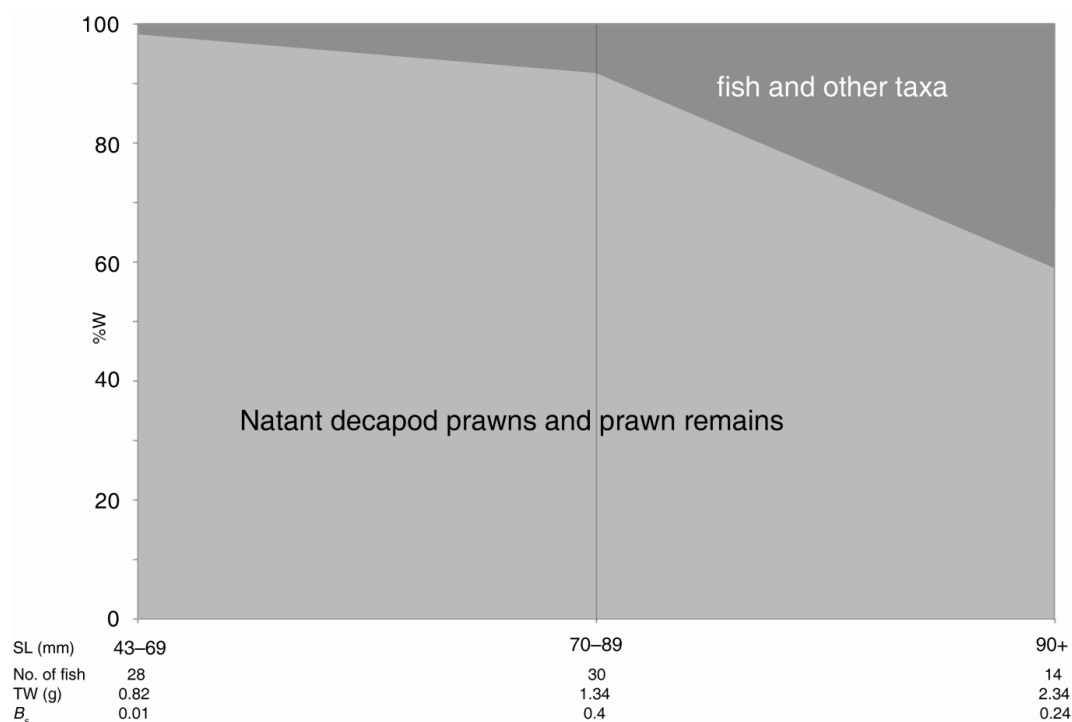


Figure 160. Diet (%W) of silver roughy from off the Wairarapa coast over three size classes ($n = 72$, SL mm): number of fish (No.) in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon. Other taxa: amphipods, calanoid copepods, and unidentified crustaceans.

Table 46. Dietary overlap values for silver roughy from off the Wairarapa coast over three size categories ($n = 72$, SL mm). Food categories are based on the lowest practical taxon. Grey rectangles indicate biologically significant dietary overlaps $>60\%$. Calculations are based on %W.

Length (SL mm)	39–69 ($n = 28$)	70–89 ($n = 30$)	90+ ($n = 14$)
39–69		0.9	0.6
70–89			0.7
90+			

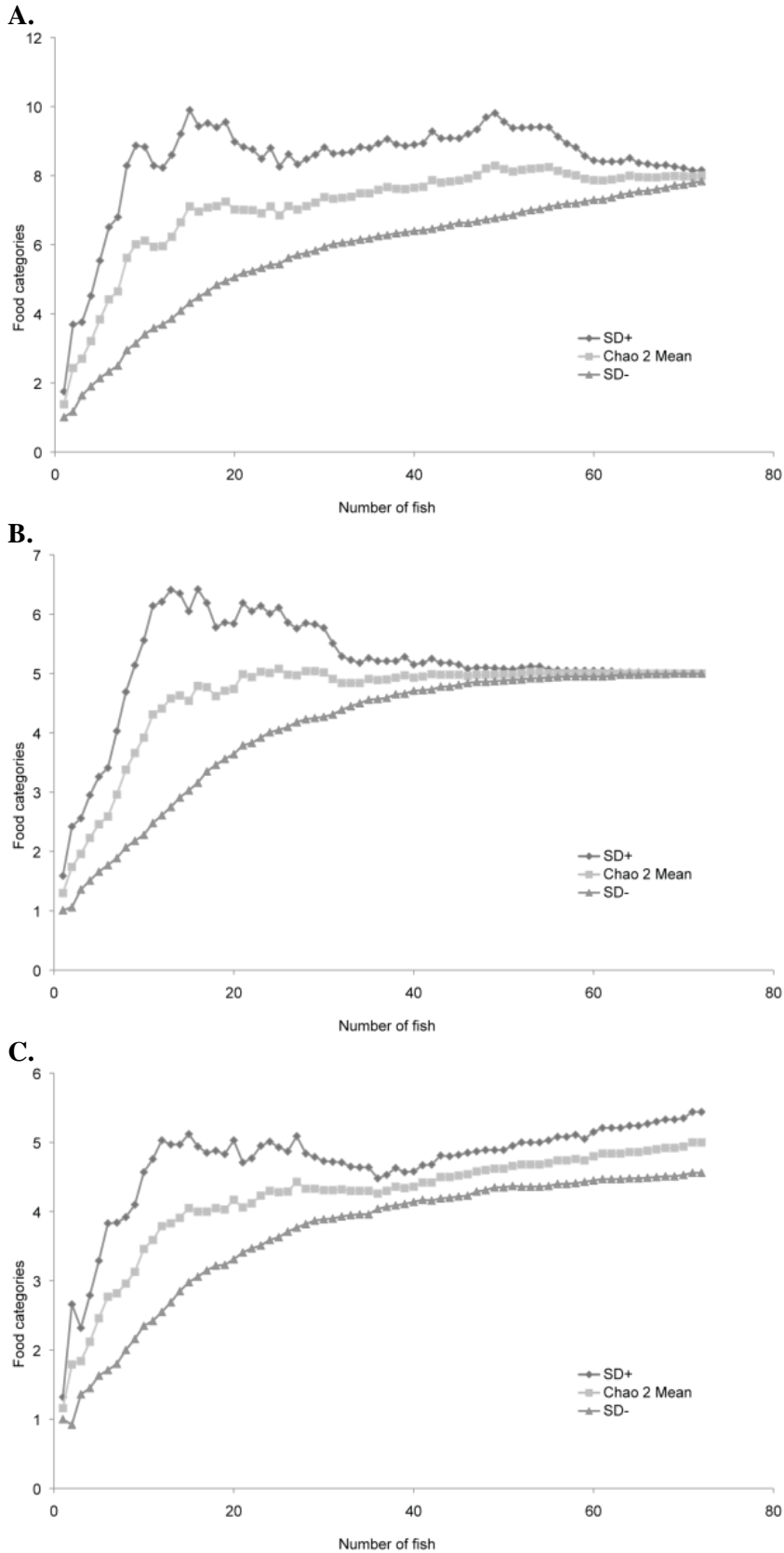


Figure 161. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of silver roughy from off the Wairarapa coast. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

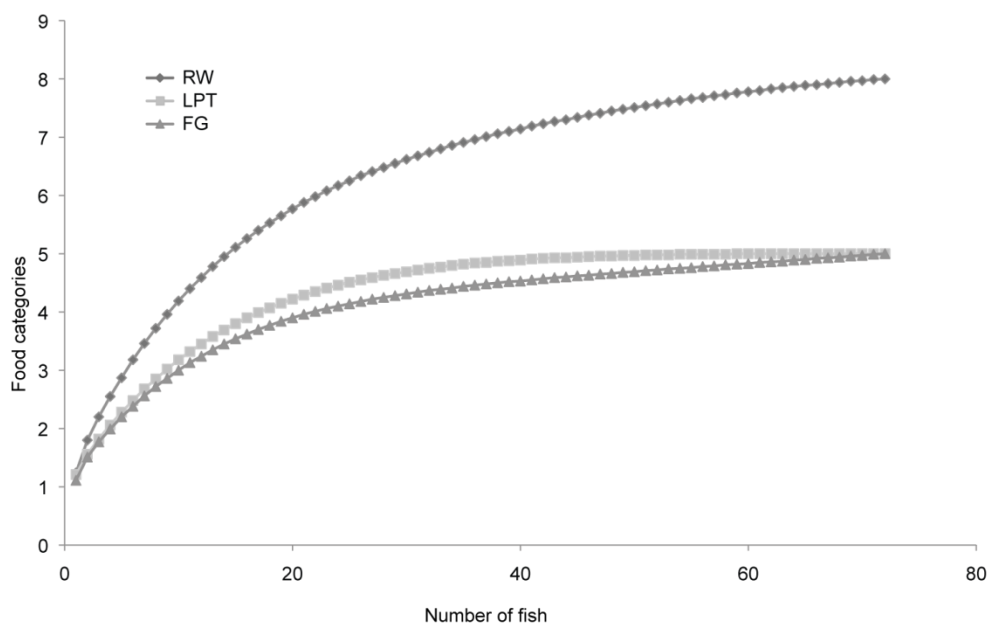


Figure 162. S_{obs} accumulation curves for the stomach contents of silver roughly from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 47. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of silver roughly from off the Wairarapa coast over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), NA: no asymptote reached, S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	18	13	
S_{max} 80%	26	18	
S_{max} 90%	40	25	
Min. total	65	55	NA
S_t	1	0	1
n	8	5	5

4.6.7. Capro dory (CDO), *Capromimus abbreviatus* ($n = 71$)

Figure 163. Capro dory, (CDO), *Capromimus abbreviatus*.

Thirty-nine of 71 capro dory examined had stomachs that contained food (**Fig. 164**), giving a PES of 45.1 percent. No stomachs were everted. Calanoid copepods were the principle food (70.6% IRI), with natant decapod prawns (28%) also important, primarily *N. magnoculus*; one fish had eaten 386 copepods, and another 316 (**Fig. 165A**). Benthic food items were also consumed (*M. gracilis*). Over the whole sample, the trophic level was 3.93. The most important functional food-item group was pelagic crustaceans (**Fig. 165B**). There was no correlation between the weight or number of food items and fish size (Spearman rank correlation $r_s = 0.007$, $P > 0.485$ and $r_s = -0.233$, $P > 0.089$). The standardised niche breadth was low (0.12). No material was recovered from the intestines.

The RW and LPT datasets were identical, so were treated as one. The dietary variation within the stomachs of capro dory was adequately described by two of the dietary classifications (RW & LPT) (**Fig 166**). The minimum total number of stomachs required to describe the dietary variation of capro dory ranged between 22 (FG) and 31 (RW & LPT) (**Fig. 167, Table 48**), and this was reflected in the S_{\max} values (**Table 48**). There were generally fewer stomachs required to describe the dietary variation when there were fewer food categories (**Table 48**).

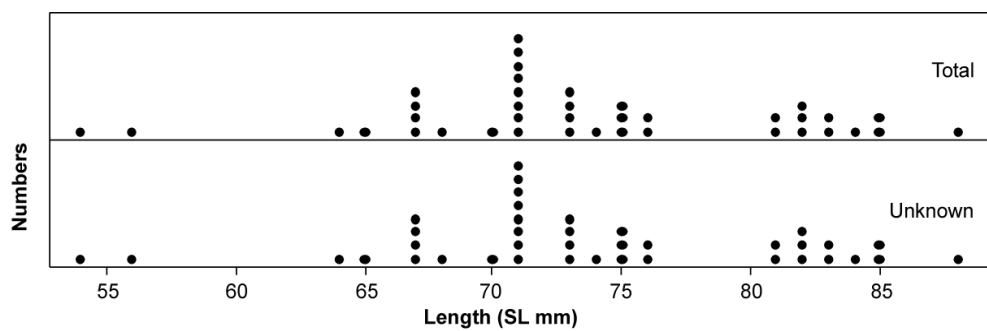
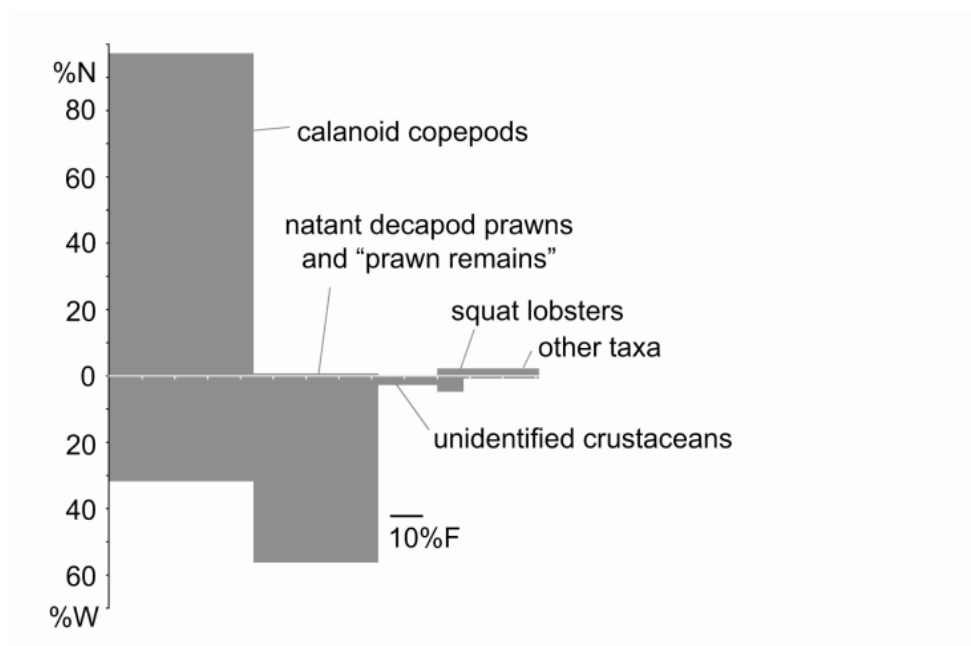


Figure 164. Size-frequency distribution for capro dory from off the Wairarapa coast (stomachs containing food) ($n = 39$, SL mm). Fish of unknown gender include those damaged and/or immature.

A.



B.

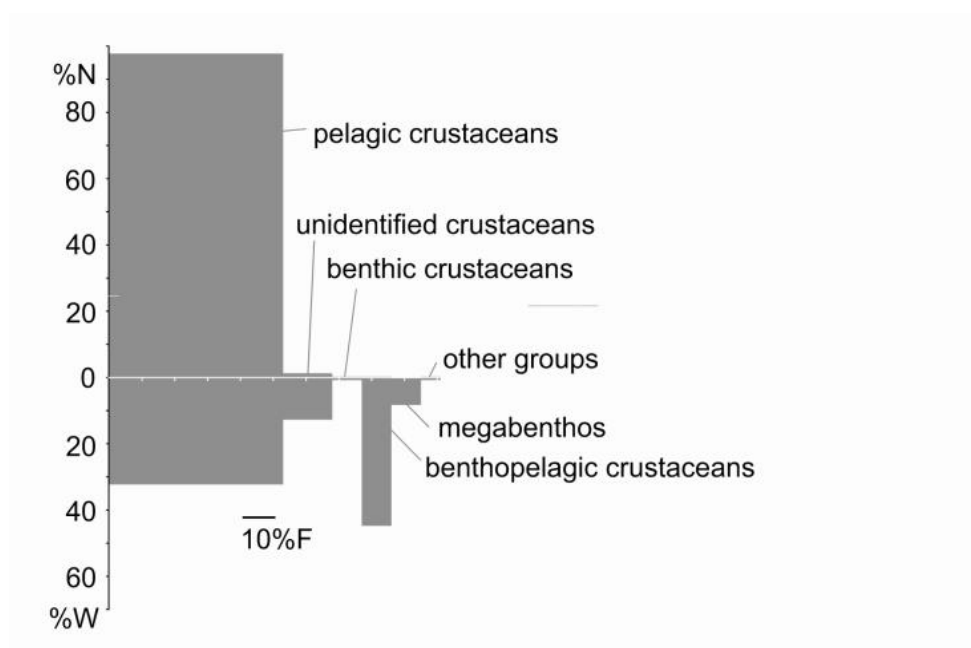


Figure 165. Diet of capro dory from off the Wairarapa coast expressed as percentage IRI area charts ($n = 39$). **A.** Lowest practical taxon: other taxa; amphipods, polychaetes, crabs, ostracods, gastropods, and foraminiferans. **B.** Functional food-item groups: other groups; polychaetes and benthic invertebrates. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

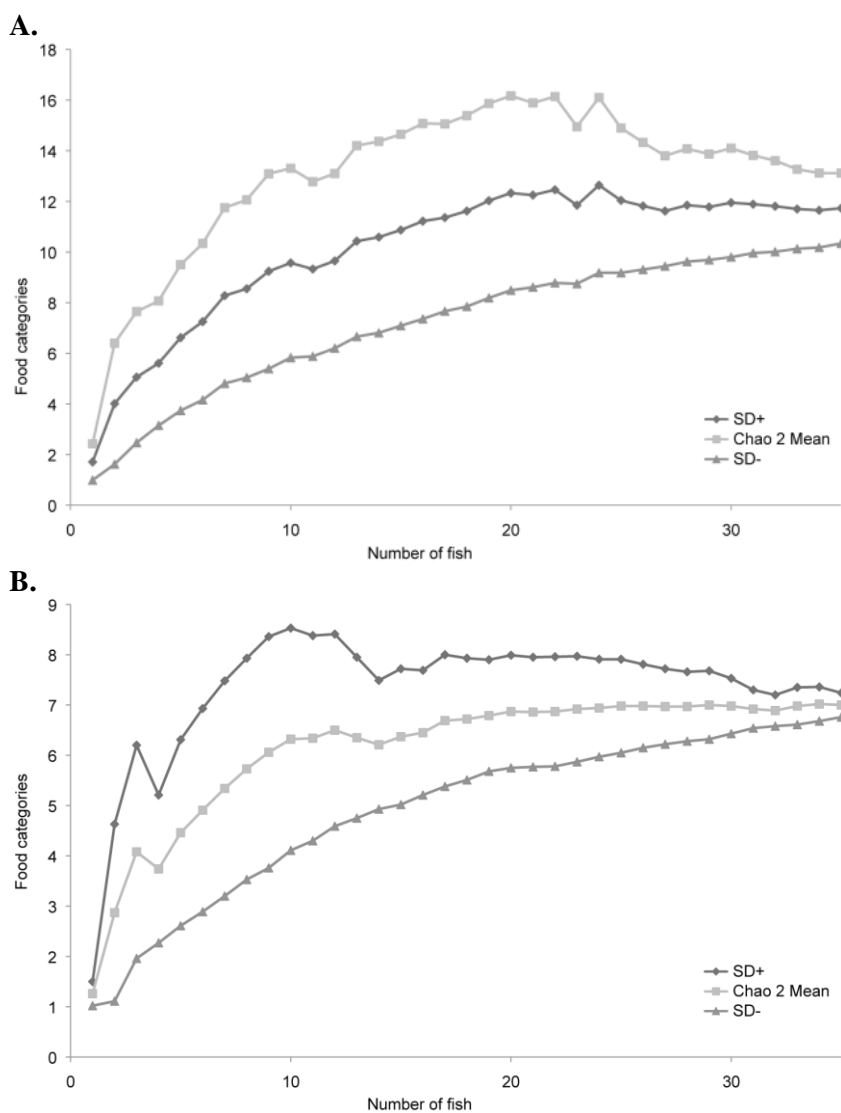


Figure 166. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of capro dory from off the Wairarapa coast. **A.** Raw data and lowest practical taxon. **B.** Functional food groups.

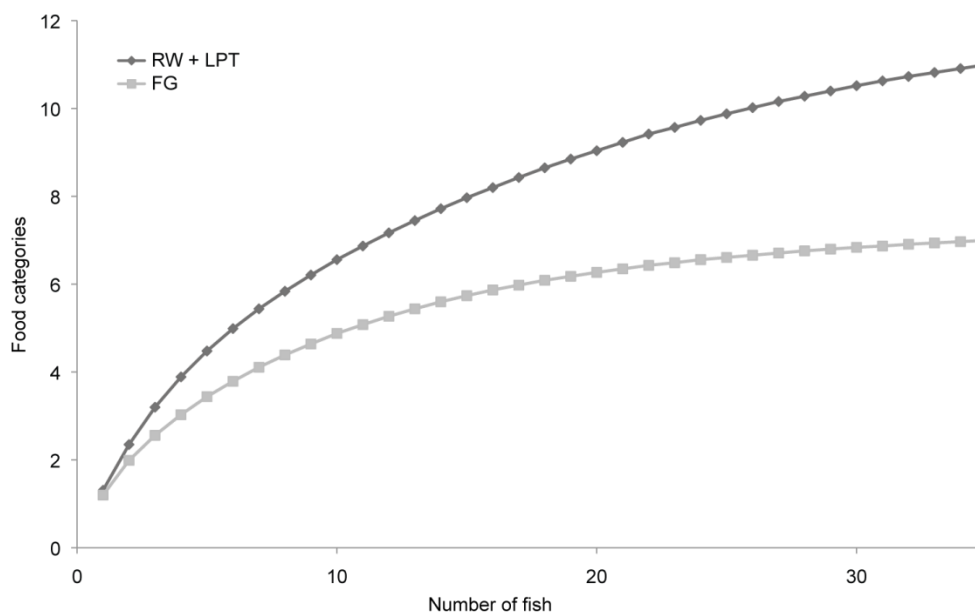


Figure 167. S_{obs} accumulation curves for the stomach contents of capro dory from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 48. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of capro dory from off the Wairarapa coast over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease. NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_i : total number of singletons in each food category.

STOMACHS	RW & LPT	FG
S_{max} 70%	13	
S_{max} 80%	18	
S_{max} 90%	24	
Min. total	31	NA
S_t	3	1
n	11	7

4.6.8. Sea perch (SPE), *Helicolenus percooides* ($n = 124$)



Figure 168. Sea perch, (SPE), *Helicolenus percooides*.

Seventy of 124 sea perch had food in their stomachs (**Fig. 169**) giving a PES of 43.5 percent. No stomachs were everted. Overall, the crab *P. victoriensis* was the most important food of this species (41.6% IRI), with natant decapod prawns (including *N. magnoculus* and *P. acutirostratus*) also important (34.5%) (**Fig. 170A**). Over the whole sample, the trophic level was 4.48. Megabenthos, pelagic crustaceans, unidentified fish, and benthopelagic crustaceans were the most important functional food-item groups (**Fig. 170B**). There was evidence for an ontogenic shift in the diet; smaller fish (75–139 mm SL) fed upon natant decapod prawns, and then switched to the crab *P. victoriensis* as they grew larger (140–179 mm) (**Fig. 171**). The largest size class (180–308 mm) was dominated by the stomach contents of the largest sea perch recorded, which itself had eaten a piece of fish (too digested for precise identification), with the stomach contents of this fish weighing more than all the other stomach contents combined. One sea perch had eaten a scarab beetle (*Acrossidius tasmaniae* Hope, 1846).

There was a significant positive correlation with the weight of food increasing with fish size, but not the number of food items per fish (Spearman rank correlation $r_s = 0.330$, $P < 0.003$ and $r_s = 0.067$, $P > 0.295$ respectively). There were two significant dietary overlaps, between the two smallest size classes (75–129 and 130–159 mm) (**Table 50**), and between the two largest size classes (140–159 and 160+ mm). The standardised niche breadth values (B_s) were low for all size classes and over the whole sample (0.17) (**Fig. 171**).

The dietary variation in the stomachs of sea perch was adequately described by two dietary classifications (RW & LPT), (**Fig 172, Fig 173, Table 51**). The minimum number of stomachs required to describe the dietary variation ranged between 57 and 62

(RW & LPT). These data were reflected in the S_{\max} values (**Table 51**), with 52 and 51 stomachs required to describe 90 percent of the dietary variation (RW and LPT). There were multiple singletons in all dietary classifications (**Table 51**).

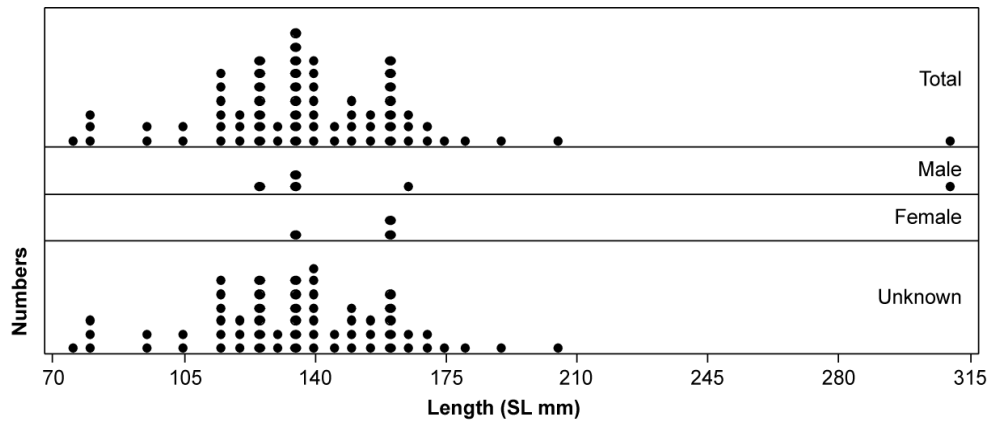
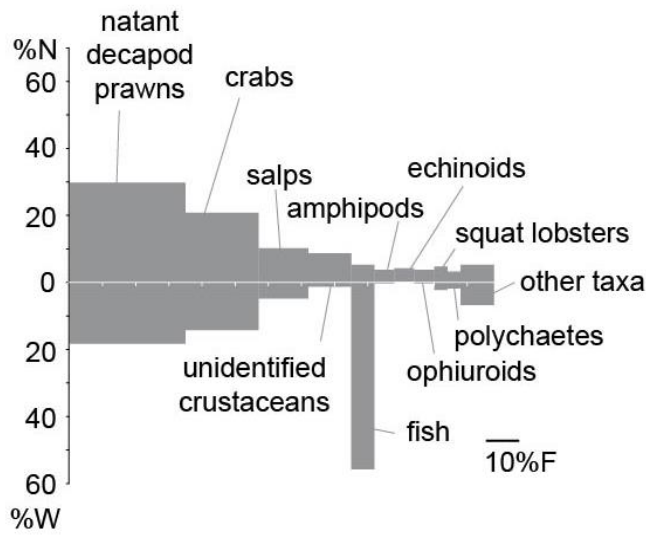


Figure 169. Size-frequency distribution for sea perch from off the Wairarapa coast (stomachs containing food) ($n = 70$, SL mm). Fish of unknown gender include those damaged and/or immature.

A.



B.

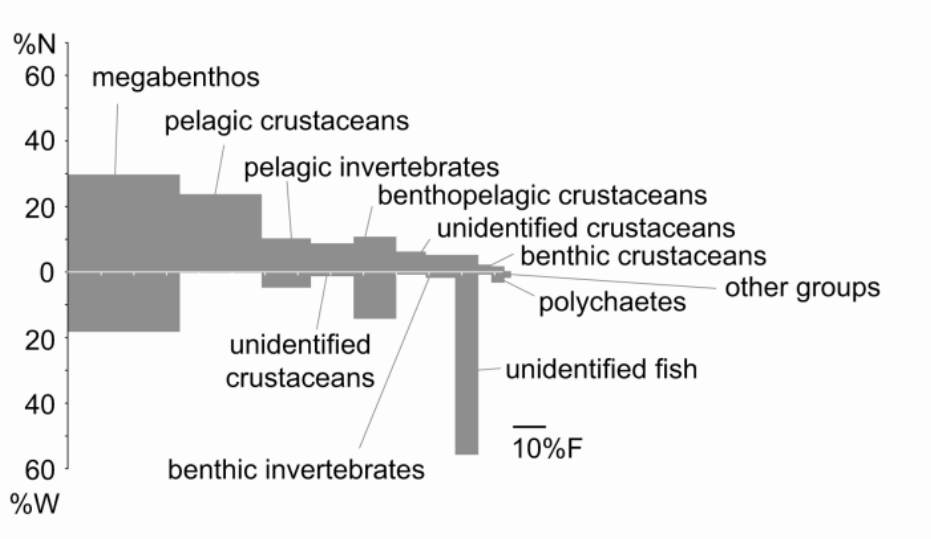


Figure 170. Diet of sea perch from off the Wairarapa coast expressed as percentage IRI area charts ($n = 70$). **A.** Lowest practical taxon: other taxa; amphipods, a Spanish lobster (*Ibacus alticrenatus*), isopods, a scarab beetle (*Acrossidius tasmaniae*), gastropods, squids, ophiuroids, and sponge remains. **B.** Functional food-item groups: other groups; insects and unidentified material. %F is the percentage contribution by frequency of occurrence, %N by number, and %W by weight.

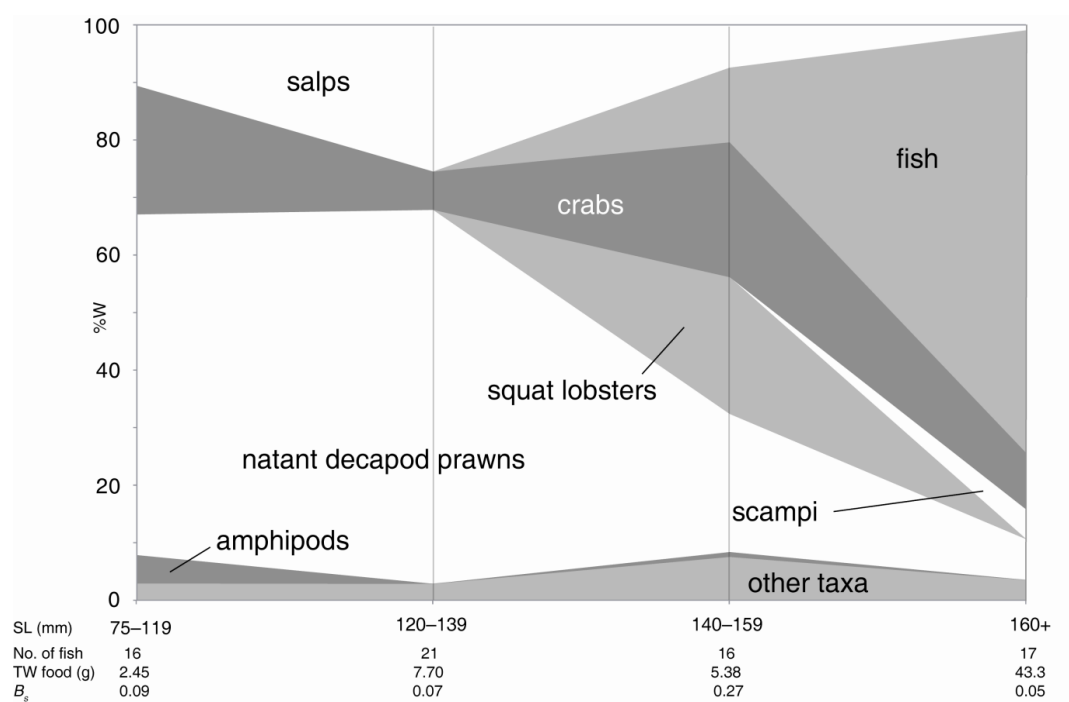


Figure 171. Diet (%W) of sea perch from off the Wairarapa coast over four size classes ($n = 70$, SL mm): number of fish (No.) in each size class, total weight of food (TW), and the standardised niche breadth B_s for each size class. Food categories are based on the lowest practical taxon. Other taxa: Spanish lobsters (*Ibacus alticrenatus*), isopods, a scarab beetle (*Acrossidius tasmaniae*), gastropods, squids, ophiuroids, and sponges.

Table 50. Dietary overlap values for sea perch from off the Wairarapa coast over four size classes ($n = 70$, SL mm). Food categories are based on the lowest practical taxon. Dark grey rectangles indicate biologically significant dietary overlaps >60%. Calculations are based on %W.

Length (SL mm)	75–119 ($n = 16$)	120–139 ($n = 21$)	140–159 ($n = 16$)	160+ ($n = 16$)
75–119		0.8	0.4	0.3
120–139			0.2	0.2
140–159				0.7
160+				

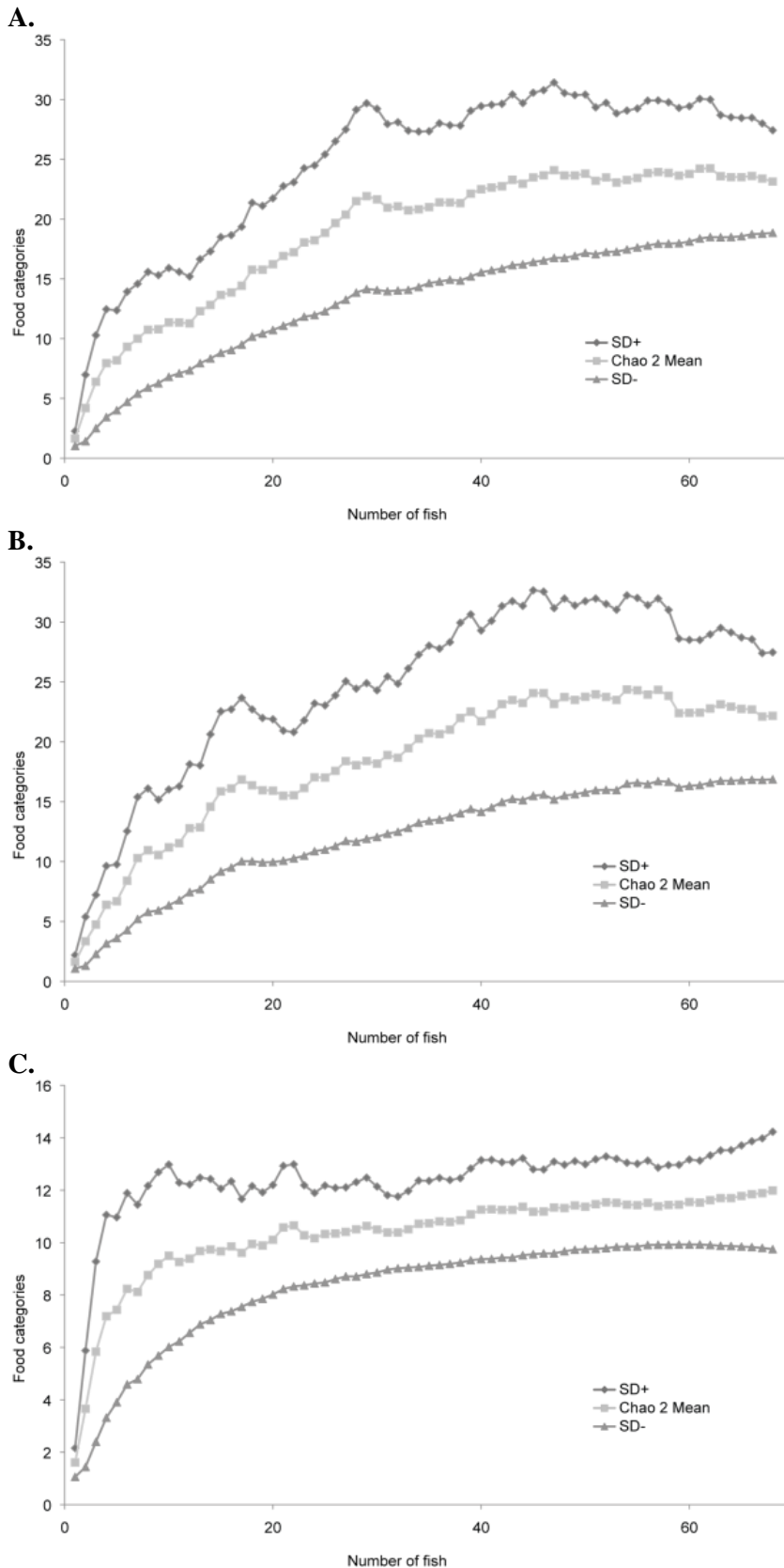


Figure 172. Mean Chao 2 estimation curves (plus and minus one standard deviation) for the stomach contents of sea perch from off the Wairarapa coast. **A.** Raw data. **B.** Lowest practical taxon. **C.** Functional food groups.

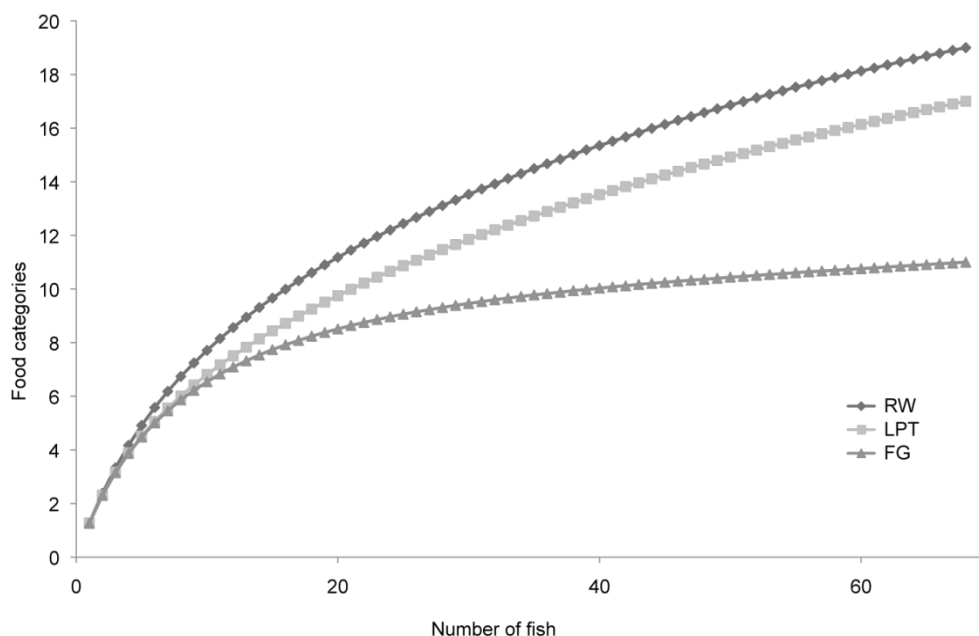


Figure 173. S_{obs} accumulation curves for the stomach contents of sea perch from off the Wairarapa coast for three dietary classifications; standard deviations are removed for clarity (RW: raw data, LPT: lowest practical taxon, FG: functional food groups).

Table 51. Number of fish estimated to describe 70–90% of S_{max} for the stomach contents of sea perch from off the Wairarapa coast over three dietary classifications, based on S_{obs} estimates. Min. total describes the minimum number of fish required for the Chao 2 estimate standard deviation to continuously decrease. NA: no asymptote reached, n : number of food categories per dietary classification (RW: raw data, LPT: lowest practical taxon, FG: functional food groups), S_t : total number of singletons in each food category.

STOMACHS	RW	LPT	FG
S_{max} 70%	27	29	
S_{max} 80%	37	39	
S_{max} 90%	48	50	
Min. total	62	64	NA
S_t	7	7	2
n	19	17	11

4.7. Principal food items of other fish species from off the Wairarapa coast

A further 19 fish species retained in the Wairarapa trawls had <10 stomach or intestinal samples containing food items; their biological data are presented in **Table 52**. Unless stated, food items are described from stomach contents.

Eight dark ghostshark, *Hydrolagus novaezelandiae*, had eaten the crab *P. victoriensis*; it occurred in every stomach examined, often more than once (23 in total). Echinoids and bivalves (*Austrotindaria benthicola* Dell, 1956 and *Saccella hedleyi* (Fleming, 1951)) had also been consumed. One ghost shark had also consumed the scarab beetle *Acrossidius tasmaniae*. One Lucifer's dogfish, *Etmopterus lucifer*, had fish remains in its stomach. Two female Dawson's catshark, *Halaelurus dawsoni*, had each eaten a lantern fish, and one had also consumed two prawns (*N. magnoculus*). Two female carpet-sharks, *Cephaloscyllium isabellum*, had eaten hermit crabs and fish; one fish also had eaten a polychaete.

Three of six hairy conger eels, *Bassanago hirsutus*, had eaten the crab *P. victoriensis*, and one had eaten scampi and Spanish lobster, *I. alticrenatus*.

Fifteen red cod, *Pseudophycis bachus*, were examined, of which six had stomachs containing food items. Each of these fish had eaten natant decapod prawns (*N. magnoculus* and *P. acutirostratus*); one of the fish also had eaten a crab (*P. victoriensis*). Analysis of the intestines of a further four individuals that had everted stomachs revealed that crabs (*P. victoriensis*) and fish (Myctophidae and Macrouridae, identified from otoliths) had also been eaten. The intestines of one red cod contained beetle remains.

A grenadier cod, *Triperophycis gilchristi*, was examined and its stomach contained prawn remains. The stomach of the single eucla cod, *Euclichthys polynemus*, was empty, although its intestines contained mysid, natant decapod prawn and unidentifiable crustacean remains. A black-spot rattail, *Lucigadus nigromaculatus*, had eaten amphipods, natant decapod prawns, unidentifiable crustacean remains, and chaetognaths.

Two alfonsino, *Beryx splendens*, were examined; the stomach of one was empty, whilst the other had eaten 18 prawns (*Pasiphaea* aff. *sivado* and *N. magnoculus*).

One immature ling, *Genypterus blacodes*, had eaten three prawns (*N. magnoculus*). A single bass, *Polyprion americanus*, had eaten scampi. Two scaly gurnard, *Lepidotrigla brachyoptera*, had eaten the prawn *N. magnoculus*. Five of seven *Epigonus denticulatus* had eaten euphausiids, with one fish consuming 12.

Nine deep-sea flatheads, *Hoplichthys haswelli*, had stomachs that contained food, in which the prawn *N. magnoculus* was the most frequently occurring item.

A pale toadfish, *Neophrynichthys angustus*, had eaten unidentifiable worm-like remains; a fish eye lens was also present.

One stargazer, *Kathetostoma giganteum*, had unidentifiable fish and crustacean remains in its stomach.

Two of three yellow boarfish, *Pentoceros decacanthus*, had stomachs containing crinoid remains. The fish with an empty stomach had material in its intestines comprising the remains of three gnathiid isopods, foraminifera, crinoid fragments, and unidentifiable crustacean remains.

Four opalfish, *Hemerocoetus macrophalmas*, were examined; the stomachs of two contained food. One had eaten a *N. magnoculus*, while the other contained unidentifiable crustacean remains.

Two of four finless flounder, *Neoachirosetta milfordi*, had stomachs containing food items. One fish contained prawn remains, while the other had consumed the prawn *P. aff. sivado*.

Twelve spotted flounder, *Azigopus pinnifasciatus*, were examined; eight contained food in their stomachs. Gastropods (*R. delecta*), and the crab *P. victoriensis* were the most frequently occurring food items.

Table 52. Mean length (mm) and weight (g) of 19 fish species (male and female) from off the Wairarapa coast; fish with <10 stomach or intestinal samples containing food items. Acronyms: PCL; pre-caudal fin length, TL; total length, SL; standard length, PAL, pre-anal fin length; co-efficient of variation (CV).

Species Code	Gender	Number	Mean length			CV	Weight (g)	CV
			(TL ¹)	(PCL) (SL ²) (PAL ³)	(mm)			
<i>Hydrolagus novaezelandiae</i> HYN	Male	0						
	Female	8	280.6		48.9	528.9	137.7	
	Unknown	0						
<i>Etmopterus lucifer</i> ETL	Male							
	Female	1	230			28.2		
	Unknown							
<i>Halaelurus dawsoni</i> DAW	Male	0						
	Female	2	283.5		4.2	314.4	44	
	Unknown	0						
<i>Cephaloscyllium isabellum</i> CAS	Male	0						
	Female	2	275		36.5	295.5	88.3	
	Unknown	0						
<i>Bassanago hirsutus</i> HCO	Male	4	529 ¹		2.3	160.6	21.2	
	Female	2	643 ¹		7.6	358.6	14.4	
	Unknown	0						
<i>Pseudophycis bachus</i> RCO	Male	0						
	Female	4	322 ²		13.1	439.9	36.6	
	Unknown	11	204 ²		52.3	128.1	71.1	
<i>Triperophycis gilchristi</i> TGI	Male	0						
	Female	4						
	Unknown	1	185 ²			26.1		
<i>Euclichthys polynemus</i> EPO	Male	0						
	Female	0						
	Unknown	1	204 ²			39.8		
<i>Lucigadus nigromaculatus</i> LNI	Male	0						
	Female	0						
	Unknown	1	31 ³			6.5		
<i>Beryx splendens</i> BYX	Male	0						
	Female	0						
	Unknown	2	291 ²		4.9	666.0	14.8	
<i>Genypterus blacodes</i> LIN	Male	0						
	Female	0						
	Unknown	1	578 ¹			724.4		
<i>Polyprion americanus</i> BAS	Male	0						
	Female	0						
	Unknown	1	485 ²			3027.6		

Table 52 (continued).

Species Code	Gender	Number	Mean length (PCL)			CV	Weight (g)	CV
			(TL ¹)	(SL ²)	(PAL ³) (mm)			
<i>Epigonus denticulatus</i> EPD	Male	0						
	Female	0						
	Unknown	7		101.9 ²		9.2	15.7	28.3
<i>Hoplichthys haswelli</i> DFL	Male	0						
	Female	0						
	Unknown	23		182.9		35.8	47.1	62
<i>Neophrynichthys angustus</i> NAN	Male	0						
	Female	0						
	Unknown	1		159 ²			123.5	
<i>Kathetostoma giganteum</i> STA	Male	0						
	Female	0						
	Unknown	1		380 ²			1536	
<i>Pentaceros decacanthus</i> YBO	Male	0						
	Female	0						
	Unknown	3		91 ²		2.0	31.1	5.9
<i>Hemerocoetus macrophalmus</i> HMA	Male	0						
	Female	0						
	Unknown	3		133 ²		8.1	6.5	55.6
<i>Neoachirosetta milfordi</i> NMI	Male	0						
	Female	0						
	Unknown	4		187.6 ²		15.4	60.6	38.2
<i>Azigopus pinnifasciatus</i> API	Male	0						
	Female	0						
	Unknown	12		109.4 ²		10.9	15.8	30.4

4.8. Stomach contents of prey animals

For completeness of trophic reconstruction for some of the larger fishes, particularly the dogfishes and rattails, it was possible to investigate the stomach contents of the fishes they had consumed; for some of the smaller species it was possible to investigate the foregut content of some of the *N. magnoculus* that they themselves had eaten. Those data are presented here.

Two long-nosed velvet dogfish from northeastern Chatham Rise had respectively eaten a notable rattail and a viperfish. Analysis of these two prey fish revealed that the notable rattail had eaten gastropods (*A. meridiana* and an unidentified turrid gastropod). The viperfish had consumed a lantern fish, which in turn had eaten several calanoid copepods.

Fourteen shovel-nosed dogfish had eaten 16 lantern fish (more than one species), although owing to the high level of their digestion it was not possible to identify the myctophids further. Ten of these myctophids had stomachs containing food, and had been feeding on calanoid copepods. The foreguts of five *N. magnoculus* from off the Wairarapa coast were examined and polychaete remains were found in one and unidentified crustacean remains in another; the rest were empty.

4.9. Selected comparisons between stomach and intestinal contents

Six fish species had enough material in their stomachs and intestines for a comparison to be made. These species were: big-scaled brown slickhead, black slickhead, serrulate rattail, four-rayed rattail from northeastern Chatham Rise and Puysegur Bank, and Bollons' rattail from off the Wairarapa coast.

4.9.1. Big-scaled brown slickhead (SBI) from northeastern Chatham Rise

Analysis of similarities (ANOSIM) analysis (on the presence or absence of food material) showed there was a significant difference between stomach and intestinal contents, $R = 0.079$, with the significance level of the sample statistic being 1.5 percent. A SIMPER test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): thaliaceans, calanoid copepods, fish natant decapod prawns, amphipods, squid, ostracods, foraminifera, and mysid prawns (**Table 53**). Calanoid copepods, fish,

ostracods and foraminifera increased in mean abundance in the intestines, while all other food items decreased (**Table 53**).

Table 53. Similarity percentage test (SIMPER) results for big-scaled brown slickhead; comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 85.58				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Thaliacea	0.40	0.30	21.82	21.82
Calanoid copepods	0.00	0.34	15.23	37.05
Fish	0.13	0.22	13.60	50.66
Natant decapod prawns	0.20	0.12	11.44	62.10
Amphipods	0.13	0.03	7.30	69.40
Squid	0.13	0.00	7.00	76.40
Ostracods	0.07	0.12	6.95	83.35
Foraminifera	0.07	0.12	6.54	89.89
Mysids	0.07	0.02	4.56	94.44

There was an increase in the intestines of some small-bodied crustaceans and invertebrates (calanoid copepods, ostracods, and foraminifera), and a decrease in larger-bodied animals (squid, natant decapod prawns, amphipods, mysids and thaliaceans). There was also an increase in fish in the intestines.

4.9.2. Black slickhead

There was no significant difference between stomach and intestinal contents $R = 0.031$, 13 percent. A similarity percentage test (SIMPER) test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): natant decapod prawns, amphipods, calanoid copepods, fish, unidentified crustaceans, ostracods, and thaliaceans (**Table 54**). Natant decapod prawns, calanoid copepods, unidentified crustacean remains, and thaliaceans increased in mean abundance in the intestines, amphipods did not change, and all other food items decreased (**Table 54**).

Table 54. Similarity percentage test (SIMPER) results for black slickhead; comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 81.50				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Natant decapod prawns	0.40	0.28	22.62	22.62
Amphipods	0.24	0.24	17.96	40.58
Calanoid copepods	0.22	0.24	17.71	58.29
Fish	0.19	0.08	12.02	70.31
Unidentified crustacean remains	0.05	0.20	11.24	81.55
Ostracods	0.09	0.04	5.62	87.17
Thaliaceans	0.02	0.08	4.90	92.06

Sixteen fish had material in both their stomach and intestines and these were significantly different ($R = 0.096$, 1.9%). A SIMPER test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): natant decapod prawns, amphipods, ostracods, fish, unidentified crustaceans, and calanoid copepods (**Table 55**). Unidentified crustacean remains and calanoid copepods increased in mean abundance in the intestines; all other food items decreased (**Table 55**).

Table 55. Similarity percentage test (SIMPER) results for black slickhead: comparisons between individual fish with both stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 84.35				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Natant decapod prawns	0.67	0.19	29.33	29.33
Amphipods	0.13	0.19	13.35	42.68
Ostracods	0.20	0.06	12.27	54.95
Fish	0.20	0.06	12.27	67.22
Unidentified crustacean material	0.00	0.25	12.00	79.21
Calanoid copepods	0.13	0.19	11.69	90.90

There was no significant difference between the stomach and intestinal contents of black slickhead when comparing all stomachs and intestines containing food items. However, there was a significant difference between stomach and intestinal contents when the stomach and intestinal contents of the same fish were analysed.

Over the whole sample of black slickhead, there was an increase in the intestines of natant decapod prawns, calanoid copepods, and unidentifiable crustacean remains, no

change in the incidence of amphipods, and a decline in fish, ostracods and thaliaceans. Fish that had material in both their stomach and intestines showed a general decrease in the abundance of larger-bodied animals in their intestines (natant decapod prawns and fish), although ostracods also declined. These declines were compensated for by increases in the abundance of amphipods, calanoid copepods and unidentifiable crustacean remains.

4.9.3. Serrulate rattail

There was a significant difference between the stomach and intestinal contents of serrulate rattail, ($R = 0.326$, 0.1%). A SIMPER test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): amphipods, unidentified crustacean remains, natant decapod prawns, polychaetes, fish, calanoid copepods, squid, ostracods, and isopods (**Table 56**). Unidentified crustacean remains and polychaetes increased in mean abundance in the intestines, whereas all other food items decreased (**Table 56**).

There were 62 fish with both stomach and intestinal contents and these were also significantly different ($R = 0.315$, 0.1%). A SIMPER test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): amphipods, unidentified crustacean remains, natant decapod prawns, polychaetes, fish, calanoid copepods, squid, ostracods, and isopods (**Table 57**). Polychaetes and unidentified crustacean remains increased in mean abundance in the intestines, whereas all other food items decreased (**Table 57**).

Table 56. Similarity percentage test (SIMPER) results for serrulate rattail: comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Food items	Average dissimilarity = 81.50		Percentage contribution of each food item	Cumulative percentage
	Stomachs Mean abundance	Intestines Mean abundance		
Amphipods	0.68	0.16	14.22	14.22
Unidentified crustacean remains	0.32	0.59	12.60	26.82
Natant decapod prawns	0.54	0.33	12.13	38.95
Polychaetes	0.63	0.86	11.19	50.14
Fish	0.44	0.19	10.28	60.41
Calanoid copepods	0.46	0.02	9.59	70.00
Squid	0.37	0.01	7.96	77.96
Ostracods	0.34	0.15	7.87	85.83
Isopods	0.26	0.12	6.17	92.00

Table 57. Similarity percentage test (SIMPER) results for serrulate rattail: comparisons between individual fish with both stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 81.50				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Amphipods	0.69	0.19	13.95	13.95
Unidentified crustacean remains	0.32	0.65	12.84	26.79
Natant decapod prawns	0.55	0.28	11.94	38.73
Polychaetes	0.61	0.88	11.17	49.90
Fish	0.45	0.20	10.35	60.25
Calanoid copepods	0.45	0.03	9.16	69.41
Squid	0.40	0.01	8.57	77.98
Ostracods	0.34	0.16	7.77	85.76
Isopods	0.27	0.14	6.42	92.17

Serrulate rattail also saw increases in abundance, in the intestines, of animals either represented by hard-parts (chaetognaths) or too digested for precise identification (unidentifiable crustacean material). There was a corresponding decrease in generally larger-bodied identifiable food items (amphipods, natant decapod prawns, fish, and squid). There was also a decrease in some smaller forms (calanoid copepods, ostracods and isopods). Fish with both stomach and intestinal contents also followed this pattern, with increases in abundance of unidentified crustaceans and polychaetes at the expense of larger-bodied or identifiable food items.

4.9.4. Four-rayed rattail from northeastern Chatham Rise

There was a significant difference between stomach and intestinal contents ($R = 0.254, 0.1\%$). A SIMPER test revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): polychaetes, calanoid copepods, amphipods, chaetognaths, unidentified crustacean remains, and natant decapod prawns (**Table 58**). Polychaetes and chaetognaths increased in mean abundance in the intestines; all other food items decreased (**Table 58**).

Ten fish had both stomach and intestinal contents and these were also significantly different ($R = 0.175, 2.3\%$). Similarity percentage test (SIMPER) results revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): polychaetes, chaetognaths, amphipods, calanoid copepods, natant decapod prawns, and unidentified crustacean remains (**Table 59**). Polychaetes and chaetognaths increased in mean abundance in the

intestines, calanoid copepods and unidentified crustacean remains did not change, and all other food items decreased (**Table 59**).

Table 58. Similarity percentage test (SIMPER) results for four-rayed rattail; comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 62.00				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Polychaetes	0.35	0.72	19.86	19.86
Calanoid copepods	0.91	0.52	18.03	37.90
Amphipods	0.57	0.08	17.46	55.35
Chaetognaths	0.30	0.54	17.02	72.37
Unidentified crustacean remains	0.34	0.30	14.67	87.04
Natant decapod prawns	0.18	0.05	6.41	93.45

Table 59. Similarity percentage test (SIMPER) results for four-rayed rattail: comparisons between individual fish with both stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 55.37				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Polychaetes	0.30	0.80	25.42	25.42
Chaetognaths	0.40	0.60	19.69	45.11
Amphipods	0.50	0.10	15.72	60.83
Calanoid copepods	0.80	0.80	12.23	73.06
Natant decapod prawns	0.30	0.00	11.15	84.20
Unidentified crustacean remains	0.10	0.10	6.75	90.95

4.9.5. Warty oreo

There was a significant difference between stomach and intestinal contents ($R = 0.258, 0.6\%$). Similarity percentage test (SIMPER) results revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): calanoid copepods, squid, natant decapod and mysid prawns, fish, and chaetognaths (**Table 60**). Chaetognaths increased in mean abundance in the intestines, all other food items decreased (**Table 60**).

Table 60. Similarity percentage test (SIMPER) results for warty oreo: comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 53.27				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Calanoid copepods	0.85	0.27	26.41	26.41
Squid	0.46	0.27	16.96	43.37
Natant decapod prawns	0.46	0.18	16.95	60.32
Mysid prawns	0.46	0.00	16.83	77.15
Fish	0.92	0.91	8.15	85.31
Chaetognaths	0.08	0.09	4.76	90.07

4.9.6. Four-rayed rattail from Puysegur Bank

There was a significant difference in the composition of stomach and intestinal contents ($R = 0.330$, 0.1%). Similarity percentage test (SIMPER) results revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): calanoid copepods, chaetognaths, unidentified crustaceans, and amphipods (**Table 61**). Chaetognaths and unidentified crustaceans increased in mean abundance in the intestines; all other food items decreased (**Table 61**).

There were 17 fish with both stomach and intestinal contents and these were significantly different ($R = 314$, 0.1%). A SIMPER test revealed that 90 percent of the dissimilarity between stomach and intestinal contents comprised calanoid copepods, chaetognaths and unidentified crustacean remains (**Table 62**). Chaetognaths and unidentified crustacean remains increased in mean abundance in the intestines, and calanoid copepods decreased (**Table 62**).

Table 61. Similarity percentage test (SIMPER) results for four-rayed rattail from Puysegur Bank: comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 57.20				
Food items	Stomachs		Intestines	
	Mean abundance	Mean abundance	Percentage contribution of each food item	Cumulative percentage
Calanoid copepods	1.00	0.22	44.04	44.04
Chaetognaths	0.72	0.74	23.61	67.65
Unidentified crustacean remains	0.17	0.37	20.49	88.14
Amphipods	0.09	0.00	3.78	91.92

Table 62. Similarity percentage test (SIMPER) results for four-rayed rattail from Puysegur Bank: comparisons between individual fish with both stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 57.20				
Food items	Stomachs	Intestines	Percentage contribution of each food item	Cumulative percentage
	Mean abundance	Mean abundance		
Calanoid copepods	1.00	0.22	50.26	50.26
Chaetognaths	0.76	0.78	24.54	74.80
Unidentified crustacean remains	0.24	0.33	23.03	97.83

4.9.7. Bollons' rattail from off the Wairarapa coast

There was a significant difference between stomach and intestinal contents ($R = 0.194$, 0.1%). Similarity percentage test (SIMPER) results revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): polychaetes, unidentified crustacean remains, crabs, ostracods, amphipods, gastropods, natant decapod prawns, isopods, bivalves, and ophiuroids (**Table 63**). Unidentified crustacean remains, crabs, ostracods, gastropods, and bivalves increased in mean abundance in the intestines; all other food items decreased.

There were 34 fish with both stomach and intestinal contents and these were also significantly different ($R = 0.132$, 0.1%). Similarity percentage test results (SIMPER) revealed that >90 percent of the dissimilarity between stomach and intestinal contents comprised (in decreasing order of percentage contribution): unidentified crustaceans, polychaetes, crabs, ostracods, amphipods, gastropods, natant decapod prawns, bivalves, isopods, and foraminifera (**Table 64**). Unidentified crustacean remains, crabs, ostracods, gastropods, bivalves, and foraminifera increased in mean abundance in the intestines; all other food items decreased (**Table 64**). This trend was also the case for fish with both stomach and intestinal food items. Polychaetes declined in abundance in the intestines.

Table 63. Similarity percentage test results (SIMPER) for Bollons' rattail: comparisons between stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 60.80				
Food items	Stomachs	Intestines	Percentage contribution of each food item	Cumulative percentage
	Mean abundance	Mean abundance		
Polychaetes	0.62	0.28	18.53	18.53
Unidentified crustacean remains	0.44	0.72	18.48	37.02
Crabs	0.56	0.89	15.76	52.78
Ostracods	0.05	0.25	8.59	61.37
Amphipods	0.23	0.08	7.99	69.36
Gastropods	0.03	0.19	6.45	75.81
Natant decapod prawns	0.15	0.02	4.67	80.48
Isopods	0.10	0.08	4.64	85.12
Bivalves	0.00	0.11	3.58	88.70
Ophiuroids	0.08	0.04	3.49	92.2

Table 64. Similarity percentage test results (SIMPER) for Bollons' rattail: comparisons between individual fish with both stomach and intestinal contents (higher mean abundance values are displayed in bold typeface).

Average dissimilarity = 59.11				
Food items	Stomachs	Intestines	Percentage contribution of each food item	Cumulative percentage
	Mean abundance	Mean abundance		
Unidentified crustacean remains	0.47	0.68	18.31	18.31
Polychaetes	0.56	0.29	18.17	36.49
Crabs	0.56	0.94	15.80	52.29
Ostracods	0.06	0.24	8.44	60.73
Amphipods	0.21	0.09	7.94	68.67
Gastropods	0.03	0.18	6.35	75.02
Natant decapod prawns	0.18	0.00	5.08	80.10
Bivalves	0.00	0.15	4.81	84.90
Isopods	0.09	0.09	4.66	89.56
Foraminifera	0.00	0.12	3.74	93.30

4.10. Food item accumulation curves

4.10.1. Stomach contents

The variation in the dietary data was adequately described for all dietary classifications for basketwork eel (BEE), four-rayed rattail from Puysegur Bank (CSUp), robust cardinal fish (EPR), and Bollons' rattail (CBO) and for all dietary classifications other than the raw data (RW), for big-scaled brown slickhead (SBI), serrulate rattail (CSE), and four-rayed rattail from north eastern Chatham Rise (CSU). The variation was adequately described for functional food groups (FG) for Baxter's dogfish from Puysegur Bank (ETBp) and orange roughy (ORH). The dietary data did not adequately describe the dietary variation in any of the dietary classifications for long-nosed velvet dogfish (CYP), Baxter's dogfish from north eastern Chatham Rise (ETB), black slickhead (BSL), Oliver's rattail (COL), and sliverside (SSI). Other fish species had varying combinations of dietary classifications that adequately described the dietary variation within the stomach contents (Table 65). For silver roughy (SRO), capro dory (CDO), javelin fish (JAV), and sea perch (SPE), the diet was adequately described by dietary classifications other than FG, whilst for warty oreo (WOE) it was for lowest practical taxon (LPT) only, and for shovel-nosed dogfish (SND) RW only. There were some species for which the reduction in food categories did not result in a curve that adequately described the dietary variation within the stomach contents: long-nosed velvet dogfish (CYP), Baxter's dogfish from north eastern Chatham Rise (ETB), black slickhead (BSL), Oliver's rattail (COL), sliverside (SSI). The food categories that did not adequately describe the variation within the stomach contents had singletons present.

4.10.2. Intestinal contents

The variation within the dietary data was adequately described for all dietary classifications for black slickhead (BSL (I)), serrulate rattail (CSE (I)), four-rayed rattail (CSU (I), CSUp (I)), ridge-scaled rattail (MCA), white rattail (WHX), and Johnson's cod from Puysegur Bank (HJOp) and all dietary classifications other than RW, for surgeon rattail (CTH), rough-headed rattail (CHY), and notable rattail (CIN). The dietary data did not adequately describe the dietary variation in any of the dietary classifications for Johnson's cod from northeastern Chatham Rise (HJO), and small-headed cod (SMC). Other species had varying combinations of dietary classifications that adequately described the dietary variation (Table 66). RW and LPT adequately

described the intestinal contents of big-scaled brown slickhead (SBI). The dietary variation within the intestinal contents of small-scaled brown slickhead (SSM) and warty oreo (WOE (I)) was adequately described by the RW and FG, and the RW and LPT classifications respectively.

Table 65. Food classifications adequately describing the dietary richness of the stomach contents of 22 fish species from northeastern Chatham Rise, Puysegur Bank and off the Wairarapa coast. Dietary classifications, which adequately described dietary richness, are displayed in grey with white text (S_{\max} 90% values for each dietary classification). Those species for which the largest numbers of food classifications are adequately described are displayed first (from RW–FG).

Species code	RW	LPT	FG
BEE	93	73	68
CSUp	38	21	10
EPR	23	9	6
CBO	28	25	17
SBI		8	11
CSE		32	5
CSU		20	4
ETBp			23
ORH			20
SRO	65	55	
CDO	24	24	
JAV	58	58	
SPE	48	50	
SND	28		
WOE		8	
CYP			
ETB			
BSL			
CBO			
COL			
SSI			
Number of asymptotes for each classification	8	12	10
RW: raw data LPT: lowest practical taxon FG: functional food groups			

Table 66. Food classifications adequately describing the dietary richness of the intestinal contents of 22 fish species from northeastern Chatham Rise, Puysegur Bank and off the Wairarapa coast. Dietary classifications, which adequately described dietary richness, are displayed in grey with white text (S_{\max} 90% values for each dietary classification). Those species for which the most number of food classifications are adequately described are displayed first (from RW–FG). (I): indicates the intestinal contents of a fish species, which also had stomach contents.

Species code	RW	LPT	FG
HJOp	9	9	8
BSL (I)	11*	11	5
MCA	26	21	12
WHX	12	14	6
CSE (I)	42	42	45
CSU (I)	66	66	20
CSUp (I)	28	28	18
CTH		9	4
CHY		2	2*
CIN		8	3
SBI (I)	43	40	
SSM	13		13
WOE (I)	8*	8*	
CBO (I)			
HJO			
SMC			
Number of asymptotes for each classification	10	12	11
RW: raw data LPT: lowest practical taxon FG: functional food groups			

4.11. Section two - Stomach parasites of serrulate and four-rayed rattail

There were more stomach parasites in serrulate rattail than four-rayed rattail (KW ANOVA, $H = 27.21$, $P < 0.000$ DF = 1, adjusted for ties), and these were mostly digeneans, and to a lesser extent, nematodes (**Table 67**).

Table 67. Total numbers of stomach parasites in serrulate (CSE) and four-rayed (CSU) rattail.

	digenean spp.	nematode spp.	trematode sp. 2	trematode sp. 3	Total	Mean (SD)
CSE ($n = 37$)	364	44	5	10	423	12.05 (14.92)
CSU ($n = 34$)	72	11			83	2.44 (4.86)

There was a significant difference in the median number of parasites in the five size classes of serrulate rattail (KW ANOVA, $H = 18.88$, DF = 4, $P < 0.001$ (adjusted for ties)), with the number of parasites significantly increasing with the size of the fish (Spearman rank $r_s = 0.744$, $P > 0.000$) (**Fig. 174**).

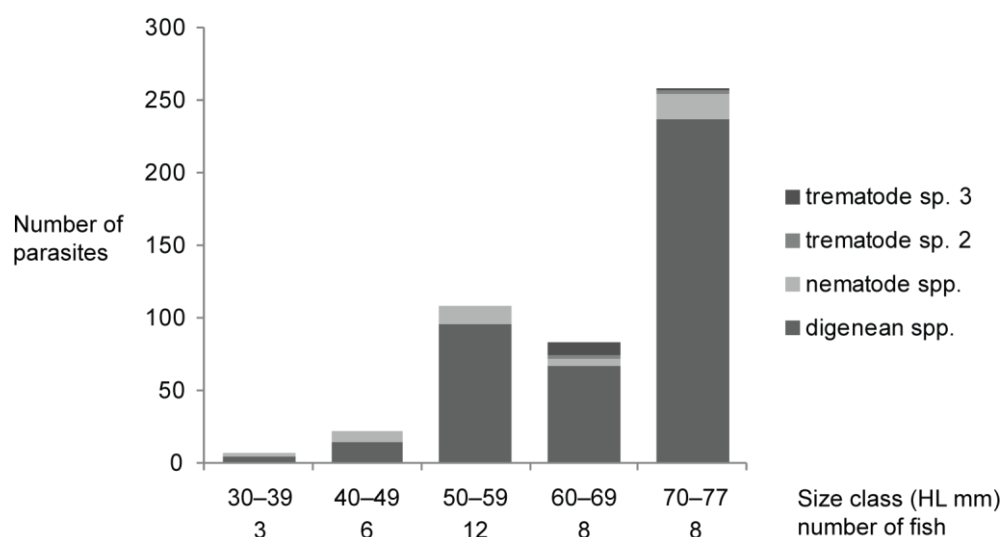


Figure 174. Number and type of stomach parasites of serrulate rattail over five size classes.

There was no significant difference in the median number of parasites in the stomach contents of four-rayed rattail over four size classes (KW ANOVA $H = 2.00$, DF = 3, $P > 0.573$ (adjusted for ties)), and apart from one fish with 29 digenean parasites (**Fig. 175**), the number of parasites did not significantly increase with increasing fish size (Spearman rank $r_s = 0.150$, $P > 0.198$).

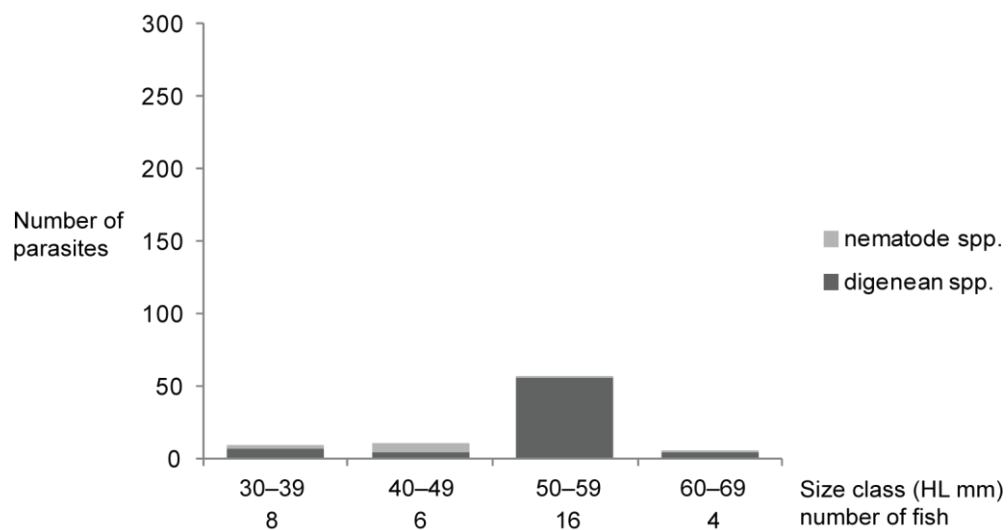


Figure 175. Number and type of stomach parasites of four-rayed rattail over four size classes.

4.12. Interspecific dietary overlaps

4.12.1. Northeastern Chatham Rise and Puysegur Bank

There were few high levels of dietary overlap between species (**Table 67**). Amongst the northeastern Chatham Rise and Puysegur Bank fish, basketwork eel (BEE), Baxter’s dogfish (ETB), orange roughy (ORH), and warty oreo (WOE) had the greatest number of dietary overlaps with other species. There was high level of dietary overlap between Baxter’s dogfish (ETB, ETBp) from the northeastern Chatham Rise and Puysegur Bank, but not for four-rayed rattail (CSU, CSUp). Four-rayed rattail from Puysegur Bank had a high overlap with robust cardinal fish (EPR) from northeastern Chatham Rise.

Table 68. A similarity matrix for the diets of 11 species of fish from northeastern Chatham Rise, and Puysegur Bank: CYP, long-nosed velvet dogfish; SND, shovel-nosed dogfish; ETB, Baxter’s dogfish; BEE, basketwork eel; SBI, big-scaled brown slickhead; BSL, black slickhead; CSU, four-rayed rattail; CSE, serrulate rattail; WOE, warty oreo; and EPR, robust cardinal fish. Fish from Puysegur Bank were: Baxter’s dogfish, EBAp, and four-rayed rattail, CSUp. High levels of dietary overlap (>0.6) are shown in grey with white text; low overlaps <0.3 are not shown for clarity. All comparisons are based on %W. Fish species codes are as listed in **Table 5**.

	CYP	SND	ETB	ETBp	BEE	SBI	BSL	CSU	CSUp	CSE	ORH	WOE	EPR
CYP		0.43	0.54	0.82	0.71					0.33	0.44	0.44	
SND				0.58	0.71					0.35			
ETB				0.56	0.50					0.35			
ETBp					0.86					0.36	0.61	0.61	
BEE											0.72	0.73	
SBI													
BSL								0.32		0.47	0.40	0.30	
CSU									0.48	0.31			0.33
CSUp													0.68
CSE													
ORH												0.87	
WOE													
EPR													

4.12.2. Wairarapa coast

Overall, the levels of dietary overlap were low between the eight fish species from off the Wairarapa coast. Capro dory (CDO) had a high level of dietary overlap with javelin fish and silver roughy. Silver roughy (SRO) and javelin fish (JAV) also had a high level of dietary overlap. There was moderate overlap between Oliver’s rattail (COL) and all other species, except silverside (SSI), also between two-banded rattail, and sea perch and Bollons’ rattail. Silverside (SSI) had low levels of dietary overlap with all other species.

Table 69. A similarity matrix, for eight species of fish from off the Wairarapa coast: CBI, two-banded rattail; CBO, Bollons' rattail; COL, Oliver's rattail; JAV, javelin fish; SRO, silver roughy; CDO, capro dory; SPE, sea perch and SSI, silverside. High levels of dietary overlap (>0.6) are shown in dark grey with white text; low overlaps <0.3 are not shown for clarity. All comparisons are based on %W. Fish species codes are as listed in **Table 5**.

	CBI	CBO	COL	JAV	SRO	CDO	SPE	SSI
CBI			0.45	0.34		0.36	0.34	
CBO			0.50					
COL				0.50	0.43	0.45	0.53	
JAV					0.79	0.73		
SRO						0.67		
CDO								
SPE								
SSI								

4.13. Feeding guilds for fish species from northeastern Chatham Rise and Puysegur Bank

4.13.1. All gut analysis

The similarity profile-based (SIMPROF) agglomerated cluster analysis of the 19 fish species from northeastern Chatham Rise and Puysegur Bank formed three main clusters, when based on the presence or absence of stomach and/or intestinal contents identified using functional food groups (**Fig. 176**). Shovel-nosed dogfish was an outlier, as its diet was almost entirely small vertically migrating pelagic/mesopelagic fishes. The second cluster was made up of benthic feeding fishes, most of which had high rates of stomach eversion, and were macrourids. The third and largest cluster was made up of the remaining 13 species, all of which were varying combinations of benthopelagic feeders. Within this cluster there were several smaller clusters, although the stress required to display the nMDS plot was quite high (0.13), which suggests that these data may not describe the relationships between these species well (**Fig. 177**).

4.13.2. Stomach contents only

The similarity profile (SIMPROF) agglomerated cluster analysis of the 11 fish species from northeastern Chatham Rise and Puysegur Bank also formed several clusters, when based on square root transformed wet weight stomach contents data identified using functional food groups (**Fig. 178**). The nMDS plot showed some structure to the data at approximately 60 percent similarity level, with three similar groups at the 60 percent level (**Fig. 179**). These were four-rayed rattail (from Puysegur Bank) and robust cardinal fish, four rayed rattail (from north eastern Chatham Rise) and

black slickhead, and Baxter's dogfish (from both areas) and basketwork eel. Orange roughy and warty oreo were approximately 59 percent similar. The other species had diets that were <60 percent similar, with shovel-nosed dogfish also an outlier. **Figs. 180–185** use bubble plots to detail the proportional contributions, made by the square root of the wet weight of each functional group, to the ordination of the nMDS shown in **Fig. 179**.

Table 70. Ten functional feeding guilds for 19 fish species from northeastern Chatham Rise, Puysegur Bank, and off the Wairarapa coast; fish species included in these guilds, and the relevant literature used to justify their inclusion; species codes are as those listed in **Table 5**.

Functional feeding guild	Fish species code	Literature used
Pelagic invertebrate feeders	SBI	Mauchline & Gordon (1983b), Clark et al. (1989), Bulman et al. (2002), Pakhomov et al. (2006).
Pelagic fish feeders	SND	Mauchline & Gordon (1983a), Clark & King (1989), Ebert et al. (1992).
Pelagic crustacean and invertebrate feeders	EPR CSU CSUp CSE BSL	Mauchline and Gordon (1983b); Clark et al. (1989); Gaskett et al. (2001); Bulman et al. (2002).
Benthopelagic fish and invertebrate feeders/scavengers	CYP ETB ETBp	Mauchline & Gordon (1983a), Clark et al. (1989), Ebert et al. (1992), Bulman et al. (2002), Dunn et al. (2010a).
Benthopelagic fish, crustacean, and invertebrate feeders (BEE may also scavenge)	ORH BEE WOE	Mel'nikov (1981), Mauchline & Gordon (1984a), Rosecchi et al. (1988), Clark et al. (1989), Bulman & Koslow (1992), Anderson (2005b).
Benthic invertebrate feeders/scavengers	SSI	Graham (1953), Clark (1985a).
Benthic crustacean and megabenthos feeders	CBI CBO	McLellan (1977), Bulman et al. (2001), Stevens & Dunn (2011).
Pelagic crustacean feeders	SRO	Mauchline & Gordon (1984a, 1987a), Kerstan (1989), Pais (2001, 2002), Madurell et al. (2004).
Benthopelagic crustacean, fish, and megabenthos feeders/scavengers	SPE	Graham (1953), Blaber & Bulman (1987), Bulman et al. (2001), Horn et al. (2012).
Pelagic and benthopelagic crustacean and megabenthos feeders	COL JAV CDO	Clark (1985a), Blaber & Bulman (1987), Clark et al. (1989), Bulman et al. (2001), Stevens & Dunn (2011).

Stomach and/or intestinal contents

Northeastern Chatham Rise and Puysegur Bank

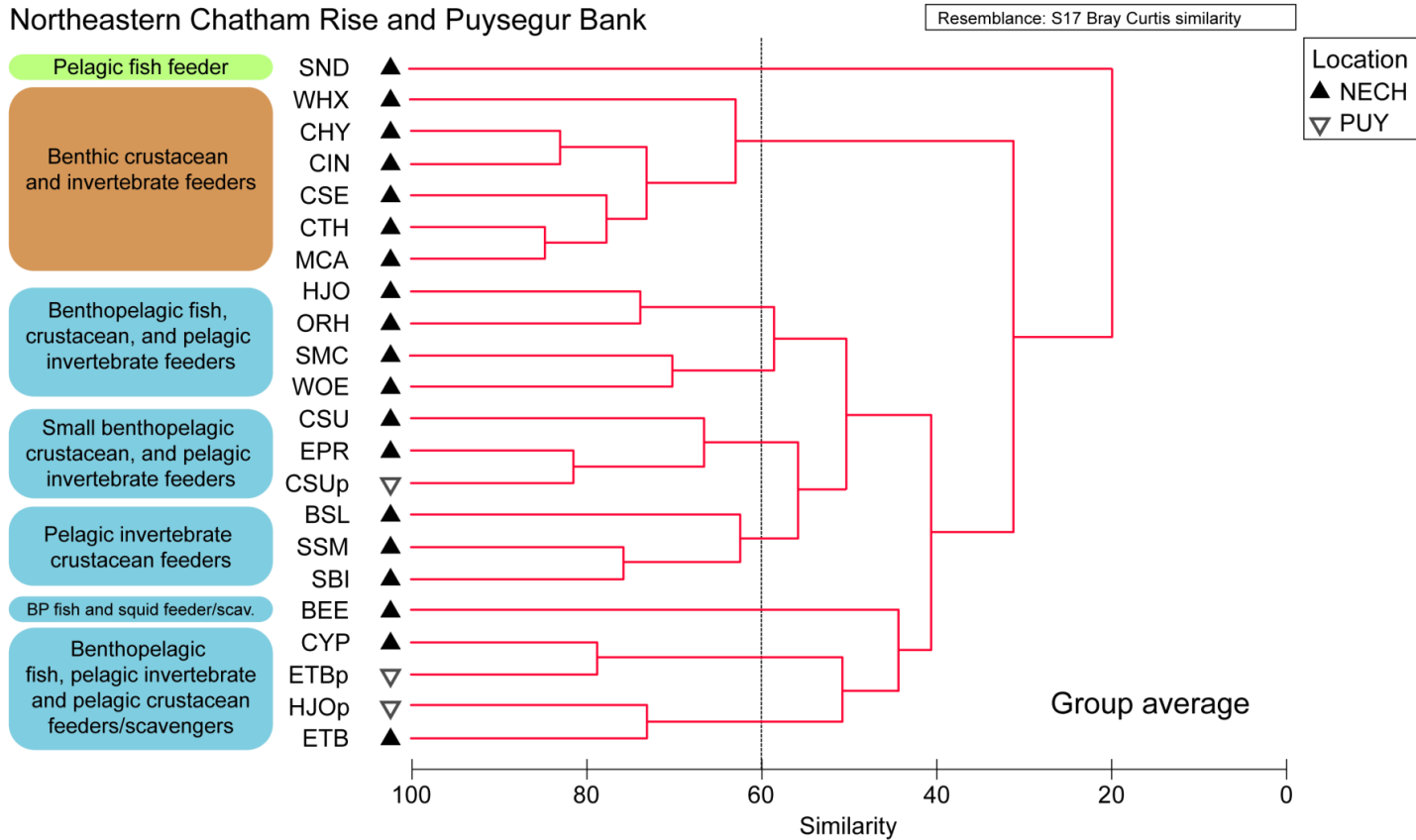


Figure 176. An agglomerated cluster analysis of 19 fish species from northeastern Chatham Rise (NECH) and Puysegur Bank (PUY). Clusters are based on averaged presence/absence data from whole gut analysis of functional food groups. The vertical bar indicates 60% similarity. Assumed feeding guilds are in rounded rectangles to the left: green rounded -rectangles indicate pelagic; brown, benthic; and blue, benthopelagic (BP) diets, scav.: scavenger. Fish species codes are as listed in **Table 5**.

Stomach and/or intestinal contents

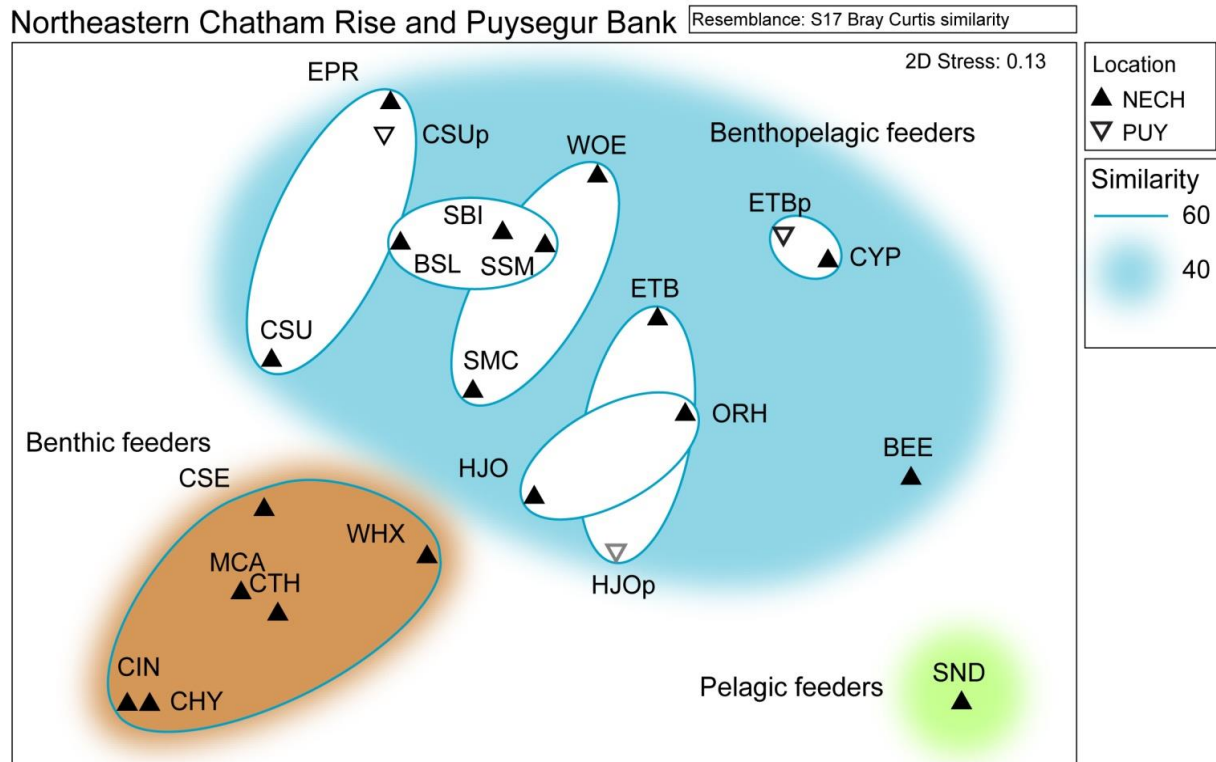


Figure 177. Non-metric multi-dimensional scaling plot (nMDS), for 19 fish species from northeastern Chatham Rise (NECH) and Puysegur Bank (PUY) (based on averaged presence/absence data from whole gut analysis of functional food groups). Dietary similarities of 60% or over are grouped within ovals, while blurred outlines indicate >40–59% similarity. Colours as are for **Fig. 176**; fish species codes are as listed in **Table 5**.

Stomach contents

Northeastern Chatham Rise and Puysegur Bank

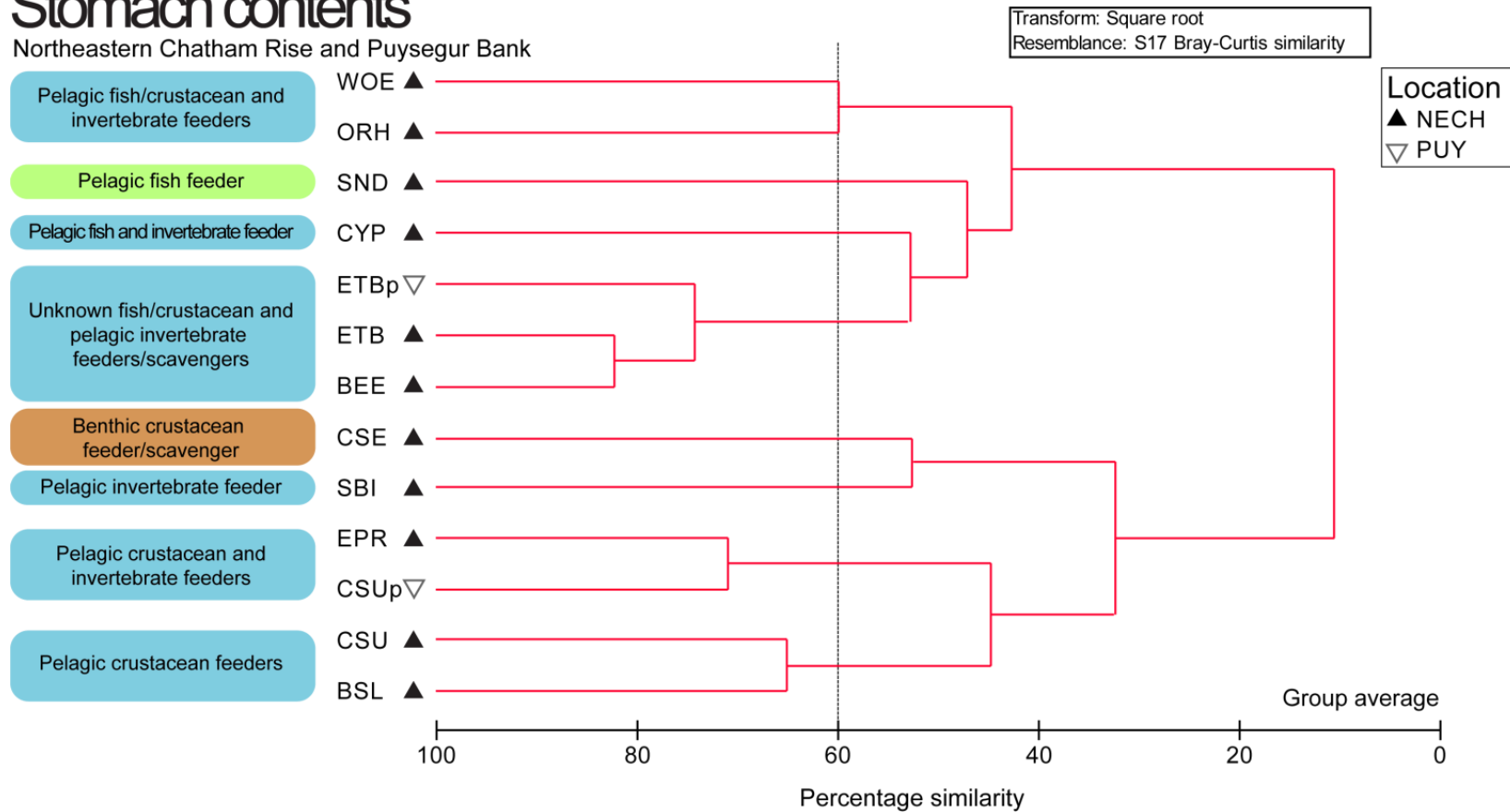


Figure 178. An agglomerated cluster analysis of 11 fish species from northeastern Chatham Rise (NECH) and Puysegur Bank (PUY). Clusters are based on square root transformed, averaged wet weight of stomach contents data based on functional food groups. The vertical bar indicates 60% similarity. Assumed feeding guilds are in rounded rectangles to the left. Assumed feeding guilds are in rounded rectangles to the left: green rounded -rectangles indicate pelagic; brown, benthic; and blue, benthopelagic diets. Colours as are for **Fig. 176**; fish species codes are as listed in **Table 5**.

Stomach contents

Northeastern Chatham Rise and Puysegur Bank

Transform: Square root
Resemblance: S17 Bray-Curtis similarity

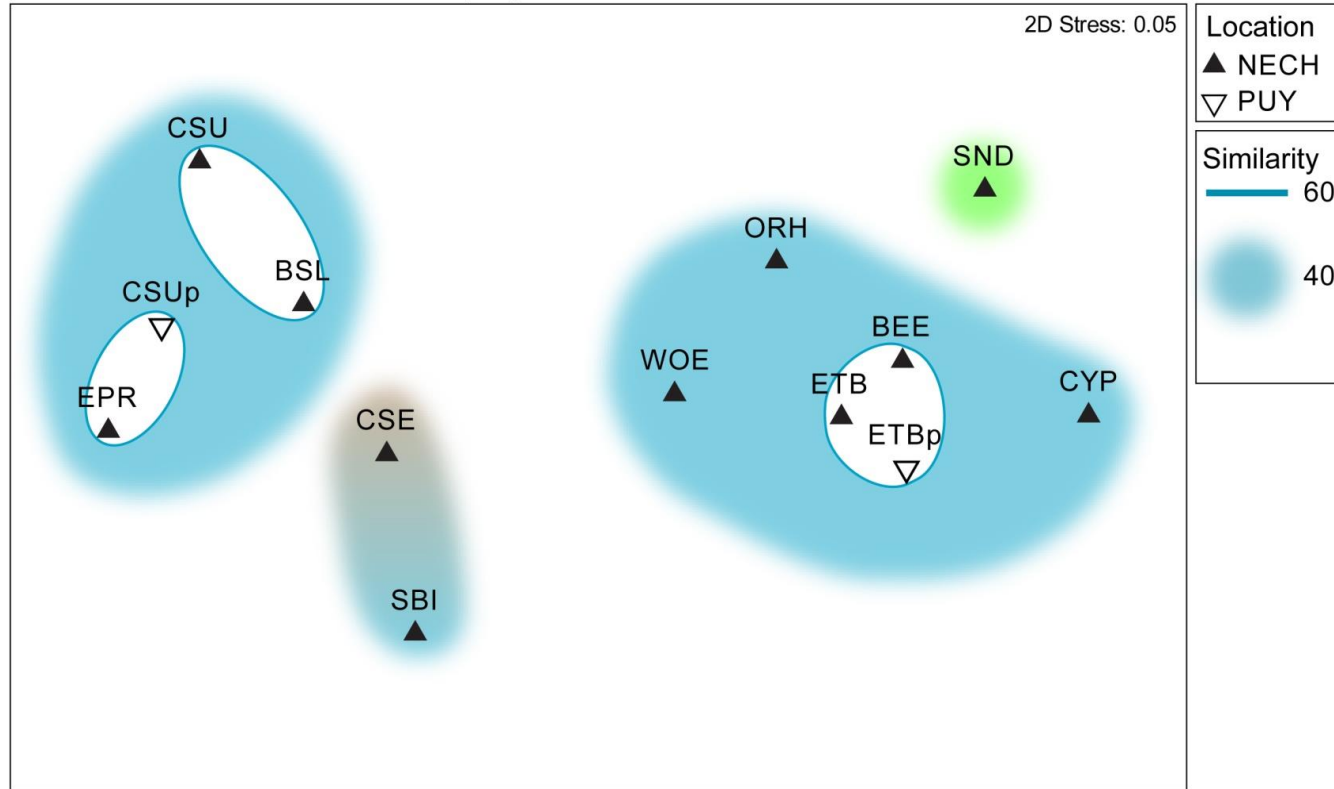
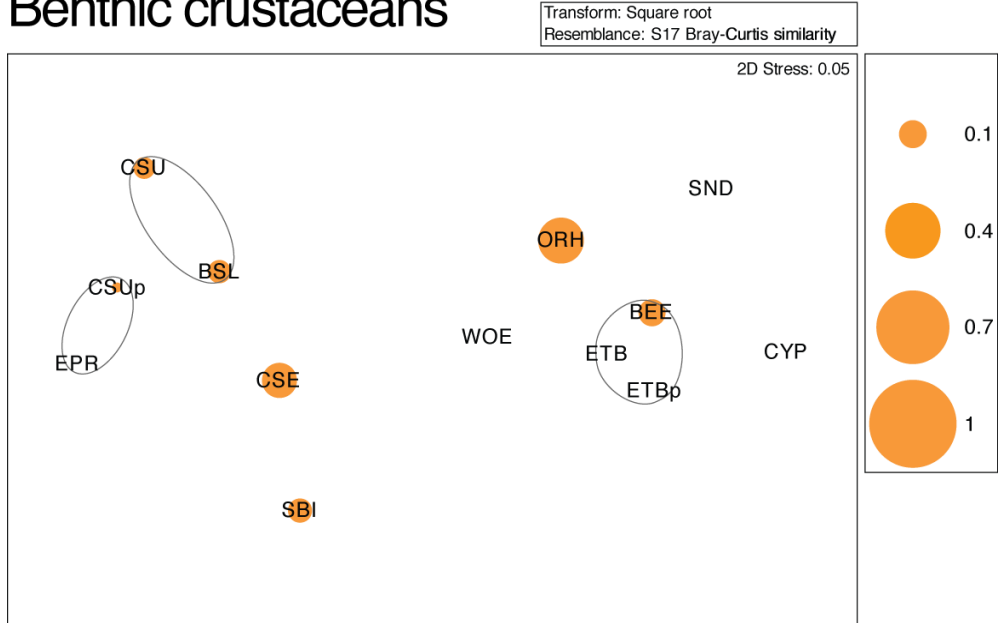


Figure 179. Non-metric multi-dimensional scaling plot, (nMDS), for 11 fish species from northeastern Chatham Rise (NECH) and Puysegur Bank (PUY) (based on averaged wet weight stomach contents data, based on functional food groups). Dietary similarities of 60% or over are grouped within ovals, while blurred outlines indicate >40–59% similarity. Colours as are for **Fig. 176**; fish species codes are as listed in **Table 5**.

Benthic crustaceans



Benthic invertebrates

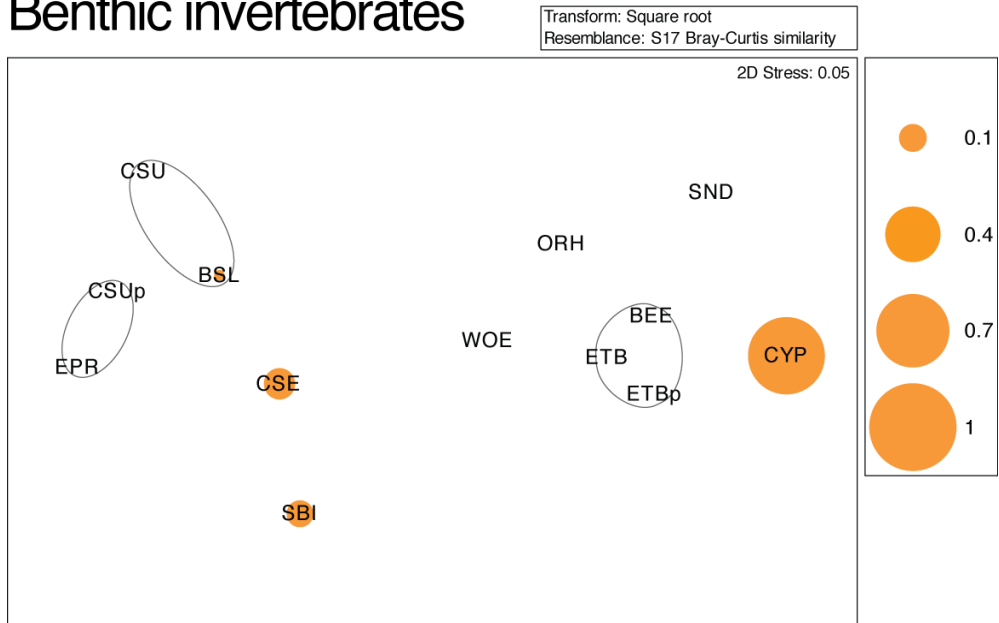


Figure 180. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Benthic crustaceans** and **Benthic invertebrates**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

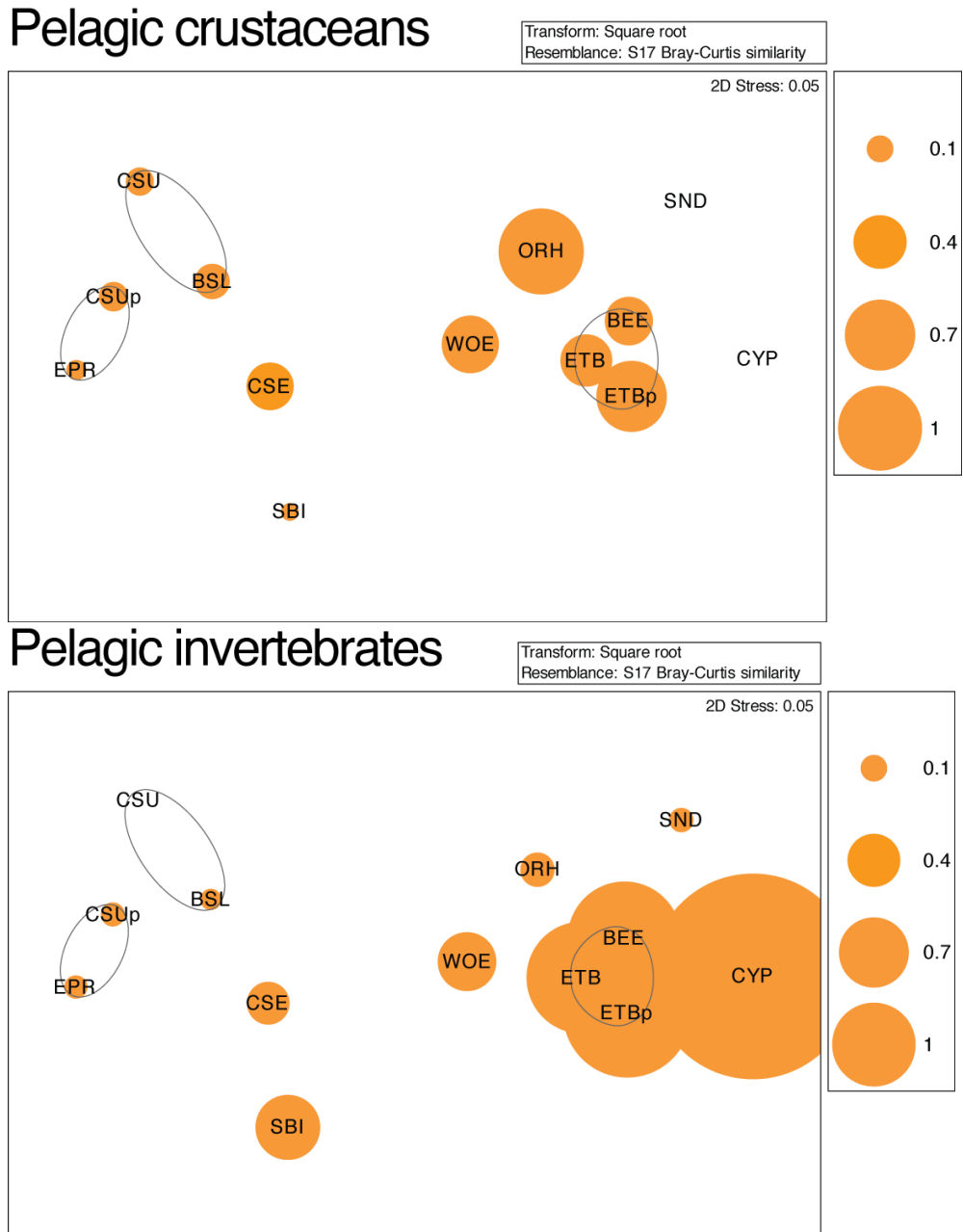
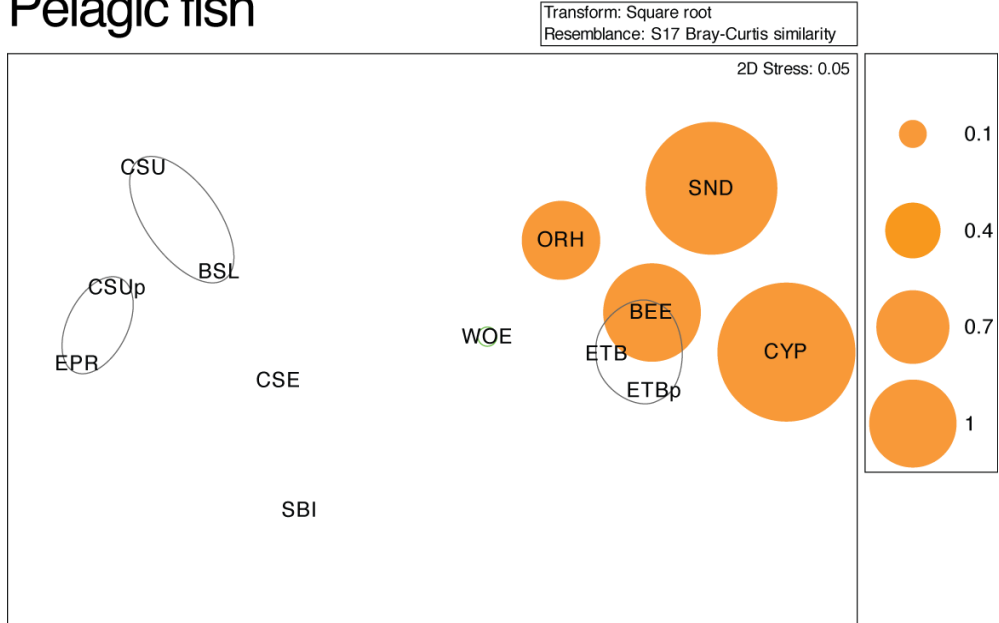


Figure 181. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Pelagic crustaceans** and **Pelagic invertebrates**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

Pelagic fish



Benthopelagic fish

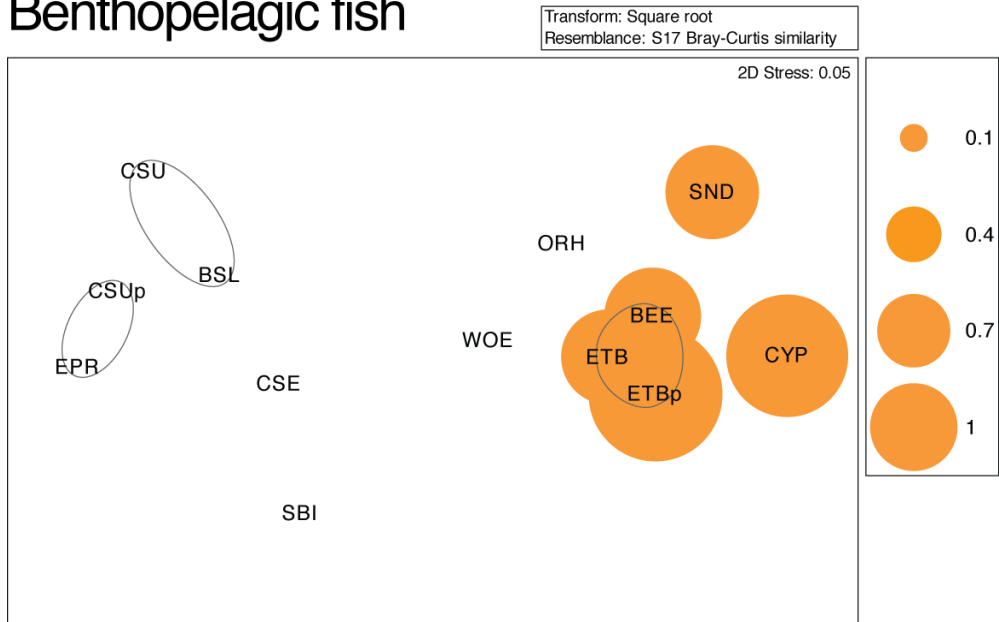
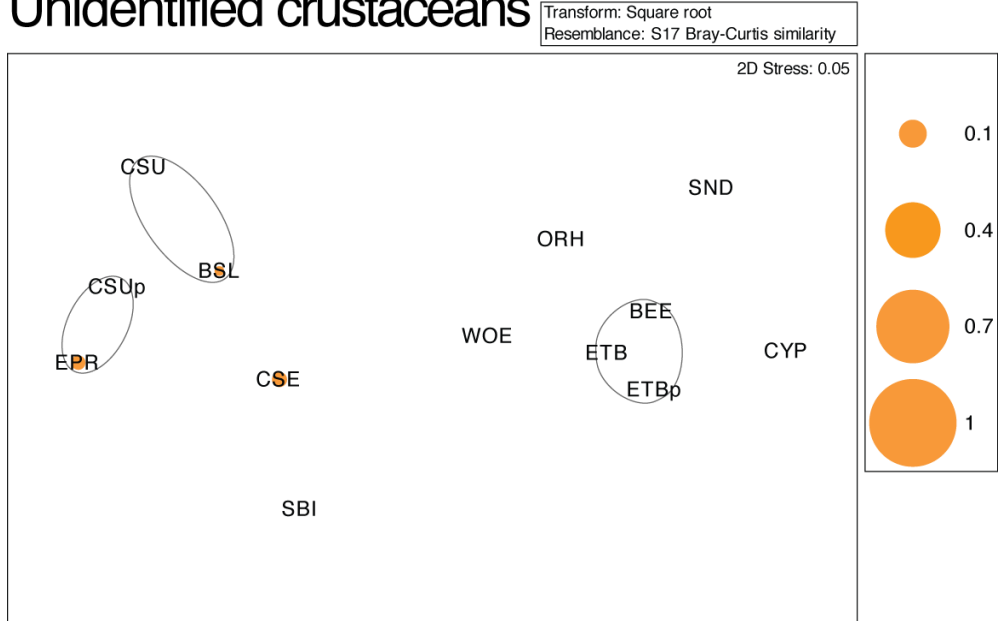


Figure 182. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Pelagic fish** and **Benthopelagic fish**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

Unidentified crustaceans



Unidentified fish

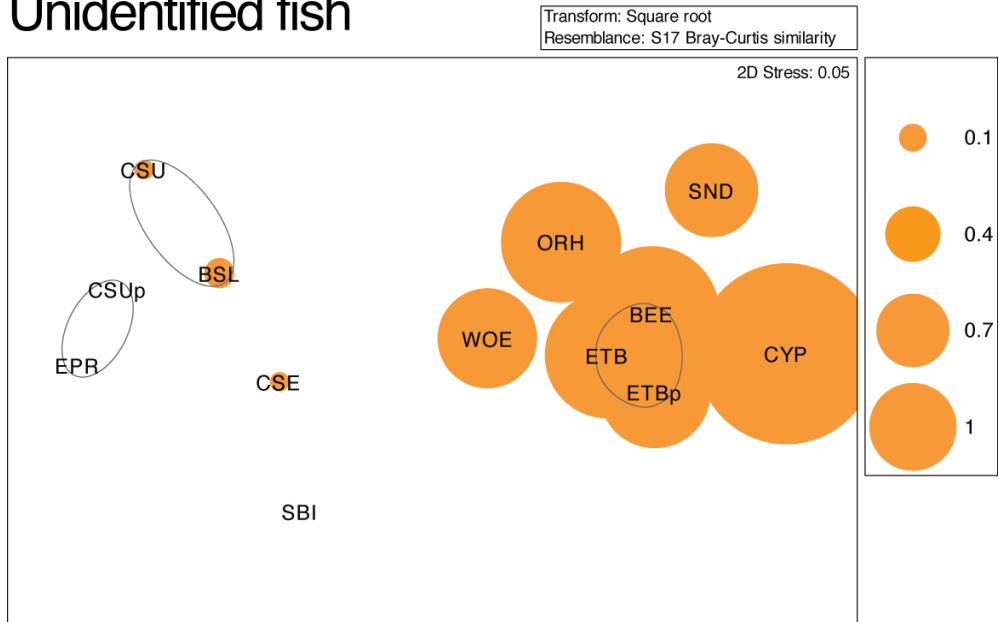
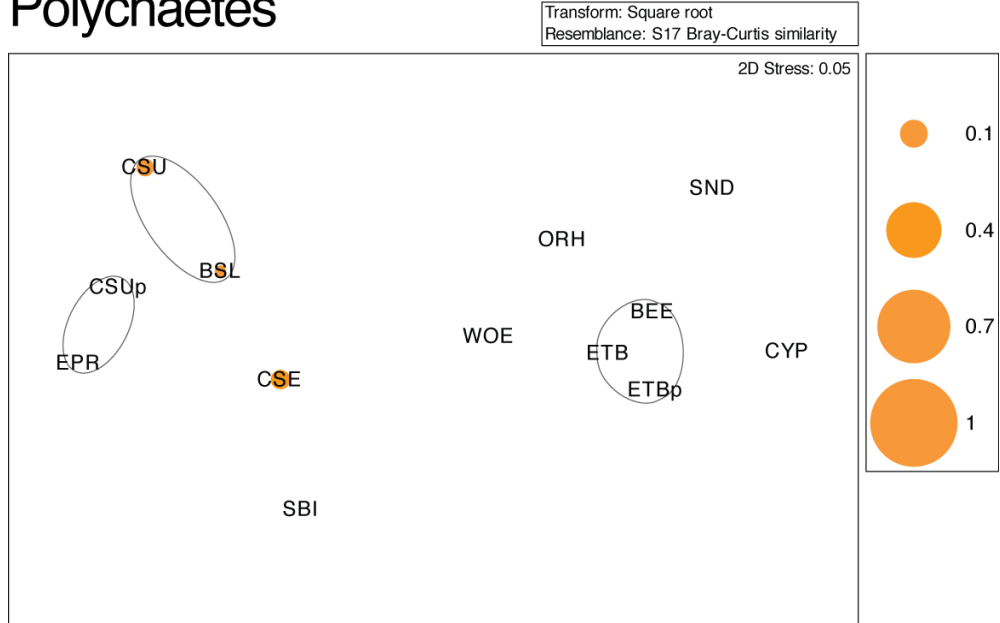


Figure 183. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Unidentified crustaceans** and **Unidentified fish**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

Polychaetes



Unidentified

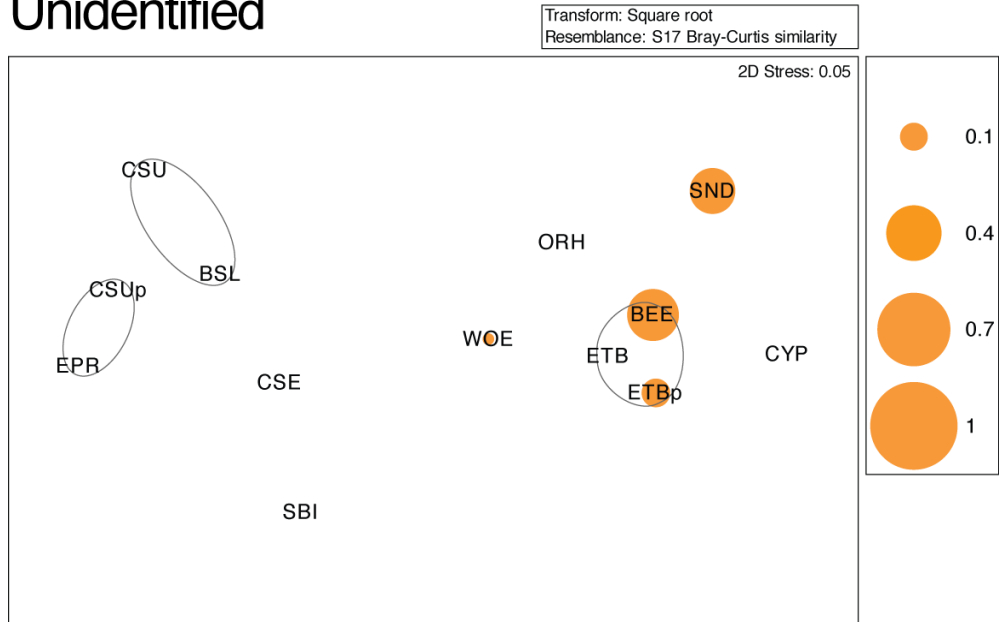


Figure 184. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Polychaetes** and **Unidentified material**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

Algae

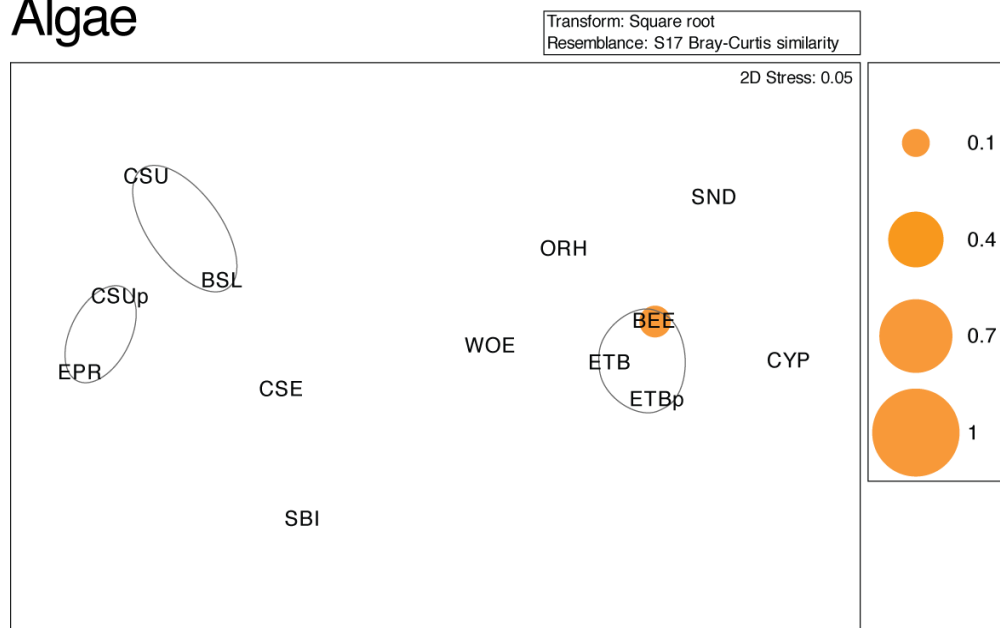


Figure 185. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for 11 fish species from northeastern Chatham Rise, and Puysegur Bank: **Algae**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

4.14. Feeding guilds for fish species from off the Wairarapa coast.

There were two groups of species with diets that were >40, but <60% similar, but only two species, javelin fish (JAV) and Oliver's rattail (COL), had diets that were >60% similar (**Fig 186, Fig. 187**). The diets of silver roughy (SRO), capro dory (CDO), Oliver's rattail (COL) and javelin fish (JAV) were similar at the 40 percent level, as were the diets of Bollons' (CBO) and two-banded rattail (CBI) , and sea perch (SPE). Silverside (SSI) was an outlier and was <30% similar to the diets of any of the other species. **Figs. 188–194** use bubble plots to detail the proportional contributions made by the square root of the wet weight of each functional group to the ordination of the nMDS shown in **Fig. 187**.

Stomach contents

Wairarapa coast

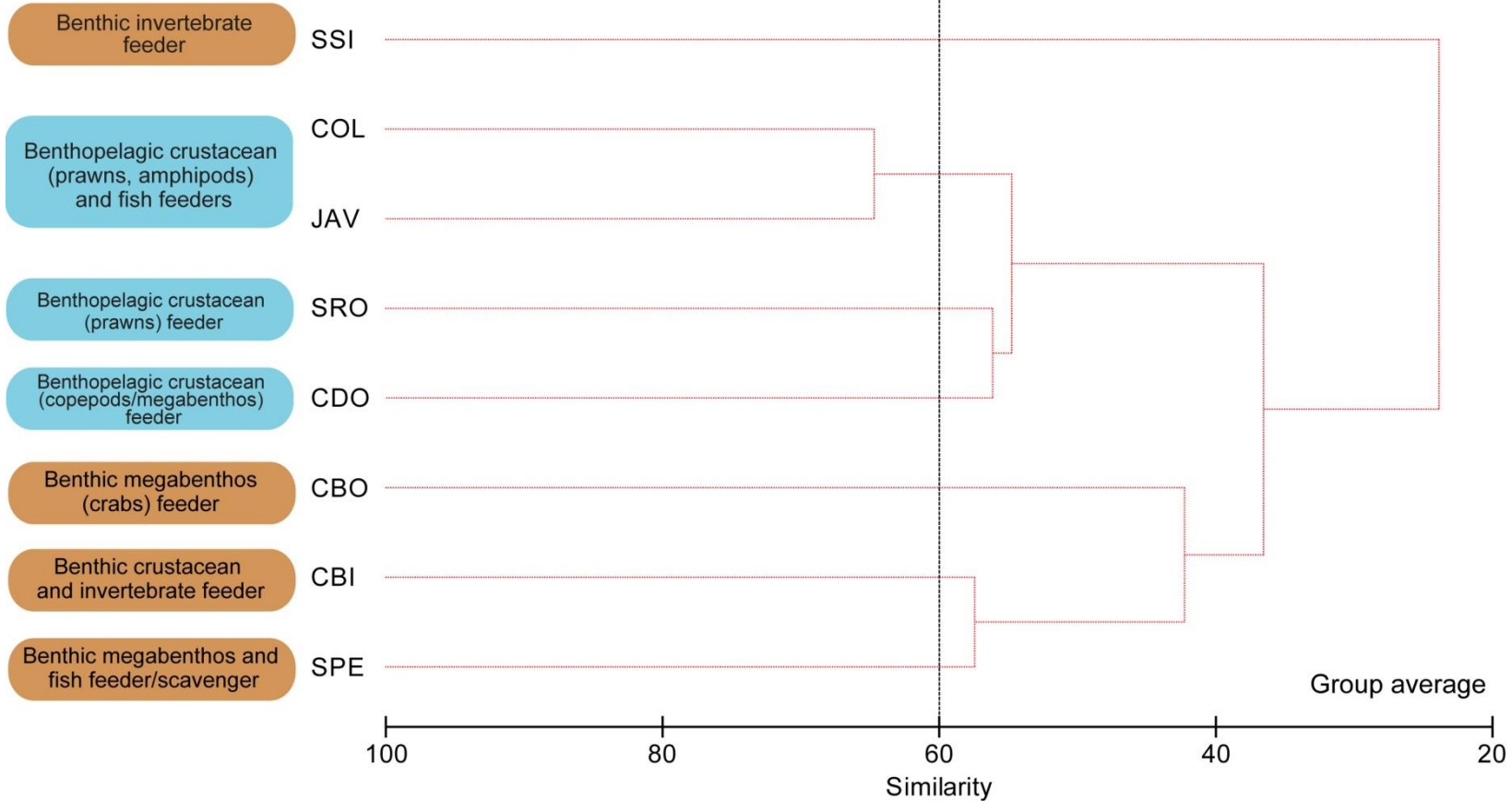


Figure 186. An agglomerated cluster analysis of eight demersal fish species from off the Wairarapa coast (WAI). Clusters are based on averaged wet weight data (g), from stomach contents, and based on functional food groups. Assumed feeding guilds are in rounded-rectangles to the left. Blue rectangles indicate a predominantly benthopelagic diet, and brown rounded-rectangles indicate a predominantly benthic diet. The vertical bar indicates 60% similarity. Colours as are for **Fig. 176**; fish species codes are as listed in **Table 5**.

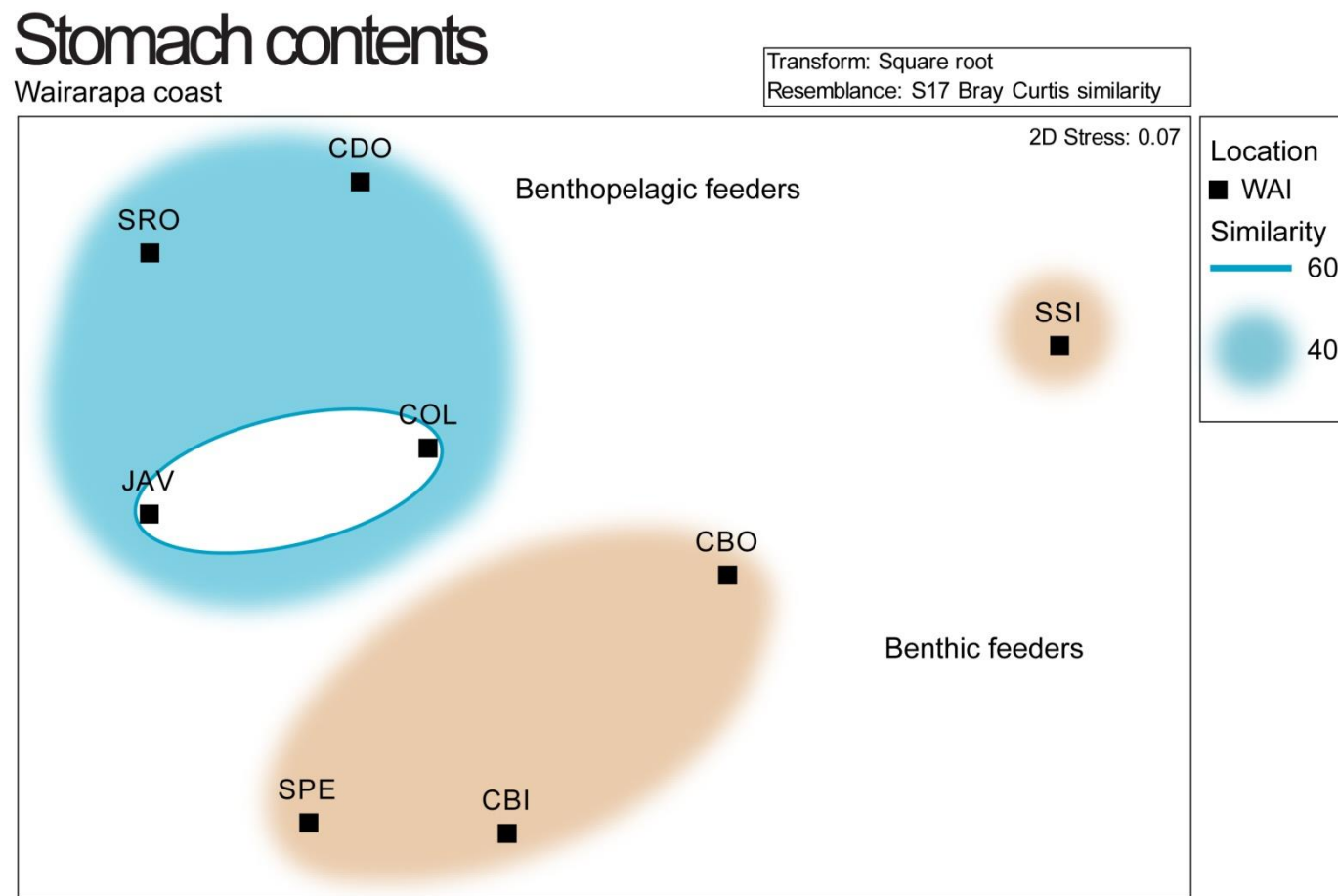
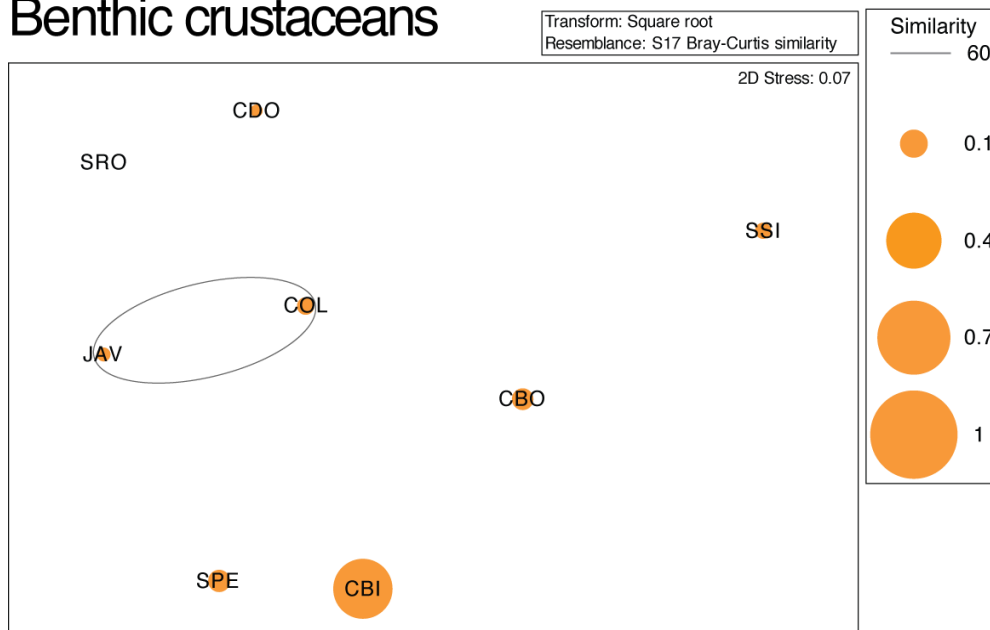


Figure 187. Non-metric multi-dimensional scaling plot, (nMDS), for eight fish species from off the Wairarapa coast (WAI) (based on square root transformed, averaged wet weight stomach contents data, based on functional food groups). Dietary similarities of 60% or over are grouped within ovals, while blurred outlines indicate >40–59% similarity. Colours as are for **Fig. 176**; fish species codes are as listed in **Table 5**.

Benthic crustaceans



Benthic invertebrates

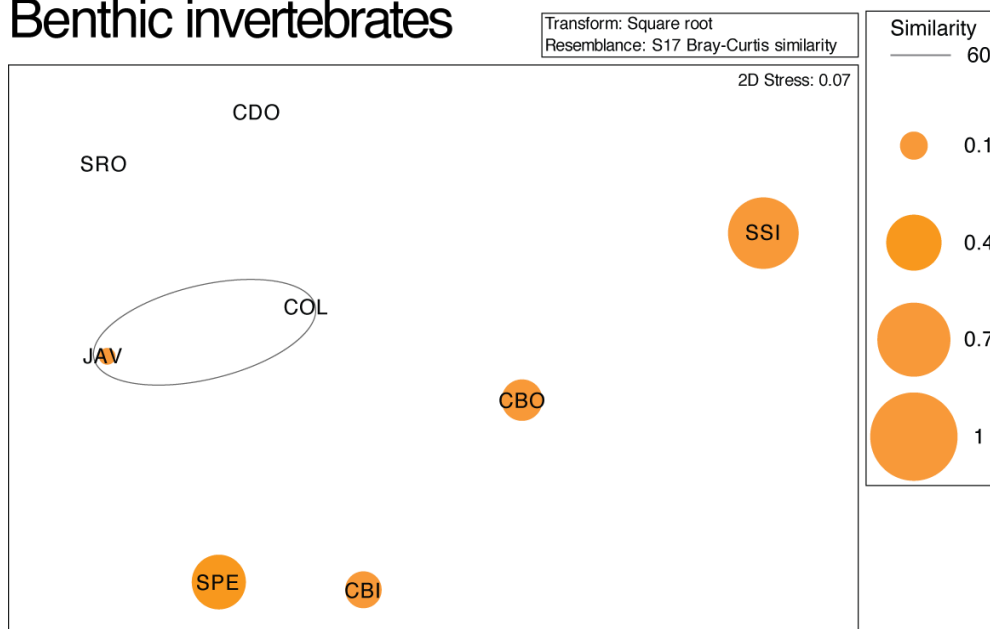


Figure 188. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Benthic crustaceans** and **Benthic invertebrates**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

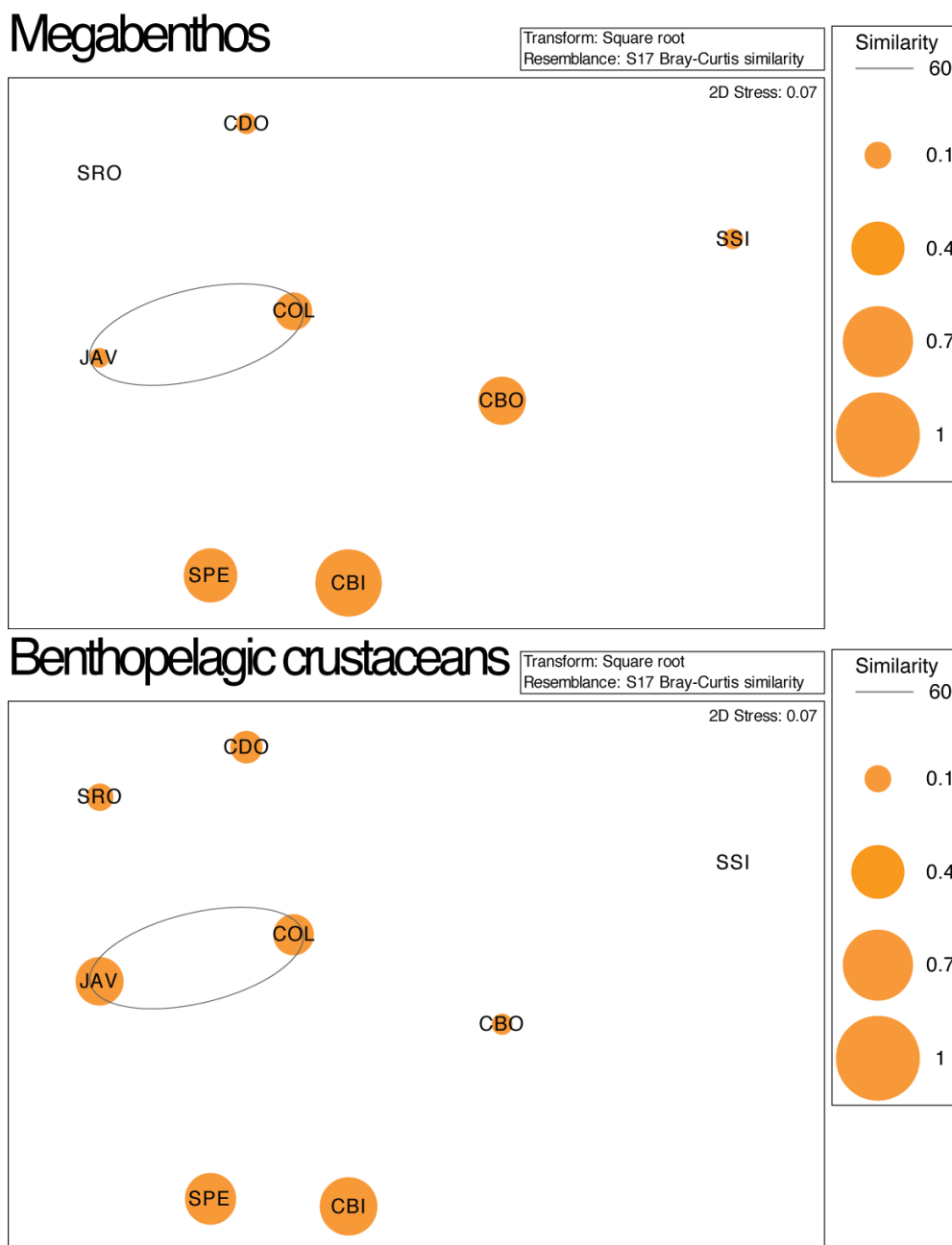


Figure 189. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Megabenthos** and **Benthopelagic crustaceans**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

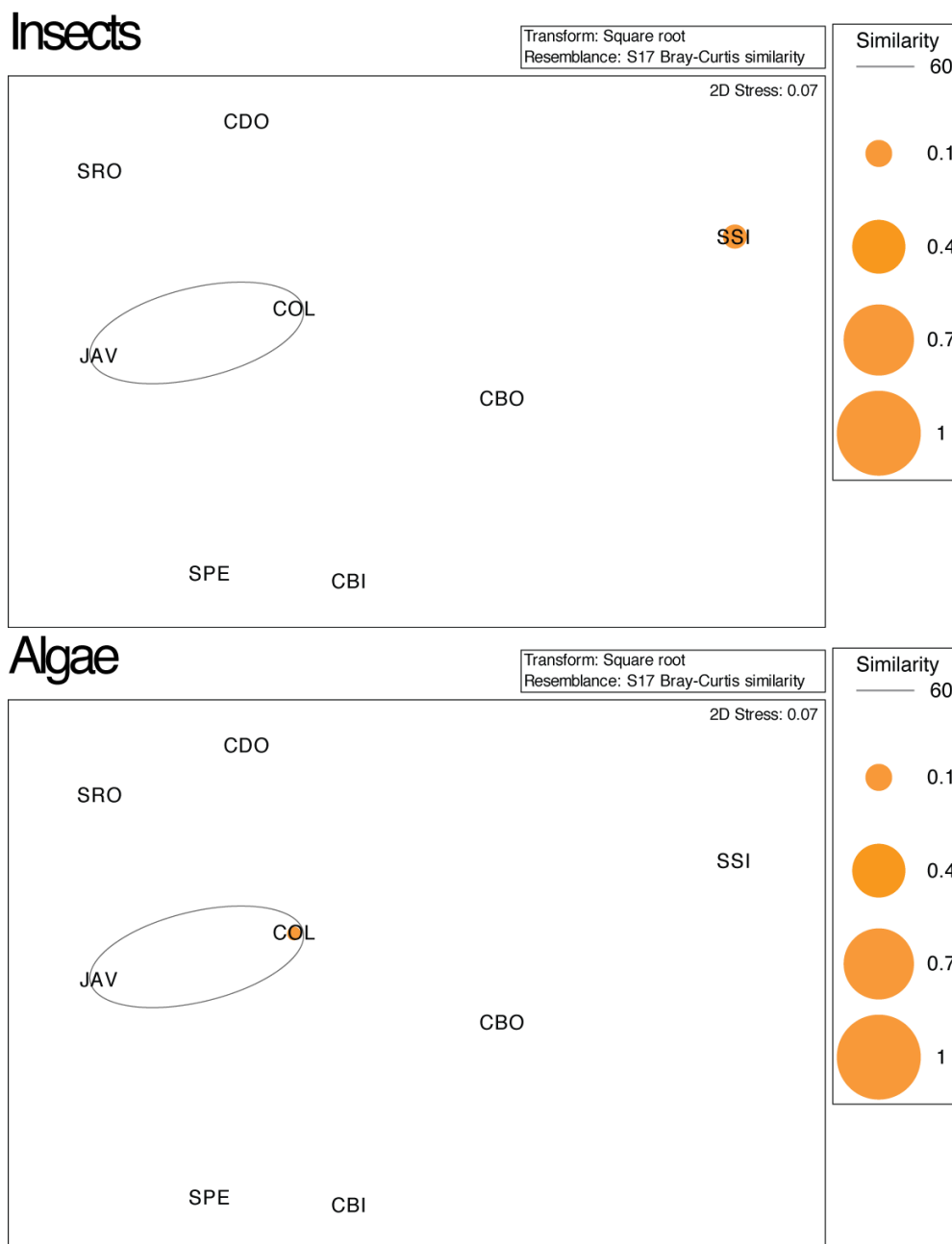


Figure 190. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Insects** and **Algae**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

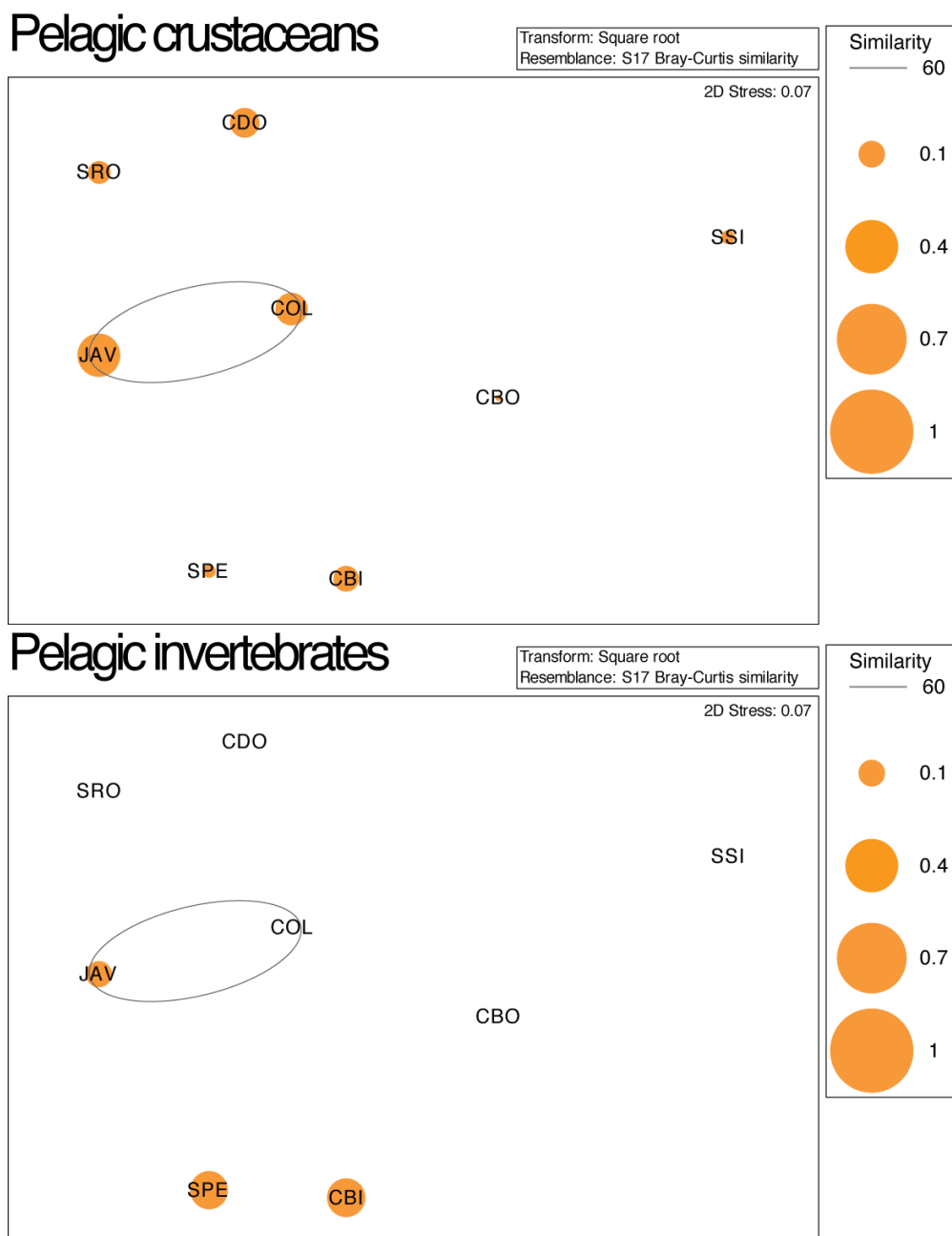


Figure 191. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Pelagic crustaceans** and **Pelagic invertebrates**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

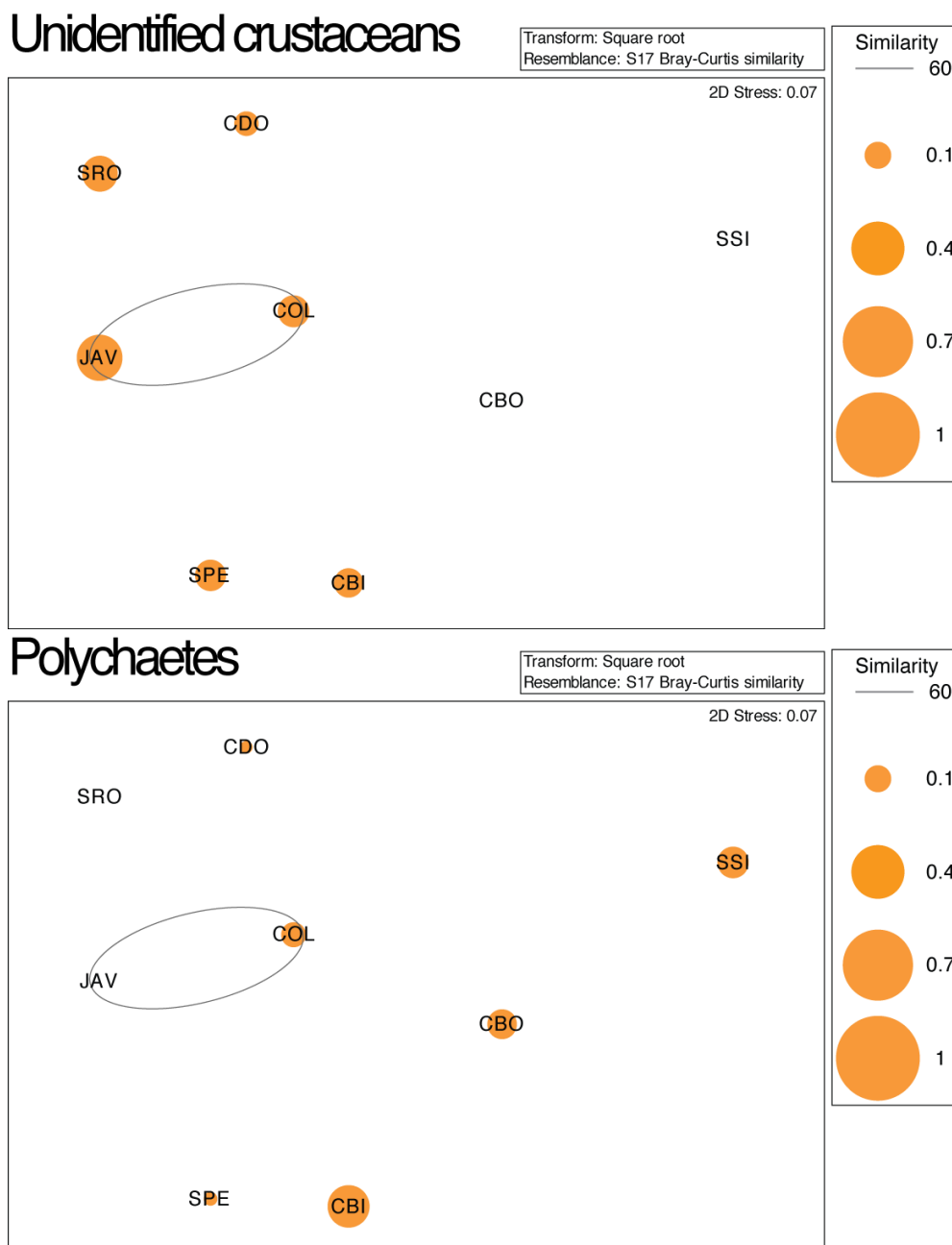


Figure 192. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Unidentified crustacean material** and **Polychaetes**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

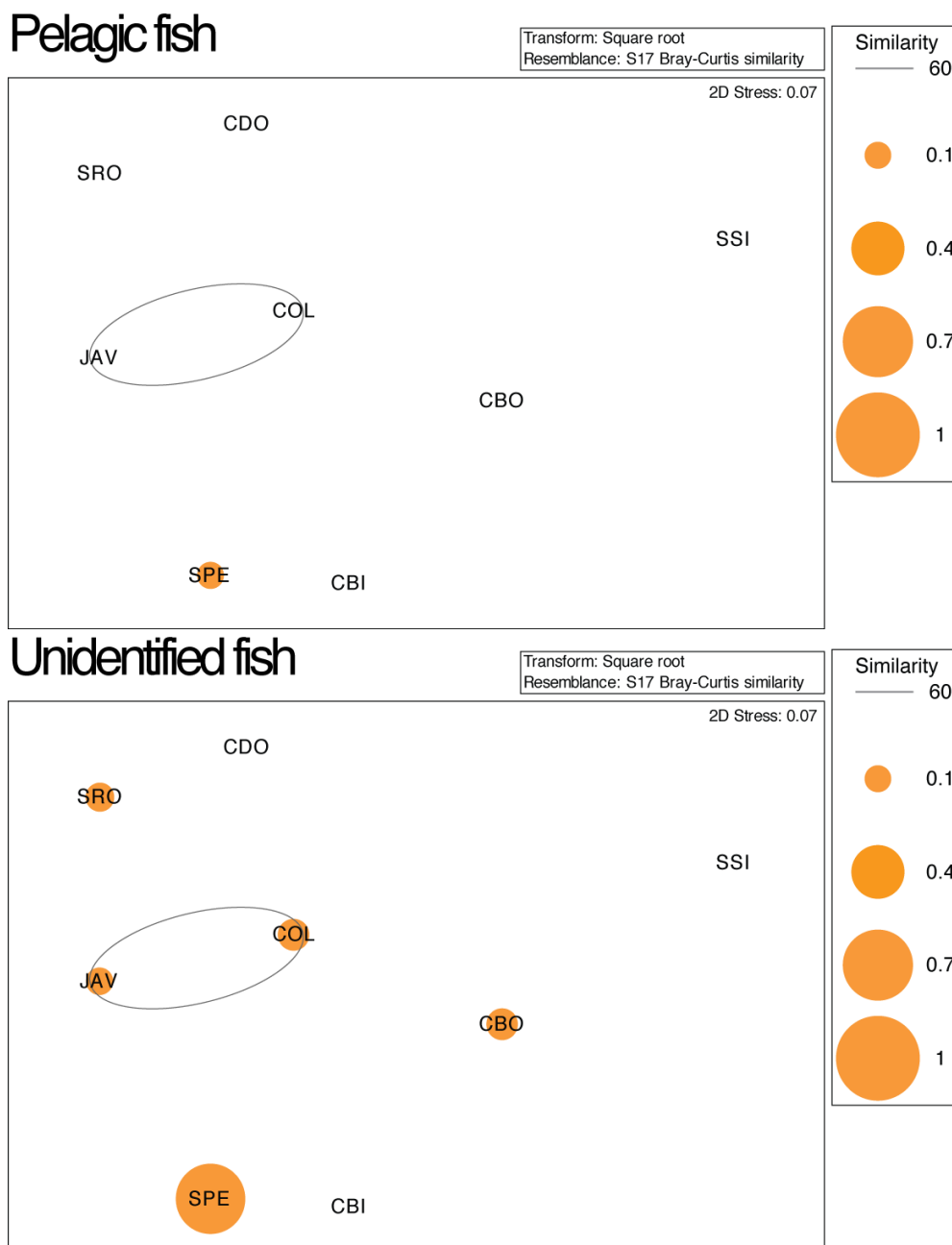


Figure 193. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Pelagic fish** and **Unidentified fish**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

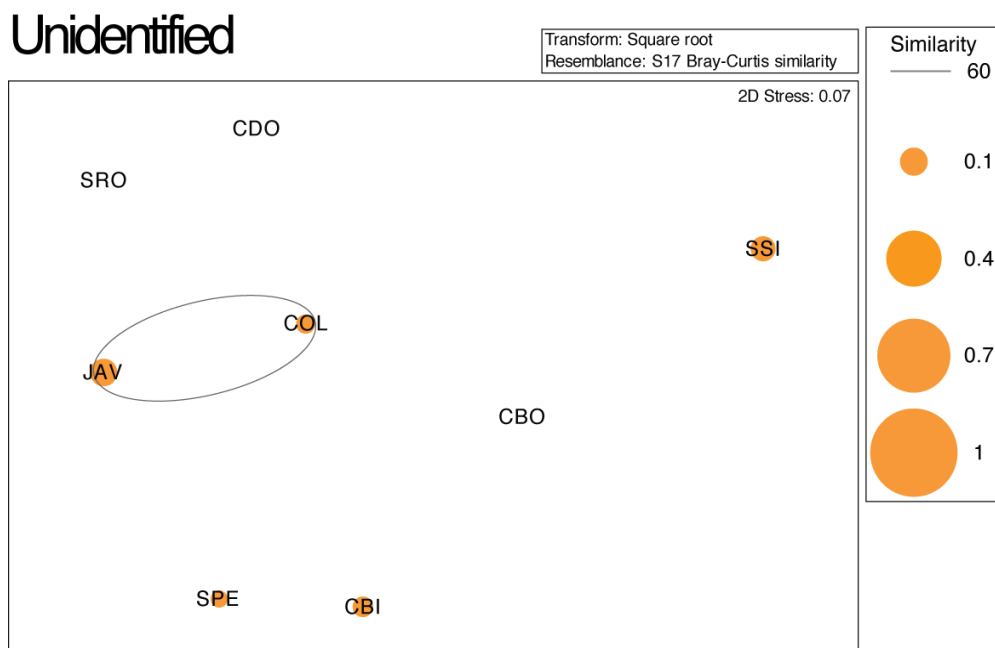


Figure 194. Two-dimensional bubble plots of square root-transformed, averaged wet-weight (g) stomach contents data for eight fish species from off the Wairarapa coast: **Unidentified material**. The size of circles represents the square root of the proportional contribution to each species by each food group (wet-weight (g)). Fish species codes are as cited in **Table 5**.

5.0 Discussion

5.0. Discussion

This discussion is divided into four sections. **Section one** discusses the diets of the fish species investigated in this study, and deals with intraspecific dietary elements: mid-slope northeastern Chatham Rise, the Puysegur Bank, and then upper slope off the Wairarapa coast. **Section two** discusses the food and interspecific feeding relationships between these species. This section focuses on the roles of thaliaceans and seaweed in the diets of these fish, and levels of dietary overlap between fish species from the northeastern Chatham Rise and Puysegur Bank. Trophic levels are discussed, then the percentage of empty stomachs/intestines. Following that, a parasite analysis of serrulate and four-rayed rattail is discussed. Feeding guilds are then described and finally, these guilds are interpreted to provide a simplified model of trophic pathways in the deep-sea and the relative trophic positions of the fishes examined in this study. **Section three** discusses the potential for the implementation of ecosystem-based fisheries management (EBFM) to orange roughy fisheries. **Section four** provides the conclusions of this study and future recommendations.

5.1. Section one — Diets of mid-slope species from northeastern Chatham Rise and Puysegur Bank

This section describes the intraspecific nature of the diets of the fish species investigated in this study: major dietary elements and ontogenic shifts are discussed and related to relevant literature. This section is split into two sub-sections; the first discusses the diets of fishes from northeastern Chatham Rise and Puysegur Bank. The second discusses the diets of upper slope fish from off the Wairarapa coast. The order of species follows **Chapter four**.

5.1.1. Chondrichthyans (dogfishes, chimaeras and skates)

Chondrichthyans are common mid-slope bycatch in orange roughy and other deep-sea fisheries in New Zealand and Australian waters, and can act as top predators in these ecosystems (Doonan et al. 2009, Blackwell 2010, Dunn et al. 2010a, Pethybridge et al. 2011). Until recently the biology of many New Zealand species has been largely unknown, and knowledge has focused around abundance data from research trawls (Wetherbee 1996, 2000; Duffy 1997; Blackwell 2010). Dietary information has also,

until very recently, been sparse (Clark & King 1989, Clark et al 1989, Jones 2008b, Dunn et al. 2010a, b; Forman & Dunn 2012).

Long-nosed velvet dogfish in this study fed on a combination of squid and fish. In the north Atlantic, off South Africa, and Tasmania, long-nosed velvet dogfish has been described as primarily piscivorous on mesopelagic species (Mauchline & Gordon 1983a, Ebert et al. 1992, Bulman et al. 2002). Recent work by Dunn et al. (2010a) investigated the diet of 19 long-nosed velvet dogfish from several upper slope (649–799 m) locations scattered over Chatham Rise, collected over three years (2005–2007), during daylight hours in the austral summer months. They found a diet dominated by fish, with squid a lesser component. They found that ten fish were adequate to describe the variation in the diet of this species. Although the sharks used in their study are a comparable size range to this study, their sharks were collected from the shallower end of this species' distribution (Anderson et al. 1998, Francis et al. 2002), and from several locations on Chatham Rise, during the austral summer, in daylight hours; so there are many confounding variables between their study and this. Although Dunn et al. (2010a) used DNA bar-coding to identify the food items in the stomachs of several New Zealand deep-sea shark species, DNA was not used to assist with the identification of the stomach contents of long-nosed velvet dogfish. More recently, Pethybridge et al. (2011) described the diet of several long-nosed velvet dogfish from off southern Australia between 2004 and 2006. They used a combination of fatty acid profiles and stomach contents and found a diet comprised of squid, benthopelagic fish and an ontogenic shift from small polychaetes.

Shovel-nosed dogfish fed primarily on small mesopelagic fish, and there was no evidence of benthic feeding or scavenging in this species' diet from northeastern Chatham Rise. The diet of shovel-nosed dogfish has previously been reported from around the northern half of North Island by Clark and King (1989) as comprising mostly of small lantern fish (Myctophidae), similar to that reported for this species in the north Atlantic (Mauchline & Gordon 1983a), off South Africa (Ebert et al. 1992), and off Tasmania (Bulman et al. 2002). Kobayashi (1986) reported more shovel-nosed dogfish caught on loglines at night than during the day, suggesting that this species could be predominantly a nocturnal feeder. This would be counter to the notion that this species feeds on vertically migrating fishes, as presumably these would be at the low point of their diel migrations (and vulnerable to shovel-nosed dogfish) during daylight hours. Shovel-nosed dogfish had a narrow niche breadth and little dietary overlap with other

species, which suggests that it occupies a defined niche. This is in contrast with the diet of this species recently reported by Pethybridge et al. (2011) from off various parts of southern Australia, who describe a diet of fish and squid. Despite the presence of an inferior mouth position (McLellan 1977) there was no evidence of benthic feeding in this species. Shovel-nosed dogfish would appear to feed above the bottom, in the water column, on small vertically migrating fish.

Baxter's dogfish fed on squid and fish, with most food items being fragmentary, which could be interpreted as evidence for scavenging. Clark et al. (1989) have previously reported the diet of this species in New Zealand waters from southwestern Chatham Rise and found a similar diet of fish, cephalopods and prawns. Despite the presence of an inferior mouth position (McLellan 1977), there was no evidence of direct benthic feeding in this species. Bulman et al. (2002) described the diet of this species from an area of seamounts off the south east coast of Tasmania and found that 88.4 percent of the diet by weight was fish, and 9.2 percent was squid. However later work by Pethybridge et al. (2011) found an increase in the proportion of squid, and suggest that this might infer a trophic cascade; the depletion of higher level trophic predators relieving predation pressure on squid. However they were unsure of this, as squid recruitment can be very uncertain. Congener (*E. spinax*) from the north Atlantic is believed to scavenge (King et al. 2006), and it is possible that this species also scavenges. It is also known to be an active net-feeder (feeding on fish caught within the net as the net is being fished along the bottom) (M. Clark pers. com.).

Generally speaking, the dogfishes from Puysegur Bank had similar diets to those from the flat areas of northeastern Chatham Rise. Puysegur Bank long-nosed velvet dogfish had fed on fish and squid, with fish more important, but the sample was small. Likewise, the small sample of Owston's dogfish (a species not retained in the northeastern Chatham Rise trawl samples) had feed exclusively on squid spermatophores. Pethybridge et al. (2011) speculate that the increases they found in squid consumption could be due to a reduction in fish predators through fishing, and a consequent trophic cascade resulting in an increase in squid, but there is a lack of the necessary historical dietary data for deep-sea sharks in New Zealand waters for this claim to be investigated. Baxter's dogfish from Puysegur Bank fed on a combination of fish, squid and prawns (in that order of importance). Some of the stomach contents of Baxter's dogfish could indicate scavenging or net feeding, as parts of orange roughy (including pectoral fins) were found in three stomachs. Whether these were taken

through predation, net-feeding, or as scavenging on fisheries discards is impossible to tell. Likewise, the whole four-rayed rattail that were consumed could be from any of these sources.

Only one of the three catsharks (*Apristurus* spp.) from Puysegur Bank had identifiable stomach contents, and these consisted of digested fish remains; possibly a myctophid lantern fish. Deep-sea catsharks are not well known in New Zealand waters and there are several undescribed deep-sea species (C. Duffy, pers. com.). One exception is the small, shallower-living Dawson's catshark (*Halaelurus dawsoni* Springer 1971). Francis (2006) examined the biology and diet of Dawson's catshark from various New Zealand localities and found that it was probably a benthopelagic or benthic feeder. Mauchline and Gordon (1983a) reported the diet of *Apristurus* spp. from the Rockall Trough and found a combination of prawns, fish and squid. One of these, species had fed on orange roughy, although Mauchline and Gordon do not state the size of the orange roughy consumed, and their data are confounded by the fact that they combined at least two catshark species.

The brain morphology of several New Zealand deep-sea chondrichthyans has been related indirectly to feeding activity. Yopak & Montgomery (2008) examined the brain morphology of 22 deep-sea chondrichthyans including Baxter's, long-nosed velvet, and shovel-nosed dogfish. They found there were differences in brain morphology between species that did not follow taxonomic lines, and while theirs was not a functional analysis, they did draw some tentative conclusions regarding a possible link between morphology and functionality. The brains of Baxter's and long-nosed velvet dogfishes were more similar than those of shovel-nosed dogfish. They also found that the brains of dogfish were morphologically distinct from those of holocephalans. They postulated that the degree of foliation (folding) in the brains of some deep-sea species was linked to activity levels; the low levels of foliation seen in Baxter's and long-nosed velvet dogfish being indicative of low activity levels in these species, and the higher level of foliation seen in shovel-nosed dogfish being indicative of a higher level of activity. This lower level of activity could be interpreted as scavenging behaviour in Baxter's and long-nosed velvet, and foraging behaviour in shovel-nosed dogfish. In this study there was no conclusive evidence for scavenging in these species. However, the diet of shovel-nosed dogfish was markedly different to that of the other sharks examined, being a diet of almost exclusively small mesopelagic fish (Myctophidae, Photichyidae, and Paralepididae). The presence of these small vertically

migrating fish could be indicative of a more active foraging strategy employed by shovel-nosed dogfish.

Pethbridge et al. (2011) suggest that Baxter's dogfish (on the basis of fatty acid profiles) could be a predator of whales, much in the same way as cookie cutter sharks (*Isistius* spp.), which can swim up to and take bites out a whale's side. However, given the low activity level predicted by Baxter's dogfish's brain morphology (Yopak & Montgomery 2008, Yopak 2012) and the likelihood that this species scavenges (M.R. Clark pers. com.), it seems more likely that Baxter's dogfish may have been feeding on whale falls, rather than actively parasitising live animals. The Portuguese dogfish *Centrocygnus coelolepis*, Bocage & Capello, 1864, is another deep-sea dogfish species that has been reported to have whale blubber in stomach contents (Clarke & Merrett 1972, Mauchline and Gordon 1983a, Ebert et al. 1992, Bulman et al. 2002). Mauchline and Gordon (1983a) suggest this is probably a result of feeding on whale falls, rather than predation, although Ebert et al. (1992) suggest it could be either. The single Portuguese dogfish examined in this study (from northeastern Chatham Rise) had an empty stomach.

Other chondrichthyan species from northeastern Chatham Rise with small sample sizes include the holocephalans, brown chimaera (*Chimaera* sp. C), and wide-nosed chimaera (*Rhinochimaera pacifica*), plus the long-nosed deep-sea skate (*Bathyraja shuntovi*). Brown chimaera had fed primarily on squid spermatophores and pteropod fragments, indicating that benthic feeding and possibly scavenging is important to this species. Pteropod fragments can give the illusion of pelagic feeding but they are in fact quite common dead, on the seabed (dead pteropod shells were a frequent occurrence in epibenthic sled and beam trawl hauls at upper and mid-slope depths on Challenger Plateau in May-June 2007, pers. obs.). The rest of the dietary material was characteristically benthic, but differed from the shallower species described by Dunn et al. (2010b) in that there were no crabs recorded, although this may be due to the small sample size herein. The single *Chimaera* sp. B from Puysegur Bank had also eaten benthic food items typical of holocephalans elsewhere (Mauchline & Gordon 1983a, Dunn et al. 2010b). A recent study by Dunn et al. (2010b) examined the diets of three chimaeroids in shallower waters from various localities on Chatham Rise. They found niche partitioning between the three species they examined, and concluded that the main driver was physical (depth), not biological (food).

Wide-nosed chimaera had unidentified fish remains in the only available stomach. Pethybridge et al. (2011) described the diet of *R. pacifica* from off southern Australia, based on fatty acid profiles, and suggested that the diet of this species is probably benthic (based on the presence of polychaete markers in liver tissues). A closely related congener, *R. atlantica*, has been reported to also have a benthic diet (Macpherson & Roel 1987).

Long-nosed deep-sea skate had fed on polychelids, natant decapods, and serolid isopods, probably indicating a benthic diet similar to other species of deep-sea skate elsewhere (Orlov 1998, Brickle et al. 2003, Ebert & Bizzarro 2007, Forman & Dunn 2012). Yopak and Montgomery (2008) examined the brain morphology of several holocephalans from New Zealand waters. They found that the brains of holocephalans were markedly different to those of the dogfishes, possibly being indicative of their benthic foraging habits.

The roles of the dogfishes examined in this study are unclear; are they predators or scavengers or a combination of both? It is probable that they are both predators (shovel-nosed dogfish), and facultative scavengers (long-nosed velvet, Baxter's and Owston's dogfishes) to varying degrees. The main issue would be: have they always been scavengers or has is this trait been augmented through fisheries interaction? There is a difference between scavenging, and scavenging on fisheries discards, and it is very hard to tell the difference (Clark et al. 1989, Dunn et al. 2010c, Horn et al. 2010a, Forman & Dunn 2012). There was evidence of scavenging on fisheries discards in the Baxter's dogfish from Puysegur Bank (orange roughy pectoral fins), although this evidence was not conclusive, and could have been net feeding. All three Owston's dogfish from Puysegur Bank had fed on spent squid spermatophores, which could also be interpreted as scavenging. All the dogfishes had an inferior mouth position, and this would facilitate obtaining carrion from the seabed.

Scavenging in the mid-slope dogfish species from northeastern Chatham Rise and Puysegur Bank inferred by dietary information is further supported by brain morphology, which suggests that these species may be passive feeders rather than active foragers (Yopak & Montgomery 2008, Yopak 2012). There is circumstantial evidence from a congener of Baxter's dogfish: *E. spinax* from the North Atlantic, which is a known scavenger (King et al. 2006), as it has brain morphology very similar to that of Baxter's dogfish (Yopak 2012). Shovel-nosed dogfish appears to be an exception to this dietary trend, as it fed almost exclusively on small pelagic fish, indicating a degree of

niche partitioning amongst the three main dogfish species examined on northeastern Chatham Rise. The chimaeras and skates were benthic feeders and also had inferior mouth positions. The chimaeras may also be facultative scavengers, as two out of the three brown chimaera had eaten squid spermatophores, although the sample was small.

5.1.2. Eels

Basketwork eel is the most abundant eel species at mid-slope depths in New Zealand waters, and is a common bycatch species in orange roughy bottom trawls (Anderson et al. 1998, Clark et al. 2000, Francis et al. 2002, Doonan et al. 2009). On northeastern Chatham Rise, basketwork eel had fed on a combination of fish, squid and, to a lesser extent natant, decapod and mysid prawns, with squid becoming slightly more important in the diets of larger eels, however there were high degrees of dietary overlap between all size classes examined. Larger eels also fed on larger species of fish, such as slickheads and Johnson's cod.

Clark et al. (1989) reported the diet of basketwork eel from southwestern Chatham Rise as comprising relatively equal combinations of fish and squid, while off Tasmania the diet of this species has been reported as comprising almost exclusively fish (Bulman et al. 2002). The diet of basketwork eel from northeastern Chatham Rise was consistent with earlier reports for the diet of this species off South Africa and Mozambique Seamount (Indian Ocean) (Anderson 2005a, Parin et al. 2008), but contrasted with earlier reports from New Zealand and Tasmania (Clark et al. 1989, Bulman et al. 2002).

Often only segments of fish were present in basketwork eel stomachs, either heads or tails; but whole animals were rare. Of the two basketwork eels that were examined from Puysegur Bank, one contained a severed orange roughy head (an obvious fisheries discard), and the other, unidentifiable fish remains. Clark et al. (1989) and Anderson (2005a) also note fragmentary food items; both came up with different but equally plausible explanations to account for this. Clark et al. (1989) found sections of hoki, sourcing them to factory trawlers operating in the immediate vicinity, and suggested that this was evidence of scavenging on fisheries discards. Anderson (2005a) suggested that the eels were biting through their prey fish and that the other section of the fish was being lost to the eel.

As with the dogfishes, it is very hard to distinguish between predation and scavenging in basketwork eel, unless it is an obviously processed discard (a severed head or a filleted frame). Recent New Zealand video footage has shown that basketwork

eels are attracted to baited cameras, which could be interpreted as possible evidence of being at least attracted to carrion (Tales from Te Papa 2011). Regardless of how the basketwork eels obtain their food, it is a predominantly benthopelagic piscivore that also feeds on squid and to a lesser extent prawns, and is likely to be a facultative scavenger.

The cutthroat eel *Synaphobranchus kaupi* is a common mid-slope eel species in the north Atlantic (Gordon & Mauchline 1996). It is closely related to basketwork eel (Sulak & Shcherbachev 1997), and is a known scavenger; frequently being seen at baited cameras (Uiblein et al. 2002, Collins et al. 2005, King et al. 2006). Wagner (2002) examined the brain morphology of *S. kaupi* and another closely related species (*Histiobranchus batyhubus*) and found that they had enlarged olfactory bulbs. He concluded that these two species were probably demersal specialists. The relatively large brain of *S. kaupi* could be related to its relatively high metabolism and swimming speeds, which in turn could be related to an active foraging lifestyle (Uiblein et al. 2002, Bailey et al. 2005).

Of the two other eel species from northeastern Chatham Rise with small samples: spineback eel (*Notocanthus sexispinus*) had intestinal material but it was too digested to be certain of its origin; hairy conger eel (*Bassanago hirsutus*) had fed on crabs and isopods and was the only species to feed on crabs in either the northeastern Chatham Rise or Puysegur Bank samples. However, the *B. hirsutus* sample was small, and without precise locality data. If it were sympatric with basketwork eel, its diet would be an example of niche partitioning between the two eel species.

5.1.3. Slickheads

The slickheads (Alepocephalidae) are commonly found at or below 1000 metres depth in New Zealand waters, and elsewhere (Anderson et al. 1998, Francis et al. 2002, Wagner 2002, Mauchline & Gordon 1984b). Like many deep-sea species in New Zealand waters slickheads are known from their appearance in research trawls and little else (Anderson et al. 1998, Francis et al. 2002, Doonan et al. 2009). There are two common species in the genus *Alepocephalus* found in austral waters at mid-slope depths: big-scaled and small-scaled brown slickhead. Unfortunately, these two species are easily confused and their identification can be uncertain. For example, Bulman et al. (2002) reported the diet of *Alepocephalus* sp. 1 and sp. 2 (probably these two species), but were unable to positively identify their species. Also, Pakhomov et al. (2006)

described the diet of “*A. antipodiana* Parrott, 1948” from the vicinity of the Prince Edward Archipelago in the sub-Antarctic.

The biology of New Zealand slickheads is currently limited to the account of Clark et al. (1989), who described the stomach contents of 26 *A. australis* from southwestern Chatham Rise. Clark et al. (1989) found a diet of mainly pelagic invertebrates, particularly salps (*S. thompsoni* and *I. zonaria*), and hyperiid amphipods (*V. stebbingi*, *Cylopus magellanicus*, and *Parathemisto gaudichaudii*). On northeastern Chatham Rise, big-scaled brown slickhead (*A. australis*) is more abundant than small-scaled brown slickhead (*A. antipodanus*) (Doonan et al. 2009). Elsewhere, Parin et al. (2008 p362) described the diet of “*A. australis*” from Mozambique Seamount, and characterised it as “shrimp, squids, fish, salps, holothurians.” However, it is unclear which species of slickhead Parin et al. (2008) examined. Whichever species Bulman et al. (2002), Pakhomov et al. (2006) and Parin et al. (2008) examined, their slickheads had been feeding in the water column, but close to the seabed. As with big-scaled brown slickhead, small-scaled brown slickhead possesses a terminal mouth (**Fig. 27**) and had a mainly pelagic diet. In the north Atlantic two closely related species, *A. bairdi* Goode & Bean, 1879, and *A. rostratus* Risso, 1820, also have been reported to have benthopelagic diets, but rely less on thaliaceans (Mauchline & Gordon 1983b). However, *Alepocephalus rostratus* taken from off Namibia and the Mediterranean had a greater reliance on thaliaceans (Macpherson 1983, Carrassón & Cartes 2002). Carrassón & Matallanas (1998) also found a temporal change in the diet of *A. rostrata*.

Many species of hyperiid amphipod have associations with salps (Harbison et al. 1977), most notably *Phoronima sedintaria*, which dwells in dead, hollowed out salp tests (Nishikawa et al. 2005). Rumour has it that *P. sedintaria* was the inspiration for the alien in the “Alien” movie series. Madin & Harbison (1977) describe hyperiid amphipods from the genus *Vibilia* as obligate salp dwellers, which feed on the particulate food gathered by the salp. Hyperiiids are also higher in energy than salps and pyrosomes (Clark et al. 1989, Bulman et al. 2002), which leads to the question: are the slickheads eating the salps and pyrosomes for the higher energy hyperiid amphipods inside?

Big- and small-scaled brown slickheads had very high PES values, which suggests they might not feed frequently. There was identifiable material in 80 of the intestines of big-scaled and 18 for small-scaled brown slickhead, which suggests that there could be a periodicity to their feeding. However, the number of trawls sampled was insufficient

for effective analysis to be made to compare the timing of stomach and intestinal contents. There was circumstantial evidence for some possible periodicity in the feeding of the two *Alepocephalus* species. Both species had fed on the pyrosome *P. atlanticum*, which is known to make large diurnal vertical migrations (Anderson 1992, Anderson & Sardou 1994), meaning that to have consumed them live, they must have been feeding during daylight hours. This, however, does not preclude feeding at other times of the day on other organisms. Dead thaliaceans can be found in large amounts on the deep-sea bed (pers. obs., Lebrato & Jones 2009; Lebrato et al. 2012), so it is possible that the slickheads could have been picking the thaliaceans dead from the sea floor, as there were occasional benthic items their diets (e.g., the gastropods *Anatoma* sp., and *N. ephamillus*).

Pyrosoma atlanticum has been reported to have an association with hyperiid amphipods (Harbison et al. 1977), however, no hyperiids were found in slickhead stomachs or intestines that also contained pyrosomes. Whether this is because the pyrosomes were dead and the hyperiids had vacated the dead pyrosome test, or that the pyrosomes were consumed living but do not always have commensal hyperiids, is not clear. Perhaps the pyrosomes do not host hyperiid amphipods at this time of year, or at this stage of their lifecycle? Maybe it is more the case that all hyperiids need to live inside pyrosomes, but not all pyrosomes need to contain hyperiids, since the hyperiids are thought to steal food from the pyrosome they live within (Harbison et al. 1977).

As with the dogfishes and eels, the brain morphology of slickheads has been investigated with a view to shedding light on their ecology (Wagner 2002). Wagner (2002) examined the brain morphology of two related alepocephalids (*Alepocephalus productus* and *X. copei*) and found they had large optic nerve and optic tectum, and suggested that these species were primarily optically focused foragers. The olfactory bulbs of *A. productus* and *X. copei* were not greatly developed, which could suggest that scavenging is not important to these two species. Given the depths these two species are found, the large optic nerve and tectum suggest that bioluminescent animals might be important prey. Pyrosomes are known to be bioluminescent (Herring 1987), and these were food for both big- and small-scaled slickheads from northeastern Chatham Rise.

In the north Atlantic, Gordon et al. (2002) found that *A. bairdi* and *X. copei* were caught significantly more frequently by bottom trawls fished with attached lights than those trawled in darkness. This could suggest that the slickhead species were attracted to

light given off by the trawl gear encountering bioluminescent animals as it progressed. However, this was only the case for *A. bairdi* <30 cm TL, so the nature of this attraction is unclear.

Thaliaceans found in the intestines of the slickheads were not well digested, which was unexpected given their gelatinous nature (Arai et al. 2003), and the high degree of digestion in the intestinal contents of other species, particularly the rattails and morid cods. This lack of digestion may indicate recent feeding, or be a reflection of a slow metabolic rate, as reported for other deep-sea fish (Smith & Hessler 1974, Smith 1978, Bailey et al. 2002, Drazen 2002, Drazen & Haedrich 2012). As far as I am aware, no attempts have been made to estimate the metabolic rates of slickheads. They can be fragile fish with watery flesh (Childress & Nygaard 1973), and lose almost all of their scales very easily when retained in trawl nets, so they are probably difficult to work on while alive.

Overall, the two brown slickheads from northeastern Chatham Rise fed mainly on bioluminescent pyrosomes and small crustaceans from the water column, with the occasional benthic item. There seems little obvious evidence for niche partitioning between the two brown slickhead species, although this may be due to the small sample of small-scaled brown slickhead. Both species possessed a terminal mouth position, which would facilitate feeding from the water column. Unlike the other slickhead species, black slickhead did not feed to the same extent on thaliaceans. Black slickhead had fed mainly on benthopelagic prawns, calanoid copepods, fish, and gammaridean amphipods, and there was no clear ontogenic change in this species diet. The biology and diet of black slickhead has not been previously reported for New Zealand waters, although in the north Atlantic Fock et al. (2004) described its distribution in the water column. Earlier, Mauchline & Gordon (1983b) described some aspects of its biology and diet, reporting an ontogenic shift in its diet and relating this to a vertical migration from the upper 200 metres down to mid-slope depths when the fish were approximately 136 mm SL. All northeastern Chatham Rise black slickhead were >238 mm SL, possibly explaining the lack of any clear ontogenic dietary shift as most already were large (**Fig. 39**). All the black slickheads came from the same (901 m) trawl, and all but two were female, which could suggest either gender partitioning in schools or a skewed sex ratio.

Black slickhead were benthopelagic/pelagic feeders, and possessed a terminal mouth position. One of the few benthic food items was the protoconch of a *Fusitriton*

magellanicus laudandus, Finlay, 1926, but this was so small it may well have still been in its planktonic stage. Wagner (2002) examined the brain morphology of black slickhead and found that they have an enlarged optic nerve and tectum, suggesting that this species (as with the other slickhead species he examined) is an optically focused forager. Black slickhead (unlike the previous two species) is a bioluminescent species (Badcock & Larcombe 1980), although how this relates to its diet is unknown. The olfactory bulbs in the brain of black slickhead were not greatly developed, so this could suggest that scavenging is not important to this species. The flesh of black slickhead was more robust and less watery (pers. obs.) than that of the two previous slickhead species, which could reflect a more active lifestyle, and their diet may reflect this as they fed on more active pelagic animals, and very much less on thaliaceans.

There was no significant difference between the stomach and intestinal contents of black slickhead when comparing all stomachs and intestines containing food items. However, there was a significant difference between stomach and intestinal contents when the stomach and intestinal contents of the same fish were analysed.

Over the whole sample of black slickhead, there was an increase in the intestines of natant decapod prawns, calanoid copepods, and unidentifiable crustacean material, no change in the incidence of amphipods, and a decline in fish, ostracods and thaliacean remains. Fish that had material in both their stomach and intestines showed a general decrease in the abundance of larger-bodied animals in their intestines (natant decapod prawns and fish), although ostracods also declined. These declines were compensated for by increases in the abundance of amphipods, calanoid copepods and unidentifiable crustacean material. Black slickhead have a terminal mouth position and this would facilitate feeding on pelagic food (**Fig. 38**).

5.1.4. Morid cods

The two species of morid cod each had high rates of stomach eversion, particularly Johnson's cod, all samples of which had everted stomachs. There was a small amount of highly digested material recovered from the intestines of Johnson's cod from both northeastern Chatham Rise and Puysegur Bank. It was not possible to identify this material with much precision, and as a consequence the description of the diet of this species is really quite vague. The intestinal material of Johnson's cod consisted of mostly benthopelagic items: fish, natant decapod prawns, calanoid copepods, and ostracods. However, it is impossible to tell if this material was taken

from live animals, or dead from the seabed, or if these were the stomach/gut contents of prey animals. Sediment was not identified from the intestinal contents, so it is possible that the intestinal material was sourced from the water column, but again this is not conclusive. The diet of this species has not been previously reported for New Zealand waters, and there is little data regarding it, despite its large distribution (probably due to the high rates of stomach eversion). Globally, there is little information regarding the diet of Johnson's cod. Mauchline and Gordon (1984b) described a benthopelagic diet of calanoid copepods and the natant decapod prawn *Segestes arcticus* for Johnson's cod from the north Atlantic.

Johnson's cod was the seventh most abundant fish species caught as bycatch on northeastern Chatham Rise (Doonan et al. 2009), and as such, probably plays an important role in the structuring of the demersal community, however the high rate of stomach eversion, coupled with the high level of digestion seen in the intestinal contents, combined to obfuscate this role. Johnson's cod possess a terminal mouth position (**Fig. 47**), and from the limited data available would appear to be a benthopelagic feeder on fish, prawns and other small crustaceans.

Small-headed cod (*Lepidion microcephalus*) had fed on a variety of benthopelagic items such as fish and natant decapod prawns, but food remains usually were fragmentary. They had also eaten characteristically benthic items, such as hermit crabs (Parapaguridae) and gastropods (*N. ephamillus*), which suggests that small-headed cod could be picking the fish remains and prawns dead from the seabed (similar to serrulate rattail). There was sediment in most of the intestines, which suggests that much of the dietary material may have been picked from the seabed. The diet of small-headed cod has also previously not been reported from New Zealand waters. Small-headed cod possess a sub-terminal mouth and fed on a variety of benthic and benthopelagic food items, and may scavenge on larger food items.

The sample of small-headed cod from Puysegur Bank had one fish with a stomach containing fish and prawn remains and a fragmentary squid beak, which suggests a benthopelagic diet and/or scavenging. In the north Atlantic, a congener, *L. eques*, has been reported to have an epibenthic component to its diet and little dietary overlap with Johnson's cod (Mauchline & Gordon 1984b). In the western Mediterranean Sea, *L. lepidion* was found to also have a mix of pelagic and benthic organisms in its diet (Carrassón et al. 1997). Small-headed cod is not found in the north Atlantic or the

Mediterranean Sea and could be filling a similar niche to *L. lepidion* and/or *L. eques*, but in austral waters.

Violet cod (*Antimora rostrata*) was the other demersal morid cod species examined; all stomachs were everted and the intestinal contents mostly unidentifiable. This species was at the shallowest end of its depth distribution and is usually found in much deeper water (Anderson et al. 1998). Ribaldo (*Mora moro* (Risso, 1810)) is a closely related species and one not retained in the samples examined in this study, although it was taken as orange roughy bycatch during these surveys (Doonan et al. 2006). Carrassón et al. (1997) found this species was also primarily a benthic feeder (although this species also had very high rates of stomach eversion; approx. 97% examined). A cursory examination of the intestines of three ribaldo caught on Challenger Plateau during the TAN0707 Oceans 20/20 voyage (June 2007) revealed fish and crustacean remains, but little conclusive material. The intestinal contents were highly digested, similar to those of Johnson's cod.

5.1.5. Rattails

Rattails (Macrouridae) are found throughout the New Zealand EEZ, and are one of the most common and specious groups of deep-sea fishes in New Zealand waters (McMillan & Paulin 1993). They are also common bycatch species in deep-water demersal trawls for orange roughy on northeastern Chatham Rise (Doonan et al. 2006, 2009), and there has been speculation they might have commercial potential as fishmeal (Stevens & Dunn 2011). Their distribution appears to be mainly influenced by depth, with a faunal transition in New Zealand waters between a characteristically upper-slope assemblage and a deeper mid-slope assemblage starting at around a depth of 700–800 metres (Francis et al. 2002).

Generally speaking, there are more species of rattail in deeper waters (Francis et al. 2002, Leathwick et al. 2006, Stevens & Dunn 2011), and after orange roughy, three rattail species are the most abundant fish species at mid-slope depths on northeastern Chatham Rise (Doonan et al. 2009). Due to their abundance they probably have an important role in the structuring of demersal and benthic communities in the deep seas around New Zealand. Like the morid cods, they have high rates of stomach eversion: up to 100 percent. As a result, they are often omitted from traditional dietary studies based on stomach contents, and for many species little is known of their biology (e.g., Clark 1985a, Clark et al. 1989, Stevens and Dunn 2011).

The feeding of the mid-slope rattails can be divided into two three broad groups. Firstly there are those fish species that feed directly from the seabed. Secondly there are species that feed from the water column, and thirdly there are species that do both. A fourth group could also be added, making up those species for which their intestinal contents were too digested to form any firm conclusions regarding their dietary preferences, or for which the sample was too small. Rattails in the genera *Coelorinchus*, *Nezumia* and *Trachyrincus* have an inferior mouth position, while those in *Coryphaenoides*, *Gadomus*, *Lepidorhynchus*, and *Macrourus* have sub-terminal mouths.

Notable rattail (*C. innotabilis*) is the second most abundant mid-slope species on northeastern Chatham Rise caught as orange roughy bycatch (Doonan et al. 2009), but also one with one of the highest rates of stomach eversion. All the dietary material for this species came from intestinal contents. Notable rattail fed on small benthic and often infaunal animals, particularly bivalves and gastropods. There was also evidence for feeding on polychaetes, but this was in the form of setae, so it is difficult to know if these were whole animals or if the heads of the worms were being cropped (seen in the feeding of shallower water rattails on Chatham Rise (Stevens & Dunn 2011)). Most of the intestines contained sediment, which suggests that the seabed was the source of their food.

The diet of notable rattail has been previously reported by McLellan (1977), and by Bulman et al. (2002), both based on samples of three stomachs (probably a reflection of this species' high rate of stomach eversion). McLellan (1977) found benthic items including gastropods, but Bulman et al. (2002) found "pelagic crustaceans", which is curious given the diet reported here. The fish that Bulman et al. (2002) examined were from seamounts, and this could indicate some plasticity in the diet of this species, related to habitat. One notable rattail was found in the stomach of a long-nosed velvet dogfish, which implies a trophic link. However, it is impossible to rule out scavenging here, as long-nosed velvet dogfish may be a facultative scavenger and notable rattail is a bycatch species usually discarded from orange roughy trawls.

Most notable rattail intestines examined contained food items, however, without stomach contents it is impossible to tell how often this species feeds. Notable rattail is a smaller rattail species (usually <35 cm TL), and while this probably precludes it from scavenging on large food falls, it could scavenge small items. The single non-everted stomach was empty of food items, but did contain eight digenean and two nematode parasites, which could be taken as further evidence of a benthic diet, as benthic feeding

fish are considered to have high gut parasite loadings (Houston & Haedrich 1986, Klimpel et al. 2010). The abundance of notable rattail, coupled with its almost exclusively benthic diet, suggests that this species could form an important link in the benthic food web.

Other rattails with smaller sample sizes include squashed face rattail (*Nezumia namatahi*), which had a diet of small invertebrates, mainly amphipods, isopods, ostracods, and foraminifera. No gastropods or bivalves were present in gut contents. This is similar to the diet of congener *N. aequalis* from the north Atlantic (Mauchline & Gordon 1984b). There was material in several of the squashed face rattail intestines and this was similar to the stomach contents. A similar-sized and closely related species, Kaiyomaru rattail (*C. kaiyomaru*), was obtained from Puysegur Bank and it also had a predominantly benthic diet of small crustaceans and carnivorous gastropods (Naticidae, Marginellidae). Bulman et al. (2002) reported the diet of 50 Kaiyomaru rattail from seamounts off southeastern Tasmania and found a similar diet comprised of benthic invertebrates.

The small sample of humpbacked rattail (*Coryphaenoides dossenus*) suggests that this species was a benthopelagic forager, having fed on natant decapod prawns (Nematocarcinidae), and a hermit crab. The single *Gadomus aoteanus* examined had eaten gammaridean amphipods. Also, the single *Coelorinchus fasciatus* had many bivalves and gastropods in its intestine. Javelin fish (*L. denticulatus*) from both northeastern Chatham Rise and Puysegur Bank had fed on benthopelagic food; natant decapod prawns and chaetognaths, similar to reports describing the diet of this species from other New Zealand localities and depths (Clark 1985, Clark et al. 1989, Jones 2009, Stevens & Dunn 2011). Javelin fish were caught at the lower limit of their depth distribution and are much more common in shallower upper-slope waters (Clark 1985a, Stevens & Dunn 2011), which may explain the small sample.

Surgeon rattail (*C. acanthiger*) and rough-headed rattail (*C. trachycarus*) are two very morphologically similar species (Iwamoto et al. 1999). Both species reach a larger adult size than notable rattail (Iwamoto et al. 1999), and had very high rates of stomach eversion, with two stomachs containing food in surgeon rattail and none in rough-headed rattail. Surgeon rattail had fed mainly on myodocopid ostracods (occurring in all intestines examined), gammaridean amphipods, and polychaete remains, although this may be a bias owing to their chitinous hard-parts being preserved in intestinal contents. No gastropods, bivalves or hermit crabs were present in the stomach or intestines

examined. Also, one of the non-everted stomachs came from the largest fish recorded (127 mm PAL), and it contained a whole myctophid. This could be seen as evidence of an ontogenic shift in diet for this species from benthic to benthopelagic feeding, but more samples would be necessary to conform this. Elsewhere, Parin et al. (2008) reported the diet of surgeon rattail (*C. acanthiger*) from Mozambique Seamount as comprising squids, shrimp, molluscs, and fish. Parin et al. (2008) is translated from Russian and based on data collected during 1976–77). Their surgeon rattail could comprise more than one species, as several similar species have been subsequently described (McMillan & Paulin 1993, Iwamoto et al. 1999).

The intestinal contents of rough-headed rattail were typically benthic items. Most abundant were the remains of polychaetes, gastropods, bivalves, hermit crabs, and amphipod fragments. The gastropods and bivalves were larger species than those found in notable rattail (e.g., the gastropod *Falsilunatia* sp., and bivalve *Parvamussium maorium*), possibly indicating both an ability to consume larger benthic prey by being a larger, but also niche partitioning. This ability to consume larger but essentially taxonomically (at higher levels at least) identical food could easily mask potential niche partitioning between notable rattail and its larger congener. There is also potential niche partitioning between rough-headed rattail and surgeon rattail, as surgeon rattail had not fed on gastropods, bivalves, or hermit crabs. Also, the intestines of surgeon rattail were noticeably more fragile than those of rough-headed rattail, which could possibly be linked to their consumption of less hard-shelled food, such as gastropods or bivalves. However, as with notable rattail, more samples are required to ascertain the true nature of any niche partitioning between these three common mid-slope rattail species. Niche partitioning has been described for congeners Oliver's rattail (*C. oliverianus*), Bollons' rattail (*C. bollonsi*), and smooth-headed rattail (*C. aspercephalus*) from shallower upper-slope depths on Chatham Rise (Stevens & Dunn 2011). So it is possible that the dietary differences between the three common mid-slope *Coelorinchus* species, surgeon, rough-headed, and notable rattail examined herein, may also facilitate niche separation at deeper mid-slope depths in a similar way to upper-slope rattails on Chatham Rise (Stevens & Dunn 2011).

Serrulate rattail (*Coryphaenoides serrulatus*) have a sub-terminal mouth position (McLellan 1977). Small individuals have a predominantly benthic diet of small invertebrates and crustaceans, particularly gammaridean amphipods. There was evidence for an ontogenic shift in diet, as small-bodied crustaceans (amphipods,

isopods, ostracods, and calanoid copepods) were less important in the diets of larger fish, and this change in diet was compensated for by an increase in larger-bodied organisms, particularly natant decapod prawns, fish, and squid. This dietary shift was coupled with an increase in the weight of consumed food items, an increase in the number of stomach parasites (**Fig. 175**), and a low level of dietary overlap between most size classes examined. This ontogenic shift in diet reflects this species' ability to consume larger food items as its own size increases, and also a probable shift from benthic foraging on small invertebrates to scavenging.

Scavenging has long been considered an important feeding strategy in rattails, especially in deeper waters (Collins et al. 1999, 2005; Drazen et al. 2001, 2009), and has been linked to a change in brain morphology in *C. armatus* (Wagner 2003). Wagner (2003) found an ontogenic change in the morphology of the brain of *C. armatus* and linked this to an ontogenic shift in diet. He found that the optic tectum decreased in size while the olfactory bulb increased in size, and related this to a behavioural change from visual to olfactory-based foraging. Wagner (2003) suggested that this behavioural change was reflected in a shift to scavenging in larger individuals, and found further supporting evidence for this in stomach contents. The presence of opercula from gastropods, squid spermatophores, gladii and beaks (often from squid larger than the fish consuming them, based upon lower beak rostral length measures (S. O'Shea pers. comm.)), and the rachis and eye lenses of fish, suggests that like small-headed cod, serrulate rattail may scavenge from the seabed. This is further supported by the frequent occurrence of sediment in the alimentary canal. Since squid beaks were only present when associated with a small amount of flesh, it is possible that these were ingested during scavenging activity.

There were differences between the composition of material obtained from the intestines of serrulate rattail and this was mainly due to an increase in the amount of hard-parts (chaetognath jaw hooks, polychaete jaws, and unidentifiable crustacean remains). There was a corresponding decrease in generally larger-bodied identifiable food items (amphipods, natant decapod prawns, fish, and squid). There was also a decrease in some smaller forms (calanoid copepods, ostracods and isopods). Fish with both stomach and intestinal contents also followed this pattern, with increases in abundance of unidentified crustacean remains and polychaete jaws at the expense of larger-bodied or identifiable food items. This increase in intestinal material may have

been due to the preferential retention of hard-to digest material, or a reflection of multiple feeding episodes being retained within the intestines.

Five serrulate rattail stomachs examined from seamount habitat on Puysegur Bank contained similar material to those of northeastern Chatham Rise: gammaridean amphipods, isopods, and the fragmentary remains of fish and squid. The diet differed from northeastern Chatham Rise in the consumption of the galatheid *Munida isos*, Ahyong & Poore, 2004, a species common to seamount habitat on Chatham Rise (Clark & Rowden 2009). The diet of serrulate rattail has not been previously reported for New Zealand waters, although off Tasmania it has been described by Bulman et al. (2002) as a “benthopelagic omnivore,” feeding on Penaeidae, Reptantia, Polychelidae, squid, holothurians, salps and fish.

Galatheids were conspicuous by their absence in the guts of fish from northeastern Chatham Rise, which may reflect a preference for seamount habitats at these depths (Probert et al. 1997, Clark & Rowden 2009). It could also demonstrate a faunal discontinuity between upper- and mid-slope soft sediment assemblages on Chatham Rise, as one of the most common upper slope benthic food items recorded in the diets of benthic feeding rattails by Stevens and Dunn (2011) was the galatheid *M. gracilis*. Although the sample is small, it does indicate a degree of spatial plasticity in the diet of serrulate rattail that could relate to habitat.

Four-rayed rattail from northeastern Chatham Rise fed mainly on calanoid copepods from the family Aetideidae (at least two *Bradydium* spp.). The aetideids are well-known as benthopelagic dwellers (Bradford-Greive 2003, 2004, Laakmann et al. 2009). These copepods are not adapted to undertake long periods of swimming, and are non-vertically migrating, often living just above the seabed in the benthic boundary layer (BBL) (Bradford 1969, Bradford-Greive 2003, 2004). Copepods from the families Aetideidae, Metridinidae and Euchaetidae are known to be bioluminescent (Herring 1987), so four-rayed rattail could be an optically based feeder. Further examination of brain morphology would likely shed some light on whether this was so (Wagner 2002, 2003).

Four-rayed rattail also preyed on gammaridean amphipods, and isopods, which also suggests a mode of feeding close to the seabed. Apart from the presence of polychaete jaws (these have yet to be further identified, so whether they were benthic or pelagic species is currently unknown), there was little evidence for feeding on either characteristically benthic species or for scavenging. These benthopelagic copepods were

supplemented by mesopelagic calanoid copepods (Metridinidae: *P. abdominalis* and *P. quadrangulata*); both latter species are mesopelagic vertical migrators (Haury 1988, Bradford-Grieve 1999, Hunt & Pakhomov 2003).

There was little evidence of any ontogenic shift in diet within the range of fish sizes examined; perhaps a small shift to fish prey in the largest specimens. As the weight of food items increased with fish size, but not their number, there may have been a shift within the composition of the copepods predated. It is also possible that the sample did not include fish of a size to exhibit a marked ontogenic shift in diet (possibly being too small to be retained or insufficient numbers of large specimens). Also, the number of parasites was fairly consistent over the four size classes and may infer that there was no change in the source of the diet (**Fig. 176**).

The diet of four-rayed rattail has been previously reported in New Zealand waters, based on the stomachs of 23 fish collected from southwest Chatham Rise during November 1984 (Clark et al. 1989); mysids (50% IRI), calanoid copepods (29%), and natant decapod prawns (15%) were reported as the most important food items. Both the northeastern Chatham Rise and Puysegur Bank stomach contents collected in July 2004 and 2006 respectively, differ from those described earlier with calanoid copepods (84.2 & 79.8% IRI respectively) the most important food items in the northeastern Chatham Rise and Puysegur Bank fish.

The dietary differences between southwestern and northeastern Chatham Rise four-rayed rattail could be influenced by spatial and seasonal changes in surface productivity, as the waters over the Chatham Rise are more productive during the spring than summer (Knox et al. 2012). Also, the western end of Chatham Rise is more productive than the east (Knox et al. 2012), and the southern flanks are more productive than the north (Probert et al. 1996, Uddstrom & Oien 1999, Murphy et al. 2001, Nodder & Northcote 2001, Knox et al. 2012), which also could account for differences in diet between southwest and northeastern Chatham Rise four-rayed rattail. Also, the four rayed rattail examined by Clark et al. (1989) were larger than those examined from northeastern Chatham Rise, which could also account for some of the dietary variance.

The diet of four-rayed rattail has also been described elsewhere: near the sub-Antarctic Macquarie Island it was reported to consist of amphipods, copepods, chaetognaths, and euphausiid prawns (Gaskett et al. 2001), and off Tasmania as being mostly crustaceans, although these were not identified (Bulman et al. 2002). Four-rayed rattails have been collected in trawls >100 metres off the sea bed (Williams & Koslow

1997, Gaskett et al. 2001) and it is possible that this species forages within the water column, similar to round-nosed grenadier (*C. rupestris*) in the north Atlantic (Mauchline & Gordon 1991), and javelin fish in shallower waters on Chatham Rise (Stevens & Dunn 2011). Stevens and Dunn (2011) suggested that javelin fish were following vertically migrating prey back up into the water column, so it possible that four-rayed rattail is doing the same when predating the metridinid copepod species. However, species of *Bradydium* have been reported to live within two metres of the seabed (Bradford-Grieve 2004), which suggests that this species on northeastern Chatham Rise is usually feeding in the water column close to the seabed, and perhaps making occasional pelagic foraging trips.

There was an increase in the abundance of polychaetes and chaetognaths in the intestines of four-rayed rattail, and a corresponding decrease in calanoid copepods, amphipods, unidentifiable crustaceans, and natant decapod prawns. The increase in polychaetes and chaetognaths in the intestines may be a result of these two taxa being mostly represented by hard chitinous jaws. Fish that had material in both their stomachs and intestines also showed an increase in polychaetes and chaetognaths in their intestines, with a corresponding decrease in amphipods and natant decapods prawns. The abundance of calanoid copepods and unidentifiable crustacean material did not change in both stomachs and intestines, although the sample was small (**Table 12**). Four-rayed rattail from Puysegur Bank displayed a similar pattern to conspecifics from northeastern Chatham Rise, with increases in the abundance in the intestines of chaetognaths and unidentifiable crustaceans, with a corresponding decrease in calanoid copepods and amphipods. This was mirrored in those fish with both stomach and intestinal contents.

There were differences between the diets of four-rayed rattail from northeastern Chatham Rise and Puysegur Bank. Four-rayed rattail species from a seamount habitat on Puysegur Bank consumed calanoid copepods of a larger mass but in lower numbers than fish from northeastern Chatham Rise. This suggests that the specific composition of the copepod species was different. The copepods that were identified were different species from those identified from Chatham Rise but they were too small a sample to be representative. As with this species from northeastern Chatham Rise there was no large-scale taxonomic ontogenic shift in diet, but there was an increase in the weight of food eaten, but not numbers, which could indicate an ontogenic shift in diet within the food categories described. Also, euphausiids were absent from Chatham Rise fish and

polychaetes, ostracods, and isopods were absent from the diet of the Puysegur Bank fish. Chaetognaths were more numerous in the diets of fish from Puysegur Bank than in fish from northeastern Chatham Rise. This could be a reflection of the differences between living over the flat soft-sediments of northeastern Chatham Rise and the rougher harder seamount substrates of Puysegur Bank. The differences in diet could also be a reflection of the differences in productivity between the two areas.

There was some evidence for an ontogenic shift in the diet of four-rayed rattail, with the weight of food items increasing (but not their numbers) with fish size, for both the northeastern Chatham Rise and Puysegur Bank fish. The composition of the diet also remained constant with increasing fish size, with a high level of dietary overlap between sizes classes. This may indicate that “calanoid copepods” was too broad a category to detect any possible ontogenic shift in the diet of this species. Four-rayed rattail have a sub-terminal mouth position (McLellan 1977), but unlike its congener *C. serrulatus* (which has a mainly benthic diet, and scavenges), its diet is benthopelagic and predatory in character.

Four-rayed rattail is one of the most abundant species at mid-slope depths on northeastern Chatham Rise (Doonan et al. 2009), and as such probably plays an important role in the structuring of the benthopelagic food web. Whether this is linked directly to the pelagic food web is dependent on the diets of the calanoid copepods on which it feeds. The benthopelagic non-migrating aetideid copepods are thought to be omnivorous or carnivorous (Bradford-Grieve 2004), and the composition of their fatty acids suggests they are not directly linked to the surface waters (Bühning & Christiansen 2001).

Bühning & Christiansen (2001) found that invertebrates that fed on phytodetritus were rich in wax-esters, but that animals that did not were rich in triglycerols. They postulated that animals that fed on the seasonal pulses of phytodetritus from spring algal blooms would contain wax-esters and that those that did not would contain more triglycerols. The triglycerols reflected a more constant steady state, while the wax-esters reflected seasonal pulses from the surface waters. They found that aetideid copepods and some polychaetes were rich in triglycerols. Four-rayed rattail from northeastern Chatham Rise fed largely on aetideid copepods, and to lesser extent polychaetes, which could suggest that at least part of four-rayed rattail's diet is linked more with the benthic detrital food web than the pelagic (Drazen et al. 2008).

Ridge-scaled rattail from northeastern Chatham Rise had a wide range of predominantly benthic food items in their intestines, with only the largest individuals having eaten fish. The diet of ridge-scaled rattail has been previously reported in New Zealand waters from the southwestern Chatham Rise by Clark et al. (1989): primarily on salps, amphipods and myctophid fish. The diet of ridge-scaled rattail off the Falkland Islands was described by Laptikhovsky (2005), as being similar to that of this species reported from southwestern Chatham Rise (Clark et al. 1989). Laptikhovsky (2005) also found that the breadth of the diet of ridge-scaled rattail changed during the year, with abundant items such as salps being consumed in summer (high numbers and low prey diversity), while in winter the breadth of the diet widened, with ridge-scaled rattail taking any available food (low numbers and high prey diversity). Ridge-scaled rattail from northeastern Chatham Rise possess a sub-terminal mouth position (McLellan 1977), and had been primarily benthic feeders on a wide range of benthic invertebrates, and could possibly be reflecting the austral winter diet characteristic of Laptikhovsky's findings (2005), with low numbers and high diversity.

Ridge-scaled rattail from Puysegur Bank had fed on a mix of benthopelagic and benthic food. The stomach contents were dominated by four-rayed rattail (three occurring in one fish and two in another). Benthic food was made up of cirrolanid isopods, the galatheid *M. isos*, and a eunicid polychaete worm. Galatheids, hermit crabs, and trochid gastropods were also recovered from the intestines. The Puysegur Bank sample was of quite large individuals, and these were the fish predated the four-rayed rattail. Despite the small sample from Puysegur Bank, the major difference between the diet of ridge-scaled rattail from northeastern Chatham Rise and Puysegur Bank was the presence of four-rayed rattail and galatheids in the diets of the Puysegur Bank fish. This is similar to serrulate rattail from Puysegur Bank and demonstrates a degree of dietary plasticity in this species that may be habitat dependent.

Both species of trachyrincine rattails exhibited total stomach eversion, and the intestines of available specimens contained a variety of benthopelagic and benthic food items, although most were highly digested and difficult to identify. An exception to this was the gastropod *Mesoginella* sp., however this may be a chance occurrence of accidental ingestion, as the gastropod in question was orders of magnitude smaller than the fish that consumed it. White rattail has an inferior mouth position (**Fig. 89**), and had benthic and benthopelagic components in its diet. The diet of white rattail has not been previously described for New Zealand waters, although a closely related species in the

north Atlantic and off Namibia, *T. trachyrincus* (Risso, 1810), has been reported to have a benthopelagic diet, with an occasional benthic component (Merrett & Marshall 1981, Macpherson 1983, Mauchline & Gordon 1984b). *Trachyrincus trachyrincus* was also a species with a high rate of stomach eversion, necessitating Merrett & Marshall (1981) also describing its diet based on intestinal contents. Recent underwater footage from baited cameras has shown white rattail attempting to feed on baits, inferring that this species is attracted to carrion (Tales from Te Papa 2011). Another closely related species from the north Atlantic (*T. murrayi*, Günther 1877) has also been observed after being attracted to baited cameras (Priede et al. 1994a). So it is possible that this species is also a facultative scavenger. The diet of unicorn rattail was also described from intestinal contents, and these were also highly digested. Identifiable remains included those from fish, amphipods and natant decapod prawns. Data were insufficient to draw meaningful conclusions regarding the dietary habits of this species, or to infer any niche partitioning between these congeners. However, it is known that the two species are separated by depth, with white rattail occurring in shallower waters than unicorn rattail (McMillan 1995, Anderson et al. 1998). White rattail also attains a larger size, which would facilitate obtaining larger prey/carrion than unicorn rattail, as been suggested by Bailey et al. (2009) for other deep-sea fish species.

5.1.6. Oreos

Warty oreo have a terminal mouth position, and fed mainly on fish, large calanoid copepods, natant decapod prawns and squid. The diet of warty oreo has not been previously reported for New Zealand waters; although off southeastern Australia Lyle & Smith (1987) reported its diet to comprise benthopelagic fish. Off Tasmania it has been described as comprising fish, crustaceans and squid (Bulman et al. 2002). Elsewhere, Mel'nikov (1981) described the diet of warty oreo from off South Africa as benthopelagic, as did Macpherson & Roel (1987) from off Namibia. Likewise, warty oreo from northeastern Chatham Rise had a benthopelagic diet, comprised primarily of fish and small crustaceans, consistent with these earlier accounts. The slight increase of chaetognaths in the intestines may be due to their being represented by hard-parts (jaws), but the sample was small.

Black oreo are far more common in colder water, on the southern flanks of Chatham Rise (Anderson et al. 1998, Anderson 2011a). Only two black oreo had stomach contents and these were a gammaridean amphipod and a salp. Clark et al.

(1989) report black oreo as a salp feeder, however Stevens et al. (2011), in a review of trawl survey data, report a diet that differs from that reported by Clark et al. (1989). Stevens et al. (2011) found that the diet of black oreo contained more fish and fewer salps than fish from southwestern Chatham Rise. Oreos are known to have high rates of stomach eversion, so the lack of usable black oreo stomach contents was expected (Clark et al. 1989).

5.1.7. Orange roughy

The diet of orange roughy on northeastern Chatham Rise was predominantly lantern fish (Myctophidae), natant decapod prawns (*Acantheephyra* spp.), and gammaridean amphipods (*E. gryllus*). In New Zealand waters, the diet of orange roughy is probably the most well-known for any mid-slope deep-sea fish species, and has been described by Liwoch & Linkowski (1986), Rosecchi et al. (1988), Anderson & Fenaughty (1996), and most recently by Dunn & Forman (2011). Between 1982 and 1994, orange roughy diet was regularly assessed as part of research trawls assessing biomass (Anderson & Fenaughty 1996).

Rosecchi et al. (1988) provide the most comprehensive orange roughy dietary work in New Zealand waters. Their investigations are based on the stomach contents of 687 orange roughy from northwest Challenger Plateau sampled over three cruises, in March, June and November, 1984. At that time, the Challenger Plateau was supporting an orange roughy TAC of 4950 tonnes (Field & Francis 2001). Supplementary data was included in the form of 652 gut contents examined in 1983, when only crustaceans were identified, 85 stomachs that were taken from the Challenger Plateau in 1981 and 33 stomachs taken from the Chatham Rise in 1984. The contents of the 85 stomachs taken in 1981 were not identified much past Order level, so were of limited use as a temporal comparison.

Comparisons were made between the three cruises; March, July and November using sub-samples, where possible giving approximately equal sex ratios, size distributions and proportions of orange roughy from the depths sampled. For the analysis of dietary change with fish size, fish ranging from 8.7 cm and 39.8 cm were divided into five size classes starting with fish <20 cm (as there were few of these) and increasing in intervals of 5 cm up to 40 cm (SL). A three-part index was used to assess stomach fullness: empty, partially full and full. There was significant variation found between seasons for stomach fullness, with July (the month of spawning) having a much

higher proportion of empty stomachs. From this, it was considered that orange roughy feed less often during the July spawning period. Over a 24-hour period, Rossetti et al. (1988) found no evidence of diel feeding using trawls taken every three hours.

The diet of orange roughy taken from the Challenger Plateau consisted mainly of crustaceans, cephalopods and fish. The most abundant and diverse crustaceans were natant decapods in the three families Oplophoridae, Pasiphaeidae and Sergestidae. Prawns in these families undertake diel migrations and ascend the water column at night (Roe 1984). Amphipods were also common, notably lysianassid scavengers and hyperiids (Vibiliidae). Copepods and isopods were rare; similar crustacean groups were also found in the Chatham Rise samples.

Identification of prey items appears to have been one of the largest challenges faced by Rossetti et al. (1988), as many prey items are only identified down to genus, and others (large numbers) referred to as “unidentifiable”. Most cephalopods were luminescent members of the order Teuthoidea, mainly Cranchiidae, Mastigoteuthidae and Onychoteuthidae, however, a large proportion were listed as “cephalopod remains”.

Many fish were found to be digested and unidentifiable. Two of the major fish families present were the Stomiidae and the Myctophidae, both strongly bioluminescent families (Haddock et al. 2010). However, it is difficult to know whether orange roughy was targeting these fish because they were bioluminescent or just because they were abundant. Most of the identifiable fish found were benthopelagic, although some benthic forms were found. There was a small amount of evidence for benthic feeding, although it was argued that this could have been an example of net-feeding. Prawns were the most abundant and frequently occurring prey, followed in decreasing numeric order by fish, squid, amphipods and mysids. By weight, fish were the most important prey items, followed by prawns and squid. There was found to be agreement between the orange roughy diet from the Challenger Plateau and the Chatham Rise sample with respect to prawns and squid, although there were a few fish found in the Chatham Rise sample not found in the Challenger Plateau sample.

Rossetti et al. (1988) observed no difference between seasons in the abundance of different prey items, although when the weight of prey was considered, the bulk of prey in March and July was fish, whereas in November it was cephalopods. Among prawn families, the Pasiphaeidae were dominant in occurrence, number and weight in March, whereas the Oplophoridae became dominant in July and November.

The same temporal reversal was also seen for the Sergestidae and the Opolophoridae, but at a lower intensity than the Pasiphaeidae.

Crustaceans decreased in importance with increasing fish length when comparing occurrence and number, whereas the proportions of fish and squid increased in size. Crustaceans were found to make up 14.3–47.2% by weight of fish >20cm (SL), fish made up 32.1–68.8%, and squid 16.3–24.8%. There was an absence of squid in fish <20 cm (SL) and a general trend towards an increase in the importance of fish as orange roughy size increased. Comparing orange roughy <25 cm (SL) with those >25 cm (SL), a significant difference in the relative proportions of crustaceans in the diet of orange roughy was apparent. Furthermore, as orange roughy size increases, so do the numbers of Opolophoridae and Sergestidae; Pasiphaeidae and amphipods stayed relatively even, while mysids appeared to decrease.

The proportions of crustaceans decreased slightly with an increase in the depth of orange roughy capture. The proportion of squid in orange roughy guts between 900–1120 metres depth was approximately twice that of orange roughy caught between 800–900 metres. There was also an increase in orange roughy guts of numbers and occurrence of prey fish, with depth. Between 900–1000 metres, the predominant prey were crustaceans, then fish and squid in descending order and between 1000–1120 metres, fish become dominant.

Liwoch & Linkowski (1986) examined the diet of orange roughy from both Challenger Plateau and Chatham Rise over a one-year period, sampling monthly from December 1980 to November 1981. They based their results on the degree of stomach fullness, concluding that orange roughy feed most intensively in April and May, correlating this with gonad development. During June–July, fish were found to almost completely cease feeding, with almost 90 percent of fish examined having empty stomachs. Liwoch & Linkowski (1986) did not go into detail regarding the identification of prey items, “The most common food components of orange roughy were fish Macrouridae, Myctophidae–35.4% and deep-water shrimps Decapoda–29.2%. Other components included squid Cephalopoda–18.8% and various crustaceans–10.4%”.

Clark et al. (2000) examined the diet of orange roughy on the Chatham Rise over a 19-year period, from 1979–1997. This investigation reviewed 19 years of research trawl data in an attempt to quantify any changes in response to ongoing fishing pressure. No discernible temporal change in diet was found, however the level of prey

identification was gross, with taxonomic scales for fish being identified to Class, crustaceans and cephalopods to Order level, and salps to Family. With this crude level of identification, any fine changes within taxonomic groups could be overlooked. Moreover, the majority of these research trawls are undertaken during spawning, and it has already been shown that up to 90 percent of stomachs during this time period were likely to be empty (Liwoch & Linkowski 1986). Early trawl surveys (data used by Clark et al. 2000) were undertaken without the benefit of a dedicated research vessel, and conditions for researchers have been described as primitive (Judd & Westerkov 1989). The large early catches, coupled with the necessity to process the fish as fast as possible, would have no doubt put pressure on the nature and extent of the data that could be gathered. It is also likely that the level of taxonomic expertise would have increased as researchers became more familiar with the material.

A similar benthopelagic diet has been described for orange roughy in the north Atlantic. Most orange roughy dietary work in the North Atlantic centres on the Rockall Trough region, off the west coast of Ireland. Mauchline & Gordon (1984b, 1986) investigated the diet of orange roughy from Rockall Trough between 1973 and 1981. Their results are consistent with Rosecchi et al. (1988) and Bulman & Koslow (1992), with the prey mainly comprising natant decapod crustaceans and fish. Major identifiable prey were the mysid *Boreomysis tridens* and the crangonid shrimp *Pontophilus norvegicus* together making up roughly 40 percent of the diet. The ontological shift from crustaceans to squid was inferred, as the fish sampled were immature. Dividing the fish into two depth zones (1000 and 1250 m) showed differences in the proportion of some prawn species. Again, many prey taxa were only identified to Order level and “unidentified tissues” made up a significant proportion (15%) of the total diet. As sampling was carried out in winter, dietary seasonality could not be assessed. Gordon & Duncan (1987) assessed the diets of orange roughy and silver roughy taken from Rockall Trough and Porcupine Sea Bight and discerned similar results. An ontological shift in diet was observed, with juvenile orange roughy <20 cm (SL) having a more diverse diet and consuming more mysid species than adult orange roughy. Adult orange roughy consumed more of the mysid *G. zoea*, in addition to small increases in the amount of fish and cephalopod prey.

Mauchline & Gordon (1986) examined foraging strategies of several deep-sea fish, including orange roughy from Rockall Trough, and concluded that orange roughy appears to have a preferred prey but, as feeding increased, so did the total number of

other prey consumed. The diet of orange roughy appears to be made up of large prey taken infrequently rather than smaller prey in large numbers. This seems especially true for fishes and squids, with one or two items per orange roughy stomach. Thomsen (1998) in a brief review of orange roughy fisheries in Faroese waters and the Mid-Atlantic Ridge, concluded that, “The stomach content of orange roughy had a great variation in the diet. This includes a broad selection of small deep-sea species, shrimps and cephalopods”. This is indicative of the level of prey identification in the few published reports regarding orange roughy diet in the North Atlantic.

Off Tasmania, Bulman & Koslow (1992) provided the first investigation into orange roughy diet around south-eastern Australia and Tasmania. Their approach was comparable to that of Rosecchi et al. (1988), but sampling was limited to the January–May period over two years (1988–89). Their objectives were to describe the diet of orange roughy in Australian waters in relation to area, depth, size and year, and to examine the food consumption and metabolism of orange roughy based on an analysis of diel feeding periodicity and digestion rate. Over this two year period, Bulman & Koslow (1992) examined the contents of 7486 stomachs, of which 41 percent contained food. The diet of orange roughy from south eastern Australian waters was found to be similar to that of orange roughy from the Challenger Plateau, although taxa were often only identified to Order level. They found the diet to consist of “natant decapods, mysids, amphipods, benthopelagic fish and squid”. They also found an ontological shift in diet, with fish and squid becoming more important in orange roughy greater than 15 cm. The daily ration of orange roughy was estimated to be one percent of body weight.

Using periodicity observed in the digestion stage of prey as a guide, Bulman & Koslow (1992) found it possible to ascertain a diel variation in mean stomach fullness for juvenile orange roughy. The highest proportion of food in the early stages of digestion were found in the afternoon and evening, with the highest proportion of food in the later stages of digestion being found in the morning. These results were thought to be consistent with feeding on the vertical migration of prey species. This pattern was not shown in adult orange roughy, as it was non-significant over the total data set. However, data collected off New South Wales over one 42-hour period showed that mean stomach fullness of adult orange roughy peaked at night and steadily declined until midday. Thus, it would appear likely that orange roughy exhibits a diel periodicity in feeding.

The diet of orange roughy has also been reported off Namibia (Macpherson 1983, Branch 2001), and the Mozambique Seamount (Parin et al. 2008). Recently, Dunn and Forman (2011) examined the diet of orange roughy from the east coast of New Zealand and found a similar benthopelagic diet to previous New Zealand studies (Rosecchi et al. 1988, Anderson & Fenaughty 1996, Jones 2007). They related this to several environmental factors and found that water temperature was correlated to diet. Orange roughy has a terminal mouth position and is a benthopelagic feeder; its diet varies spatially, temporally, with depth and ontogeny (e.g., Liwoch & Linkowski 1986, Rosecchi et al. 1988, Anderson & Fenaughty 1996, Dunn & Forman 2011).

5.1.8. Robust cardinal fish

The diet of robust cardinal fish consisted of benthopelagic and pelagic items; calanoid copepods, chaetognaths and thaliaceans. The copepods identified were mesopelagic species: *Pleuromamma abdominalis*, *P. quadrangulata*, and *Lucicutia bicornuta*, which could indicate feeding further off the bottom than four-rayed rattail (the other common small copepod feeder at mid-slope depths on northeastern Chatham Rise (Doonan et al. 2009)). Its diet has not been previously reported for New Zealand waters, although off Tasmania Bulman et al. (2002) described its diet ($n = 5$) as being almost exclusively calanoid copepods. Robust cardinal fish have a terminal mouth position and this would no doubt facilitate the predation of pelagic food. Robust cardinal fish had a high PES (82.9%), indicating that this species may not feed frequently, and the few intestines that were examined were empty. One notable feature of this species was its oily flesh, which could be used as an energy store between feeding episodes. The diet of robust cardinal fish had the closest similarity to that of four-rayed rattail from Puysegur Bank, rather than four-rayed rattail from northeastern Chatham Rise. This similarity was, in the main, due to the consumption of chaetognaths by robust cardinal fish, and the increased consumption of them by Puysegur Bank four-rayed rattail. Niche partitioning between robust cardinal fish and four-rayed rattail could be occurring through the predation of slightly more pelagic prey than in four-rayed rattail on northeastern Chatham Rise.

5.2. Diets of upper-slope species from off the Wairarapa coast

The fish species retained in scampi bycatch tended to be towards the small end of their species size distribution. This could be due to the shallowness of the scampi trawls; capturing these species at the shallow ends of their depth distributions (Anderson et al. 1998), or it could be related to the trawl gear used to fish for scampi, which typically has a low headline height, which could enable larger (presumably faster swimming) fish to escape over the top of the trawl (Hartill et al. 2006, Ballara & Anderson 2009). As a consequence, the dietary information is predominantly for juvenile fishes compared with more recent studies on the diet of conspecifics from Chatham Rise (e.g., Stevens & Dunn 2011). There are also some common upper-slope species that these trawls did not sample well, notably ling and hoki, possibly for the same reasons.

5.2.1. Silverside

Silverside examined from off the Wairarapa coast appeared to have a benthic diet; this in contrast to Clark (1985a), who reported the diet of silverside from Campbell Plateau as comprising almost exclusively salps (*I. zonaria* and *S. thompsoni*), although he also recorded gastropods and polychaete worms. Graham (1953) described the diet of this species from the Otago region and found it to comprise primarily benthic fauna; the crab *Cyclograpsus lavauxi* (Edwards, 1853), which is likely a misidentification of *P. victoriensis* given the almost supralittoral boulder-shore distribution of the former (Morton & Miller 1968); “whalefeed” (the squat lobster *M. gregaria*), and “...isopods and worms (especially *Glycera ovigera*).” It seems likely that the diet of this species is benthic.

Clark (1985a) suggested that the salps consumed by silverside from Campbell Plateau were evenly distributed throughout the water column and the feeding of silverside simply reflected the lower range of this distribution. However, dead salps were common both in benthic video and still photography, and in epibenthic sled tows at these depths on Challenger Plateau during the 2007 Oceans 20/20 TAN0707 voyage (pers. obs.), so it is possible that silverside simply picked these normally pelagic organisms dead from the seabed. The diet of this species could be predominantly benthic in origin, in contrast with the account of Clark (1985a). Silverside has a terminal mouth (**Fig. 128**), but does not appear to have a pelagic diet.

5.2.2. Rattails

The diets of the macrourids from off the Wairarapa coast were similar to the deeper mid-slope species from northeastern Chatham Rise in that they exhibited a range of feeding strategies: benthic and benthopelagic, and combinations thereof (Jones 2008a, b, 2009). The diet of two-banded rattail from off the Wairarapa coast was predominantly benthic invertebrates, particularly the squat lobster *M. gracilis*, several species of polychaete worm, and the crab *P. victoriensis*. The benthic/benthopelagic prawn *N. magnoculus* was also eaten. The lack of any relationship between the size or sex of the fish was probably due to the small sample. Previously, Graham (1953) examined two two-banded rattail stomachs and found crustaceans (although these were not identified further). Two-banded rattail are possibly the shallowest-living species in this genus in New Zealand waters, with a mean depth of 296 metres (Anderson et al. 1998), and possibly this relatively shallow distribution gives them a degree of niche partitioning from their deeper living congeners. Two-banded rattail can attain a size of approximately 70 cm (Stevens & Dunn 2011); almost twice the size of the fish examined herein. As a consequence, these data probably reflect the diet of juvenile two-banded rattail.

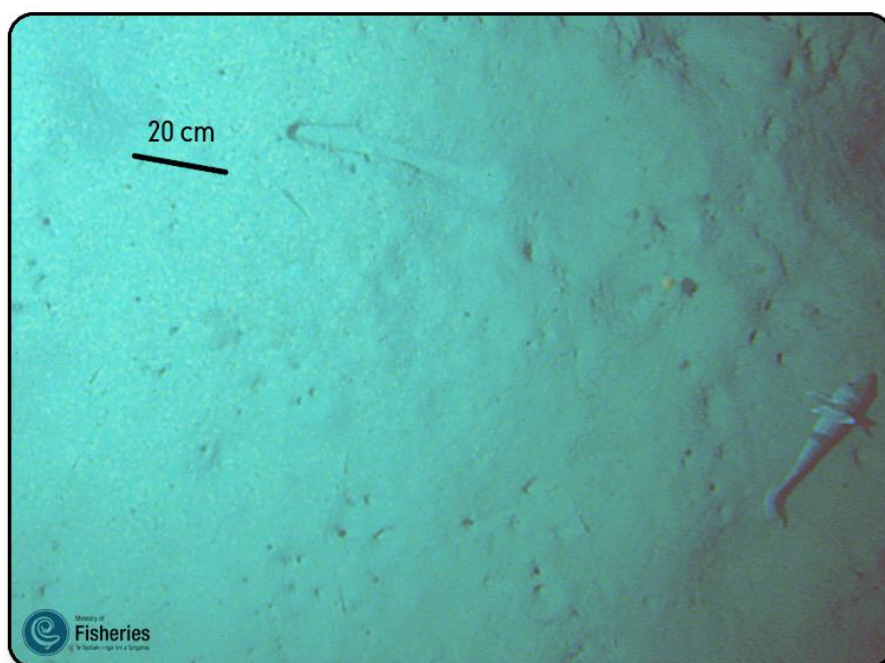


Figure 195. A two-banded rattail swims just above the seabed: 200–500 metres water depth, off the Wairarapa coast (KAH0401). A scampi burrow sits upper left-center. The bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

The diet of Bollons' rattail was predominantly benthic invertebrates: crabs (almost exclusively *P. victoriensis*) and polychaetes. There was an increase in the abundance of unidentifiable material in the intestines, but also an increase in animals with hard-part remains (crabs, ostracods, gastropods, and bivalves), which was expected. This trend was also the case for fish with both stomach and intestinal food items. Polychaetes declined in abundance in the intestines. A cohort of juvenile/immature fish (**Fig. 140**) dominated the sample, which probably biases it towards smaller fish. Recently published work by Stevens and Dunn (2011) describes the diet of Bollons' rattail from various locations on the Chatham Rise. They report a diet dominated by polychaetes in the smallest sizes of their Bollons' rattail, and speculate that the predominance of crabs in the diet of the Bollons' rattail from off the Wairarapa (this sample) is due to a recent spat fall of crab larvae. This is possible, as the Wairarapa is under the influence of the Wairarapa Eddy (WE), and this oceanic feature is linked to the coastal retention of pelagic larvae of other benthic crustacean species (Chiswell & Roemmich 1998, Chiswell & Booth 1999, 2005). The feeding of Bollons' rattail from the Wairarapa on crabs could possibly be an indication of a latitudinal difference in diet between the Wairarapa coast and the more southerly Chatham Rise, although this could be confounded by the small size of the fish from the Wairarapa.

Oliver's rattail was a benthopelagic feeder feeding on natant decapod prawns (*N. magnoculus*, and *Pontophilus* sp.), crabs (*P. victoriensis*) and amphipods (gammaridean and hyperiidean). Clark et al. (1989) previously reported the diet of ten Oliver's rattail from southwestern Chatham Rise as comprising calanoid copepods (60% IRI) and hyperiidean amphipods (35%), suggesting that the overall diet of this species could be a mix of benthic and benthopelagic organisms. More recently, Stevens and Dunn (2011) described the diet of Oliver's rattail from various locations on Chatham Rise. They also found a diet dominated by calanoid copepods, and perhaps Oliver's rattail fills a similar niche to four-rayed rattail, but in shallower waters.

Stevens and Dunn (2011) found little in the way of an ontogenetic shift in diet but did describe a slight latitudinal gradient in its composition, with natant decapod prawns becoming more important in the diets of fish from northern Chatham Rise. Whether this extrapolates to the dominance of natant decapod prawns in the diet, Oliver's rattail from the Wairarapa further north is open to speculation, but it might indicate that water temperature is important to the food of this species. Stevens and Dunn (2011) suggest

that due to a link between primary productivity and copepod biomass, the lack of copepods in the diets of the Wairarapa fish may be related to lower rates of primary productivity off the Wairarapa Coast, compared with Chatham Rise. However, satellite images of Chlorophyll *a* concentration show little difference between the Wairarapa coast and Chatham Rise between 1998 and 2007 (Knox et al. 2012), so perhaps there is an alternative explanation. Investigations into the diet of Oliver's rattail from other, more northerly, New Zealand locations would shed light on this. Oliver's rattail have an inferior mouth position (McLellan 1977), and the diet of this species would appear to be a mixture of benthic, benthopelagic, and pelagic organisms.

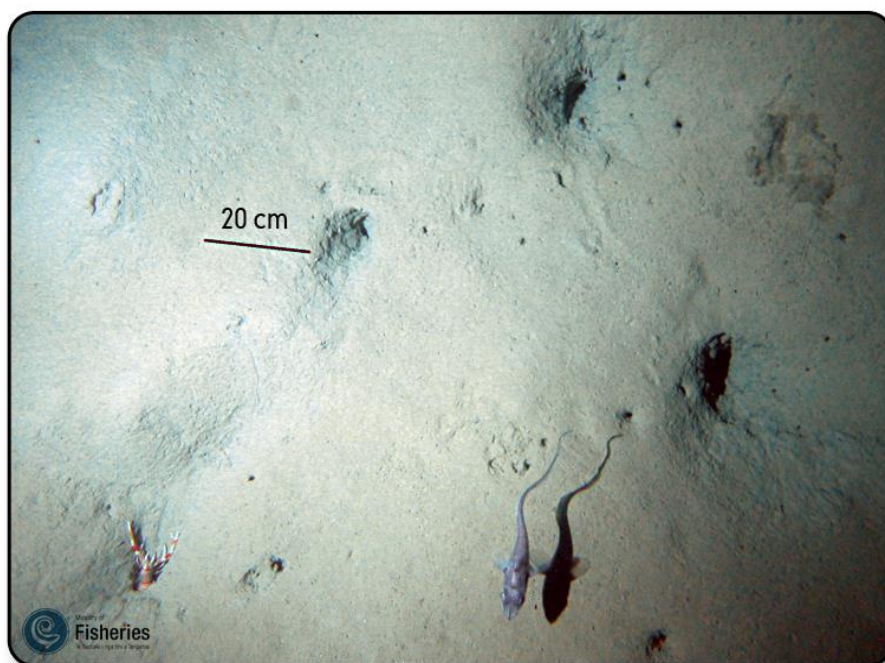


Figure 196. An Oliver's rattail swimming above the seabed: 200–500 metres water depth, off the Wairarapa coast (KAH0401); a scampi sits in a burrow entrance in the lower left hand corner. The scale bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

Javelin fish fed mainly upon natant decapod prawns, particularly *N. magnoculus* and *Pasiphaea* aff. *sivado*, and these two species also became more important in the diets of larger fish. Clark (1982, 1985a, b) reported the diet of javelin fish from Campbell Plateau, southeast of New Zealand, and found natant decapod prawns (*Pasiphaea* sp.), hyperiidean amphipods (*Vibillia stebbingi*), and squid (mainly *Iridoteuthis maoria*) to be important food items; Clark (1982) also found that the diet of

javelin fish changed spatially, temporally, and ontogenically, with mysid and natant decapod prawns becoming more important in the diets of larger fish. In the current study hyperiidean amphipods and squid (*I. maoria* (beaks only)) were recorded, but these were infrequent.

More recently, Stevens and Dunn (2011) described the diet of javelin fish from various locations on Chatham Rise, and also found it to be a benthopelagic feeder, preferring prawns (natant decapod and euphausiid). The javelin fish examined by Stevens and Dunn (2011) were of a larger size than the ones examined herein (2.9–253.7 g for the Wairarapa sample, compared with 10–515 g for Chatham Rise). This probably reflects limitations of the net size used in their trawls, which were primarily targeting hoki, a much larger fish (Stevens et al. 2009). As a consequence, their sample focuses on the diets of larger fish species. However, despite differences in sampling protocols in the two studies, there are strong similarities between the diets of javelin fish from Chatham Rise and off the Wairarapa coast.

Both the Chatham Rise and Wairarapa samples were notable in that there was an ontogenetic shift in diet to larger prawns, but not fish, which was unexpected. Perhaps this could be a seasonal effect, as both samples were obtained during the summer months. In Australian waters, Coleman & Mobley (1984) examined the diet of javelin fish from off the Victorian coast and found them to be eating fish; Blaber & Bulman (1987) examined the diet of javelin fish from off southeastern Tasmania and also found seasonal shifts in its diet; during winter this species fed upon the myctophid *Lampanyctodes hectoris*, and during spring its diet was dominated by euphausiid prawns. In New Zealand waters, the diet of javelin fish appears to change spatially, temporally and ontogenically, but was principally benthopelagic, and primarily crustacean in nature.

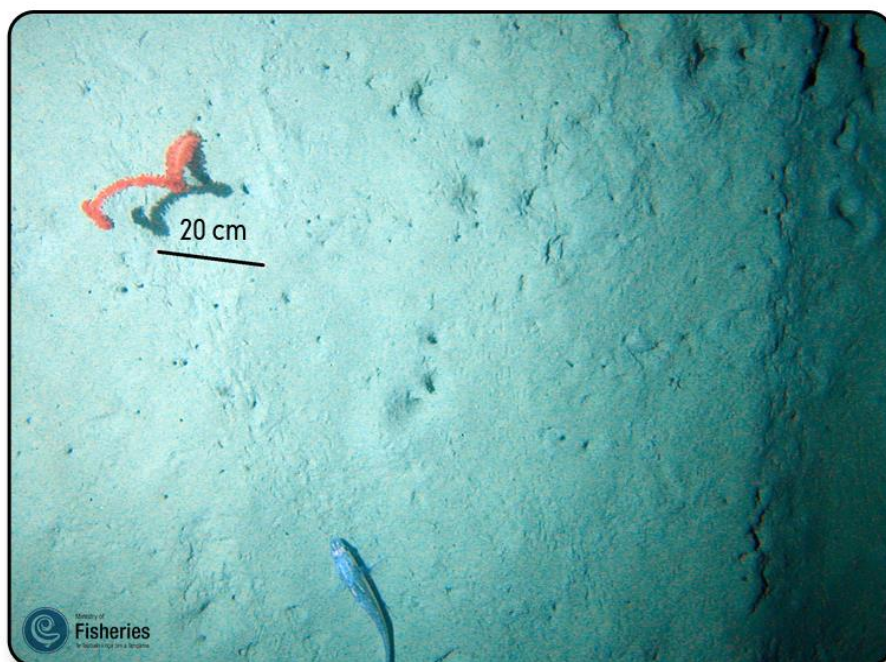


Figure 197. A javelin fish (lower center) swims just above the seabed: 200–500 metres water depth, off the Wairarapa coast (KAH0401). The scale bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

5.2.3. Silver roughy

Silver roughy have a wide distribution, being found from their type locality in the Mediterranean Sea (Madurell et al. 2004, Madurell & Cartes 2005b, Fanelli & Cartes 2010) through the north Atlantic (Mauchline & Gordon 1984b, Gordon & Duncan 1987) down to South African (Hoffmann 1982) and in New Zealand waters, where they dwell on the upper slope (Kerstan 1989, Anderson et al. 1998). They have a terminal mouth position and a benthopelagic/pelagic diet made up predominantly of prawns. They also have an ontogenetic dietary shift to fish in the largest individuals. The diet of silver roughy has been previously described from the north of North Island in New Zealand waters (Kerstan 1989), Rockall Trough in the north Atlantic (Mauchline & Gordon 1984b, Gordon & Duncan 1987), off Portugal (Pais 2001, 2002), the Mediterranean Sea (Madurell et al. 2004, Madurell & Cartes 2005b, Fanelli & Cartes 2010), and off northwestern Africa (Hoffmann 1982). The fish in this study were all of relatively small size, and this was indicated by their lack of maturity (**Fig. 159**), and could infer why no clear ontogenetic shift in diet was detected (**Fig. 161**).

5.2.4. Capro dory

Capro dory are endemic to New Zealand waters (Froese & Pauly 2011) and their diet has not been previously reported. Capro dory have a terminal mouth position and were a predominantly benthopelagic feeder (calanoid copepods, occasionally in great numbers, and natant decapod prawns), with the occasional benthic item taken (squat lobsters (*M. gracilis*) and the benthic prawn *N. magnoculus*). Capro dory would appear to feed close to, and occasionally from, the seabed.

5.2.5. Sea perch

Sea perch have a terminal mouth position (**Fig. 169**) and have a mostly benthic diet, with the occasional benthopelagic item. The diet of sea perch has been previously reported from the Otago region by Graham (1938, 1953), who found over ten species of crab (including *Leptomithrax longipes*) and more than three species of “shrimp-like animals” (including *Squilla armata* and *M. gregaria*), and three of “worm” (including *Glycera ovigera*, *Physalidonotus squamosus*, and *Nereis ammblyodonta*). Graham (1938, 1953) also noted that no “shellfish” were found in the 300–350 stomachs he examined, and concluded that the diet of this species was crabs and shrimps.

Paul (1998) also described the diet of sea perch from New Zealand waters as being benthic crustaceans and fish.

The diet of this species from off the Wairarapa coast was also predominantly benthic, dominated by the crab *P. victoriensis*, and the natant decapod prawns *N. magnoculus* and *P. acutirostratus*; the latter two species also became more important in the diets of larger fish, with fish possibly important to the diet of the largest specimens (**Fig. 172**). The diet of sea perch has also been reported off southeastern Australia, where Bulman et al. (2001) described them to be “benthopelagic omnivore and epibenthic invertebrate feeders specialising in megabenthos and benthic crustaceans.” Blaber & Bulman (1987) reported an ontogenic change in the diet of this species from eastern Tasmania, with small fish feeding on benthic crabs and other benthic crustaceans, and larger fish shifting their diet to fish. This was consistent with the fish from off the Wairarapa coast, although the Wairarapa sample had far fewer large fish than the eastern Tasmanian sample. Sea perch from Wairarapa fed predominantly on crabs and prawns and there was some evidence of an ontogenic shift to feeding on fish in the largest fish available (**Fig. 172**).

More recently, Horn et al. (2012) investigated the diet of sea perch from upper-slope depths on Chatham Rise. They describe a similar diet to that reported from the Wairarapa coast: the crab *P. victoriensis* and thaliaceans. However, the diet of sea perch on Chatham Rise varied with location on Chatham Rise and with fish size; indicating both a spatial and an ontogenic shift in diet from small to large crustaceans. However, a possible reason for this variation could be the relative sizes of the fish studies, as the fish from Chatham Rise were larger than those from off the Wairarapa coast.

Horn et al. (2012) also found inter-annual variability in the percentage of thaliaceans present in the diet of sea perch, with the percentage varying between 10 percent in 2007, 20 percent in 2005 and 30 percent in 2006. This variation in the proportion of thaliaceans eaten was also found in two warehou species sampled concurrently on Chatham Rise (Horn et al. 2011), and suggests the contribution of thaliaceans to the diets of these species is related to annual thaliacean availability. Thaliaceans were 4.9 percent of the total diet of sea perch from the off the Wairarapa coast by weight, but this may have been either a reflection of thaliacean availability or the size of the sea perch sampled. This variation between years also suggests that inter-annual variation be taken into account when analysing the diets of fish based on a single sampling episode.

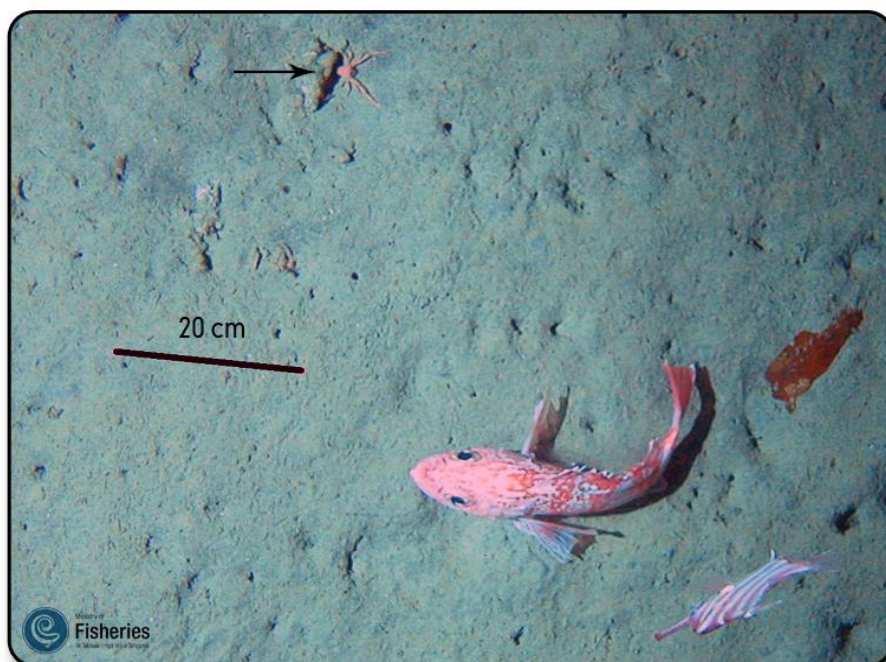


Figure 198. A sea perch and a banded bellows fish (*Centriscops humerosus* (Richardson, 1846)), (lower right corner), from 200–500 metres water depth, off the Wairarapa coast (KAH0401). A squat lobster (*Munida gracilis*) sits in the top left hand corner (arrow). The scale bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

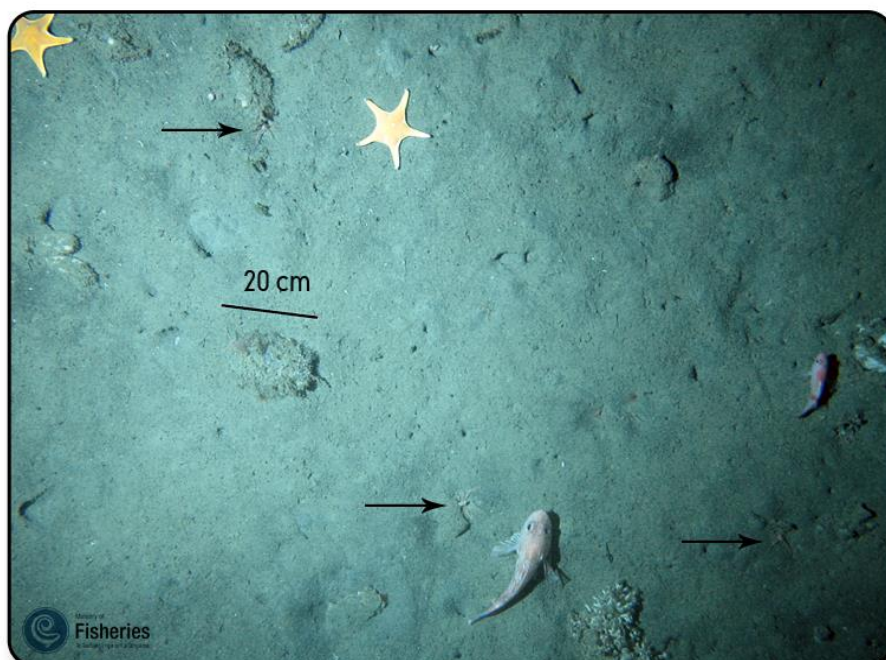


Figure 199. Two sea perch (lower right) and squat lobsters (*M. gracilis*) (arrows); 200–500 metres water depth, off the Wairarapa coast (KAH0401). A scampi burrow can be seen in the lower left hand corner. Two starfish, possibly *Dipsacaster magnificus* (Clark 1916), are in the upper left corner. The scale bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

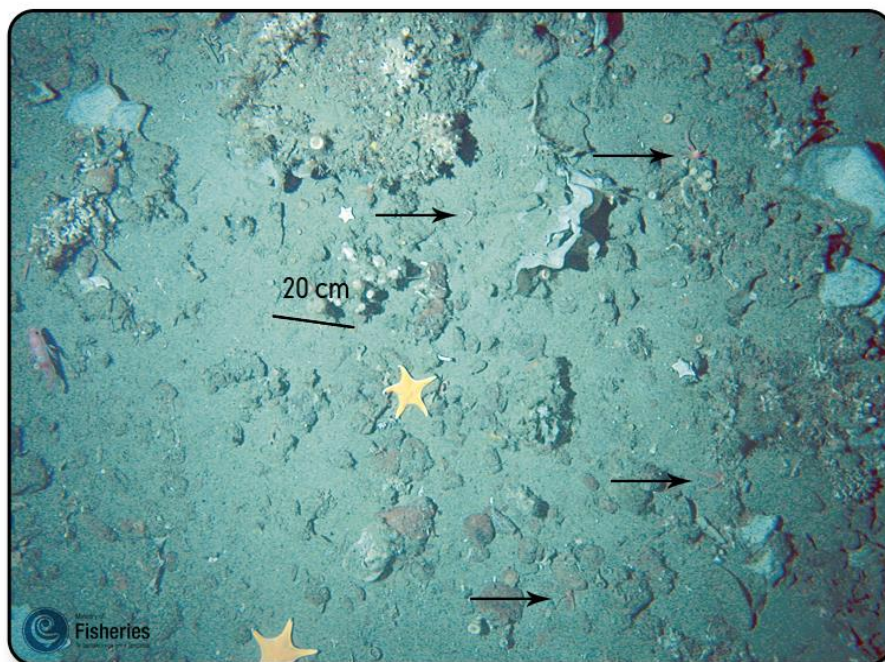


Figure 200. One sea perch (mid-left hand edge), and several squat lobsters (*M. gracilis*) (arrows); 200–500 metres water depth, off the Wairarapa coast (KAH0401). The large white structures are sponges, and two starfish, possibly *Dipsacaster magnificus* (Clark 1916), are in the centre and lower edge. The scale bar indicates the distance between two laser pointers (20 cm): image courtesy of the New Zealand Ministry of Fisheries.

5.2.6. Diets of other fish species from off the Wairarapa coast

Several fish species were obtained from off the Wairarapa coast, with sample sizes of less than ten stomachs or intestines containing food. Despite this, some of these had quite distinct diets. Dark ghost shark (*Hydrolagus novaezealandiae*), had feed on benthic food items, mostly the crab *P. victoriensis*, which made up approximately 53 percent, and echinoids (approx. 41%) of the diet by (wet) weight. The consumption of *P. victoriensis* was consistent with later work by Dunn et al. (2010b), who found that *P. victoriensis* was the most common brachyuran encountered in stomach contents and approximately 40 percent (wet-weight) of this species diet from Chatham Rise. However, the Chatham Rise dark ghost shark fed on comparatively fewer echinoderms (approx. 15%), but this may be a reflection of the small Wairarapa sample. Hairy conger eel (*Bassanago hirsutus*) was another benthic feeder with a small sample ($n = 6$). This species also targeted crabs (*P. victoriensis* (approx. 34%)) but also prawns (*N. magnoculus* approx. 26%), and benthic crustaceans: *I. atlicrenatus*, and scampi (approx. 15%). Spotted flounder (*Azygopus pinnifasciatus*) ($n = 8$) was also a benthic

feeder feeding on *P. victoriensis*, polychaetes, foraminifera and gastropods. Deep sea flathead (*Hoplichthys haswelli*) ($n = 9$) was more a benthopelagic than a benthic feeder. It had fed mostly on prawns (*N. magnoculus*) and fish (Myctophidae). Larger samples would likely indicate the degree of niche partitioning between these benthic/benthopelagic feeders.

All seven denticulate cardinal fish (*Epigonus denticulatus*) had fed on euphausiid prawns (one had fed on 12). Off Tasmania, this species also fed on euphausiids (Blaber & Bulman 1987). The diet of this species from off Namibia was similar: euphausiids, natant decapods, and mysids (Macpherson & Roel 1987). This species from the Mediterranean Sea fed mostly on euphausiids during summer, but not at other times of the year, when the diet was made up of copepods and myctophids (Matallanas 1982). These data suggest this species is a pelagic crustacean feeder, with the data from the Mediterranean suggesting a seasonal plasticity in the diet.

5.3. Section two — Role of thaliaceans in the diets of fish species from all study areas

This section is made up of three sub-sections. The first describes the roles of selected dietary components and relates them to the ecology of the fish species consuming them. The second sub-section discusses the role of the PES/PEI, which is then discussed as a possible proxy for productivity. The parasite analysis of the two rattail species is also then discussed in the light of its usefulness as an indicator of dietary preferences. The third sub-section discusses dietary overlap between species, feeding guilds and potential deep-sea trophic pathways.

Thaliaceans are known to form large swarms after spring plankton blooms (Bradford & Chapman 1988; Anderson & Sardou 1994; Nishikawa & Tsuda 2001a, b). As such, they have been suggested to be an important vector for the rapid deposition of organic material to the deep-sea benthos through their fecal pellets when alive (Wiebe et al. 1979, Iseki 1981, Bathmann 1988, Madin et al. 2006, Phillips et al. 2009, Robinson et al. 2010), and through the benthic deposition of their bodies when dead (Lebrato & Jones 2009). These thaliacean swarms are patchy and are not always annual, or of the same magnitude (Bathmann 1988, Zeldis et al. 1995b, Madin et al. 2006, Lebrato & Jones 2009). The fish collected from southwestern Chatham Rise by Clark et al. (1989),

were collected in the austral spring of 1984, when productivity is high in this area (Bradford-Grieve et al. 1999, Nodder & Northcote 2001). Many of the species in that study had salps as a large component of their diet (e.g., black oreo, ridge-scaled rattail). It seems likely that these fish were taking opportunistic advantage of a salp swarm feeding on a spring plankton bloom on southwestern Chatham Rise, and that this may partially explain the differences in the diets of congeners from southwestern Chatham Rise, northeastern Chatham Rise and Puysegur Bank. For example, the diet of black oreo recorded subsequent to Clark et al. (1989) contained far fewer salps (Stevens et al. 2011). While thaliaceans have been an important part of the diets of many deep-sea fish species in previous New Zealand studies (Clark 1985a; Clark et al. 1989), they did not play an important role in the diets of many fish from any of the three areas sampled in this study (the exception being the two brown slickhead species, which fed on the pyrosome *P. atlanticum*).

5.3.1. Relationship between hyperiid amphipods and thaliaceans

Hyperiid amphipods are known to be associated with gelatinous zooplankton (Harbison et al. 1977). Madin & Harbison (1977) describe hyperiid amphipods from the genus *Vibilia* as obligate salp dwellers, which feed on the particulate food gathered by the salp. Consequently, it could be expected that the consumption of either taxa would coincide. Several species of fish had either fed on salps or on hyperiids from the genus *Vibilia*. Of the eight incidences of hyperiid amphipods in the diets of javelin fish, only one of these coincided with a thaliacean. Hyperiids were encountered eight times ($n = 21$) and thaliaceans three times ($n = 3$). There were five instances of hyperiids in the stomachs (one in each) of Oliver's rattail, but no instances of thaliaceans. Also, there were two instances of hyperiids in sea perch stomachs, and ten of thaliaceans ($n = 2$), but no concurrent occurrences. On the basis of these data, it could be suggested that these hyperiids are not obligate thaliacean dwellers at this time of the year, as if they were, it could be expected that thaliaceans and hyperiids would have occurred together in the stomachs of the fish that ate them. An alternative explanation could be that these thaliaceans were consumed dead, and that the hyperiids had vacated their host on its demise.

Similar results were obtained for thaliaceans and amphipods consumed by the three slickhead species from northeastern Chatham Rise. Black slickhead had 11 incidences of hyperiids (not identified further) and three of thaliacean remains, but these

did not coincide. Out of the six incidences of pyrosomes found in the stomachs of big-scaled brown slickhead, there were three incidences of amphipods. The amphipods did not coincide with the occurrence of pyrosomes. There was one incidence of an amphipod occurring in the intestine of a big-scaled brown slickhead with a pyrosome, and it was not a hyperiid. Pyrosomes occurred twice in the stomachs of small-scaled brown slickhead, and hyperiids also twice. There was one occurrence of a hyperiid and a pyrosome together in the same stomach. Overall, although these data are limited they do suggest that if there is a relationship between hyperiid amphipods and pyrosomes, it did not transfer into the diets of the fish species that consumed them, in this study.

5.3.2. Depth transition in the thaliacean feeding guild on Chatham Rise

Horn et al. (2011c) studied the diets of silver (*Seriolella punctata*) and white (*S. caerulea*) warehou from upper-slope depths on Chatham Rise and found that they were both thaliacean feeders. They also found hyperiid amphipods in the stomach contents along with thaliaceans, but could not discern whether the hyperiids were being consumed accidentally along with the salps. It would appear that the warehou fulfil a similar niche to the slickheads, but in shallower waters, thus indicating a faunal transition in the thaliacean-feeding guilds between upper- and mid-slope depths on Chatham Rise.

5.3.3. Thaliaceans in the diets of benthic-feeding fishes

Thaliaceans were also found in the diets of fish that had largely otherwise benthic diets. For example, Clark (1985a) records the diet of silverside from Campbell Plateau as dominated by salps. However, the rest of the diet was typically benthic food; crabs, polychaetes, and gastropods. Although the sample from off the Wairarapa coast was much smaller, thaliaceans were absent and the diet of this species was almost exclusively benthic. Sea perch from Wairarapa also fed on thaliaceans (4.9%, wet weight), but otherwise had a mostly benthic diet. It is probable that these thaliaceans were not taken live from the water column, but dead from the seabed. As such, they are most likely an example of opportunistic scavenging in sea perch. Dead and moribund thaliaceans can be found on the deep seabed in great numbers subsequent to the formation of large swarms (e.g., Lebrato & Jones 2009). I have also seen dead thaliaceans on the seabed on Challenger Plateau during the 2007 Oceans 20/20 voyage; they were also a common occurrence in epibenthic sled hauls during that voyage

(TAN0707). The falling bodies of thaliaceans represent a rapid influx of gelatinous food from the surface waters, similar to large jellyfish (Billett et al. 2006, Yamamoto et al. 2008, Robinson et al. 2010). Swarms of thaliaceans may also be indicators of previous high pelagic productivity (Iseki 1981, Bathmann 1988, Anderson & Sardou 1994, Zeldis et al. 1995b, Madin et al. 2006, Lebrato & Jones 2009).

5.4. Role of seaweed and insects in the diets of fish species from all study areas

There were some unexpected items found in the diets of several fish from northeastern Chatham Rise and off the Wairarapa coast. Brown seaweed (possibly *Durvillea* sp.) was found twice in the stomachs of basketwork eels, and from a pale toad fish from northeastern Chatham Rise. Brown seaweed was also found in the stomachs of javelin fish and Oliver's rattail from the Wairarapa. This is perhaps not as surprising as first thought, as a search through deep-sea dietary literature revealed that seaweed has also been reported from the stomach contents of oreos from southwestern Chatham Rise by Clark et al. (1989). It is possible that these rare occurrences may be accidental ingestions, but there is a body of evidence that suggests that they may not. Jefferies et al. (2010) conducted experiments using baited cameras with spinach as bait, and found that several fish species were not only attracted to the baits, but also actively fed on them. Further work by Jefferies et al. (2011) used phytodetritus deposits to investigate whether phytodetritus would be consumed in a similar way to spinach, and found that it was, and rapidly. Their lander deposited a patch of phytodetritus on the seabed at approximately 3000 metres water depth, and the patch was significantly decreased in size within two hours of deposition. Rattails and cusk eels were the first species actively attracted to the patch and later invertebrates (crabs, amphipods and elapsoid holothurians). The phenomenon would appear to be complex, as a similar experiment conducted in the Mediterranean Sea did not attract phytodetritus-feeding fish, but only invertebrates (Jefferies et al. 2011). Jefferies et al. (2011) attribute this to phytodetritus deposits being rare in this region of the Mediterranean Sea. Although in Jefferies et al. (2010, 2011) the scavenging fish species were rattails, and the depths were deeper than this study, it nevertheless demonstrates that scavenging species of deep-sea fish will actively target plant material if it is available. This unexpected trophic pathway could have the effect of lowering the trophic level of these fish species.

Another example of unexpected items in the diets of deep-sea fish was the presence of beetles in several fish species from off the Wairarapa coast. Seven species

of fish from the Wairarapa had beetles either in their stomach or intestinal contents. The beetles were rare, only occurring once in each species, but in the case of silverside made up approximately 8 percent of the total weight of prey. There were two types of beetle, firstly weevils from the family Curculionidae, and the scarab beetle *A. tasmaniae*.

The nocturnal scarab beetle *A. tasmaniae* was originally described from Tasmania (see Strebicka 2001), and is known from South Australia, Victoria, and New South Wales, where it is most active during the first two months of the year (Steinbauer & Weir 2007). It was first recorded in Canterbury in 1916 (Brown 1967), and is now a common pest of pastures in New Zealand. Its high-activity period in New Zealand is from November to March (Strebicka 2001), which coincides with the timing of the trawl survey during which the fish were collected. It is somewhat remarkable that these beetles were eaten by fishes obtained from depths to 418 m, up to 30–40 km offshore. It is possible that the beetles were caught up in the trawl nets on deck before their deployment. However, as three of the beetles were recovered from the intestines of two fishes it seems unlikely that the beetles would have had time to be digested, and enter the intestines during the trawl duration. Another possibility is that the beetles were consumed on the surface by nocturnal vertically migrating fishes. Interestingly, the weevils were found in species with benthopelagic diets (javelin fish and Oliver's rattail), whilst the scarabs came from species with benthic diets (Bollons' rattail, sea perch, ghost shark, and silverside). Beetle remains were also found in the intestines of a red cod, but they were too fragmentary for further identification.

Acrossidius tasmaniae can form large swarms at dusk (Steinbauer & Weir 2007). It is postulated that one or more of these swarms has been blown offshore by the prevailing offshore westerly winds, fallen into the sea, drowned, and then sunk to the upper-slope seabed. There they were eaten by benthic feeding fish, much in the same way Saharan dust was found in offshore Atlantic deep-sea sediments (Kremling & Streu 1993). The vector for the weevils is unknown, but probably similar. Even though the beetles were rarely found, the large latitudinal range over which they were found (approx. 0.9° of latitude) suggests that this is possibly a large-scale occurrence. The presence of beetles provides an opportunistic influx of terrestrial food, much in the same way (although on a much smaller scale) as the seasonal deposition of dead salps (Lebrato et al. 2012), pyrosomes (Lebrato & Jones 2009), or jellyfish (Yamamoto et al. 2008). The presence of both seaweed and insects in the diets of these deep-sea fish

provides an example of small, but previously overlooked, examples of connectivity with surface (seaweed), and terrestrial (beetles) ecosystems through opportunistic and/or seasonal food-falls.

5.5. Percentage of empty stomachs/intestines (PES, PEI) for fish species from northeastern Chatham Rise and Puysegur Bank

As most food of deep-sea fish comes from the surface waters, it is reasonable to assume that feeding of deep-sea fish will reflect the level of productivity in the waters above them (McClatchie et al. 1997, 2005, Drazen et al. 2008). Also, in times of abundant food fish will take advantage of abundant food items (Clark et al. 1989, Laptikhovsky 2005, McClatchie et al. 2005). Conversely, when food is scarce fish will feed less often (Arrington et al. 2002, Laptikhovsky 2005, Vinson & Angardi 2011). Vinson & Angardi (2011) reasoned that PES values would relate to productivity, and also to the size of the fish; that larger fish, feeding on more energy-dense, higher trophic level food items, would find these more scarce, and hence would feed less often than small fish feeding on less energy-dense, lower trophic-level food items. Also, PES values would be higher for pelagic compared to benthic feeders, and linked to season, with lower PES values in summer and higher in winter, overall reflecting prey availability. In this way, the PES could be used to predict levels of productivity between different regions using conspecifics, and possibly also infer their trophic position.

On northeastern Chatham Rise, the PES values ranged between 4.2 percent for serrulate rattail (a benthic feeder) to 92.3 percent for big-scaled brown slickhead (a pelagic feeder). Other species with PES levels of over 50 percent were also pelagic or benthopelagic feeders: orange roughy, warty oreo, shovel-nosed, and Baxter's dogfish, and robust cardinal fish. Serrulate and four-rayed rattail, long-nosed velvet dogfish, black slickhead, and basketwork eel all had PES values of <50%. Four-rayed rattail was an exception to this trend, having a benthopelagic diet and a PES of 9.3 percent. The low PES values for serrulate and four-rayed rattails may be confounded by their respective rates of stomach eversion, as it is impossible to tell if an everted stomach contained food at the time of sampling. Also, it is difficult to know if there is a size-related trend in the PES values, as most of the fish caught in the mid-slope trawls were less than a metre long. However, four-rayed rattail and robust cardinal fish, the two smallest species examined from northeastern Chatham Rise, had dramatically different PES values: 9.3 percent for four-rayed rattail and 83.0 percent for robust cardinal fish,

so perhaps food availability at this time of year is more important than fish size or food quality. The PES for big-scaled brown slickhead was also high, and it fed on low energy-dense pyrosomes for most of its diet, which again suggests that food availability may be the most important variable.

The PES values for the two Puysegur Bank fish were 50 percent for Baxter's dogfish and 13 percent for four-rayed rattail, so there was no evidence for lower PES values in the presumably higher productivity seamount habitat of Puysegur Bank. The PES value for Baxter's dogfish was lower, but the value for four-rayed rattail was higher, which was contrary to expectations; if the seamount habitat is more productive than the flatter soft-sediments of northeastern Chatham Rise. However, this could be confounded by the difference in year between the samples (and the prevailing oceanographic conditions), the fish species retained, which may not be representative (from Puysegur Bank), and the method of their capture, which was not random in either case. Despite this, the PES has the potential to be used as a metric for productivity comparisons between areas in the absence of other data (**Fig. 201**).

The mean PES for the eleven species from northeastern Chatham Rise and Puysegur Bank was 47 percent, which is higher than the value of 26.4 percent provided for shallow and fresh water fish populations by Vinson and Angardi (2011). This could possibly be an indication of lower rates of feeding/food availability, and of the metabolism displayed by deep-sea fish. Alternatively, it could be caused by the trauma of being caught, causing the fish to regurgitate their stomach contents, which would confound the PES value. For species with intestinal contents, the PEI revealed a similar trend to the PES, with low PEI values for the benthic feeders from northeastern Chatham Rise. Johnson's cod had the highest PEI (67.4%), and small-headed cod the lowest (9.5%). Both species of brown slickhead had high levels of PEI. The PEI suffers from the same limitations as any analysis using intestinal contents; the main limitation being that it is impossible to tell how many feeding episodes intestinal contents represent, but it is useful in the absence of other data.

Four-rayed rattail is the most abundant orange roughy bycatch species on northeastern Chatham Rise at mid-slope depths, and is four times more abundant than the next most abundant species: notable and serrulate rattails (Doonan et al. 2009).

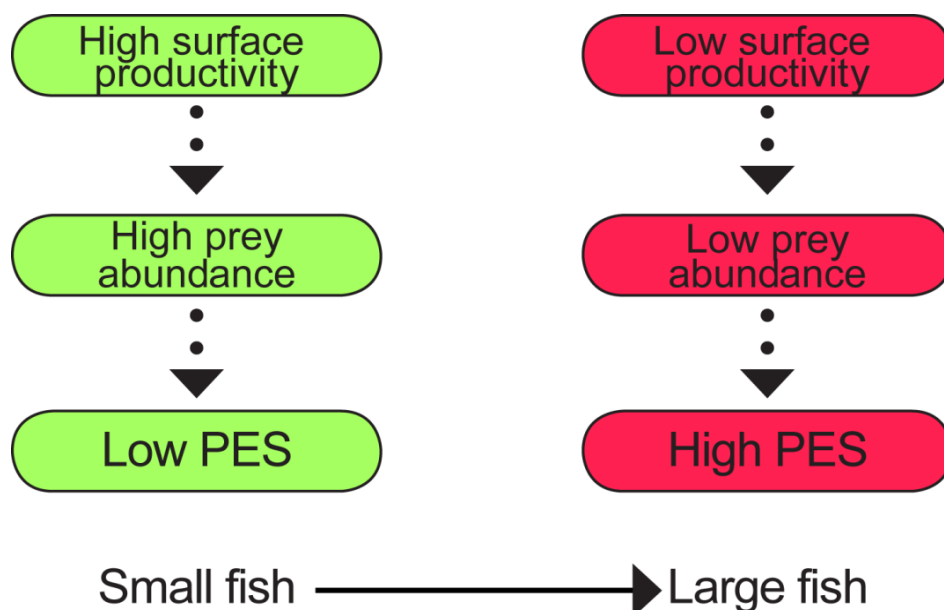


Figure 201. A simple conceptual model using PES values of deep-sea fish from northeastern Chatham Rise and Puysegur Bank as a proxy for productivity.

However, it is quite a small fish with a mean length of approximately 270 mm TL and 60g weight (**Table 5**). Small fish feed more often than bigger fish and this is inferred by their low PES (9.3%). If rate of feeding can be extrapolated from PES, it is likely that this species is very important in the structuring of the demersal ecosystem. Selective removal of this species could cause an increase in the benthopelagic and, to a lesser extent, mesopelagic copepods it feeds on, and a corresponding decrease in the food of those copepods. The consequences of this small trophic cascade are unknown and probably complex, but might include a decrease in the particulate matter entering the benthic boundary layer (as it is eaten by the increased copepod biomass), and then reaching the benthos. This could in turn provide less food for benthic deposit feeders on soft-sediments, or filter feeders on harder seamount substrates.

There is very little information regarding the feeding rates of deep-sea fish from mid-slope depths in New Zealand waters. Liwoch & Linkowski (1986) found that orange roughy fed less during the winter months, so it possible that the high numbers of empty stomachs found in other mid-slope species on Chatham Rise reflect a lack of feeding at this time. It is possible that PES values could be used as a proxy for feeding periodicity over large temporal scales, but more samples would be needed for confirmation.

5.5.1. Percentage of empty stomachs (PES) values from fish from off the Wairarapa coast

The PES values for the Wairarapa fish ranged from 0.0 percent for the benthic feeders two-banded and Bollons' rattail to sea perch, which had a PES of 43.5 percent. The pelagic/benthopelagic feeders had relatively low PES values, with 3.4 percent for javelin fish and 16.7 percent for capro dory. This generally agrees with the trends predicted by Vinson & Angardi (2011), with the main exception being sea perch, which may need an alternative explanation. The low PES value for javelin fish may be related to the rate of stomach eversion, even though this was low in this species. The low rates of PES in the Wairarapa samples are not comparable to those from the deeper samples, owing to confounding variables of depth, time of year, and method of collection. The Wairarapa coast samples were collected during the summer months and food may have been more plentiful than at other times of the year, as suggested by Stevens & Dunn (2011), and Horn et al. (2012).

5.5.2. Temporal feeding periodicity

The opportunistic nature of the sampling in this study precluded the evaluation of any periodicity in feeding beyond the PES/PEI values, which are not really indicative of any feeding cycle by themselves. However, feeding cycles do exist in many species of deep-sea fish, for example, hoki (Bulman & Blaber 1986, Connell et al. 2010) and orange roughy (Rosecchi et al. 1988, Bulman & Koslow 1992, Dunn & Forman 2011). Blaber & Bulman (1987) have found diel periodicity in the feeding of deep-sea fish species from off Tasmania. They used stomach fullness to demonstrate that three species had distinct diel variation in diet: both silver scabbard fish (*Lepidopus caudatus*) and the rattail *Coelorinchus* sp. 2 were predominantly nocturnal feeders, while sea perch fed more in the afternoon.

On a larger temporal scale, Wagner et al. (2007) found that biological rhythms are present in deeper-living fish (*C. armatus* and *S. kaupi*), and their periodicity is linked to lunar cycles. Wagner et al. (2007) suggest that tidal currents may act as a zeitgeber for deep-sea fish in the Porcupine Sea Bight region of the north Atlantic. In shallower New Zealand waters on Chatham Rise, Horn et al. (2010) attempted to relate the diet of alfonsino (*Beryx splendens* Lowe, 1834) to the lunar cycle, and while no significant relationship was found, (possibly because they only sampled fish during daylight hours), it does highlight a possible linkage between tidal cycles and feeding that is an

extension of Wagner et al. (2007)'s work. It also suggests there is likely to be a periodicity in the feeding of these deep-sea fish species, and that it is likely to exist over several temporal scales, from the diel, lunar, seasonal, and annual.

5.6. Parasite analysis of serrulate and four-rayed rattail from northeastern Chatham Rise

The number of parasites in the stomachs of four-rayed rattail was generally low, and stayed relatively constant over the full size range of the sample. This correlated well with previously reported data that suggests fish species with pelagic diets have low parasite loadings compared with benthic feeding fish (Campbell et al. 1980, Houston & Haedrich 1986, Klimpel et al. 2010). This low parasite loading also agrees with the dietary description of four-rayed rattail herein being a benthopelagic feeder without a marked ontogenic shift in diet (at least over the size range examined in this study); feeding close to but rarely (if at all) from the bottom. Possible vectors for these parasites could be benthopelagic copepods and chaetognaths, as these have been reported as being intermediate digenean hosts elsewhere (Blend et al. 2000, Bray 2004).

The parasite loading of serrulate rattail was significantly higher than for four-rayed rattail, and this correlated with the benthic diet shown by serrulate rattail. The numbers of parasites increased sharply with fish size and this could be a correlation with the ontogenic shift from benthic/benthopelagic foraging to benthic scavenging in larger serrulate rattail. Digeneans are the most common deep-sea fish parasites between the depths of 200–4000 metres depth (Bray 2004), and these were also the most numerous of the stomach parasites found in the two rattail species. There may also be more than one digenean species represented, but these are currently unidentified.

Campbell et al. (1980) reported an ontogenic shift in parasite loading for *C. armatus* from the New York Bight, and related this to ontogenic changes in diet. In *C. armatus* there are also changes in brain morphology that is thought to be connected to an ontogenic shift in diet; the optical centers of the brain reduce in size and the olfactory centers increase (Wagner 2003). Wagner (2003) related this change to a shift from optically based foraging on small invertebrates to chemosensory based foraging for carrion. A similar pattern could be occurring with serrulate rattail.

The parasite fauna of deep-sea fishes is not well known in New Zealand waters or indeed elsewhere (Bray & Gibson 1995, Bray 2005), although they have been used in stock differentiation in orange roughy (Lester et al. 1988), and digeneans have been

obtained from Bollons' rattail for taxonomic purposes (Bray & Jones 1993).

Parasite analysis could be useful in determining the diets of fish that feed infrequently, as the numbers and composition of the parasite fauna are related to the dietary habits of the fish species concerned. The low parasite loadings of deep-sea fish with a pelagic/benthopelagic diet could be related to their food supply, much in the same way as the PES/PEI.

5.7. Trophic levels of fish species from northeastern Chatham Rise, Puysegur Bank and off the Wairarapa coast

The trophic levels of fish from Chatham Rise ranged between 4.01 for black slickhead, to 5.48 for long-nosed velvet dogfish. The trophic levels obtained from estimates based on intestinal contents were lower, and ranged between 3.68 for notable rattail and 4.24 for Johnson's cod. Similar values were obtained from the Puysegur Bank fish. These levels are higher than those reported by Bulman et al. (2002) (3.0–4.9) for fish species from mid-slope depths on seamounts off Tasmania. However, this may be due to differences in the trophic definitions of prey between this study and theirs. For instance, they assumed all their calanoid copepods were herbivores (2.0). Other work has shown that many benthopelagic copepods are either carnivorous or omnivorous (Bühning & Christiansen 2001, Bradford-Grieve 2004, Laakman et al. 2009), but since the ratio of carnivory to omnivory is unknown, it was assumed in this study that they were all feeding at the third trophic level. This could be an overestimate, as not all the copepods were benthopelagic species; some were vertical migrators, which may have been herbivores or detritivores. Trophic levels estimated from intestinal contents may also be biased as they are based on the presence or absence of food items, not their proportional weights.

The trophic levels for the eight fish species from off the Wairarapa coast ranged between 3.27 for silverside and 4.48 for sea perch. Generally speaking, the benthic feeders had lower trophic levels than the benthopelagic/pelagic feeders. However, as for the Chatham Rise and Puysegur samples, the lack of trophic knowledge regarding prey species limits the conclusions that can be drawn from these calculations.

Overall, the trophic levels of benthic feeding fish were generally lower than those recorded for benthopelagic/pelagic feeding fishes, the exception being the two brown-slickhead species. These trophic values are in contrast to the enriched deep-sea benthic food web predicted by Iken et al. (2001), Drazen et al. (2008), and Boyle et al. (2012).

It is possible that these low trophic values for the benthic feeders are a result of the assumptions made regarding the trophic levels of their food items, many of which are not ecologically well-known. As a consequence, these values are unlikely to be precise, but could serve as the basis for further work.

5.8. Dietary overlaps between fish species from northeastern Chatham Rise and Puysegur Bank

Generally speaking, there were low levels of dietary overlap between most species on northeastern Chatham Rise and Puysegur Bank. There were some high levels of dietary overlap and these were found between the largest fish species; two of the dogfishes and basketwork eel. Long-nosed velvet dogfish's diet overlapped with basketwork eel and Baxter's dogfish (from both Puysegur Bank, and northeastern Chatham Rise). Basketwork eel's diet also overlapped with Baxter's dogfish from Puysegur Bank and with shovel-nosed dogfish. The dietary overlap between basketwork eel and shovel-nosed dogfish, orange roughy, and warty oreo maybe an artifact caused by the aggregation of all identified and unidentified fish into one category, as the species of fish consumed by basketwork eel were much broader in variety than shovel-nosed dogfish that had fed on small mesopelagic vertically migrating fish.

The dietary overlap between basketwork eel and long-nosed velvet dogfish could be explained if both species were scavenging, as they might have had access to the same types of carrion. The dietary overlap between Baxter's dogfish from Puysegur Bank and long-nosed velvet dogfish and basketwork eel could also be interpreted as possible scavenging by Baxter's dogfish. Baxter's dogfish from northeastern Chatham Rise only had a moderate degree of dietary overlap with its conspecific from Puysegur Bank, and this may have been due to the small size of the Chatham Rise sample.

The highest level of dietary overlap was between orange roughy and warty oreo, and Bulman et al. (2002) also report the diet of warty oreo as being very similar to that of orange roughy off Tasmania. Although both samples were small, this high level of dietary overlap could be seen as an indication that warty oreo is a species that could benefit from the reduction in orange roughy biomass on northeastern Chatham Rise. However, given the long time frames for change in the deep-sea, this may take a long time to observe.

There was little in the way of dietary overlap between the large >400 mm TL and small <400 mm TL fish species, indicating clear niche separation. The only high level

of dietary overlap between small fishes was between four-rayed rattail from Puysegur Bank and robust cardinal fish. As a group, the slickheads had little dietary overlap with any other species and nor did the rattails.

On Puysegur Bank there is evidence for cold seeps in an area adjacent to where the Puysegur bank fish were sampled (Carey 1993, Lewis & Marshall 1996). However, there was no evidence of cold seep fauna in the diets of the benthic feeders from Puysegur Bank, although this may be due to the small sample size of the benthic feeders.

Both Chatham Rise and Puysegur Bank are under the influence of the STF, so are areas of heightened primary productivity (e.g., Knox et al. 2012). However, the northern flanks of Chatham Rise are less productive than the southern (Uddstrom & Oien 1999, Murphy et al. 2001, Knox et al. 2012), so northeastern Chatham Rise may be less productive than Puysegur Bank, especially during winter months when the STF moves southwards and its influence over the northeastern Chatham Rise is presumably lessened (Uddstrom & Oien 1999).

The two species from Puysegur Bank with more than ten stomach samples, Baxter's dogfish and four-rayed rattail, had similar diets to conspecifics on northeastern Chatham Rise, which suggests that at the functional level there is little difference in their feeding between seamounts and adjacent slope. There was some evidence for more fine scale differences in diet for four-rayed rattail, as the small number of calanoid copepods that were identified from Puysegur Bank were different species from those from northeastern Chatham Rise. The mean weight of copepods in the diets of Puysegur Bank fish was higher than those for northeastern Chatham Rise, which also infers a difference in species composition. The presence of *N. tonsus* in four-rayed rattail could indicate a link between the surface waters and this species, as *N. tonsus* overwinters at depth before vertically migrating back to the surface the following spring (Ohman 1987, Bradford-Grieve et al. 2001). However, the numbers of copepods identified were too small for solid conclusions to be drawn.

Four-rayed rattail from Puysegur Bank fed more on chaetognaths and had a diet more similar to robust cardinal fish than its conspecific from northeastern Chatham Rise (suggesting a more pelagic diet). It is difficult to know if this is due to four-rayed rattail feeding more on pelagic food on Puysegur Bank, or if this is a reflection of the benthic faunal composition on seamounts, which is known to differ from the surrounding slope (Probert et al. 1997, O'Hara et al. 2008, Rowden & Clark 2009). Another confounding

factor could be the difference in years between sampling, as there could be inter-annual differences in diet. This inter-annual variance in food items could also be linked to surface variations in primary productivity, as suggested for Oliver's rattail and sea perch in shallower water on Chatham Rise (Stevens & Dunn 2011, Horn et al. 2012).

5.8.1. Dietary overlaps between fish species from off the Wairarapa coast

Levels of dietary overlap between species were generally low, indicating clear niche separation between the eight species examined. The highest dietary overlap values between the stomach contents of Wairarapa fish species were between javelin fish and silver roughy, both of which consumed benthopelagic prawns. There were also high levels of dietary overlap between javelin fish and capro dory, and silver roughy and capro dory.

There is probably more dietary separation between javelin fish and capro dory than this indicated, given the large difference in size between the two species (McMillian et al. 2011). Javelin fish is a much larger fish than capro dory, and it seems reasonable to suggest that capro dory feed on prawns of a much smaller size than javelin fish. This is less likely for capro dory and silver roughy, as they were of more similar sizes, although silver roughy is still bigger. However, capro dory occasionally fed on large numbers of calanoid copepods, and occasionally small galatheids, which silver roughy did not; also silver roughy fed occasionally on fish, which capro dory did not. This is possibly another example of where a food category is too broad to detect a more subtle difference in diet. In this case "natant decapod prawns" encompassed the predominantly benthic *P. acutirostratus*, *N. magnoculus*, and the benthopelagic *Sergestes* sp. and *P. aff. sivado*. This suggests that measures of dietary overlap need to be sensitive to the size of the fish species examined, as broad dietary categories may miss subtle interactions between species.

Bollons' rattail and silverside had fed principally on benthic food. Oliver's rattail had fed upon a combination of benthopelagic and benthic food, as had sea perch. The natant decapod prawns *N. magnoculus* and *P. aff. sivado* were generally important to the benthopelagic feeders, while the crab *P. victoriensis*, and to a lesser extent the squat lobster *M. gracilis*, were important food of the benthic feeders. This suggests these upper slope fish species were closely associated with the seabed, either feeding directly on the benthos, or on free-swimming animals closely associated with the seabed.

An interesting morphological feature is that the species that had benthopelagic diets, Oliver's rattail, javelin fish, silver roughy, and capro dory, are all silver-sided fishes. Those that fed predominantly from the bottom were either drab browns; Bollons' and two-banded rattail, or had mottled red patterns; sea perch. The silvered sides of these fish could aid in camouflaging them if they forage away from the bottom. However, an exception to this was silverside, which had a predominantly benthic diet, so perhaps this is a coincidence, or there is an alternative explanation.

5.9. Feeding guilds for fish species from northeastern Chatham Rise, Puysegur Bank, and off the Wairarapa coast

Dietary data from northeastern Chatham Rise and Puysegur Bank based on the presence or absence of food items, interpreted from all gut analyses, indicated several clusters of fish species with similar diets. There was a cluster made up of benthic feeders (rattails), and another cluster made up of varying combinations of benthopelagic feeders (**Fig. 176, Fig. 177**). Shovel-nosed dogfish was a clear outlier and fed on small pelagic fish. Within the broad cluster of benthopelagic feeders, assumed feeding guilds were roughly based around the 60 percent similarity mark. Some of the smaller clusters may have been affected by the presence/absence transformation. For example, the three slickhead species are probably less similar in diet than indicated, as black slickhead consumed far fewer thaliaceans than the other two species. Also, the grouping of orange roughy and Johnson's cod is more to do with the low resolution of the Johnson's cod intestinal contents than any dietary overlap with orange roughy (although this is possible). This is also probably the case with Johnson's cod from Puysegur Bank and Baxter's dogfish from northeastern Chatham Rise. Likewise, small-headed cod had fed on fish, but also hermit crabs (Paguridea) and other benthic food, so this species could be a scavenger, and therefore also unlikely to compete for food with orange roughy. These seemingly anomalous results highlight the limitations of using functional feeding groups based on very imprecise dietary data. Basketwork eel was an outlier within the benthopelagic feeders, while long-nosed velvet dogfish from northeastern Chatham Rise and Baxter's dogfish from Puysegur Bank had quite similar diets. Four-rayed rattail from Puysegur Bank had a diet more similar to robust cardinal fish than conspecifics from northeastern Chatham Rise, although the three fish could, broadly speaking, be considered part of a small pelagic crustacean feeder guild. When only stomach contents were considered, the guilds were similar to those based on all gut contents (**Fig. 178,**

Fig. 179). There was still a pelagic fish feeder guild made up of shovel-nosed dogfish, but there was only one fish, which had a benthic diet, and while serrulate rattail fed on pelagic crustaceans and invertebrates, these could have been taken dead from the seabed, as the rest of this species's diet was benthic in origin.

The guilds are very similar to those reported for 12 mid-slope species from seamounts off southeastern Tasmania by Bulman et al. (2002). As fish with everted stomachs (and only intestinal contents) were excluded from this analysis, there is a potential bias towards fish that feed in the water column. However, Bulman et al. (2002) were able to include the stomach contents of 50 Kaiyomaru rattail, and categorise it as a benthic invertebrate feeder. They classified serrulate rattail as a benthopelagic omnivore. The stomach contents of two of this species from Puysegur Bank were similar. The inclusion of intestinal contents included more benthic feeders into the analysis from northeastern Chatham Rise. The role of the seabed in the diets of mid-slope fish is probably underestimated as a consequence of the high stomach-eversion rates of bottom-feeding fishes, and their subsequent exclusion from trophic studies.

The upper-slope fish species from off the Wairarapa coast formed four main feeding guilds (**Fig. 186, Fig. 187**). Silverside was a benthic invertebrate feeder, two-saddle and Bollons' rattails were benthic crustacean and megabenthos feeders, and Oliver's rattail, sea perch, javelin fish, and capro dory were pelagic crustacean and megabenthos feeders. The shallower upper-slope rattail species from off the Wairarapa coast did not suffer as much from stomach eversion as their mid-slope northeastern Chatham Rise congeners. Consequently they provide a more complete picture of the feeding at these depths, with the rattails (apart from javelin fish) being predominantly benthic feeders.

5.10. Food webs — trophic pathways (northeastern Chatham Rise)

A further interpretation of the feeding guilds of fish species from northeastern Chatham Rise suggests there may be three overlapping demersal food webs at mid-slope depths (**Fig. 202**). Fish species may exploit more than one pathway seasonally, and at different points of their life history. The first trophic pathway is fed by vertically migrating nekton (prawns and other small crustaceans, mesopelagic fishes, squid and other invertebrates), also known as the biological pump (Longhurst & Harrison 1989, Angel 2003, Buesseler et al. 2007, Robison 2009). The fish species that generally fed in the water column benefitted from this pathway, feeding on these vertically migrating

animals at the low point of their daily migrations, or where their vertical migration is interrupted by raised bathymetry (e.g., seamounts (Rogers 1994, Koslow 2007, Pitcher et al. 2007)). Examples of these fish from northeastern Chatham Rise were orange roughy, warty oreo, shovel-nosed dogfish, and the three slickhead species. Fish that may also exploit this pathway are Johnson's cod, white rattail, four-rayed rattail (seasonally (Clark et al. 1989)), robust cardinal fish and long-nosed velvet dogfish. Basketwork eel may also partially exploit this pathway.

The second pathway is phytodetritus-based, and driven by the passive falling and then sequential recycling of phytodetritus up through the benthic food web (Iken et al. 2001, Drazen et al. 2008, Boyle et al. 2010). Fish that exploit this pathway are typically benthic feeders; notable, rough-headed, and surgeon rattail, but could include some benthopelagic feeders: ridge-scaled rattail (Laptikhovsky 2005), small serrulate and all four-rayed rattail (Bühring & Christiansen 2001). Four-rayed rattail is included here due its consumption of aetideid copepods, which are considered to be high in triglycerols and therefore linked to the benthic food web (Bühring & Christiansen 2001). White rattail and small-headed cod may also use this pathway, but may also exploit the carrion-based pathway.

The third pathway is based on the falling of surface carrion and bypasses the benthic food web (Drazen et al. 2008). Fish exploiting this pathway are more difficult to identify owing to the difficulty in ascertaining the nature of carrion in their diets. However, there is evidence from brain structure (Wagner 2002, 2003; Yopak & Montgomery 2008), and from gut contents (Clark et al. 1989, Anderson 2005a, Dunn et al. 2010a, Horn et al. 2012) to infer that some of these species may utilise this pathway: Baxter's and long-nosed velvet dogfish, basketwork eel, large serrulate rattail, and small-headed cod. White rattail (Tales from Te Papa 2011) and brown chimaera may also exploit this pathway. This third pathway may also be augmented further by carrion in the form of fisheries discards (Clark et al. 1989, Forman & Dunn 2012, Horn et al. 2012).

It is likely that fish will exploit a combination of these pathways depending on the seasonal availability of food items. For example, serrulate rattail fed on a combination of small benthic items when small, but shifted its diet to scavenging ontogenically (Jones 2008a). This dietary shift was reflected in this species' parasite loading, which also increased with fish size. Laptikhovsky (2005) reported a seasonal shift in the diet of ridge-scaled rattail, which could also be a reflection of a shift between pathways.

The differences between the diet of ridge-scaled rattail from the southwestern and northeastern Chatham Rise may also be a reflection of a seasonal shift (Clark et al. 1989, Jones 2008a). However, in the latter case this may be confounded by methodological differences between the two studies.

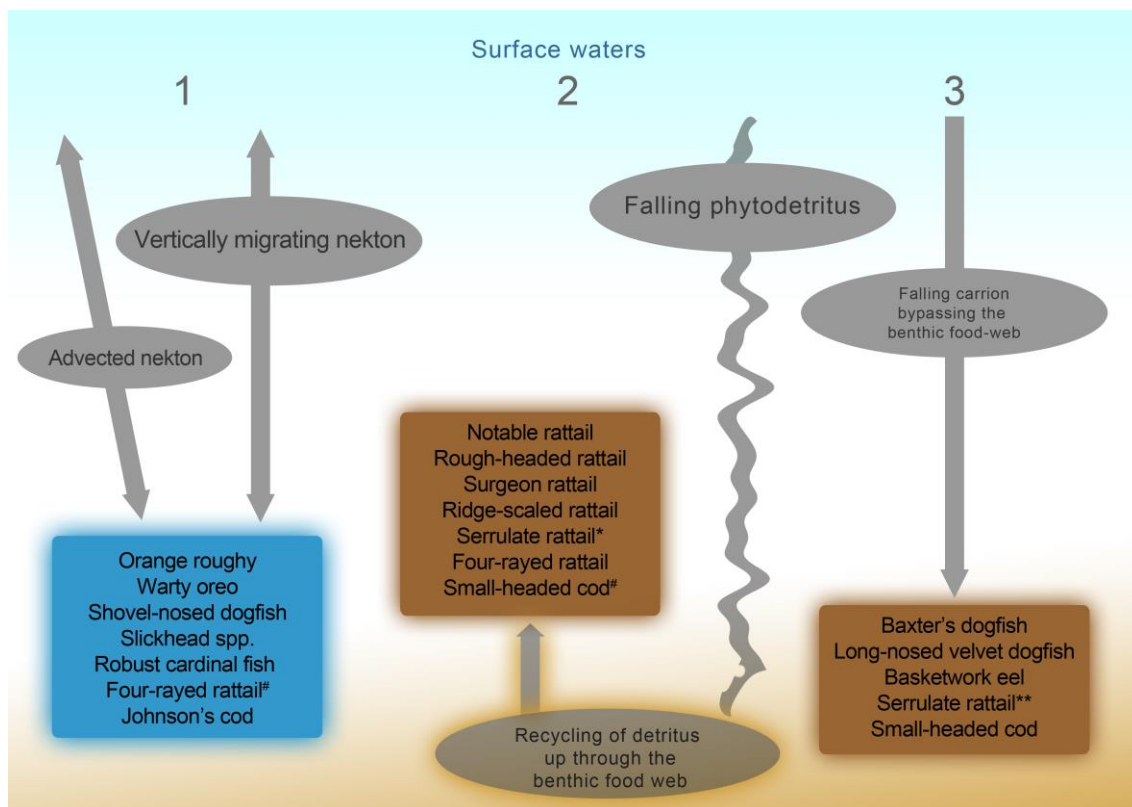


Figure 202. A simplified graphical interpretation of three deep-sea trophic pathways on northeastern Chatham Rise, and the fish species that may utilise them (after Drazen et al. 2008). 1. Biological pump pathway (including advected sources). 2. Detritus-based benthic pathway. 3. Carrion-based benthic pathway. Four-rayed rattail#, small-headed cod#: may utilise two pathways. Serrulate rattail*: small. Serrulate rattail**: large.

5.10.1. Food webs — trophic pathways (Wairarapa coast)

The trophic pathways for Wairarapa fish are less clear than those for the deeper northeastern Chatham Rise (**Fig. 203**). Javelin fish feed in the water column, as does silver roughy, and they could be relying on the biological pump pathway. However, some of the prawns both species fed on are benthic, so they could be linked to the phytodetritus-based benthic food web. However, there was no evidence of scavenging in either of these species so it is unlikely that they utilise this pathway. Capro dory and Oliver's rattail could also be linked in this way, but with a bias towards the phytodetritus-based benthic food web, as they also fed on benthic food. Fish relying predominantly on the phytodetritus-based benthic food web were two-banded and Bollons' rattail, as has been shown for Bollons' rattail on Chatham Rise (Stevens & Dunn 2011). Sea perch and silverside were also benthic feeders, and rely on the phytodetritus-based and carrion-based food web. Silverside has been shown to feed on seasonal pulses of salps as has sea perch, so they could be seen as at least partial benthic scavengers (Clark et al. 1989, Horn et al. 2012).

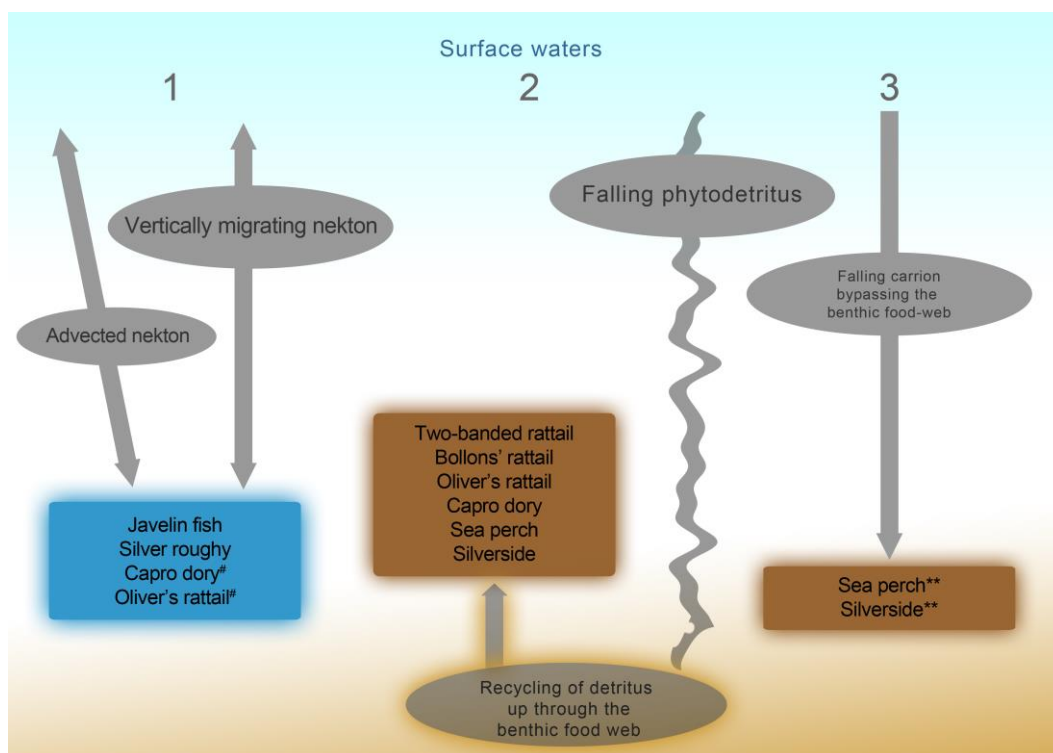


Figure 203. A simplified graphical interpretation of three deep-sea trophic pathways off the Wairarapa coast, and the fish species that may utilise them (after Drazen et al. 2008). 1. Biological pump pathway (including advected sources). 2. Detritus-based benthic pathway. 3. Carrion-based benthic pathway. Capro dory and Oliver's rattail[#], sea perch and silverside^{**} may utilise two pathways.

5.11. Section three — Feeding guilds and dietary implications

This section provides a general dietary summary for all the fish species analysed. It then provides discussion based on issues raised by these analyses. Based on the findings of this thesis, further discussion is provided regarding the potential for the application of EBFM to orange roughy fisheries in New Zealand waters.

The mid-slope demersal fish ecosystem on Chatham Rise is structured primarily by depth (Bull et al. 2001, Francis et al. 2002, Leathwick et al. 2006). The Puysegur Bank fish assemblage is likely similar (Tracey et al. 2004). On a finer scale, the fish species are segregated by diet and hence food availability (Jones 2008a, b; Stevens & Dunn 2011). The demersal ecosystem on northeastern Chatham Rise at mid-slope depths, based on stomach contents, is different to viewing it using all gut contents (stomach and intestines).

As the target of a major bottom trawl fishery, orange roughy was the most common mid-slope fish species on northeastern Chatham Rise (Doonan et al. 2006, 2009). Based on stomach contents, the diet of orange roughy on these flat soft-sediment plains is not too dissimilar to that reported from other areas, or at other times (e.g., Rosecchi et al. 1988, Anderson & Fenaughty 1996, Dunn & Stevens 2011). As for the other common bycatch species, only broad comparisons are possible owing to the lack of previous data for most of them.

The feeding of the mid-slope fish species can be divided into several narrow or broad feeding guilds. From stomach contents alone, shovel-nosed dogfish is a pelagic piscivore, while big-scaled brown slickhead is a thaliacean feeder. Pelagic crustacean feeders comprise black slickhead, robust cardinal fish and four-rayed rattail, although black slickhead could be considered more of a prawn feeder than the other two species. Perhaps this grouping demonstrates an inadequacy of the pelagic crustacean food group, so this group could be further sub-divided into small and large pelagic crustaceans. Also, many of the copepod species consumed were benthopelagic species (e.g., *Bradydium* spp.), which do not undergo vertical migrations, so describing them as pelagic crustaceans could be misleading. Robust cardinal fish and four-rayed rattail were copepod feeders, and could be classified as small-benthopelagic crustacean feeders, although robust cardinal fish may be feeding higher in the water column than four-rayed rattail (also, the consumption of benthopelagic aetideid copepods by four-rayed rattail links this species to the benthic food web). Warty oreo and orange roughy are benthopelagic omnivores, and by

weight and food groups have very similar diets (although warty oreo fed more on calanoid copepods than orange roughy). Baxter's dogfish and basketwork eel could be classified as benthopelagic fish and squid and prawn feeders, although it is likely that they both scavenge. Long-nosed velvet dogfish is a squid and fish feeder, but like the previous two species could also scavenge. Serrulate rattail is the only species in this group that could be termed a benthic feeder, and even then a cursory glance at its diet could suggest that it was another benthopelagic omnivore. All but one of the species' diets based on stomach contents would suggest a benthopelagic or pelagic diet.

Analysis of the diets of fish based on all gut contents reveals a more detailed picture of the mid-slope demersal fish community on northeastern Chatham Rise, as a further eight species were included into the analysis, plus further intestinal data from some of the previous eleven. The biggest change in the view of the demersal community is the inclusion of at least two guilds of benthic feeders (**Fig. 178, Fig. 179**). All but one of these would have been excluded from recent dietary studies on the basis of stomach eversion. Some caution needs to be exercised when interpreting these results, as the transformation of the data is extreme (presence/absence) and as such accentuates the differences between some dietary elements by giving them all equal weighting. As a consequence, a conservative approach has been applied to the structure of the guilds.

Notable, surgeon, rough-headed, serrulate, ridge-scaled, and white rattail are all considered to be benthic invertebrate feeders, or in the case of serrulate rattail, a benthic or benthopelagic feeder, with an ontogenic shift in diet to benthic scavenging. White rattail may also be a scavenger, based on its attraction to baited cameras (Tales from Te Papa 2011). Small-headed cod may also be a benthic feeder/scavenger. Warty oreo are benthopelagic feeders (fish and small invertebrates). Johnson's cod and orange roughy are also benthopelagic feeders, but the resolution of the Johnson's cod intestinal contents was quite low, so this grouping may be artificial. Baxter's and long-nosed velvet dogfish are benthopelagic fish and squid feeders, and probably scavenge. The pelagic feeders are made up of shovel-nosed dogfish, which remains a pelagic fish feeder, and a clear outlier. The thaliacean (pyrosome) feeders were big- and small-scaled brown slickhead and, to a much lesser extent, black slickhead. This inclusion of black slickhead in this guild may be a result of the presence/absence data transformation, as thaliaceans were rare in the diet of this species. There would be an argument for separating squid and thaliaceans into separate trophic groups, as there

appear to be species that are thaliacean specialists (Horn et al. 2011). Four-rayed rattail and robust cardinal fish form a similar small-crustacean feeder guild, with the diet of four-rayed rattail from Puysegur Bank being more similar to that of robust cardinal fish than to conspecifics from northeastern Chatham Rise.

There were differences in diet between conspecifics from the flat soft-sediments of northeastern Chatham Rise and the seamount habitat of Puysegur Bank. Baxter's dogfish from both areas had very similar diets, although the specific composition was different. There was an inference that fish species from Puysegur Bank may have been scavenging on orange roughy discards, for example, basketwork eel. The diet of four-rayed rattail from Puysegur Bank was different from northeastern Chatham Rise, in that more chaetognaths and larger calanoid copepods (by weight) were eaten. Puysegur Bank four-rayed rattail had fed on the calanoid copepod *N. tonsus*, which is known to overwinter at depths greater than 500 metres depth (Bradford-Greive et al. 2001). Conversely, four-rayed rattail from Puysegur Bank did not feed on polychaetes, isopods or amphipods. These dietary differences are probably not enough evidence to be interpreted as reflecting differences in habitat type, however there were some examples of differences between other rattail species from the two areas. Serrulate and ridge-scaled rattail from Puysegur Bank had fed on the galatheid *M. isos*. This galatheid is known to be associated with seamount habitat, and not with flat soft-sediments (Probert et al. 1997). The diet of Johnson's cod from both areas was quite similar, but as mentioned earlier, the intestinal contents of this species were highly digested, and detailed dietary descriptions were not possible. It needs to be mentioned that these samples were collected two years apart and under different oceanic conditions, so these confounding factors might account for some of the dietary variation between the two areas.

The area on Puysegur Bank from which the fish were trawled is very close to an area known to contain cold seeps (Carey 1993, Lewis & Marshall 1996). Despite this, there was no obvious evidence of seep fauna in the diets of any of the Puysegur Bank fish. This may be inconclusive however, as few benthic feeders were obtained from Puysegur Bank.

Scampi was conspicuous by its absence in the diets of almost all fish species examined from off the Wairarapa coast. The fish species that consumed scampi were larger fish species: bass (*P. americanus*) and hairy conger eel (*B. hirsutus*), and a large (for this sample) sea perch (205 mm SL) (**Table 5**). Even then, the occurrences were

singletons. Studies on Chatham Rise (Dunn et al. 2010c) on the diet of ling have demonstrated scampi predation. Also that scampi in the diet of ling were large, but infrequent compared the squat lobster (*M. gracilis*). Sea perch on Chatham Rise also predated scampi, but they were not an important dietary component (Horn et al. 2012). If scampi is predated by larger fish species, then this is a potential limitation of this study, as most fish retained in the scampi trawls from the Wairarapa coast were <400 mm TL. However, no juvenile scampi were recorded from the diets of the benthic invertebrate feeders (apart from the two previously mentioned species). This suggests that either juvenile scampi are not targeted by the smaller fishes in this demersal community, or they are not available to them as prey at this time of the year.

There are, as yet, no benthic protected areas (BPAs) within the Wairarapa scampi fishery. The interactions between scampi and the fish species off the Wairarapa coast were previously unknown. In the current study, feeding on scampi was rare and mainly undertaken by larger >500 TL fish; bass and hairy conger eel. There was no evidence of predation on juvenile scampi. On Chatham Rise, scampi has been preyed upon by ling (Dunn et al. 2010c) and by large smooth skate (Forman & Dunn 2012). The proportion of scampi in the diet of ling decreased with depth, which probably reflects the depth distribution of scampi. Ling mostly fed on the squat lobster (*M. gracilis*), but the proportion decreased with increasing fish size, and was replaced by larger-bodied food items (macrourid fishes, scampi, campylonitid prawns), and some evidence of scavenging.

The squat lobster (*M. gracilis*) was an important food item in a number of the benthic feeding fishes examined from off the Wairarapa coast. In the Bay of Plenty, Cryer et al. (2002) found an increase in the numbers of *M. gracilis* in trawled areas. Shackell et al. (2010) describe the overfishing of a large ground fish population as resulting in exponential increases in their prey species. In the Wairarapa scampi fishery it is impossible to ascertain whether something similar has occurred, as there are no baseline studies describing the benthic population structure before trawling commenced. Trying to ascertain a possible cause for this increase in abundance leads to more questions than answers. What kind of trophic cascade leads to *M. gracilis* being more abundant? Has the biomass of *M. gracilis* increased due to the selective removal of a predator or through the increase in food supply or through the discarding of bycatch, or is there some other forcer involved? Is there a climate effect: southern oscillation or el nino? Perhaps trawling has removed another more preferred prey species and *M.*

gracilis is now able to flourish in its absence? Cryer et al. (2002) also found decreases in other species of benthic invertebrates, notably large, fragile, and/or epibenthic species (e.g., *Alcithoe pseudolutea* Bail & Limpus, 2006, *Provocator (Iredalina) mirabilis* Finlay 1926, and *Penion cuvieranus* (Powell 1927)).

Anecdotal reports from shell collectors also noted declines in large volutid gastropods (*A. benthicola* (Dell 1963) and *A. fissurata* (Dell 1963)) in the late 1980s being obtained as bycatch from scampi trawls. Although these anecdotal reports are not verifiable, and the fine scale abundances of two species were not really known prior to the commencement of scampi trawling, they were probably high-trophic level benthic predators, due to their large size (approx. 200–300 mm for *A. benthicola*) and the biology of closely related shallow water species (Powell 1979). Volutes are direct developers; they have no planktonic larval stage and lay few eggs (Powell 1979). From these eggs can hatch one to three small volutes; a K-selected reproductive strategy making them vulnerable to extirpation. Furthermore, in New Zealand waters there are several regional species that are hard to identify, and to the untrained eye look alike (with the possible exception of *P. (I.) mirabilis*) (Powell 1979, Bail & Limpus 2006). These are species that could easily be removed from a benthic ecosystem without being noticed; the effects of their absence would be unknown and now, possibly, unknowable.

5.12. Ecosystem-based fisheries management (EBFM) and New Zealand fisheries for orange roughy

The application of EBFM principles to the harvesting of orange roughy seems a significant challenge, given the biology of the species and the destructive method of capture (e.g., Watling et al. 2010, Nourse et al. 2012). However, it might be possible, as ecosystem-based approaches to fisheries management could be implemented in an incremental fashion, and from within the QMS (Hilborn 2011); some of these approaches are being to be applied to New Zealand orange roughy fisheries (Mfish 2011). The localised nature of seamount-based orange roughy fisheries lend themselves to the place-based nature of EBFM (Clark et al. 2011). The introduction of feature limits for some North Island seamounts, the creation of deep-sea BPAs, the addition of other species into the management plans for orange roughy, and the closure of some fisheries (voluntary and enforced) are steps towards a more ecosystem-based approach (Helson et al. 2010, Clark et al. 2011, Mfish 2011). However, the lack of knowledge regarding the

ecosystem interactions of the fish species at these depths has been a significant obstacle to this progress.

Hobday et al. (2011) have built a risk assessment model for EBFM, based on the model of Levin et al. (2009). This model is designed to be of use in fisheries where data is poor, and differs from Levin et al. (2009)'s through the incorporation of risk as a function of the probability of management targets/goal not being achieved. As such it is a more complex model, and has recently been adopted by the MSC as part of their assessment protocols (MSC 2012). Some orange roughy fisheries have been described as a data poor, in terms of habitat/fisheries, and trophic interactions (Campbell & Gallagher 2007), therefore the Hobday et al. (2011) model could be used to leverage synergies between the works of Clark et al. (2010a, 2011, 2012), and the geospatial benthic habitat models of New Zealand's EEZ being developed by NIWA (Clark & Tittensor 2010, Bowden et al. 2011). This could then help to achieve MSC certification for orange roughy and its sustainable exploitation.

The New Zealand Ministry of Fisheries Deepwater Plan (2010) outlines an aspiration to have biological reference points for orange roughy fisheries by 2011. However, Tuck et al. (2010) concluded there were not enough concurrent or consistent studies at mid-slope depths to provide conclusive ecosystem indicators in mid-slope orange roughy fisheries in New Zealand waters. This in itself provides a significant ongoing barrier to the immediate implementation of EBFM to orange roughy fisheries. However, great strides have been made in recent years in the provision of a biogeographic classification for the New Zealand EEZ (Bowden et al. 2011), and seamounts within (Clark & Tittensor 2010, Clark et al. 2011). Biological reference points are important, as it has recently been found that New Zealand deep-sea fish species assemblages can vary over quite small spatial scales (Tracey et al. 2012).

The lack of an obvious deep-sea ecological indicator species is probably due to the long time-scales involved with regard to deep-sea organisms; they are often long-lived, slow growing, and difficult to study (e.g., Tracey et al. 2011). Also, perhaps there could be a search for a potential keystone/ecological indicator species/species group that could come under protection. The obvious choice has been deep-sea corals as a potential indicator species. However, while they have the advantage of being large and relatively charismatic, they do have three major disadvantages. Firstly, they are restricted to hard substrates and therefore are unsuitable for soft-sediment environments (Tracey et al. 2011). Once they are removed they are no longer any use as an ecological indicator

species, and thirdly, they are very slow growing and their recovery times are too long for them to be a valid metric for recovery.

It is known that deep-sea corals have associations with other species (Husebø et al. 2002, Costello et al. 2005, O'Hara et al. 2008), so perhaps the presence of an associated animal could be used. In New Zealand mid-slope depths there is little information regarding fish species associations with deep-sea corals, as species assemblages have been described on large spatial scales (Francis et al. 2002, Tracy et al. 2004, Bowden et al. 2011). Also, it is not known how much coral is necessary for these associations to function (Clark & Rowden 2009). In addition, recent work by Tracy et al. (2012), on the Graveyard Complex of seamount features on Chatham Rise, has shown that fish species assemblages can vary quite dramatically over quite small spatial scales; adding a further layer of complexity to this issue.

In soft sediments, bioturbators have been shown to be important in the recycling of nutrients and detritus in both shallow (Berkenbusch et al. 2000; Lohrer et al. 2004; Widdicombe et al. 2004; Giangrande et al. 2005, Lohrer et al. 2010), and deep waters (Bailey et al. (2006). For example, Bailey et al. (2006) found a temporal relationship between the numbers of echinoids and rattails of the genus *Coryphaenoides* at abyssal depths (approx. 4100 m) of the northeast Pacific. However, they were only able to speculate on the nature of this linkage, but suggested that the numbers of rattails was influenced in a bottom-up nature by the numbers of echinoids (with a time lag of nine to twenty months). However, this would link them to the benthic food web, not the carrion-based food web subsequently described by Drazen et al. (2008), so perhaps there is another driver at work here.

Nematodes have been shown to be important in the functioning of deep-sea benthic ecosystems (Danovaro et al. 2008). As with polychaete worms, as these have been shown to be important in the rapid sequestering of organic carbon (e.g., maldanid polychaetes on the North Carolina continental slope (Levin et al. 1997)), and to form hotspots of biological diversity (De Leo et al. 2009). Echinoids, nematodes, and polychaetes were all components of the diets of the benthic feeding fish examined in this study, but their contributions to the diets of these species is likely to be difficult to quantify, owing to the high rates of stomach eversion in these fish species.

Perhaps an alternative to trying to find ecological indicator species impacted by fishing would be to find species that could be re-colonising areas after disturbance, and visible on a time scale meaningful to humans. Clark & Rowden (2009) found small

hydrocorals on trawled seamounts in the Graveyard complex on Chatham Rise and suggested that these might be a better alternative to using the presence or absence of stony corals. Gage et al. (2005) found xenophyophores in recent trawl tracks and suggested they might be fast growing re-colonisers of trawled ground. Another group that could be looked at for its potential to re-colonise trawled areas would be polychaete worms or nematodes, as nematode diversity has been related to faunal disturbance (Danovaro et al. 2008).

Other deep-sea fish caught with orange roughy could also be used as potential ecological indicator species. Cardinal fish (*Epigonus telescopus*) has been moved into the deepwater management plan for orange roughy, and is managed in conjunction with orange roughy, since they are often caught together over seamounts (Mfish 2011). If this proves not to be a useful addition, perhaps there could be a search for a potential limiting species, in much the same way that rattails are considered in the Antarctic toothfish fishery (Watling et al. 2010).

Marine protected areas have proved to be a popular device to protect habitat and to promote biodiversity in shallow waters (Pinnagar et al. 2000, Mfish & Department of Conservation 2008). The setting aside of benthic protected areas in New Zealand's EEZ, while not providing total protection for deep-sea habitats, could be seen as providing protection from some of the most damaging fisheries impacts (Clark & Rowden 2009, Rowden et al. 2010b, Helson et al. 2010). Benthic protected areas do not provide protection from the impacts of fishing in the overlying waters (Mfish and Department of Conservation 2008, Mfish 2009). This could be an issue, given that most of the energy at these depths comes from the surface (Drazen et al. 2008, Ramirez-Llodra et al. 2011). Any extraction of biomass above these habitats and the subsequent discarding of fisheries waste could have unforeseen effects on the benthic ecosystem.

Some thought could be given to the protection of the food of orange roughy, as like hoki they feed off the seabed on vertically migrating fish (e.g., lantern fish: Myctophidae) (Connell et al. 2010, Dunn & Forman 2011). Lantern fishes have a relatively high calorific value (Childress & Nygaard 1983), and act as forage fish (Tacon & Metian 2009) in the deep-sea, providing a linkage between the surface waters and the deep-sea as part of the biological pump (Kozlov 1995, Moku et al. 2000, McClatchie et al. 2005, O'Driscoll et al. 2009). The trawling of forage fish in shallow waters has been considered to have unforeseen effects on higher trophic level species (e.g., Smith et al. 2011). Lantern fishes, although abundant, are not very fecund and, as

such, are vulnerable to over-exploitation (Catul et al. 2011). Thus, mid-water trawling could impact on their abundance and limit the food supply of deeper-living fish species.

One of the challenges facing the orange roughy fisheries in New Zealand for many years was the lack of information regarding juveniles, as without them it is impossible to tell if there is recruitment occurring. Orange roughy (<6 cm: 0+ to 1+ cohort) were almost unknown. In New Zealand waters, quantities of juveniles were known from two locations; north-east Chatham Rise at depths of 800–900 metres (Mace et al. 1990), and from the west coast of North Island from 250 metres depth in February 1984 (Gauldie 1998). Chatham Rise juveniles were taken from trawls in February, June and September of 1988, and were found over 100 km east of a known major spawning area (the Spawning Box), suggesting that the eggs are advected some distance (Mace et al. 1990). Gauldie (1998) does not specify where exactly on the west coast of the North Island the juveniles were caught, so determining the area from which they were likely to be spawned was not possible.

There has been some debate regarding whether juvenile orange roughy dwelt in the mesopelagic layers (Shephard et al. 2007), or in shallower waters further up the continental slopes (Mace et al. 1990). Recent meta-analysis of historical trawl data by Dunn et al. (2009) has revealed the location of orange roughy nursery grounds on Chatham Rise. Dunn et al. (2009) believe that the nursery grounds are in shallower waters (850–900 m water depth), and on the southern part of Chatham Rise, and bounded by a thermal front; the nursery grounds being found on the warmer side. It is inferred that since these were bottom-trawls, the juvenile orange roughy were associated with the seabed, perhaps for shelter or for feeding, as juvenile orange roughy are known to feed on benthic scavenging amphipods (e.g., *E. gryllus*) (Rosecchi et al. 1988, and this study). As a consequence, repeated trawling of these areas may remove the source of shelter for these juveniles, rendering them vulnerable to predation.

As orange roughy are long-lived, mature late (23–30 years), and the original population was so large, it is possible that New Zealand fisheries are still exploiting the virgin population. Recent trawls through these areas (NIWA 2008) yielded no orange roughy smaller than 23 cm SL, using a 6–10 cm cod-end mesh (Tracey pers. com.), suggesting there has been no orange roughy recruitment since the fishery was first exploited in the early 1980s. Should this be the case, then the future of orange roughy fisheries on Chatham Rise could be bleak, especially given that recent work on orange roughy from the east coast of North Island New Zealand has shown that a predicted

stock recovery has failed to take place, and that population numbers remain low (Dunn et al. 2011). In the north Atlantic, orange roughy biomass was very quickly fished down to approximately 30 percent of the original estimated biomass, and it is now thought that even with a cessation of fishing it will take about a century for stocks to recover (Watling et al. 2010).

Pinkerton's (2011) trophic model for the whole Chatham Rise is useful in identifying gaps in the current knowledge regarding deep-sea food webs in this area. The fish dietary data used by Pinkerton (2011) is mostly based on data from shallower than 800 metres (one limitation of this model is that for all but orange roughy and oreo species it only uses fish diet data from shallower than 800 metres. It does cite data from Clark et al. (1989), which was collected during spring from arguably the most productive area on Chatham Rise (Nodder & Northcote 2001). Thus it could be overestimating the productivity of the whole area if it is based on data from the most productive region, at the most productive time of the year.

Modelling work requires the use of stomach contents for the description of fish diet, and through it the flow of energy through the ecosystem (e.g., Aydin & Mueter 2007). The problem of stomach eversion (forcing the fish's stomach inside out, out through the mouth) either by the pressure expanding the gas-filled swimbladder, or by the weight of the trawl above, has long been a problem in deep-sea trophic studies (e.g., Clark et al. 1989, Drazen et al. 2001, Boyle et al. 2012). Fish with everted stomachs are usually excluded from dietary analysis, and as a consequence their role in food-web models is not represented (e.g., Bradford-Grieve et al. 2003). An example in this study is notable rattail, a small <40 cm (TL) benthic forager living at a mean depth of 985 metres in New Zealand waters (Anderson et al. 1998). As the second most abundant fish caught as bycatch in orange roughy trawls on northeastern Chatham Rise (**Table 2**), it is an important species in the demersal fish community. However, it also has a very high rate of stomach eversion, and as a consequence would be excluded from any study using stomach content analysis, or for that matter any study using stable isotope, fatty acid or DNA analysis, as the current trend for these studies is to have stomach contents available to verify these indirect methods (e.g., Stowasser et al. 2009, Dunn et al. 2010a, Pethybridge et al. 2011, Boyle et al. 2012). Notable rattail probably plays an important role in the structuring of the benthic food web, and its exclusion from trophic studies would possibly bias them.

Notable rattail is by no means the only mid-slope benthic feeding species that would be excluded from any study relying on stomach content analysis in this region. Surgeon, rough-headed, ridge-scaled, white, and unicorn rattails would also be excluded, in addition to the other rattail and cod species with small sample sizes. The same can be said for Johnson's cod, the seventh most abundant mid-slope species on northeastern Chatham Rise (**Table 2**). Indications from literature (e.g., Mauchline & Gordon 1984a) and this study indicate Johnson's cod is likely to have a benthopelagic diet and is therefore also likely to have a role in the structure of the mid-slope benthopelagic community. Leathwick et al (2006) found that the highest fish species diversity occurred between 800–1000 metre water depth, so it is very likely that there are many other species also found at these depths that would be likely to have high rates of stomach eversion (e.g., banded, filamentous, Kaiyomaru, Kermadec, and Mahia rattails, and black javelin fish). If these species also prove to be benthic feeders, further unravelling the phytodetritus-based benthic food web may lead to a greater understanding of this increased biodiversity.

Reasons for the high diversity of fish species at this depth are unclear; perhaps the high diversity in fish species is reflected in the high diversity of benthic invertebrates at mid-slope depths. It would be convenient to group these rattail species as benthic feeders, but this would be misleading, as the food and feeding of rattail species in this study varied within (ontogenically) and between species. For example white rattail, is a large rattail species (to approx. 0.7 m TL), and its role in the demersal community is currently unknown. It could be a facultative scavenger, as it has been attracted to baited cameras (Tales from Te Papa 2011). Evidence from intestinal contents suggested a mix of benthic and benthopelagic food, but this was not conclusive. The intestinal contents examined in this study were highly digested, which could suggest that white rattail does not feed often, but all intestines examined contained food, which could suggest otherwise. However, since gut evacuation rates are unknown for most deep-sea fish, this is open to speculation.

The exclusion of fish with high rates of stomach eversion could have a significant impact on studies that exclude them, especially the exclusion of benthic feeders. As a consequence, a deep-sea food web constructed solely based on stomach contents has the potential to exclude linkages between the benthos and benthopelagic realm.

The sustainability of New Zealand orange roughy fisheries has been in question for some time (Clark 2001, Francis & Clark 2005). On one hand Mfish, believes that

they are sustainable (Mfish 2010), but on the other there is a growing body of literature that suggests they are not (Clark 2001, Francis & Clark 2005, Watling et al. 2010, Dunn & Forman 2011). Alternatively, if orange roughy fisheries are sustainable they may be at reduced catch sizes, which might not prove to be economically viable in the long term (Watling et al. 2010). Meanwhile, the fishing of orange roughy worldwide has been akin to mining, with a sequential series of 'boom and bust' fisheries giving the illusion of sustainability (Clark 1999, Francis and Clark 2005, Watling et al. 2010, Nourse et al. 2012). In New Zealand waters it has been the sheer size and distribution of the virgin population that has allowed this to continue (Clark 1999, Branch 2001, Dunn & Forman 2011).

Watling et al. (2010) believe that it is theoretically possible for deep-sea fish species to be harvested successfully, but they note that there are several caveats that need to be addressed before this could happen. Firstly, they believe that no deep-sea fishery that has significant bycatch or habitat impact can be sustainable. Deep-sea organisms are not adapted to cope with the impacts of heavy bottom-trawl gear and are quickly damaged or removed by them (e.g., corals and other erect biogenic habitat) (Rogers 1999, Rogers et al. 2007, Clark & Rowden 2009). As a result, bottom-trawling should be avoided under any circumstance in the deep-sea (Watling et al. 2010). Traps and long-lines are considered to have less impact, although long-lines fish indiscriminately. Mid-water trawling would avoid impacts with the bottom, and while this is possible with orange roughy spawning plumes orange roughy exhibit a dive-flight response to towed objects and avoid mid-water trawls (Koslow et al. 1995a, Clark 1995b). Koslow et al. (1995a) demonstrated that orange roughy reacted to a towed acoustic transducer when came within 130 metres of a spawning aggregation. The aggregation was shown to contract into a 25 metre pyramid shape. Also a metal bar was dropped over the side over the aggregation, causing a similar avoidance response.

However, orange roughy have proved quite passive when approached by submersibles (Lindsay et al. 2000; Lorange et al. 2002; Uiblein et al. 2003). Lorange et al. (2002) report approaching an aggregation (estimated at over 4000 fish) with the submersible "Nautil", and not eliciting a dramatic avoidance response. This particular aggregation was located in a canyon with almost zero ambient current, so it is possible that orange roughy aggregate not only to spawn and to feed but also to allow energetic recovery between foraging trips onto open water (Koslow 1996; Uiblein et al. 2003). It is possible that orange roughy are in a state of heightened awareness and display

avoidance behaviour only during spawning season, but even so, perhaps mid-water trawling could be a technique that could be revisited.

Orange roughy are active foragers, not scavengers, and tend to take their prey whole (pers. obs.), so it would seem unlikely they could be caught on hooks with longlines. This would be the least ecologically destructive method of catching them, although longlines are unselective, so bycatch could become an issue. Perhaps longlines through aggregations might work, but then the ‘dive-flight’ reflex could become an issue. The main problem with these alternative methods of capture would be ensuring their economic feasibility. Watling et al. (2010) suggest that the rebranding of orange roughy as a ‘boutique fish’ could possibly be a way forward here. Perhaps there could be a synergy with the rebranding of orange roughy in this way, coupled with MSC certification, so as to fit in with Mfish's aspirations.

Hilborn (2010) argues that the concept of maximum sustainable yield (MSY) could be supplanted by the concept of ‘pretty good sustainable yield’. However, this could be achieved through applying the precautionary principle, and reducing TACs until they achieve ecosystem-based goals (Gibbs 2008). Reducing the TAC for orange roughy and closing fisheries would be the most obvious action that could be undertaken by the ministry, and indeed this is what has happened (Mfish 2011). The issue here is that recent information from Dunn and Forman (2011) suggests that for at least one fishery this has not worked, and that these stocks have continued to decline. If the ministry were to close the fisheries to allow stocks to recover, they may have to close them for a very long time; effectively forever, in economic terms (Watling et al. 2010). It is perhaps a reflection of the lower productivity of life in the deep-sea that the fisheries collapses that took 50 years to occur in coastal waters have only taken 5–10 years in deep-sea fisheries (Nourse et al. 2012). Nourse et al. (2012) concur with Watling et al. (2010); it is unlikely that a deep-sea fishery can be sustainable where there is significant bycatch or habitat impact.

Management of orange roughy fisheries using EBFM principles is possible, but only with an increased knowledge of the surrounding ecosystem and the interactions within it. The success of the QMS will probably mean EBFM aspirations will be incorporated into existing single-species management plans, rather than the implementation of a separate ecosystem-wide management plan. This study helps our understanding of the food and feeding relationships of mid-slope depth fish at two sites

and augments data for the food and feeding of upper-slope fish from a third. As such, it helps to fill some knowledge gaps and assists in the further implementation of EBFM in New Zealand waters.

5.13. Section four — Conclusions

This section includes the conclusions of this study plus recommendations for further research.

There is evidence to suggest there are three food pathways in the demersal fish assemblages on both the mid and upper slopes in New Zealand waters. The first of these three is based on the biological pump, the second on the recycling of detritus up through the benthic food web, and the third on the bypassing of the benthic food web through the consumption of carrion from the surface waters, including the dead (or moribund) bodies of thaliaceans (or other pelagic animals originating from seasonal blooms). In addition, this pathway may be augmented by fisheries bycatch. Fish species may utilise more than one of these pathways at a time and may move between them seasonally, or ontogenically.

The benthic detritus-based food web has fish as top predators. Many of these benthic-feeding fishes have high rates of stomach eversion and are typically excluded from dietary studies. As a consequence, their roles in mediating the structure of the benthic community have hitherto been underestimated. Dietary reconstruction based on intestinal contents is possible in the absence of stomach contents, as long as appropriate precautions are followed. The slickhead species had a great deal of identifiable material in their intestines. Conversely, the intestinal contents of Johnson's cod and white rattail were highly digested and provided much less dietary information.

Of the 19 species from northeastern Chatham Rise (>10 stomach or intestinal samples), eight species' diet were described largely from intestinal contents. Of those eight, six were predominantly benthic feeders. This was reflected in the feeding guilds, as those guilds based on all gut contents provided different results from those based on stomach contents.

There were generally low levels of dietary overlap between species from northeastern Chatham Rise, indicating clear niche partitioning between most species. Species pairs with the highest levels of dietary overlap were Baxter's and long-nosed velvet dogfish, basketwork eel and shovel-nosed dogfish, and orange roughy and warty

oreo. Levels of dietary overlap were generally high within species, with the exception of serrulate rattail, which had a clear ontogenic shift in diet.

There may be evidence for dietary shifts for conspecifics between the soft-sediment flats of northeastern Chatham Rise and the harder seamount terrain of Puysegur Bank. There were slight differences between the diets of conspecifics from the flat soft sediment of northeastern Chatham Rise and the seamount terrain of Puysegur Bank. Four-rayed rattail from Puysegur Bank had a diet more similar to robust cardinal fish from northeastern Chatham Rise than its conspecific. This may reflect a more pelagic diet for four-rayed rattail on Puysegur Bank, but this could be confounded by sample year. There were some small differences between the diets of serrulate and ridge-scaled rattail on Puysegur Bank compared with northeastern Chatham Rise, but samples were too small for conclusive analysis.

Parasite analysis of two closely related rattail species indicated a potential for parasite analysis to be used to elucidate dietary relationships. Four-rayed rattail had a fairly consistent diet and little in the way of an ontogenic shift in diet or parasite loading. Conversely, serrulate rattail had a pronounced ontogenic shift in diet and parasite loading. Four-rayed rattail fed primarily on benthopelagic/pelagic food, while the diet of serrulate rattail was benthic/benthopelagic with an ontogenic shift to scavenging. This shift coincided with a dramatic increase in stomach parasites. Therefore there is some potential for the use of stomach parasites as a proxy for diet.

The percentage of empty stomachs in a given sample for a given species could be used as a proxy for the immediate productivity of an area at a given time. On northeastern Chatham Rise many fish species did not appear to feed frequently and this may be related to the seasonal food supply. The percentage of empty stomachs may be confounded by the rate of stomach eversion in some species.

5.16. Recommendations

This research has led to the identification of possible further avenues of enquiry.

These are outlined below:

Further investigations into the trophic pathways into the deep-sea: can this phenomenon be verified? If so, does it occur on greater scales: geographically and seasonally? Are there any depth related trends?

What are the habitat preferences of these fish species? More detailed comparisons are needed between habitat usage and diet, with a view to investigating the diets of fish on seamounts versus adjacent soft-sediments.

Are there fish species that benefit from the reduction in orange roughy biomass?

Could there be species replacement in the deep-sea?

Can the parasite loadings of these deep-sea species be used as dietary, and therefore ecological, indicators? Can the number of parasites be related to scavenging activity: do more parasites mean more scavenging?

To what extent can the PES/PEI be used as a proxy for local productivity?

Do these non-commercial species migrate, or are they resident at particular sites?

What is the diet of these fish species elsewhere in New Zealand waters? Are there latitudinal gradients?

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Appendices

Appendices

Limitations of this study

Due to the opportunistic nature of the sampling on northeastern Chatham Rise, several species fish were not available for sampling, or the samples retained were very small. These were in the main QMS species: the two oreo species (black and smooth), hoki, black cardinal fish (*Epigonus telescopus*), alfonsino (*Beryx splendens*), hake (*Merluccius australis*, Hutton, 1872), ribaldo (*Mora moro*), pale ghost shark (*Hydrolagus bemisi*, Didier, 2002), and ling (*Genypterus blacodes*). However, apart from the oreo species, none of the others made up >1.02 percent of the catch, and none of them were amongst the eight most abundant (by number) bycatch species on northeastern Chatham Rise estimated by Doonan et al. (2009).

Fish retained from Puysegur Bank were also collected opportunistically by the New Zealand Ministry of Fisheries Scientific Observer Programme (under instructions to collect rattails and sharks), so many typical mid-slope species were likely to be omitted (Francis et al. 2002). As for the Wairarapa sample, these fish were collected using scampi trawl gear, which is lighter, has a smaller mesh size, and has a lower headline height than orange roughly bottom trawl gear. As a consequence, the Wairarapa material is not directly comparable with the deeper northeastern Chatham Rise, or Puysegur Bank material.

There are known issues with using stomach contents to elucidate fish diet, the main one being that they represent but a snapshot of a fishes diet (e.g., Clark et al. 1989). Another issue is that if the fish suffers from mechanically induced regurgitation or pressure induced stomach eversion, then the stomach contents can be lost. Fish affected in this way are routinely excluded from dietary analyses (e.g., Clark et al. 1989; Connell et al. 2010; Horn et al. 2010a, b; Dunn et al. 2010a, b, c; Stevens & Dunn, 2011).

The use of intestinal contents as a substitute for stomach contents also has limitations, as most obviously intestinal contents have been digested (fully or partially), meaning that often only hard parts remain. The two main limitations are: it is impossible to tell how many feeding episodes intestinal contents represent, or over what time period, so they are in some ways ‘time-averaged’, but the time period is unknown. It is also impossible to distinguish between the fish’s food, and its prey’s food.

Fish species were combined within each sampling region, both over depth and time. For fish from northeastern Chatham Rise there were insufficient replicates to allow meaningful comparisons to be made between either depth and, or time of the trawls. For example, all black slickhead came from one trawl, and all but one was female. For Puysegur Bank, the dates but not the time-of-day for the trawls was known, so these comparisons were also not possible. For the Wairarapa coast sample, fish species were arbitrarily and unevenly spread between depth and latitude, and this precluded meaningful analysis between either. It is possible that this agglomeration of samples may obfuscate some latitudinal or depth variation in the diets of the northeastern Chatham Rise and Wairarapa fish. However, any analyses would have been confounded by the size of the fish, the time of day it was caught, the depth, and the small sample size available.

Publications

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