Trophic ecology of Gould’s arrow squid (*Nototodarus gouldi*) in Aotearoa New Zealand

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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 which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

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Abstract

Deep-sea squids (order Oegopsida) are recognised for their integral role in marine ecosystems, which can be investigated through detailed trophic studies. Gould's arrow squid (*Nototodarus gouldi*) is a commercially exploited species in the southwest Pacific. Although prey composition has been reported from Australia, no research to date has been published on this species' diet in Aotearoa, New Zealand. This integrative study combined morphological, DNA analyses and helminth parasite identification to provide the first data on the prey of *N. gouldi* in Aotearoa, New Zealand*.* Gut contents were visually screened for parasites and hard parts of prey remains—including otoliths, eye lenses, squid beaks, crustacean exoskeletons and soft tissues. The conservative DNA barcode region (cytochrome *c* oxidase subunit I [COI]) was sequenced for representative pieces of soft tissue (which could not be visually identified). Overall, 26 species from across six phyla were reported, including 18 novel species herein reported for the first time in the diet of *N. gouldi.* This baseline information on the prey species and parasites of *N. gouldi* may serve as a foundation for ecosystem-based fishery management and understanding trophic interactions and prey dynamics within the south Tasman region.

Acknowledgement

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1.0 Introduction

For millennia, society has imposed demands on products and services provided by marine ecosystems. In this century, the prevalence of modern technology has accelerated the impacts of anthropogenic-induced alteration and degradation on our oceans. One of the major challenges we face is the unsustainable exploitation of oceanic resources, which in combination with climate change, could explain the continuous global decline of wild fish stocks and multiple fishery collapses (Wang et al., 2022; Wootton et al., 2021). Many current fishing practices overlook the ecological expense of exploiting a target species and the multi-species nature of many harvesting methods. Therefore, to preserve and sustain stocks and habitats for future generations, it is increasingly vital for policy goals and management actions to be guided by an ecosystem-based fishery approach (Francis et al., 2007; Pikitch et al., 2004). Although this concept has been applied earlier to terrestrial systems such as forests, the underlying themes are relevant to the management of marine fisheries (Brodziak & Link, 2002; Francis et al., 2007).

A holistic management approach

Ecosystem-based fishery management is recognised as a holistic approach that incorporates multifaceted information about the ecosystem into the policies and management of fishery stocks. It aids in the decision process and aims to achieve objectives such as reducing ecosystem degradation and building overall long-term resilience, while achieving often-conflicting societal goals and maintaining fishery supply (Brodziak & Link, 2002; Francis et al., 2007; Pikitch et al., 2004). Ecosystem-based modelling merges historical single-species management and monitoring approaches and further accounts for multiple dimensions, including critical habitats, population dynamics, prey of the target species, and anthropogenic factors (Pikitch et al., 2004). Relevant stakeholders first form policy goals that directly translate into quantifiable metrics (Brodziak & Link, 2002). Metrics are utilised in ecosystem models to evaluate and quantify management actions and are categorised into three mutually interactive measures: abiotic, biotic and human (Brodziak & Link, 2002). A fundamental part of biotic metrics is described by performance measures such as single species parameters, connectivity in food webs and community-level diversity (Brodziak & Link, 2002, Francis et al., 2007).

Analysing food webs is essential in biotic metrics that evaluate specific goals identified for ecosystem-based management (Brodziak & Link, 2002, Francis et al., 2007). Assessing the taxonomy present within assemblages is fundamental in understanding potential interactions between species that make up a food web community (Francis et al., 2002). Food webs and associated cross-linkages between species form the scaffolding for larger trophic-level interactions and are essential when building indices that can communicate community dynamics and the status of the habitat, such as species richness and diversity (Paine, 1980). When ecosystem models are coupled with existing single-species models, these reference points can reflect the overall status or achievement of the goal (Howell et al., 2021; Townsend et al., 2019). Yet, ecosystem and single-species models are both limited by insufficient information on linkages that occur in the marine food web and empirical data on the role many species play in food webs across their various life stages (Brodziak & Link, 2002; Clegg et al., 2018; Cury et al., 2005). Hence, studying species occurrence or prey abundance within predator diets can fill these gaps and provide insight into potential interactions between target fishery species and the environment at the time of feeding (Francis et al., 2002; Ibánez et al., 2021; Lansdell et al., 2007).

Complications of studying cephalopod fisheries

Fisheries for squids (order Teuthida) present unique challenges for ecosystem-based fisheries management. The global commercial cephalopod fisheries are estimated to be 10.2 billion USD, making up approximately 6.8% of total global exports of seafood (Food and Agriculture Organisation of the United Nations [FAO], 2022). In 2020, wild-caught squids made up one-third of the total captured mollusc species; of this are two major commercially targeted squid groups: the coastal family Loliginidae (order Myopsida) and the Ommastrephidae (order Oegopsida) (FAO, 2022). Although fishing these species can be economically rewarding because of their fast growth and high abundance, their semelparous lifecycle with a short lifespan makes their stocks complicated to manage (de la Chesnais et al., 2019; McGregor & Tingley, 2016). In addition, regional cephalopod biomasses and abundances are influenced by seasonal components and environmental factors (Lansdell & Young, 2007, McGregor & Tingley, 2016). Gathering ecological data on squids is further complicated by their diverse life stages with species from

Ommastrephidae in particular, are migratory and use a range of pelagic feeding strategies, which decrease the chance of sampling success (Cherel, 2020). In addition, shelf-living squids are more commonly sampled, making squid stocks in the high seas less accessible and relatively unknown (Cherel, 2020; Moustahfid et al., 2021). These factors contribute towards large fluctuations within global squid fisheries, which makes their population numbers and distribution difficult to predict (Moustahfid et al., 2021).

Independent of their utility to humans, cephalopods—especially squids—play integral roles in marine ecosystems (de la Chesnais et al., 2019). Cephalopods serve as key prey for higher trophic levels (Staudinger et al., 2013), as underlined by studies on pelagic ray-finned fishes (Logan et al., 2021; Young et al., 2006), elasmobranchs (Rosas-Luis et al., 2016), seabirds (Flemming et al., 2013), and marine mammals (Kirkwood et al., 2008). In addition, squids are also voracious predators known to feed opportunistically, reflected by their versatile feeding behaviours (Becerril-Garcí et al., 2020; Coll et al., 2013; Ibánez et al., 2008). Many migrating neritic squids occupy different depths across their lifespan, exchanging resources among diverse coastal shelf systems to continental slopes, forming the essential links between smaller prey and apex predators (Arkhipkin, 2013; Coll et al., 2013). Even partial consumption of prey, a behaviour common to squids, brings remnants to oligotrophic communities feeding benthic fauna (Arkhipkin, 2013). Squids play a significant role in the world's oceans; models stimulated by Coll et al. (2013) have shown that removing large biomass of squids or environmental decline of primary production will likely have a large-scale bottom-up effect on marine ecosystems. The significant linkages in the marine food web consequently become their demise, with their role as conveyors for pollutants such as heavy metals (Lischka et al., 2019; Lischka et al., 2020) and plastics (Rosas- Luis, 2016; Sambolino et al., 2023); with the long-term effects on the animal such as metabolism and trophic effect yet to be understood.

In Aotearoa New Zealand, two ommastrephid squid species are commercially harvested. The endemic southern arrow squid, *Nototodarus sloanii* (Gray, 1849), occurs around Te Waipounamu (the South Island), and the northern (or Gould's) arrow squid *Nototodarus gouldi* (McCoy, 1888) occurs in the northern part of the NZ Exclusive Economic Zone (EEZ) and westward into eastern Australian waters. Although no juvenile *N. gouldi* have been reported from the east and southern coasts of the South Island, paralarvae and juveniles of *Nototodarus* 'sp.' were reported in large numbers in coastal waters (Uozumi & Forch, 1995; Uozumi, 1998). Similarly, juvenile and adult *Nototodarus* spp. appear concentrated on the shelf and upper slope (Francis et al., 2002), later migrating to deeper waters with age (Uozumi & Forch, 1995). After mating, females migrate to shallower shelf regions to spawn, whilst males are hypothesised to remain in slope waters (Uozumi & Forch, 1995; Uozumi, 1998). Spawning occurs throughout the year when mass quantities of eggs are produced; these hatch into paralarvae, and eventually, surviving individuals are recruited into the population (McGregor & Tingley, 2016) with *Nototodarus* sp. living for about one year reflecting a new annual stock.

Within Aotearoa, both species together are estimated to contribute 30,081 metric tonnes in annual landings (Ministry for Primary Industries [MPI], 2022a plenary report). Despite their mostly non-overlapping distributions, within the Fisheries Act, *Nototodarus gouldi* and endemic sister species *N. sloanii* continue to be managed under the same quota management system (QMS) as a single stock (Smith et al., 1987). This is fundamentally problematic since individuals of one species cannot 'balance out' the potential overharvesting of the other species (H. Braid, pers. comm.). Different higher and lower trophic-level species will also be impacted by fluctuations in these two squid species populations. *Nototodarus gouldi* is a prevalent prey item for many marine vertebrates having been reported in particularly high frequency from the stomachs of generalist predators such as common dolphin, *Delphinus delphis* (Linnaeus, 1758) (Meynier et al., 2008); New Zealand fur seal, *Arctocephalus australis forsteri* (Lesson, 1828) (Emami-Khoyi et al., 2016); and protected taonga species Maui and Hector's dolphin, *Cephalorhynchus hectori maui* (Baker, Smith & Pichler, 2002) and *Cephalorhynchus hectori* (Van Beneden, 1881) (Miller et al., 2013) although some interspecific differences exist. To date, the diet of *N. gouldi* itself has only been studied in Australian waters, where it is known to prey on a broad spectrum of benthic and pelagic species (Braley et al., 2010; O'Sullivan & Cullen, 1983; Pethybridge et al., 2012). Thus, knowledge of *N. gouldi* feeding ecology would help us to characterise predator-prey interactions, which are fundamental in composing the biotic metrics within ecosystem-based models and trophic web construction (Ibánez et al., 2021), an approach Aotearoa New Zealand wants to adopt by 2030 (Department of Conservation [DOC], 2020).

Squid ecology: Complexities and techniques

Despite its significance in the ecosystem, there is a paucity of data on the trophic ecology of squids due to the complexity and biases of reconstructing cephalopod diets (Ibánez et al., 2021). All squids possess a sharp beak that cuts prey items into small pieces, which are then funnelled down a narrow oesophagus (Jackson et al., 2007; Bolstad & O'Shea, 2004), which means prey items are masticated into multiple unidentifiable pieces (Braid & Bolstad, 2014; Ibánez et al., 2008; Uozumi, 1998). Furthermore, under natural feeding circumstances, factors such as stress, body weight and meal size all influence squid digestive rates (Wallace et al., 1981). The analysis becomes more complex for researchers utilising various preservation methods that degrade stomach samples along with rapid digestion where already fragmented hard structures like fish scales, otoliths and bones get bleached or eroded, limiting the scope of visual identification (Ibánez et al., 2008; Jobling & Breiby, 1986; Wallace et al., 1981). Earlier studies on diet reconstruction of the trophic ecology of *Nototodarus* spp. have often relied solely on visual identification of prey remains (e.g., Pethybridge et al., 2012). However, studies on other oegopsids, such as *Idioteuthis cordiformis* (Chun, 1908) (Braid & Bolstad, 2014) and *Moroteuthopsis ingens* (Smith, 1881) (McBride et al., 2023) have proven the advantages of using integrated methods. Utilising a combination of morphological and molecular techniques to overcome limitations posed by the integrity of stomach contents can help improve the number of prey taxa identified with a high degree of confidence.

Present study

We present the first dietary study on Gould's arrow squid *Nototodarus gouldi* sampled within Aotearoa New Zealand's exclusive economic zone (EEZ). Based on morphology, DNA sequencing, and helminth parasite identification, an integrative approach is applied to gut contents analysis to investigate *N. gouldi*'s feeding ecology. The resulting information will improve our understanding of this species' role within local trophic food webs and this species' potential as an intermediate host for parasites, supporting ecosystem-based management goals.

2.0 Materials and methods

2.1 Sample collection

Nototodarus gouldi specimens collected in January 2012 were from the Chatham Rise, while samples collected in August 2013 and February and April 2015 were from the west coast of Te Waipounamu, Aotearoa (South Island, New Zealand) (**Table 1**). Squid specimens (n = 70) were collected by researchers from the National Institute of Water and Atmospheric Research, Ltd (NIWA), the Scientific Observer Programme, and the AUT Lab for Cephalopod Ecology & Systematics (ALCES). NIWA collections were conducted onboard the RV *Tangaroa*, utilising a Hoki bottom trawl, which captured *N. gouldi* at depths of 90 – 397 m. The station number, coordinates, depth of capture, mantle length, and sex were recorded. Stomach caeca were dissected and frozen at -20ºC before being sent to AUT (Auckland, New Zealand) for analysis.

Table 1.
Summary of the caecum samples collected in Aotearoa New Zealand between 2012, 2013 and 2015 (N = 70). Location is based on coordinates where the sample was taken. Depth of capture (m), voyage number, and number of *Nototodarus gouldi* samples caught per voyage are listed.

Date	Location	Depth (m)	Voyage	# of samples
January 2012	43º4'S 177º7'E	333 – 338	TAN1201	14
August 2013	-40º7' to -41º7'S 169º9' to 171º5'E	208 – 397	TAN1308	21
February 2015	-40º3'S 173º6'E	73 – 78	TRIP4299	6
April 2015	-38º5' to -38º6'S 173º9' to 174º E	90 – 98	TRIP4299	16
March to April 2015	-40º5' to -41º5'S 171º1 to 173º1'E	24 – 395	KAH1503	13
			Total caeca	70

2.2 Stomach caecum analysis

Stomach caeca were thawed at room temperature. All stomach caecum contents were extracted individually, and a qualitative assessment of gut content was recorded following methods adapted from Jackson et al. (1998) following modifications by Chantheran (2022). All prey items were categorised by hard parts or representative soft tissue through examination under a Leica dissection microscope. Identifiable hard parts, including bones, eye lenses, scales, squid beaks, suckers, gladius fragments, and crustacean exoskeletons, were stored individually and preserved in 70% ethanol. Otolith identifications were confirmed by Darren Stevens (NIWA Wellington, New Zealand). Photographs of hard parts, such as chelipeds, sternum, abdomen and telson (**Fig. 2B**) were confirmed as brachyuran crab megalopa fragments by Jeff Forman (NIWA Wellington, New Zealand) and Wilma Blom (Tāmaki Paenga Hira, New Zealand). Images of peduncles, shards of white shell, and modified thoracic appendages or cirri belonging to lepadid barnacles, commonly known as gooseneck barnacles was confirmed by Wilma Blom (Tāmaki Paenga Hira, New Zealand) and John Buckeridge. Wilma Blom (Tāmaki Paenga Hira, New Zealand) and Andrea Alfaro (Auckland University of Technology, New Zealand) provided insight into the photographs of an invertebrate worm (**Fig. 2E** and **F**). Conspecific otoliths were tallied and divided by two to infer the minimum number of individuals consumed.

Representative soft tissue samples were selected due to variable texture, colour and morphology, then re-frozen at -20ºC until DNA extraction. Hard parts that had soft tissue remains attached were subsequently DNA barcoded (see Section 2.3 below) to confirm their identifications (**Appendix 1**). Macroscopic helminth parasites found in the lining of the stomach caecum membrane or within the contents were extracted and stored in 95% ethanol before being sent to Jerusha Bennett (University of Otago, Dunedin, New Zealand) for identification. Photographs were taken of all the representative parts of the stomach, otoliths, and distinguishable contents that required further identification (**Fig. 1** and **2**).

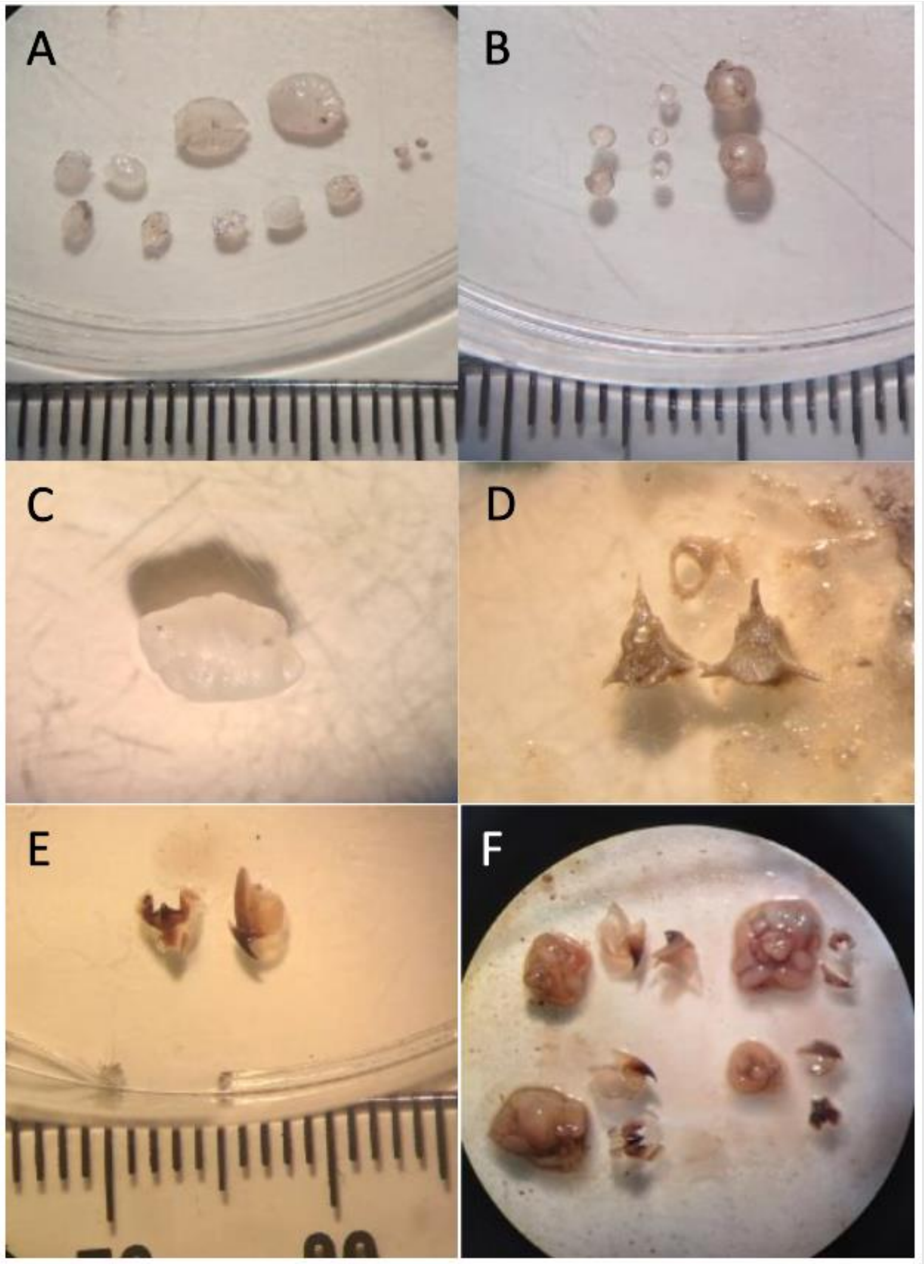


Figure 1. Characteristic hard parts and associated soft tissues from *Nototodarus gouldi* caeca collected from the West Coast of the South Island and the Chatham Rise, Aotearoa New Zealand. **A)** Otoliths of *Symbolophorus boops* (Richardson, 1845) (large) and *Lampanyctodes hectoris* (Günther, 1876) (small) (sample NOG13-020); **B)** fisheye lenses (sample NOG13-020); **C)** otolith of *Gnathophis* sp. (sample NOG15-047); **D)** vertebrae of *Gnathophis* sp. with soft tissue (sample NOG15-047); **E)** *Stoloteuthis maoria* (Dell, 1959) beak (sample NOG12-030); **F)** *Nototodarus gouldi* (McCoy, 1888) beaks (right) beside the associated buccal mass (left) (sample NOG15-024). The scale bar shows 1-mm increments.

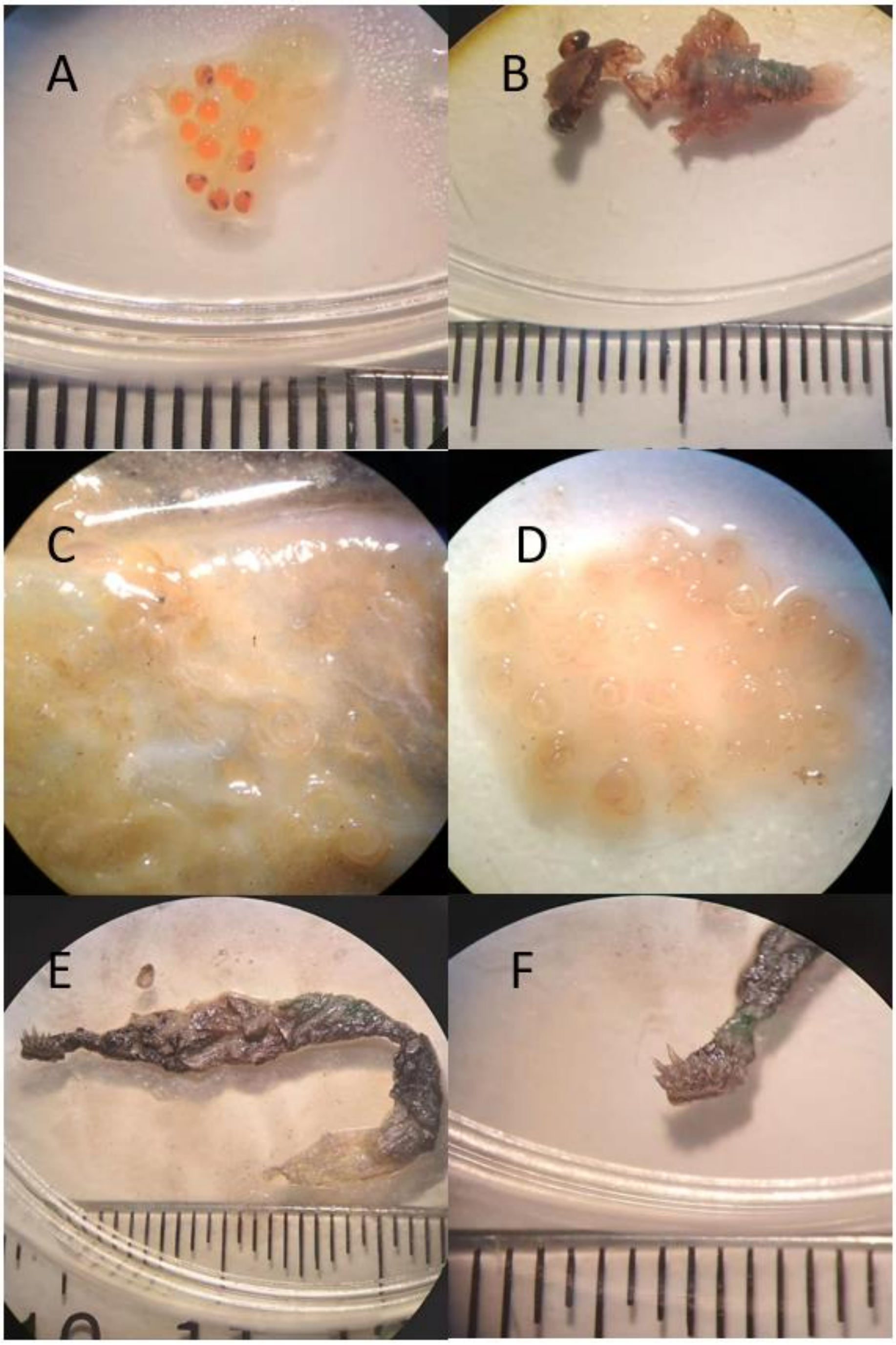


Figure 2. Prey remains and parasites from *Nototodarus gouldi* caeca collected from the West Coast of the South Island and the Chatham Rise, Aotearoa New Zealand. **A)** *Ibacus alticrenatus* (Spence Bate, 1888) mid-stage eggs (sample NOG13-025); **B)** *Guinusia chabrus* (Linnaeus, 1758) megalopa head, abdomen, and telson (sample NOG15-017); **C)** *Anisakis pegreffi* (Campana-Rouget & Biocca, 1955) parasites in the caceum lining (sample NOG15-038); **D)** *Anisakis pegreffi* parasites dissected out of caecum lining (sample NOG15-038); **E)** unidentified worm species (sample NOG13-048); **F)** close up of the head of unidentified worm species from figure 2E (sample NOG13-048). The scale bar shows 1-mm increments.

2.3 DNA barcoding

DNA extraction followed DNEasy Blood and Tissue Kit (Qiagen) protocols using Qiagen reagents and EconoSpin columns (Epoch Life Science). DNA was eluted with 100ul of elution buffer (Buffer AE, Qiagen). The 648–bp region of the cytochrome *c* oxidase subunit I (COI) gene was amplified with primer set LCO1490/HCO2198 (Folmer et al., 1994) following protocols in Braid and Bolstad (2019). For samples that failed to yield a single clear band on a 1% agarose gel stained with GelRed (Biotin), a subsequent PCR was performed using mammal cocktail primers (C_VF1LFt1/C_VR1LRt1; Ivanova et al., 2007).

Samples with LCO1490/HCO2198 primers were placed into the thermocycler with the following profile: Hot start of 94°C for 1 min; 5 cycles of 94°C for 40 s, 45°C for 40 s, 72°C for 1 min; 35 cycles of 94°C for 40 s, 51°C for 40 s, 72°C for 1 min; extension at 72°C for 5 min, and held 4°C indefinitely. Samples amplified using C_VF1LFt1/C_VR1LRt1 mammal cocktail primers were amplified using the following profile: hot start of 94°C for 1 min; 5 cycles of 94°C for 30 s, 50°C for 40 s, 72°C for 1 min; 35 cycles of 94°C for 30 s, 54°C for 40 s, 72°C for 1 min, an extension of 72°C for 10 min, hold 4°C indefinitely, following thermocycling protocols from Braid et al. (2012). All PCR products were analysed on a gel as previously described, and only those showing a single clear band were sent for sequencing. Samples were sequenced by Macrogen (Korea) using the same primers used for amplification for FOLMAR LCO1490/HCO2198 or M13-tailed mammal cocktail primers C_VF1LFt1/C_VR1LRt1.

Raw sequences were edited, arranged into contigs, and aligned in CodonCode Aligner v10.0.2. Sequence identifications were made using the Barcode of Life Data Systems (BOLD) NZ. Identification Engine (using the All Barcode Records on BOLD database) and the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information (NCBI). A species-level identification was made when sequences had a 99% similarity or higher (following Wong & Hanner, 2008). Specimens that yielded 94–97% matches were not definitively identified at the species level but added to the results as a genus (see discussion). Finally, relative significance of DNA derived prey items was calculated on frequency of occurrence (%). Based on the following equation (1):

$$Frequency\ of\ occurrence\ (FO\%) =$$

$$\left(\frac{Number\ of\ stomachs\ in\ which\ the\ taxon\ was\ identified\ in\ \ (n)}{Total\ number\ of\ stomachs\ (N)}\right) \times 100$$

3.0 Results

A total of 70 stomach caeca were analysed through a combination of morphological and/or DNA analyses (**Tables 2, 3, and 5**). Three caeca (4.3%) were empty (containing no soft tissue or hard parts). The nematode parasite *Anisakis* sp. was only observed embedded within the caecum lining and is not included as a prey item. Fish prey was the most diverse (14 species), followed by crustaceans (n = 4) and cephalopods (n = 4). Prey items encountered most frequently were *Nototodarus gouldi*, opalfish (*Hemerocoetes* sp.) and red rock crab (*Guinusia chabrus)* (Linnaeus, 1758)*,* with the frequency of occurrence (FO%) 24.29%, 11.46% and 5.72%, respectively. At least nine stomachs contained two or more prey items (see discussion) (**Table 4**). Based on the 99% threshold for species identifications defined in the method section, 54 sequences were identified at the species level, while nine additional sequences were identified to higher taxa (**Table 3**).

3.1 Morphological identification

Among the 70 caeca analysed, a total of 26 prey taxa were identified. Based on the previously defined stomach caecum digestion stages, caeca from 2012 (n = 14) and 2013 (n = 21) were well-digested or very well-digested, while samples from 2015 (n = 35) contained moderately or partially digested prey items (see discussion). Through morphological identification of hard parts, 15 species were identified across five phyla (**Table 2**). In the phylum Annelida, an intact specimen of a potential *Chaetopterus* sp. (A. Alfaro, AUT, pers. comm.) was identified based on morphology (**Fig.**

2E). However, the hard parts observed on this specimen could suggest another potential species: *Glycinde* sp. (family Goniadidae) (W. Blom, Tāmaki Paenga Hira, pers. comm.) (**Fig. 2F**). In the phylum Arthropoda, 38.6% of caeca (n = 27) had crustacean hard parts such as shells, chelipeds, sternum and peduncles. Two species were identified from the morphological hard parts: a brachyuran megalopa and a gooseneck barnacle (Lepadidae). From the phylum Mollusca, of the stomach caeca with squid gladius or suckers, 15 had beaks, of which 7 had flesh or buccal mass attached, and morphological features such as arms suggest prey from the order Teuthida (**Fig. 1F**). A calcareous spiral was also found and was tentatively identified as a foraminiferan (Retaria) (D. Stevens, NIWA, pers. comm.) (**Table 2**)**.**

Finally, the phylum Chordata was represented by a total of 39 fish otoliths found across 15 *N. gouldi* caeca. 14 of those caeca included other fish hard parts such as eye lenses, bones or scales (see Appendix). Based on otolith morphology, eight fish species were identified (**Table 2**), including an unidentified sagitta from the sample NOG15-014 (D. Stevens, pers. comm.). For one pair of otoliths from sample NOG13-005, the fish size and maturity were estimated and found to be from a juvenile hoki (*Macruronus novaezelandiae)* (Hector, 1871) (see discussion). The stomach caecum that contained the greatest number of myctophids (sample NOG13-020) had approximately four individuals of Hector's lanternfish (*Lampanyctodes hectoris*) (Günther, 1876) and one bogue lanternfish (*Symbolophorus boops*) (Richardson, 1845)*.* Opalfish (*Hemerocoetes* sp.) were found in five *N. gouldi* caeca and were identified through DNA analysis (see discussion). Finally, multiple macroscopic nematode parasites (*Anisakis pegreffii*) (Campana-Rouget & Biocca, 1955) were also observed embedded in the lining of 68.6% of caeca (**Figs 2C** and **D**) (J. Bennett, University of Otago, pers. comm.).

Table 2.

Morphologically identified prey items of *Nototodarus gouldi* sampled on the Chatham Rise of Aotearoa, New Zealand. Species names in bold represent novel records of this prey species in *N. gouldi*. “N” indicates the number of stomachs in which this prey item was identified based on morphology; “Max consumed” indicates the highest number of prey individuals encountered in any single stomach caecum, extrapolated from otoliths and characteristic hard parts.

Sample Year	Phylum	Family	Taxon	N	Max consumed
	Annelida				
2013		**Chaetopteridae**	***Chaetopterus* sp. ?***	1	1
		Goniadidae	***Glycinde* sp. ?***		
	Arthropoda				
2013, 2015			Brachyuran megalopa*	5	-
2015		Lepadidae	**Gooseneck Barnacle***	1	-
	Chordata				
2013		Argentinidae	Silverside – ***Argentina elongata?***	2	1
2015		Congridae	Conger – *Gnathophis* sp.	1	1
2013		Cyttidae	Silver dory – *Cyttus novaezealandiae*	1	1
2013		Macrouridae	Javelin fish – *Lepidorhynchus denticulatus*	2	1
2013		Merclucciidae	Hoki – *Macruronus novaezelandiae*	1	1
2013		Moridae	Red codling – ***Pseudophycis bachus?***	1	1
2013		Myctophidae	Hector's lanternfish – *Lampanyctodes hectoris*	1	4
2013			Bogue lanternfish – ***Symbolophorus boops***	1	1
2013		Percophidae	Narrow opalfish – ***Hemerocoetes artus****	3	2
2013, 2015			Opalfish – ***Hemerocoetes* sp.?**	2	1
	Mollusca				
2012, 2013, 2015			Teuthida*	15	4
	Other				
2013			**Foraminifera?**	1	1

? Tentative identification due to erosion or fragmentation of the otolith
*See discussion; maximum number of individuals based on beaks / buccal bulbs / otoliths

3.2 DNA barcoding

From 77 samples, 63 sequences were recovered and identified using online reference databases, while 14 sequences were determined to be contamination or failed samples. Following Wong and Hanner (2008), only 56 sequences with a similarity of 99% and above the threshold could be definitively attributed to species, yielding 21 prey identifications down to the genus level. The remaining seven sequences fell below the cut-off identification criteria and corresponded to two genera: opalfish (*Hemerocoetes* sp.) and nematode (*Hysterothylacium* sp.); see **Table 3** and discussion. Thus, 23 prey taxa across five phyla were identified based on DNA analysis (**Table 3**). Fishes were the most diverse prey group (at least 13 species from 13 genera in 12 families), followed by Mollusca and Arthropoda (4 species each). Based on DNA barcodes, 17 caeca yielded fish species, while cephalopods were found in 15 of the caeca (27.3%), with the majority comprised of *N. gouldi* (n = 14), followed by a single sequence representing *Nototodarus sloanii*, *Idioteuthis* cf. *cordiformis* and *Stoloteuthis* sp. Top recurring prey species in stomach caeca based on DNA sequencing included Gould's arrow squid, *Nototodarus gouldi* (n = 14); opalfish, *Hemerocoetes* sp. (n = 5)*;* and red rock crab, *Guinusia chabrus* (n = 4). Red codling (*Pseudophycis bachus*) (Forster, 1801)*,* conger eel (*Gnathophis* sp.) and opalfish (*Hemerocoetes* sp.) were initially identified by otoliths and later confirmed by DNA sequencing. Based on DNA results, six caecum samples contained two or more prey items (**Table 4**). Of the stomach caeca with multiple prey items, the contents contained either both squid and fish samples, multiple fish species, or a combination of either fish or squid with nematodes (**Table 4**).

3.3 Parasites

Two species of parasites were identified in the caecum lining and contents of *N. gouldi*. Nematodes identified as *Anisakis pegreffii* (J. Bennett, University of Otago, pers. comm.) were extracted from the caeca lining and were observed in 48 out of the 70 stomachs (68.6%), with up to 30 nematodes infesting in two stomach caeca (**Fig.2C** and **D**). Individual nematodes varied in in length and width; all appeared translucent and did not show any visual character differences. Two caeca also contained free-floating nematodes identified as *Hysterothylacium* sp. (**Table 3**).

Table 3.

DNA sequenced prey items within stomach caeca of *Nototodarus gouldi* across 21 stations (west coast of the North Island and east coast of the South Island – incl. Chatham Rise) between the years 2012, 2013 and 2015. Taxa highlighted in bold represents new findings. (n) represents number of stomachs from which the taxon was identified in. All species are FO% = frequency of occurrence.

Sample year	Phylum	Family	Taxon Identified by BOLD or GenBank	Similarity	FO%
	Arthropoda				
2015		Hyperiidae	**Amphipod – *Themisto* sp**.*	99.83%	1.43
2015		Lepadidae	**Gooseneck barnacle – *Lepas australis***	99.62 – 99.74%	2.86
2015		Plagusiidae	**Red rock crab – *Guinusia chabrus***	99.50 – 99.67%	5.71
2013		Scyllaridae	*Slipper lobster – Ibacus alticrenatus**	100%	1.43
	Mollusca				
2012		Mastigoteuthidae	**Love-heart squid –*Idioteuthis cordiformis***	100%	1.43
2012, 2013, 2015		Ommastrephidae	Gould's arrow squid – *Nototodarus gouldi*	99.81 – 100%	18.57
2012			**Southern arrow squid – *Nototodarus sloanii***	100%	1.43
2012		Sepiolidae	**Bobtail squid – *Stoloteuthis maoria***	100%	1.43
	Chordata				
2013		Argentinidae	**Silverside – *Argentina elongata***	99.65%	1.43
2012		Chimaeridae	**Dark ghost shark – *Hydrolagus novaezealandiae*****	99.83%	1.43
2015		Clupeidae	Pacific sardine – *Sardinops sagax*	99.83%	1.43
2015		Congridae	Congrid eel – *Gnathophis* sp.	99.24 – 99.67%	1.43
2012		Cyttidae	*Silver dory – Cyttus novaezealandiae*	99.83%	1.43
2012		Macrouridae	Javelin fish – *Lepidorhynchus denticulatus*	100%	1.43
2013		Merclucciidae	**Hoki – *Macruronus novaezelandiae***	100%	2.86
2015			**Southern Hake – *Merluccius australis***	100%	1.43
2013		Moridae	**Red codling – *Pseudophycis bachus***	100%	1.43

2013	Myctophidae	**Lanternfish – *Symbolophorus* sp.**	99.8 – 99.82%	1.43
2015	Paraulopidae	**Cucumber fish – *Paraulopus nigripinnis***	100%	1.43
2013	Percophidae	**Opalfish – *Hemerocoetes artus*****	94.75 – 95.33%	7.14
2012	Sternoptychidae	Pearlside – *Maurolicus walvisensis***	100%	1.43
Nematoda				
2013, 2015	Raphidascarididae	***Hysterothylacium* sp.***	97.46 – 97.62%	2.86
Rhodophyta				
2015		***Bangiophyceae* ***	99.36%	1.43

*****Recovered above identification threshold from GenBank

**See discussion

Table 4.

List of multiple prey species identified from within single *Nototodarus gouldi* caeca, using combined morphological and molecular methods. Collections were conducted on the West Coast of Te Waipounamu South Island and Chatham Rise of Aotearoa, New Zealand. MA indicates morphological analysis, whilst DA infers DNA analysis. The year and sample number allow reference to Appendix one. Common and Latin names highlighted in bold represent prey items observed for the first time in *N. gouldi* diet. For *species, please read the discussion.

Year	Sample	Species 1	Species 2	Species 3	Method applied
2012	001	Javelin fish – *Lepidorhynchus denticulatus*	**Love-heart squid –*Idioteuthis cordiformis***		DA
	039	**Southern hake – *Merluccius australis***	Gould's arrow squid – *Nototodarus gouldi*		DA
2013	005	**Hoki – *Macruronus novaezelandiae***	**Silverside – *Argentina elongata***		MA and DA
	020	**Bogue lanternfish – *Symbolophorus boops***	Hector's lanternfish – *Lampanyctodes hectoris*		MA and DA
	027	**Opalfish – *Hemerocoetes* sp.**	**Foraminifera**		MA
	045	**Silverside – *Argentina elongata***	*Gould's arrow squid – *Nototodarus gouldi*	**Nematode – *Hysterothylacium* sp.**	MA and DA
	048	Javelin fish – *Lepidorhynchus denticulatus*	**Opalfish – *Hemerocoetes* sp.**		MA and DA
2015	021	**Nematode – *Hysterothylacium* sp.**	**Red algae – Bangiophyceae**		DA
	066	**Opalfish – *Hemerocoetes* sp.**	*Gould's arrow squid – *Nototodarus gouldi*	**Nematode – *Hysterothylacium* sp.**	MA and DA

4.0 Discussion

This study reports the first data collected on the trophic ecology of Gould’s arrow squid (*Nototodarus gouldi)* in Aotearoa, New Zealand. Following successful methods of gut content analysis from previous studies, an integrative approach was conducted involving visual identification and DNA sequencing to maximise taxonomic resolution (Braley et al., 2010; McBride et al., 2023). Based on qualitative analysis, of the 35 samples collected in 2012 (n = 14) and 2013 (n = 21), approx. 80% was characterised as very – fully digested while approx. 65.7% were very digested caeca from 2015 (n = 35). Cephalopods such as carnivorous *Octopus* sp. contain two-stage digestion, where rapid digestion and passage of food occur before the slower second phase for complex nutrients to be absorbed (Bastos et al., 2020), both acidic and alkaline enzymes are known to work at various times to rapidly digest and metabolise protein (Bastos et al., 2020; Gallardo et al., 2017). Experiments by Bastos et al. (2020) have highlighted lower enzymatic activity at temperatures of 10–20°C and the presence of soluble proteins as a function of prey digestion up to 400 minutes after feeding. Although the thermal ranges of *N. gouldi* caeca enzymes should be investigated, it is possible that the accumulation of enzymes from the salivary glands and in the caecum continued to digest protein whilst frozen or at least during the thawing process. Despite this advanced state of digestion from the current samples, a diverse range of fish, cephalopod and crustacean species were identified in the diet of *N. gouldi.* In total, this study identified 26 prey taxa, 18 for the first time, including eight species from the phylum Chordata, three species from Arthropoda, three species from Mollusca, and one species each from Annelida, Nematoda, Rhodophyta, and Retaria*.* Four major prey taxa fishes, cephalopods, crustaceans, and parasites will be broken down and discussed in this section.

4.1 Fishes

Fifteen species of ray-finned fishes (Actinopterygii) and one species of cartilaginous fish (Elasmobranchii) were identified as prey items in *N. gouldi* stomach caeca. Five of these fish prey species are managed under the New Zealand Fisheries’ Quota Management System (NZ QMS): dark ghost shark (*Hydrolagus novaezealandiae*), sardine (*Sardinops sagax*), hoki (*Macruronus* *novaezelandiae*), southern hake (*Merluccius australis*), and red cod (*Pseudophycis bachus*). In general, the known distributions of the fishes encountered as *N. gouldi* prey items overlap with the sampling depths for fish specimens and the known vertical distribution for *N. gouldi* (**Table 5.**). Based on the field guide published by McMillan and Struthers (2019), most prey items found in *N. gouldi* stomachs caeca are demersal, with the exceptions of sardine (*S. sagax*), Hector's lanternfish (*Lampanyctodes hectoris*) and pennant pearlside (*Maurolicus australis*), which are all midwater pelagic species. Most of *N. gouldi*'s prey species reside below 200 m in depth in the mesopelagic zone of the oceans (e.g., southern hake, *M. australis* up to 1100 m and, javelin fish *Lepidorhynchus denticulatus* up to 1200 m (McMillan & Struthers, 2019)) although some juvenile stages do prefer shallower regions (hoki, *Macruronus novaezelandiae*) and others migrate offshore to spawn (conger eel, *Gnathophis* sp.). Known prey sizes published by McMillan and Struthers (2019) range from standard lengths of up to 5 cm for pennant pearlside to 142 cm in hoki. While some fish species were identified based only on morphology (e.g., narrow opalfish *Hemerocoetes artus*) others were only identified by DNA barcoding (e.g., Southern hake *M. australis*), supporting the value of using an integrative approach in constructing a more complete understanding of squid prey species. Eight species were reported here for the first time and new insights into the specific prey ecology of the *N. gouldi*. are discussed in more detail below. More studies are required to confirm whether these species are regularly encountered as prey items or were anomalies from the method of teleost capture.

4.1.1 Actinopterygii

Vertebrate communities made up of a network of interacting species are complex and difficult to define; thus, identifying taxa within assemblages is the first step to elucidate this complexity (Francis et al., 2002). Across all previous dietary studies on *N. gouldi*, only the sardine (*Sardinops sagax*) has been repeatedly reported (see **Table 5**), suggesting the importance of this pelagic inshore prey taxon throughout *N. gouldi*'s geographic range from southeast Australia to New Zealand (Francis et al., 2002). Other previously reported prey species included conger eel (*Gnathophis* sp.), New Zealand dory (*Cyttus novaezealandiae*), javelin fish (*Lepidorhynchus denticulatus*), Hector's lanternfish (*Lampanyctodes hectoris*), and pennant pearlside (*Maurolicus* *australis*). The two latter species are known to migrate vertically in the water column linking primary consumers to the upper trophic systems (Christiansen et al., 2018; McMillan & Struthers, 2019). It is possible that the abundance of large biomasses generated by schooling midwater lanternfishes *L. hectoris* becomes the preferred prey. A notable observation in this study that supports this opportunistic behaviour to exploit readily available resources is the presence of four individuals of *L. hectoris* from a single *N. gouldi* stomach. Similar findings are observed for generalist predators such as the common dolphin (*D. delphis*) and Hector's dolphin (*Cephalorhynchus hectori*) that occupy the same region as *N. gouldi* (Meynier et al., 2008; Miller et al., 2013). Thus, aggregating behaviour and diel migration from deep waters to the shelf and upper layers of the continental slope by prey species could be contributing factors to the high numbers found in the single *N. gouldi* stomach.

Javelin fish (*Lepidorhynchus denticulatus*) is a mesopelagic forager (Stevens & Dunn, 2011) appearing as bycatch in the scampi fishery at depths that coincide with hoki trawls (Jones, 2009). They are abundant on the east coast of South Island and Chatham Rise (Jones, 2009; McMillan & Struthers, 2019), with a seasonal variation in *L. denticulatus* dietary habits. Populations are also recorded to consume crustaceans: natant decapods, calanoid copepods and hyperiid amphipods *T. australis* with similar prey overlap with *N. sloanii* (Dunn, 2009; Stevens & Dunn, 2011). Similarly, javelin fish further north in Wairarapa fed primarily on benthopelagic invertebrates, including decapod prawns, salps, and foraminifera (Jones, 2009). This raises the idea that the presence of foraminifera present in one stomach caecum was potentially secondarily ingested, which is supported by the presence of fish bones and scales in the same stomach (although no viable DNA could be barcoded from the fish remains in our molecular studies).

The presence of a congrid eel was sequenced in a 2015 stomach and is supplemented by a pair of otoliths, a pair of fish lenses and vertebrae corroborating the ingestion of one individual. In New Zealand, large numbers of *Gnathophis* sp. occur in the south-east of the North Island and the Cook Strait between October and December (Castle & Robertson, 1974). Castle and Robertson (1974) further described a long dispersal duration of *Gnathophis* sp. leptocephali (pelagic larval phase) of up to ten months, whereby movement is highly influenced by currents, although more updated information on this species is required before confirmation. However, *Gnathophis* sp. was represented in small proportions in the diet of mammalian predators *D. delphinus* and the east coast of the South Island population of Hector's dolphin, suggesting a wide regional overlap of prey consumption with *N. gouldi* (Meynier et al., 2008; Miller et al., 2013). Future studies can investigate the life history and distribution of *Gnathophis* sp., as literature on this species is scarce.

4.1.2 Elasmobranchii

The remains of the dark ghost shark (*Hydrolagus novaezealandiae*), a NZ QMS managed species, was a novel encounter in one *N. gouldi* stomach caecum. Although *H. novaezealandiae* has recently been reported as a prey item for *N. sloanii* (Chantheran, 2022), this study reports the first chimaera in the diet of *N. gouldi.* Demersal dark ghost sharks are often captured in deep-water and coastal fisheries at mean depths between 25–950 metres (Weigmann, 2016; Finucci et al., 2021). Endemic to Aotearoa, *H. novaezealandiae* distribution ranges from North Cape to the east coast of the South Island (including Bounty Plateau, Challenger Plateau and Chatham Rise) (Beentjes et al., 2002; Dunn et al., 2010; McMillan & Struthers, 2019). Juveniles of this species are more abundant in regions shallower than 200 metres, which could explain, in part, a habitat overlap with the current *N. gouldi* samples, which were also caught on the east coast of South Island within the same depth (Dunn et al., 2010; Finucci et al., 2018). Dietary analyses of bottom-trawled *H. novaezealandiae* individuals from the Chatham Rise found prey items to include a variety of benthopelagic species, including polychaetes, isopods, brachyuran crustaceans, amphipods and annelids and multiple unidentified items (Dunn et al., 2010). However, the taxonomic resolution was limited in the study by Dunn et al. (2010) due to only morphological identification of digestive tract contents. Therefore, integrative methods using morphological and DNA analysis would enhance taxonomic resolution and elude whether there are significant dietary and foraging overlaps between *H. novaezealandiae* with *N. gouldi* and *N. sloanii,* which occupy the same depths and locality in South Island, New Zealand.

4.1.3 NZ QMS fishes

Three NZ QMS species from two families were reported for the first time in this study: red cod *P. bachus* (Moridae), hoki *M. novaezelandiae* and southern hake *M. australis,* both from Merluccidae. All three species are reported to inhabit a similar depth strata as *N. gouldi*, with a high overlap in preferred depth (Beentjes et al., 2002; Francis et al., 2002). Based on demersal bottom trawls on the east coast of the South Island, *P. bachus* was the most abundant species in winter and summer, attributed to the consistently high mean catch rates in both seasons (Beentjes et al., 2002), whereas hoki was more abundant in summer sampling effort; this could impart competition for *N. gouldi* foraging for similar prey items in the same region. Bias too should not be dismissed as the *N. gouldi* specimens were caught during trawl surveys targeting the QMS species, therefore net feeding could potentially confound natural dietary results.

Hoki is reported to perform vertical migrations and exhibit ontogenetic shifts in diet. A notable similarity is that both *N. gouldi* and hoki target larger prey as a function with increased size, suggesting the increasing significance of cephalopod and fish in mature animals (Clark,1985). Juvenile hoki often found in shallower regions consume predominantly small crustaceans shifting toward lanternfish (Myctophidae) with maturation, while larger hoki commonly inhabiting depths below 400 metres prey on rattails (Macrouridae) (Connell et al., 2010; McMillan & Struthers, 2019). On the Chatham Rise, dietary intake is further influenced by prey distribution and spatial variability (Connell et al., 2010). Clark (1985) dietary study on hoki along the Chatham Rise reported multiple prey items that overlap with the *N. gouldi* prey, including six fishes (i.e. Hector's lanternfish, *Lampanyctodes hectoris*; red cod, *Pseudophycis bachus*; Mueller's pearlside, *Maurolicus muelleri*; javelin fish, *Lepidorhynchus denticulatus*; narrow opalfish, *Hemerocoetes artus* and silverside, *Argentina elongata*); two cephalopods (i.e. *Nototodarus* sp. and a bobtail squid, *Stoloteuthis maoria*) and one crustacean (amphipod, *Themisto gaudichaudii*). These similarities suggest that N. gouldi and hoki are mesopelagic feeders preying on species performing diel vertical migrations (i.e., lanternfish, pearlsides) and demersal species (i.e., red cod, silverside). By consuming a variety of benthic and pelagic species, *N. gouldi* exhibits a generalist diet, and the overlap in foraging depth for similar resources could suggest a heightened chance of hoki predation or, to a certain extent, competition.

4.1.4 Novel fish findings

While not an NZ QMS species, the opalfish *Hemerocoetes* sp. (Percophidae) was a novel yet frequently encountered prey item found in a total of eight stomachs. These bottom-dwelling temperate species are endemic to New Zealand’s subtidal continental shelf waters (McMillan & Struthers, 2019). This is consistent with *Nototodarus gouldi*’s diet composition of notably benthic fish, with over 80% (13 of the 16 fish prey species) considered demersal. Otoliths of opalfish (*H.* spp.) are particularly difficult to differentiate. However, the two pairs of otoliths found in the stomach caeca of the present study were identified as *H. artus,* because the otoliths were deeper with a more rounded rostra (D. Stevens, NIWA, pers. comm.). Five individuals were morphologically identified down to genus level (three to *H. artus* species level*,* D. Stevens, NIWA, pers. comm.) and were further corroborated by DNA barcoding from three stomachs. However, the sequences only aligned with a 94% match to reference *H. artus*. To date, only four of the five species identified in Aotearoa have been sequenced: *H. artus, Hemerocoetes macrophthalmus* (Regan, 1914), *Hemerocoetes monopterygius* (Schneider, 1801), and *Hemerocoetes morelandi* (Nelson, 1979) Thus, the sequences obtained in this study may represent *Hemerocoetes pauciradiatus* (Regan, 1914), the barcode of which has yet to be confirmed. An updated review could ascertain *H. artus* and *H. pauciradiatus* distribution since publishing by Moore and Wakelin (1997) based on a dietary study of yellow-eyed penguin *Megadyptes antipodes* (Hombron & Jacquinot, 1841) suggest their range to be in subantarctic islands or lower South Island. However, the current presence of *H*. sp. in *N. gouldi* stomach 13-002, 13-027, 13-041, and 13-054, all caught on the west coast of South Island, points to a larger opalfish distribution. A thorough revision of the distribution and genetic composition of five opalfish species in Aotearoa should be conducted, as McMillan and Struthers (2019) did not define any species boundaries or niche partition. The current study suggests that the sequences we obtained could belong to the fifth not-yet-sequenced species: *Hemerocoetes pauciradiatus.*

The final two novel actinopterygiid fish species are silverside *Argentina elongata* (Argentinidae); and bogue lanternfish *Symbolophorus boops* (Myctophidae). Clark (1985) and Jones (2009) studies on demersal and pelagic fish diets in New Zealand have indicated silverside to have a benthic diet. Consisting of predominantly salps at the lower range of their distribution and multiple benthic crustaceans (Clark, 1985; Jones, 2009). This would not be surprising as McMillan and Struthers (2019) have reported that the physiology of the small mouth meant this demersal species would consume small food items. Silverside resides on the upper slope, whereas *N. gouldi* dwells mainly on the shelf (Francis et al., 2002); predation of silverside could occur during the lower limits of migration by *N. gouldi*. However, this requires further observation. Another fish that requires attention is the bogue lanternfish. Its presence in the same stomach with four individuals of lanternfish (*L. hectoris) suggests* the overlap within prey species foraging for the same mesozooplankton resources (Christiansen et al., 2018). However, Christiansen et al. (2018) have proposed to re-evaluate and identify *S. boops* in southern waters. Although these novel accounts of fish species provide an indication of community assemblages associated with *N. gouldi,* whether predation occurred naturally or is an anomaly should be taken with caution. A detailed investigation should be conducted on multiple species (i.e., *Hemerocoetes* sp., *S. boops, L. denticulatus*) due to the paucity of data available within the exclusive economic zone (EEZ) of Aotearoa, New Zealand.

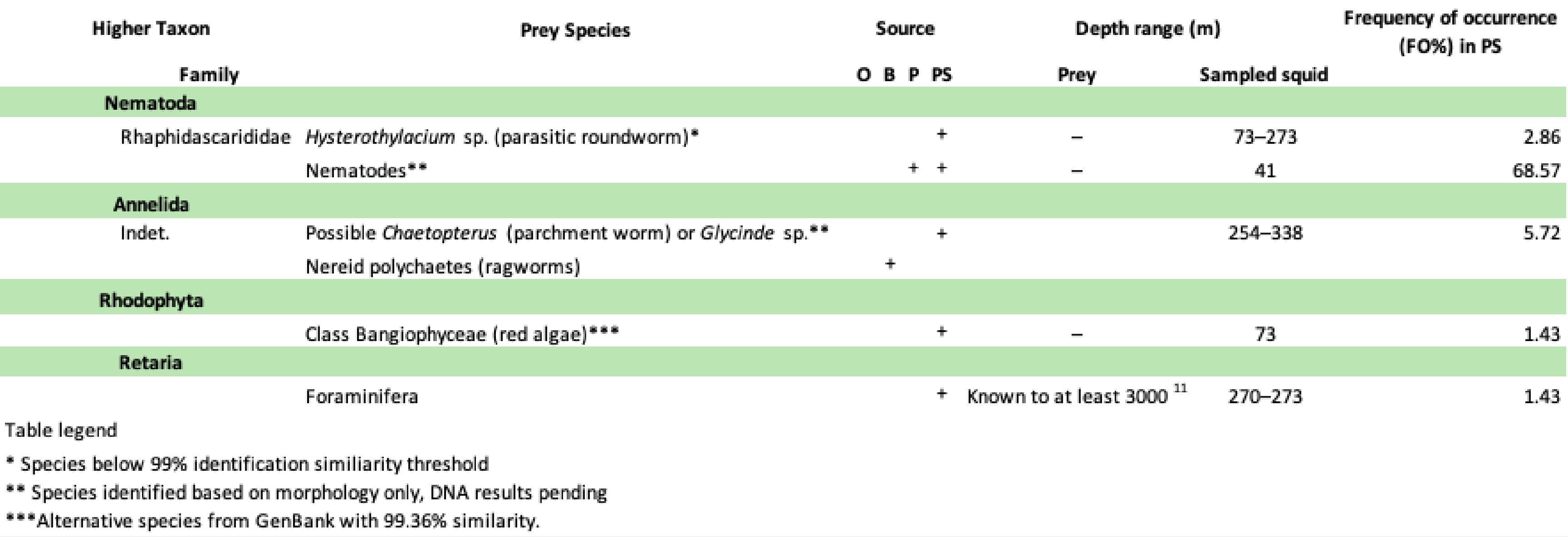
Table 5.

Summary of known prey of *Nototodarus gouldi* from Australia and Aotearoa New Zealand. Known fish prey depth distributions and sampled squid depths infer the vertical ranges of trawl depth where individual prey items are encountered. O = Australian *N. gouldi* study by O'Sullivan and Cullen (1983); B = Australian *N. gouldi* study by Braley et al. (2010); P = Australian *N. gouldi* study by Pethybridge et al. (2012); finally, PS = present study. The superscript indicates the reference used to recover prey depth. FO% is the frequency of occurrence in the present study based on equation (1).

Higher Taxon	**Prey Species**	**Source**				**Depth range (m)**		**Frequency of occurrence (FO%) in PS**
Family		**O**	**B**	**P**	**PS**	**Prey**	**Sampled squid**	
Chordata								
Argentinidae	*Argentina elongata* (silverside)				+	100–700 ^{1}	254–321	4.3
Arripidae	*Arripis* sp. (Kahawai)		+					
Atherinidae	*Atherinason hepsetoides* (smallscale hardyhead)	+						
Carangidae	*Trachurus declivis* (jack mackerel)		+					
Chimaeridae	*Hydrolagus novaezealandiae* (dark ghost shark)				+	25–900 ^{2}	333–338	1.43
Clupeidae	*Etrumeus sadina* (red-eyed herring)		+					
	Sardinops sagax (sardine)	+	+	+	+	Up to 60 ^{1}	41–44	1.43
	Clupeidae indet.		+					
Congridae	*Gnathophis* sp. (conger eel)		+		+	Up to 370 ^{1}	41–44	1.43
Cyttidae	*Cyttus australis* (silver dory)			+				
	Cyttus novaezealandiae (NZ dory)			+	+	200–400 ^{1}	270–338	2.86
Emmelichthyidae	*Emmelichthys nitidus* (redbait)		+					
Engraulidae	*Engraulis australis* (anchovy)		+					
Gempylidae	*Thyrsites atun* (barracouta)	+	+					
	Gempylidae indet.*		+					
Hemiramphidae	*Hyporhamphus melanochir* (southern garfish)	+	+					
Isonidae	*Iso rhothophilus* (Surf sardine)		+					
Macrouridae	*Coelorinchus* sp. (rattail fish)			+				
	Lepidorhynchus denticulatus (javelin fish)			+	+	250–1200 ^{1}	73–338	4.3
Merlucciidae	*Macruronus novaezelandiae* (hoki)				+	10–1200 ^{1}	254–378	2.86
	Merluccius australis (southern hake)				+	5–1100 ^{1}	101–106	1.43
Moridae	*Pseudophycis bachus* (red codling)				+	5–600 ^{1}	270–273	1.43
Mullidae	*Upeneichthys lineatus* (Blue-striped mullet)		+					
Myctophidae	*Diaphus danae* (Dana lanternfish)			+				
	Diaphus ostenfeldi (Ostenfeld's lanternfish)			+				
	Diaphus sp.			+				

Higher Taxon	**Prey Species**	**Source**				**Depth range (m)**		**Frequency of occurrence (FO%) in PS**
Family		**O**	**B**	**P**	**PS**	**Prey**	**Sampled squid**	
Chordata								
Myctophidae	*Electrona risso* (electric lanternfish)			+				
	Hygophum hanseni (Hansen's lanternfish)			+				
	Lampanyctodes hectoris (Hector's lanternfish)			+	+	Up to 300 [1]	224–225	1.43
	Lampanyctus australis (southern lanternfish)			+				
	Symbolophorus boops (Bogue lanternfish)				+	Midwater depth unknown [1]	224–225	1.43
	Symbolophorus sp.				+	Depth unknown [1]	224–225	1.43
Paraulopidae	*Paraulopus nigripinnis* (cucumber fish)				+	2–600 [1]	164	1.43
Percichthyidae	*Percichthyidae indet.* (perches)			+				
Percophidae	*Hemerocoetes artus* (narrow opalfish)*				+	–	208–397	8.6
	Hemerocoetes sp.**				+	Up to 550 [1]	42–270	2.86
Phosichthyidae	*Phosichthys argenteus* (silver lightfish)			+				
Scombridae	*Scomber australasicus* (blue mackerel)	+	+					
Sternoptychidae	*Maurolicus muelleri* (Mueller's pearlside)			+				
	Maurolicus australis (pennant pearlside)**			+	+	150–400 [1]	333–338	1.43
Trachichthyidae	*Trachichthyidae indet.* (roughies)		+					
Indet.	Fish indet.	+	+	+				
Mollusca								
Atlantidae	*Atlantidae* sp. (sea snail)	+						
Loliginidae	*Sepioteuthis australis* (southern reef squid)		+					
Mastigoteuthidae	*Idioteuthis cordiformis* (loveheart squid)				+	750–1500 [3]	333–338	1.43
Ommastrephidae	*Nototodarus gouldi* (Gould's arrow squid)	+	+		+	Known to at least 500 [4]	73–338	24.29
	Nototodarus sloanii (southern arrow squid)				+	Known to at least 600 [5]	333–338	1.43
	Todarodes filippovae (Antarctic flying squid)	+						
	Ommastrephidae indet.	+	+					
Sepiolidae	*Stoloteuthis maoria* (bobtail squid)				+	274–366 [6]	333–338	1.43
Indet.	Cephalopoda indet.	+	+	+				
	Octopoda indet.	+						
	Teuthida indet.	+						

Higher Taxon	Prey Species	Source				Depth range (m)		Frequency of occurrence (FO%) in PS
Family		O	B	P	PS	Prey	Sampled squid	
Arthropoda								
	Brachyuran adult	+						
	Brachyuran megalopa larvae	+			+	Known to at least 55 [7]	–	
Bodotriidae	Bodotriidae indet. (cumacean)	+						
Calanidae	*Calanoides carinatus* (copepod)	+						
Cirolanidae	*Cirolana* sp. (isopod)	+						
Corophiidae	Corophiidae indet. (amphipod)	+						
Cymothoidae	*Ourozeuktes* sp. (isopod)	+						
Euphausiidae	*Nyctiphanes australis* (krill)		+					
Gammaridae	Gammaridae indet.	+						
Hyperiidae	*Themisto* sp. (Amphipod)*				+	Known to at least 3000 [8]	78	1.43
	Hyperiidae indet.	+						
Lepadidae	*Lepas australis* (gooseneck barnacle)				+	–	90–98	2.86
Pandalidae	Pandalidae indet. (caridean shrimp)		+					
Plagusiidae	*Guinusia chabrus* (red rock crab)				+	Intertidal depth unknown [9]	95	5.72
Polybiidae	*Liocarcinus corrugatus*	+						
Scyllaridae	*Ibacus* sp. (slipper lobster)	+			+	25–1401 [10]	270–273	1.43
Serolidae	*Serolis* sp. (isopod)	+						
Sphaeromatidae	*Cymodoce aculeata var. grandis* (isopod)	+						
	Cymodoce sp.	+						
	Sphaeromatidae sp.	+						
Indet.	Amphipod indet.	+						
	Copepod indet.	+						
	Crustacean indet.	+	+	+				
	Eumalacostraca indet.		+					
	Isopod indet.	+						
	Mysid indet.	+						
	Ostracod indet.	+						



Higher Taxon		Prey Species	Source				Depth range (m)		Frequency of occurrence (FO%) in PS
	Family		O	B	P	PS	Prey	Sampled squid	
Nematoda									
	Rhaphidascarididae	*Hysterothylacium* sp. (parasitic roundworm)*				+	–	73–273	2.86
		Nematodes**			+	+	–	41	68.57
Annelida									
	Indet.	Possible *Chaetopterus* (parchment worm) or *Glycinde* sp.**				+		254–338	5.72
		Nereid polychaetes (ragworms)		+					
Rhodophyta									
		Class Bangiophyceae (red algae)***				+	–	73	1.43
Retaria									
		Foraminifera				+	Known to at least 3000 [11]	270–273	1.43

Table legend

* Species below 99% identification similiarity threshold

** Species identified based on morphology only, DNA results pending

***Alternative species from GenBank with 99.36% similarity.

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All literature cited can be found in the references section at the end of this dissertation.

4.2 Cephalopods

Four cephalopod species were identified among the stomach caeca contents from DNA sequences: *Nototodarus gouldi*, *Nototodarus sloanii*, *Idioteuthis cordiformis*, and *Stoloteuthis maoria* (Dell, 1959). Where possible, tissue associated with beaks found in the gut contents was sampled to minimise the likelihood of contamination from host DNA (although this cannot be ruled out). Cannibalism on conspecifics was evident in *N. gouldi* and has been previously reported by Braley et al. (2010), O'Sullivan and Cullen (1983), and Uozumi (1998). However, this is the first report of predation on congeneric *N. sloanii* based on DNA sequences from two *N. gouldi* stomach caeca captured in the Southern Taranaki Bight.

4.2.1 Gould's arrow squid

Numerous sequences of *N. gouldi* were obtained from prey tissues in this study. While contamination from the parent specimen is a possibility, most of the *N. gouldi* sequences were obtained from the multiple small cephalopod buccal masses observed within the gut content samples. These usually contained small, intact beaks representing juvenile squids (less than 1mm lower rostral length; **Fig. 1F**) from samples such as 15-024 (See appendix 1). This is not surprising as past studies have captured large numbers of juvenile *N. gouldi* on the shelf up to 300 metres along the west coast of the North and South Islands (Uozumi, 1998), which overlaps with the 2015 study area. Furthermore, the Northern Taranaki Bight has been speculated as a main spawning site for *N. gouldi* as surveys have captured both paralarvae and mature adults in the region (Uozumi and Forch, 1995). This repeated finding conforms with two previous publishing having also found *N. gouldi* in the diet analysis although there was no mention of the prey's size or age (Braley et al., 2010; O'Sullivan & Cullen, 1983).

The present findings support the idea of filial cannibalism, a form of inter-cohort interaction where larger members of conspecifics predate on their own offspring (Ibánez & Keyl, 2010). The ingestion of young conspecifics could suggest there was a lack of size segregation within this particular *N. gouldi* cohort in 2015. Adult and juvenile *N. gouldi* squids are known from across a broad range along the west coast with no clear size composition (Uozumi & Forch, 1995), which could incite cannibalism. This type of behaviour is common and has been thought to be an interplay between the density of the spawning population and the size of females observed (Ibánez & Keyl, 2010). In the case of giant squid *Architeuthis dux,* aggression, mating or autophagy could have been the contributing factor of conspecific material found in the stomach caecum (Bolstad & O'Shea, 2004) Albeit the strong cannibalism theory from our study, it should be noted that not all stomach caeca could have contained *N. gouldi* as prey since there is a chance of contamination or accidental sequencing of the host DNA. Items found in 2013 sample 045 and 2015 sample 066 were both very digested, although the 2015 sample contained more noticeable coloured membranous tissue and more defined and intact hard parts like fish scales and vertebrae. Despite DNA sequencing highlighting the presence of *N. gouldi* both samples failed to encounter non-digestible squid beaks or suckers (See appendix 1 and **Table 4**). Dietary study on the deep-sea hooked squid *Moroteuthopsis ingens* by McBride et al. (2023) also highlighted the inability to distinguish between host DNA contamination and cannibalism. Thus, cannibalism has occurred in samples such as 15-024, but in other stomach caeca, the idea of host contamination cannot be ruled out.

Our study again highlights the importance of complementing morphological analysis with DNA analysis to reveal species presence and biological measures such as life stage that DNA alone cannot convey. We recommend sampling tissue from buccal bulbs where possible as evidence for cephalopod prey items to minimise the likelihood of host tissue contamination. Although not encountered in this study, another idea that could support the idea of net feeding or recent ingestion is where a very digested stomach caecum possesses no notable hard parts but contains large tissue pieces with little to no signs of digestion. Thus, it would be advantageous to record *N. gouldi* body state (i.e. any tissue missing or tentacles/arms sections missing) at the time of capture. Alongside imaging techniques (e.g., Meynier et al., 2008) to aid in piecing together the in situ cannibalistic behaviour of mesopelagic predator *N. gouldi* from Aotearoa, New Zealand.

4.2.2 Novel cephalopod findings

This is the first report of *Nototodarus sloanii* as prey for *Nototodarus gouldi*. Sampled from the Chatham Rise in 2012, these two species can co-occur in Cook Strait and along the west coast of the South Island. Mature *N. gouldi* can also migrate and may be found over continental shelves up to 500 m depth, overlapping the known depth of occurrence for *N. sloanii* (Uozumi, 1998). Although the densities of these biomasses notably taper off with increasing depth (Jackson et al., 2000). Unlike members of other highly migratory Ommastrephids, e.g., *Illex argentinus*, it is suggested *N. sloanii* undergoes localised small-scale migrations, moving to deeper shelf waters before transitioning to shallow inshore after copulation, thus exploiting the resources between and within each region (Jackson et al., 2000; Uozomi, 1998). An aspect that is reflected in the current study is the prey items consumed: ranging from benthopelagic to neritic prey species. Since *N. gouldi*'s feeding strategy is closely tied to the squid's energy expenditure, this requires constant external prey input to meet and maintain regular function and growth (McGarth & Jackson, 2002). Thus, many individuals of *N. gouldi* sampled by McGrath and Jackson (2002) possessed food in their stomachs, a notable attribute also observed in this study where only three stomach caeca were empty (4.3%).

Two other cephalopod species were identified here for the first time. The large, deep-sea 'love-heart' squid (*Idioteuthis cordiformis*) was a surprising finding since this benthic mastigoteuthid species was recently reported to be a top-level trophic predator by Jackson et al. (2021). In New Zealand, adults of this species are associated with seamounts and have been caught at depths of 750–1500 m (Braid & Bolstad, 2014). The tissue sample sequenced from the present study was not associated with any morphologically identifiable remains, so the size class of the consumed individual remains unknown. It is possible that a large individual was scavenged or that a small individual (which may dwell higher in the water column) was predated upon by *N. gouldi*. Although having large sclerotised beaks is important to justify the presence of a prey species, it can also be misleading as it could have accumulated over a period of time and does not directly translate into a recent prey item as observed in albatross stomachs by Xavier et al. (2011). Thus, by compiling known stable isotopes (e.g. Braid & Bolstad, 2014) with new isotope findings of *L. cordiformis* and

N. gouldi from tissue and beak samples (Woods et al., 2022), we can help elucidate the complex trophic assemblage of deep-water cephalopods in Aotearoa New Zealand.

One sequence for *Stoloteuthis maoria* was also recovered from a caecum off the west coast of South Island, constituting the first report of this small sepiolid (subfamily Heteroteuthinae) as a prey item for *N. gouldi*. Literature on this species is scarce, but Drerup (2022) has reviewed species of this subfamily Heteroteuthinae to have a mostly pelagic lifestyle. Often collected at sites associated with seamounts and submarine ridges, inhabiting depths of up to 1600 m with the potential of adults in this subfamily to migrate up the water column at night (Drerup, 2022). The current known distribution of *S. maoria* extends to southern Australia (Reid, 2021) and paratypes of *S. maoria* from Cook Strait were caught at depths of approximately 274 to 366 m (Dell, 1884), which would overlap comfortably with the known distribution of *N. gouldi*. Finally, complementing this DNA analysis is the presence of a pair of small beaks (See **Figure 1E**), which further confirms the presence of *S. maoria* in the caecum; however, the taxonomy can be re-evaluated (Reid, 2021).

The holopelagic theory of *S. maoria* is debated, and mature females from the subfamily Heteroteuthinae are presumably benthic when spawning on the seafloor (reviewed by Drerup, 2022). One example that suggests demersal feeding by *N. gouldi* in the current study was from sample 13-081. Although no viable DNA was extracted, characteristic squid hard parts and sand sediments were found in the caecum. Clark (1985) also identified this *S. maoria* in the stomach contents of hoki (*Macruronus novaezelandiae*) and javelin fish (*Coelorinchus australis*) (the latter also noted in Jones (2009)). This study also encountered both fish species as prey items of *N. gouldi,* once again suggesting foraging overlap. We highlight the need for in situ observations using camera systems for passive monitoring of *N. gouldi*'s demersal foraging behaviour.

4.3 Crustaceans

At least five species of crustaceans were recovered from *Nototodarus gouldi* caeca. These span the widest depth range of any observed prey group from intertidal (red rock crab, *Guinusia chabrus*) to depths of at least 3000 m (amphipod, *Themisto* sp.). The sizes of all prey items from this phylum range from a couple of millimetres in *Themisto* sp. to approx. seven centimetres in gooseneck barnacles (*Lepas australis*) (Darwin, 1851). Understanding the life stages of these arthropods and whether dispersal depths and distribution overlap can help demystify their presence in *N. gouldi*'s stomach and inform foraging behaviour.

4.3.1 Brachyuran megalopae

Planktonic brachyuran megalopae are extremely diverse and often difficult to assign to known species (Marco-Herrero et al., 2021). Dietary studies based on DNA analysis alone can provide high-resolution (often to genus-level) evidence of prey but generally do not report which life stage of the ingested animal. Thus, supplementing DNA methods with morphological analysis can be valuable; here, at least two megalopa phases (See **Fig. 2B**) were identified to match with DNA sequences of the red rock crab (*Guinusia chabrus*) (Linnaeus, 1758) (from two North Taranaki Bight samples NOG15-014 and NOG15-017; see appendix 1). Many *G. chabrus* fragments were found in the caeca of *N. gouldi*. It is likely that these were directly consumed by *N. gouldi* as NOG15-017 only contained crustacean parts, but secondary ingestion is also possible since NOG15-014 also had otoliths present. It is not surprising to see substantial amounts of individuals belonging to the same prey species in one caecum, as this could suggest opportunistic feeding by the *N. gouldi* on abundant resources when available locally.

4.3.2 Novel crustacean findings

Three of the five crustacean species identified among the stomach caeca contents are new prey records for *N. gouldi*. A key zooplankton species identified through DNA analysis was the hyperiid amphipod *Themisto* sp. Two studies by O'Sullivan and Cullen (1983) and Chantheran (2022) have retrieved *Themisto* sp. from *Nototodarus gouldi* and *N. sloanii* stomach caeca samples (respectively) during the austral summer. The prevalence of *Themisto* sp. in previous and current *N. gouldi* dietary studies suggest that this pelagic predator could form a regular component of the *N. gouldi* diet. This is unsurprising as static modelling by Coll. et al. (2013) has reported a high bottom-up effect on squid in the Pacific Ocean. In this present study, only one sample yielded the genus *Themisto*, with two possible species identities: *Themisto australis* (Stebbing, 1888) or

Themisto gaudichaudii (Guérin, 1825), the former occupying the southeast Pacific and the latter in both temperate to polar regions (Havermans et al., 2019). Large congregations of *T. gaudichaudii* have been observed in Antarctic waters because of the reproductive season, often coinciding with the increase in primary productivity (Watts & Tarling, 2012). In the North Atlantic Ocean, juvenile members of this species are reported to migrate to the upper 50 metres of the water column, with the greatest abundance during summer (Williams & Robins, 1981). This conforms to a study by Padovani et al. (2012), where *T. gaudichaudii* formed the predominant biomass in the stomach of predatory fish in summer. Yet the minimal presence in the present study could suggest an alternative feeding pathway for *N. gouldi*. Additionally, the distribution of adult *T. gaudichaudii* can be patchy within the upper 250 metres, representing the local productivity of the region (Havermans et al., 2019) or the ability to actively evade sampling tows (Williams & Robins, 1981). The range *T. gaudichaudii* occupies around Aotearoa, New Zealand, should be revised since it is widely consumed by multiple NZ QMS species, i.e., hoki *M. novaezelandiae* (Clark, 1985) and *N. sloanii* (Chantheran, 2022).

The most unexpected crustacean identified was the southern gooseneck barnacle *Lepas australis,* which was encountered in two stomach caeca. Global natural dispersal of these sessile animals is via macroalgae such as floating kelp *Durvillaea antarctica* (Chamisso Hariot, 1892) and *Macrocystis pyrifera* (Linnaeus, 1820), where multiple epibionts are picked up or carried over vast distances, including from New Zealand to Antarctica (Avila et al., 2020; Fraser et al., 2018). In this present study, there is a possibility that *L. australis* was consumed within the trawl net, as gooseneck barnacles have often observed attached to the buoyant kelp on each Chatham Rise survey (i.e., in a bottom trawl) (D. Stevens, NIWA, pers. comm.). Studies have reported that in addition to the natural deterioration of floating kelp, epipelagic *L. australis* and multiple other species of epibionts also drive macroalgal foodfalls when colonisation of drifting kelp rafts becomes overloaded (Avila et al., 2020; Graiff et al., 2016). Thus, another speculation is that gooseneck barnacles were consumed opportunistically by *N. gouldi* while sinking kelp rafts were encountered, although no kelp fragments were observed in any stomach. Gooseneck barnacles have also been observed attached to pelagic medusae (B. Robison, MBARI, pers. comm.), providing an additional potential explanation, although no cnidarian remains were identified. We also cannot dismiss the idea of secondary ingestion since residual fish components such as scales, lenses and bones were also found in one sample (15-033, see Appendix 1), although sample 15-037 only possessed digested barnacle fragments without any apparent fish remains. The idea of opportunistic feeding from decaying matter could be further explored using non-invasive imaging systems, thus more light can be shed on the versatile feeding behaviour of the *N. gouldi.*

As a widespread species across southern temperate latitudes, the red rock crab *Guinusia chabrus* (family Plagusiidae) largely inhabits intertidal and subtidal habitats, feeding on green and red algae scraped off rock surfaces (Bento & Paula, 2018; Griffin, 1971; Griffin, 1973). In New Zealand, they are only found on the mainland of the North Island and the north of the South Island predominantly inhabiting subtidal zones with high wave action (Wear, 1970). Thorough biological Information on *G. chabrus* from New Zealand is scarce; literature from Australia suggests egg-laying or ovigerous females from Tasmania are found in the months of July to late February (Griffin, 1971). The presence of only megalopa stage of *G. chabrus* in April 2015 sample suggests a similar brooding season as Australian studies, and Wear (1970) has mentioned *G. chabrus* females could incubate more than one batch of egg per season. Thus, the potential for multiple cycles of hatched zoea developing into megalopa in one season can constantly supply the marine food web in the local region, reflecting the presence in *N. gouldi* caeca independent of any other prey items. Dietary reconstruction of benthic cephalopods such as common octopus *Octopus vulgaris* has identified *G. chabrus* as an important prey species (Smith, 2003), *s*ince megalopa is the final stage of a crabs' larvae cycle before the transition to benthic adult, (Wear, 1970). However, our study shows that the planktonic earlier life stages of *G. chabrus* is significant and consumed by mesopelagic *N. gouldi.*

Although slipper lobster was found in the earlier study by (O'Sullivan & Cullen, 1983), this finding presents the first sequencing of intact *Ibacus* sp. eggs in the caecum of the *Nototodarus gouldi*. Currently, two species are reported in New Zealand. *Ibacus brucei* (Holthuis, 1977) occupying the northern waters surrounding Rangitāhua (the Kermadec Islands) and the western range of Norfolk Ridge, would be ruled out as it lies beyond the sampling area of this study. The second, more likely species is the ‘prawn killer’ *Ibacus alticrenatus* (Spence Bate, 1888), introduced into the NZ QMS in 2007. Primarily landed as bycatch from commercial scampi trawlers, records show their common depths of capture ranges between 100 to 400 metres (MacGibbon, 2015; MPI, 2022b). The stock boundaries also coincide with scampi fisheries (MacGibbon, 2015; MPI, 2022b). Despite exhibiting burying behaviour in soft sediments, this deep-water benthic species is especially vulnerable to prawn fisheries due to the small-meshed nets employed by prawn fisheries, which retain all-sized crustaceans (Lavalli & Spanier, 2007, MacGibbon, 2015). On the west coast of South Island, there is a minor proportion of *I. alticrenatus* captured from tows targeting species such as hoki (*M. novaezelandiae*); tarakihi (*Nemadactylus macropterus*) (Forster, 1801); barracouta (*Thyrsites atun*) (Euphrasen, 1791); silver warehou (*Seriolella punctata*) (Forster, 1801) and hake (*M. australis*) (MacGibbon, 2015). Aside from bottom trawls, only midwater trawls made within five metres from the seabed would catch this benthic crustacean (MacGibbon, 2015); this suggests depth overlap with the demersal feeding *N. gouldi*.

Demersal trawls in Queensland also exploit this species, and past studies reported ovigerous *I. alticrenatus* to occur along the eastern Australian coast from New South Wales to Tasmania between April and October, peaking in the month of July (Haddy et al., 2005, Lavalli & Spanier, 2007). A re-examination of slipper lobster biology and latitudinal distribution should be undertaken in New Zealand to inform *I. alticrenatus* stock management. The current finding of genetically sequenced eggs from August 2013 *N. gouldi* stomach caecum confirms the presence of mid-stage eggs (orange eggs with two eye spots) belonging to an ovigerous slipper lobster on the west coast of South Island, Aotearoa, New Zealand (See **Fig. 2A**).

4.4 Parasites

Two nematode taxa, *Hysterothylacium* sp. (family Raphidascarididae) and *Anisakis pegreffii* (family Anisakidae), were identified from within the gut contents and embedded in the caecum lining of *Nototodarus gouldi,* respectively. In both specimens where *Hysterothylacium* sp. was present, *N. gouldi* tissue was also encountered, as well as fish remains (*A. elongata* in one, *Hemerocoetes* sp. in the other; **Table 4**). Although all sequences of *Hysterothylacium* sp. in this study fell below 99%

threshold of identification, this parasite was found in multiple marine species. Bennett et al. (2022)'s recent summary of marine parasite from NZ waters reported this heteroxenous endoparasite to infect species such as arrow worm (*Serratosagitta tasmanica*) (Thompson, 1947), decapods, and cnidarian jellyfish. Although cephalopod hosts were not published by Bennett et al. (2022), *Hysterothylacium* sp. could have been ingested from an infected prey item; albeit no crustacean or cnidarian remains were observed in the same caeca, *Hysterothylacium* sp. has been recorded inside the stomach, intestine and body cavity of opalfish and silverside both of which are prey items for *N. gouldi* (Hewitt & Hine, 1972).

Here, *Anisakis pegreffii* was also found within the lining of *N. gouldi* caecum. Two samples had the heaviest *Anisakis pegreffii* parasite loading, with over 30 individuals within a single caecum lining (samples NOG13-093 and NOG15-038 – see appendix and **Fig. 2c** and **2d**). Although no DNA was sequenced from the two samples, crustacean and fish hard parts were present independently in each of the stomach caeca. Larval *Anisakis* sp. has been observed enclosed in the integument of the viscera and mesenteries of *N. gouldi* prey silverside (Hewitt & Hine, 1972). Similarly, in the Mediterranean, Palomba et al. (2021) have observed high levels of ascaridoid nematode infestations in the gonads and musculature of two deep-sea histioteuthid specimens suggesting a higher transmission probability to marine mammal definitive hosts. As long-lived trophically transmitted helminths, these nematodes rely on an aquatic intermediate host before maturing in a definitive host to complete their lifecycle (Jacobson et al., 2019). This is the first record of this parasite in *N. gouldi* and could suggest that this squid preys on intermediate hosts and may play a role in this nematode being transmitted further up the trophic system. However, further studies should be conducted to investigate the complex linkages between *N. gouldi,* the host, and parasites.

Helminth species in New Zealand remain understudied, with more studies on vertebrates than invertebrate host taxa and over 50% of records still needing to be resolved for further taxonomic identification (Bennett et al., 2021). Despite the paucity of data, past studies have utilised parasites to better understand target species and even population-level inferences. For example, the infestation rate of Anisakidae was used to describe the asymptotic length of endemic sister species *N. sloanii* in New Zealand (Gibson & Jones, 1993). More recently, Jacobson et al. (2019) examined a subpopulation of sardines in the Northeast Pacific, where multiple parasites (including Anisakidae and Raphidascarididae) served as biological tags to re-examine stocks and migration patterns. When mixed outcomes are presented, the integration of parasites often complements genetics, stable isotope signatures and otolith morphometric studies. These results can help infer host dispersal limitations, trophic pathways, and spatial gradients of the focal species. Helminth ecology can be integrated in the future to distinguish the two subpopulations of *N. gouldi* and *N. sloanii* that are still categorised under the same NZ QMS.

4.5 Dietary comparison with *N. sloanii*

Although *Nototodarus gouldi* diet has not been previously reported in Aotearoa, New Zealand, multiple studies have explored the diet of *N. sloanii* (Chantheran, 2022; Dunn, 2009; Uozumi, 1998). Most recently, Chantheran's (2022) integrative study on feeding habits concluded that *N. sloanii* appeared to be a generalist and even opportunistic predator preying predominantly on mesopelagic species. This is consistent with the high biomasses of *N. sloanii* reported by Jackson et al. (2000) distributed at depths of 200–300 metres. In general, at least seven species from Chordata; one species from cephalopoda, and two species from crustacea identified from the diet of *N. gouldi* were reported as prey for *N. sloanii*. However, this is an underestimation as it is likely that previous papers' methods based on behavioural observation and morphology alone resulted to low taxonomic resolution (e.g., Dunn, 2009; Uozumi, 1998). All three studies, however, reported the presence of mesopelagic species: Mytophidae and *Nototodarus* sp., with Dunn (2009) and Chantheran (2022) reporting Hector's lanternfish and pearlside as the predominant fish species found in the stomach — both with the highest percentage of occurrence. The two *Nototodarus* sp. also both appear cannibalistic, consuming members of their own species, as well as preying upon congenics. Here, we identified *N. sloanii* remains in two *N. gouldi* stomach caeca. The possibility of this cannibalistic behaviour has also been speculated by Uozumi (1998) with the identification of congenic *N. gouldi* in the stomach caeca of *N. sloanii*.

An observable trend reported by Uozumi (1998) was the changes in prey categories (fish, crustaceans, cephalopods, and others) between *Nototodarus gouldi* and *Nototodarus sloanii* throughout the year. Comparing the two species' mantle length and prey consumption, there is a notable increase in squid and fish species consumption with increased mantle length. While *N. sloanii* continues to consume crustaceans, for *N. gouldi* individuals growing past 200 mm in mantle length, there was a drop in crustacean frequency encountered in the stomach (Uozumi, 1998). However, Uozumi (1998) stated that multiple factors could explain this, including year, season, area, dorsal mantle length (DML), sex and maturation stage. Jackson et al. (2000) added oceanographic properties, including currents and temperature, as variables to consider for growth rate. This highlights how complex indirect factors influence somatic growth and protein metabolism, consequently, the feeding behaviours of *Nototodarus* sp. The regions where the two species mix, most notably southeast of the North Island and northwest of the South Island (Uozumi, 1998), can be further sampled to investigate the extent to which these prey species are consumed and during what life stage by the predatory squids. With the rise of high throughput sequencing, underwater echosounder and machine-trained imaging technologies, a future study that looks deeper into the prey distribution and foraging behaviours of both *N. gouldi* and *N. sloanii* would be beneficial for evaluating this fishery stock in Aotearoa New Zealand.

4.6 Limitations and Complications

Our study captured the short-term dietary ecology of the *N. gouldi* based on the digested remains of prey items and parasites from the years 2012, 2013 and 2015. One limitation was the level of digested items from the years 2012 and 2013, where prey remains were highly digested and contained few distinguishable soft tissues. As reviewed by Ibánez et al. (2021) biases arise from basing prey taxonomy presence only on morphological parts. Future stomach caeca contents analysis would benefit from understanding the acidic and alkaline levels in the caeca and how the pH level correlates with the level of digestion. For diagnostic purposes, it is important to note that only the largest otolith, sagittae are useful (D. Stevens, NIWA, pers. comm.). Therefore, enhancing current methods to prevent unnecessary digestion would reduce erosion of otolith and characteristic hard parts, as well as tissue sample degradation, benefiting morphological studies.

When expert knowledge is applied, fish size and maturity estimations can be made (e.g., a pair of sagittae from sample 13-002 was confirmed to belong to a small juvenile hoki by D. Stevens). However, if research is beyond specialists’ scope, for the case of degraded hard parts such as squid beaks or the currently unknown specimen from Annelida, suggested as *Chaetopterus* sp. (A. Alfaro, AUT, pers. comm.) or *Glycinde* sp. (W. Blom, Tāmaki Paenga Hira, pers. comm.). Techniques such as using stable isotopes, fatty acid and trace element analysis and parasite ecology can help resolve the life history and trophic ecology of the organism (Braid & Bolstad, 2014; Gibson & Jones, 1993; Pethybridge et al., 2012) although an integrative approach is highly recommended (Braley et al., 2010; Ibánez et al., 2021).

The possibility of gelatinous organisms cannot be ruled out as Hays et al. (2018) have proposed soft-bodied zooplankton's widespread role in the marine food web. This could imply *N. gouldi*’s consumption of the medusae substrate carrying the epibiont gooseneck barnacle or parasite *Anisakis pegreffii* but has gone undetected by the rapid digestion of gelatinous tissue in the stomach caecum. Another potential source of bias is prey items such as hoki (*M. novaezelandiae*) or *N. gouldi* found in the caecum with no associated hard parts. This could point to secondary ingestion or net feeding during trawls; however, *N. gouldi* has not been observed to net feed when caught in trawls (D. Stevens, NIWA, pers. comm.). As mentioned by Uozumi (1998), there is a chance of underestimating consumed species based on the size of fragmented prey or lack of identifiable pieces (as seen in highly digested stomachs with indistinguishable parts from studies by Dunn (2009) and Uozumi (1998)). Further biases could be introduced if *N. gouldi* opportunistically scavenges, or avoids certain parts of prey items, such as fish heads. To complement dietary studies investigating the foraging ecology of *N. gouldi* using passive equipment such as imaging systems with machine learning, animal mounted video loggers or echosounders moored in areas of known fish-prey biomasses (Becerril-García et al., 2020; Christiansen et al., 2019; Hays et al., 2018; Meynier et al., 2008), we can opportunistically capture *N. gouldi*’s in situ behaviour in a non-invasive way.

5.0 Conclusion

Our understanding of trophic dynamics and energy transfers within marine ecosystems in Aotearoa is not complete without the study of the natural diets of mid-level predators such as *Nototodarus gouldi*. To date, only Australia conducted dietary studies on *N. gouldi* (**Table 3**), highlighting a gap in knowledge for this species in Aotearoa, New Zealand. Here, we report that *N. gouldi* feeding in Aotearoa ingests a wide range of fish, crustacean and cephalopod prey items, some coinciding with what has been reported in Australian populations and southern *N. sloanii* studies conducted by Chantheran (2022), Dunn (2009) and Uozumi (1998). The taxonomic diversity represented by some caeca containing at least three species also reflects the wide range of prey sizes consumed from a few centimetres in juvenile *N. gouldi*. to approx. 370 mm large adult silverside. Similar to the observations made on common dolphins by Meynier et al. (2008), consuming diverse species of prey from a wide spectrum of sizes could suggest opportunistic foraging behaviour, where predators would consume what was most abundant and readily available.

This study also highlights the importance of an integrated approach when reconstructing diets. The identification of multiple species to a high taxonomic resolution was enabled by combining morphology and DNA analysis, and on multiple occasions, the life stage of the prey was determined through morphological records and the presence of characteristic hard parts like otoliths and beak assisted in providing robust evidence of prey presence when reconstructing diets. However, these methods are not without limitations, and we cannot entirely rule out sampling bias from capture techniques and secondary ingestion of prey items. We highly encourage using an integrated approach in re-evaluating the taxonomy of *Hemerocoetes* spp. and unidentified annelid species from the present study. By complementing techniques, we can better understand the presence of unexpected prey items such as pelagic gooseneck barnacles *Lepas australis* and the large deep-sea squid *Idioteuthis cordiformis*; these items could point to scavenging behaviour in *N. gouldi.*

Gould’s arrow squid, *Nototodarus gouldi*, plays a crucial role in the marine food webs of Aotearoa, New Zealand. Based on this first dietary study, we urge the ongoing collection of a long-term trophic data set on *N. gouldi* in relation to predator distribution to help make trophic linkages across regional and temporal scales. Future work could be expanded to include biochemical methods such as stable isotope analysis, fatty acid analysis and molecular techniques to assess longer-term trophic trends for individual and predator specimens. The use of camera systems, echosounder and deep learning could help overcome biases in conventional dietary reconstruction methods such as net feeding and host DNA contamination. This could provide valuable information on the focal squid species and community assemblages whilst helping to inform fishery stock management in regions vulnerable to environmental or anthropogenic change. Therefore, prey ecology and feeding habits of *N. gouldi* serve as the basis for biotic metrics within ecosystem-based models and, along with single-species analysis, can be applied to reach New Zealand’s 2030 fishery management goal.

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Appendix

Appendix 1:

Raw data for *N. gouldi* gut contents analysed from Aotearoa New Zealand, 2012–2015 (N = 70)

Cruise/Stn	Fish						Squid							Crustacean	Parasites	Other	# samples for DNA barcoding
	Tissue	Bones	Scales	Lenses #	Otoliths #	Other	Tissue	Lenses #	Statoliths #	Suckers/hooks	Gladius	Beak	Other				
NOG15-066	Y	Y	Y	1	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8
NOG15-065	Y	NA	Y	NA	NA	NA	Y	Y	NA	NA	Y	Y	NA	Y	NA	NA	3
NOG15-064	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	Y	NA	NA	1
NOG15-063	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5
NOG15-061	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	1
NOG15-060	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1
NOG15-059	Y	Y	Y	NA	NA	Y	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	3
NOG15-054	NA	NA	NA	NA	NA	NA	Y	Y	NA	Y	Y	Y	NA	NA	NA	NA	5
NOG15-053	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	3
NOG15-052	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	5
NOG15-050	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1
NOG15-048	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5
NOG15-047	Y	Y	Y	2	2	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	6
NOG15-046	Y	NA	Y	9	1	NA	Y	1	NA	NA	Y	Y	NA	Y	Y	NA	16
NOG15-043	NA	NA	NA	NA	NA	NA	NA	4	NA	NA	NA	3	NA	Y	NA	NA	3
NOG15-042	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	1
NOG15-040	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	1
NOG15-039	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	NA	Y	Y	NA	3
NOG15-038	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	3

NOG15-037	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	Y	5
NOG15-036	Y	Y	Y	5	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	Y	NA	2
NOG15-033	NA	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	Y	15
NOG15-024	?	NA	NA	NA	NA	NA	Y	Y	NA	NA	Y	Y	NA	NA	NA	NA	9
NOG15-022	?	NA	NA	NA	NA	NA	?	NA	NA	NA	NA	NA	NA	NA	NA	?	8
NOG15-021	Y	Y	NA	NA	NA	NA	Y	NA	NA	NA	Y	Y	NA	NA	Y	NA	9
NOG15-018	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	NA	Y	NA	Y	Y	NA	2
NOG15-017	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	3
NOG15-016	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	3
NOG15-015	NA	NA	NA	NA	NA	NA	?	Y	NA	Y	NA	Y	NA	Y	NA	NA	5
NOG15-014	NA	NA	NA	NA	Y	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	2
NOG15-011	Y	Y	Y	Y	NA	NA	?	NA	NA	NA	Y	Y	NA	NA	Y	NA	2
NOG15-010	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	Y	NA	NA	7
NOG15-009	?	Y	Y	NA	NA	NA	?	NA	NA	Y	NA	Y	NA	Y	Y	Y	8
NOG15-008	NA	NA	NA	NA	NA	NA	Y	4	NA	NA	Y	NA	NA	NA	Y	NA	2
NOG15-001	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	NA	4
NOG13-093	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	10
NOG13-085	NA	NA	NA	NA	NA	NA	Y	3	NA	NA	Y	NA	NA	NA	NA	NA	4
NOG13-081	NA	NA	NA	NA	NA	NA	Y	3	NA	NA	Y	Y	NA	NA	NA	NA	2
NOG13-080	Y	Y	Y	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	3
NOG13-054	?	Y	Y	2	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1
NOG13-048	Y	Y	Y	Y	Y	NA	Y	NA	NA	Y	NA	NA	NA	NA	Y	?	9
NOG13-045	Y	Y	Y	1	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	4
NOG13-041	?	Y	Y	NA	6	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	1
NOG13-038	Y	Y	Y	3	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	2
NOG13-037	Y	Y	Y	1	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	?	5
NOG13-036	Y	NA	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	1
NOG13-029	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	2
NOG13-027	NA	Y	Y	2	3	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	1

NOG13-026	Y	Y	Y	1	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	?	4
NOG13-025	?	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	?	3
NOG13-023	Y	Y	Y	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	?	2
NOG13-020	?	NA	Y	7	14	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	4
NOG13-009	?	Y	Y	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	1
NOG13-005	Y	Y	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	?	12
NOG13-003	?	Y	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	10
NOG13-002	Y	Y	Y	2	3	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	1
NOG12-039	Y	Y	Y	2	NA	NA	Y	2	NA	Y	NA	NA	NA	NA	Y	NA	3
NOG12-036	?	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	NA	2
NOG12-032	?	NA	Y	NA	NA	NA	?	NA	NA	NA	NA	NA	NA	NA	Y	NA	1
NOG12-030	NA	NA	Y	NA	NA	NA	Y	4	1	Y	NA	Y	NA	NA	Y	NA	7
NOG12-025	Y	NA	NA	NA	NA	NA	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	5
NOG12-020	Y	Y	NA	NA	NA	NA	Y	NA	NA	NA	NA	NA	NA	Y	Y	NA	5
NOG12-019	Y	Y	Y	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	5
NOG12-017	?	Y	NA	?	NA	NA	Y	?	NA	Y	NA	NA	NA	NA	Y	NA	5
NOG12-016	Y	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	Y	8
NOG12-012	?	Y	Y	NA	NA	NA	NA	NA	NA	Y	NA	NA	NA	Y	Y		4
NOG12-010	NA	NA	NA	NA	NA	NA	Y	NA	NA	Y	NA	NA	NA	Y	Y	NA	3
NOG12-009	?	NA	NA	NA	NA	NA	?	NA	NA	NA	NA	NA	NA	NA	Y	NA	3
NOG12-002	Y	Y	Y	4	NA	NA	NA	NA	NA	NA	NA	NA	NA	?	Y	Y	4
NOG12-001	Y	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Y	NA	4

Appendix 2:

List of literature containing *N. gouldi* dietary information, with date sampled, study site and method of capture.

Literature reference	Date sampled	Study site	Method of capture
O'Sullivan & Cullen, (1983)	November 1979 – April 1980	Bass Strait, south-eastern Australian waters	Japanese jigging vessels
Braley et al., (2010)	February 2005 – March 2007	East of the Great Australian Bight	Plastic jigs and dab nets conducted at night
Pethybridge et al., (2012)	March 2007 – February 2008	Coastal waters off eastern South Australia & western Victoria (between 37856′ – 38843′S and 139859′ – 141836′E)	Trawled opportunistically
Current study	January 2012, August 2013, February & April 2015	Chatham Rise and west coast of Te Waipounamu, South Island.	Trawled opportunistically