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Feeding Ecology of Gould's Arrow Squid *Nototodarus gouldi* (Cephalopoda: Ommastrephidae) in Aotearoa New Zealand Waters

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ABSTRACT

Squids are important components of marine ecosystems because of their role as both predator and prey. Across the Tasman Sea, Gould's arrow squid (*Nototodarus gouldi*) is a commercially targeted ommastrephid squid that supports an economically important fishery. However, the ecology of this species in Aotearoa New Zealand (NZ) waters remains poorly understood. This study is the first integrative analysis of the feeding ecology of *N. gouldi* within the NZ Exclusive Economic Zone. We analyzed gut contents by combining morphological observations to identify hard parts, DNA barcoding to identify soft tissue, and a parasite analysis to further understand trophic linkages and parasite-host associations. In total, 29 prey taxa spanning six phyla were identified, including 17 prey species not previously reported in the diet of *N. gouldi*. The most frequently occurring prey items include cephalopods (with evidence of cannibalism), crab megalopa, red rock crab, and opalfish. Two parasites were identified, which can be associated with anisakiasis in humans. Most individuals (68.8%) had *Anisakis* sp. larvae encysted in the wall of their stomach caecum, and three individuals had *Hysterothylacium* sp. within their gut contents. Our results suggest that *N. gouldi* has a diverse and opportunistic feeding strategy and plays an important role in coupling pelagic and benthic food webs. This ecological information is important for the development of ecosystem-based fisheries management models.

1 | Introduction

Gould's arrow squid, *Nototodarus gouldi* (McCoy et al. 1888), is one of the two cephalopod species commercially targeted in Aotearoa New Zealand (NZ) waters. It is distributed around southern Australia and northern NZ, while the other commercially targeted species, *N. sloanii* (Gray 1849), is endemic to NZ, occurring in its eastern and southern waters (Uozumi et al. 1998). The distribution of these two species overlaps on the west coast of Te Waipounamu South Island, Cook Strait, the east coast of the lower Te Ika-a-Māui North Island, and the northern Chatham Rise (Smith et al. 1987). These two species are collectively managed as a single stock under the Quota Management System (QMS) (Ministry for Primary Industries et al. 2025). Understanding the ecological role that arrow squids play in the local ecosystem is essential for the implementation of ecosystem-based fishery management (Brodziak and Link 2002; Pikitch et al. 2004; Tuck et al. 2009).

Ecologically, *N. gouldi* plays an important role in the environment. This species is an important prey item for marine mammals; for example, *Nototodarus* spp. made up approximately half of the mass of stomach contents of the common dolphin, *Delphius* sp., occurring as bycatch around Te Ika-a-Māui North Island (Meynier et al. 2008). Similarly, *N. gouldi* appeared to make up the bulk of the diet

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in stranded specimens of long-finned pilot whales, *Globicephala melas* (Beatson, O'Shea, and Ogle 2007, Beatson, O'Shea, Stone, et al. 2007). The findings of both studies were limited by the exclusive use of beaks to determine squid identifications, which is reliable at the genus level but cannot differentiate the two species of arrow squid. Despite this importance as prey, little is known about the feeding ecology of *N. gouldi* itself in NZ waters. Previous studies on the diet of *N. gouldi* have found it to primarily consume fish, cephalopods, and crustaceans (O'Sullivan et al. 1983; Braley et al. 2010; Pethybridge et al. 2012). However, these studies focused on populations in Australian waters, leaving a gap in knowledge around the prey species of *N. gouldi* locally.

Morphology and genetics have both been previously used to analyze oegopsid squid gut contents (e.g., Clough et al. this volume; Lischka et al. in review; McBride et al. 2023), including the gut contents of *N. gouldi* in Australian waters (e.g., Braley et al. 2010). Morphological methods have revealed that this species feeds on a wide variety of teleosts, cephalopods, and crustaceans (Braley et al. 2010; O'Sullivan et al. 1983; Pethybridge et al. 2012). Although a morphological analysis is beneficial for the identification of hard parts, genetic analyses can improve identification of soft prey remains (Braley et al. 2010). Both methods were compared by Braley et al. (2010), who removed hard parts from the gut contents for morphological identification, and then amplified and sequenced the mitochondrial 16S ribosomal RNA gene for soft remains. Both methods recovered some of the same prey taxa, but others were only detected through one method, and they reported that identifications using genetics could be made to the genus or species level significantly more often (Braley et al. 2010). While 16S rRNA continues to be used in some gut content studies (e.g., Lischka et al. in review), the DNA barcode region (648bp from the 5′ end of cytochrome *c* oxidase subunit I [COI]) may be a more powerful tool for prey identification in squids, since sequences can be searched and compared on the large reference database housed within the Barcode of Life Data Systems (BOLD; Ratnasingham et al. 2024). Several recent studies have used COI to analyze squid diets in NZ (e.g., Braid et al. 2014, McBride et al. 2023), but this is the first local dietary analysis of any kind for *N. gouldi*.

The present study therefore aims to increase our understanding of the ecological role of *N. gouldi* within the NZ Exclusive Economic Zone (EEZ). We apply an integrative approach to assess the feeding ecology of this species by combining morphological identification and DNA sequencing of gut contents with helminth parasite identification. Our results provide baseline data on the food spectrum of *N. gouldi*, which will be essential in establishing an ecosystem-based fisheries framework (Department of Conservation et al. 2020) and for monitoring potential dietary shifts that may occur in our changing oceans.

2 | Methods

2.1 | Sample Collection

Specimens ($n = 70$) of *N. gouldi* were collected between 2012 and 2015 from the Chatham Rise and the west coast of Te Waipounamu South Island by Earth Sciences New Zealand (ESNZ; formerly the National Institute of Water and Atmospheric Research, Ltd [NIWA]) and the Scientific Observer Programme (SOP; Table 1; Figure 1). ESNZ voyages collected samples during daylight hours between 0616 and 1750 using bottom trawls, while time and gear data was not available for SOP samples. Samples were collected at depths of 73–397 m and frozen whole at −20°C at sea. Specimens were later thawed to measure mantle length, determine sex, and remove the stomach caecum, which was re-frozen at −20°C until analysis.

TABLE 1 | Collection data for *Nototodarus gouldi* samples ($n = 70$). Voyage indicates the trip number for the RV *Tangaroa* (TAN), RV *Kaharoa* (KAH), and specimens collected as part of the scientific observer programme (TRIP). Scientific observer location data has been truncated to a single decimal point.

Date	Location	Depth, m	Voyage	n
Jan 2012	43.386°S, 177.661°E	333–338	TAN1201	14
Aug 2013	40.668°S to 41.721°S, 169.899°E to 171.508°E	208–397	TAN1308	21
Feb 2015	40.3°S, 173.6°E	73–78	TRIP4299	6
Apr 2015	−38.5°S to −38.6°S, 173.9° to 174°E	90–98	TRIP4299	16
Mar/Apr 2015	40.763°S to 41.3°S, 171.140°E to 173.129°E	24–395	KAH1503	13
			Total specimens	70

2.2 | Morphological Analysis

Stomachs and stomach caeca were thawed at room temperature before sorting. A qualitative assessment of digestion state was recorded following methods adapted from Jackson et al. (1998) as modified by Chantheran (2022). Individual prey items were sorted and categorized into hard parts or soft tissue through examination under a dissecting microscope. Identifiable hard parts—including teleost otoliths (sagittae), eye lenses, scales, squid beaks, suckers, gladius fragments, and crustacean exoskeletons—were stored individually and preserved in 70% ethanol. Hard parts from fishes and squids were identified following Smale and Watson (2024), Stevens et al. (2024), and Xavier and Cherel (2021). When possible, fish standard length (SL) was calculated based on sagitta length. The regression equation from Beatson and O'Shea (2009) was used to estimate the mantle length of *Nototodarus gouldi* prey items using the lower rostral length of their beaks. Conspecific otoliths were tallied and divided by two to infer the minimum number of individuals consumed. Experts were consulted for the identification of hard parts from barnacles, worms, and crustaceans.

2.3 | Parasite Identification

A subset of nematodes found within the wall of the stomach caecum were stored in 95% ethanol before molecular analysis by Li et al. (this volume). Specimens found free floating in the stomach

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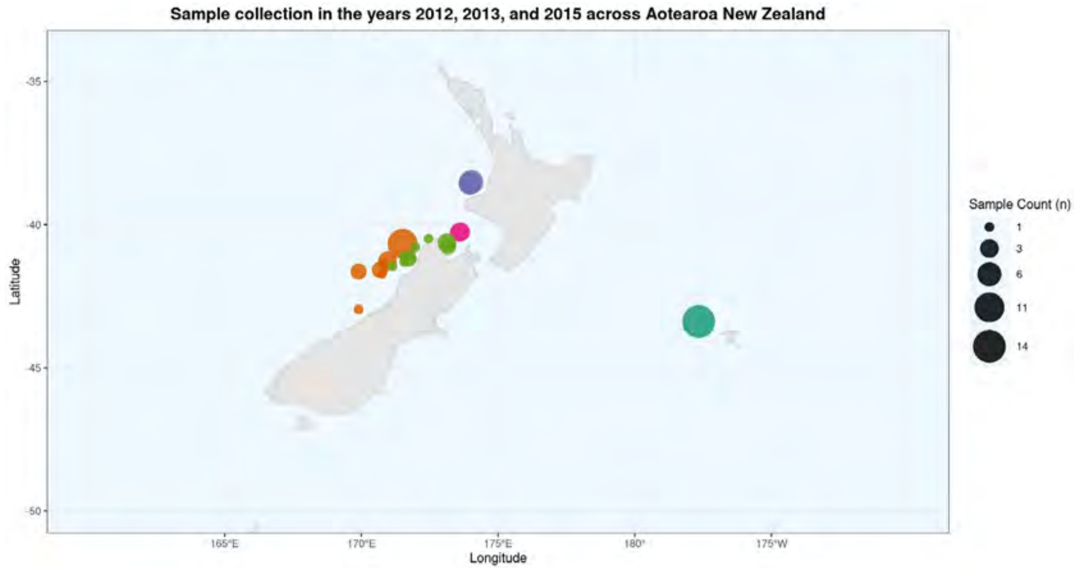

FIGURE 1 | Sample collection localities for *Nototodarus gouldi*. Circle size indicates sample size (n). Samples were collected on five cruises at different times: January 2012 (TAN1201; teal), August 2013 (TAN1308; orange), February 2015 (TRIP 4299; pink), April 2015 (TRIP 4299; purple), and March/April 2015 (KAH1503; green).

caecum contents were removed and kept frozen at −20°C until they could be genetically identified.

2.4 | DNA Barcoding

Representative soft tissue samples were selected due to variable texture, color, and morphology, then re-frozen at −20°C until DNA extraction. Hard parts that had soft tissue remains attached were subsequently DNA barcoded to confirm their identifications. DNA extraction followed DNEasy Blood and Tissue Kit (Qiagen) protocols using Qiagen reagents and EconoSpin columns (Epoch Life Science). The DNA barcode region (648-bp region from the 5′ end of the cytochrome *c* oxidase subunit I [COI]) was amplified using universal invertebrate primers (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), an additional PCR was performed using mammal cocktail primers (C_VF1LFt1/C_VR1LRt1; Ivanova et al. 2007) following protocols from Braid et al. (2012).

The two primer sets were amplified using different reaction profiles. Universal invertebrate primers used 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. Mammal cocktail primers used 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. All PCR products showing a single clear band on a 1% agarose gel were sent to Macrogen (Korea) for sequencing. PCR products using universal invertebrate primers used the same primers for sequencing, while products amplified using mammal cocktail were sequenced with M13R-pUC.

Sequences were edited using CodonCode Aligner v10.0.2. Sequences were uploaded to the public BOLD project titled "Gut Contents of *Nototodarus gouldi* from Aotearoa" (project code: GCNGA) and accessioned on GenBank (PZ407899-PZ407958). Identifications were made using the Barcode of Life Data Systems (BOLD) Identification Engine (using the All Barcode Records on the BOLD database) and the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information (NCBI). Species-level identifications were confirmed when sequences had a 99% similarity or higher to reference sequences (following Wong et al. 2008). Specimens that yielded 94%–97% matches were identified to the genus level.

2.5 | Frequency of Occurrence

We report the relative significance of prey items based on frequency of occurrence (FO%). This calculation was made separately for prey items identified through DNA barcoding and morphology. This frequency was derived from the following equation:

$$\text{Frequency of occurrence (FO\%)} = \left(\frac{\text{Number of stomachs in which the taxon was identified } (n)}{\text{Total number of stomachs } (N = 70)}\right) \times 100 \quad (1)$$

3 | Results

A total of 70 stomach caeca (67 containing prey remains) were analyzed through a combination of morphological analysis and DNA barcoding, revealing 26 prey taxa (Table 2), of which 17 were only detected using one method (morphology or sequencing). Overall, the diversity of fish prey was the highest (14 species), followed by crustaceans ($n = 4$) and cephalopods ($n = 4$). Prey items

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TABLE 2 | Prey items for *Nototodarus gouldi* from Aotearoa New Zealand waters. First report = prey taxon not previously reported for *N. gouldi*, NC = number of stomach caeca that contained a specific prey item, FO% = frequency of occurrence (for FO of morphologically identified items, bold text indicates that COI sequences for the same taxon from the same stomach were recovered), Ind = total number of prey individuals identified morphologically. DNA barcode IDs were determined using the Barcode of Life Data System (BOLD) and the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information (NCBI), and the %Match indicates the similarity to sequences of that taxon in these databases. Morphological identifications include the estimated number of prey taxa that were consumed (No. ind.), calculated from otoliths and characteristic hard parts. Sample year indicates when the samples were collected.

Taxon		Common name	First report	DNA barcode ID		Morphological ID		Sample year
				% Match	NC (FO%)	Ind	NC (FO%)	
Annelida								
Unidentified annelid			✓	—	—	1	1 (1.43%)	2013
Arthropoda (Crustacea)								
Brachyura								
		Crab megalopa		—	—	—	5 (7.15%)	2013, 2015
Hyperiidae								
	Themisto sp.	Amphipod	✓	99.83	1 (1.43%)	—	—	2015
Lepadidae								
	Lepas australis	Gooseneck barnacle	✓	99.62–99.74	2 (2.86%)	—	**1 (1.43%)**	2015
Plagusiidae								
	Guinusia chabrus	Red rock crab	✓	99.50–99.67	4 (5.71%)	—	—	2015
Scyllaridae								
	Ibacus alticrenatus	Slipper lobster		100	1 (1.43%)	—	—	2013
Chordata								
Argentinidae								
	Argentina elongata	Silverside	✓	99.65	1 (1.43%)	1	2 (2.86%)	2013
Chimaeridae								
	Hydrolagus novaezealandiae	Dark ghost shark	✓	99.83	1 (1.43%)	—	—	2012
Clupeidae								
	Sardinops sagax	Pilchard		99.83	1 (1.43%)	—	—	2015
Congridae								
	Gnathophis sp.	Conger		99.24–99.67	1 (1.43%)	1	**1 (1.43%)**	2015
Cyttidae								
	Cyttus novaezealandiae	Silver dory		99.83	1 (1.43%)	1	1 (1.43%)	2012, 2013
Macrouridae								
	Lepidorhynchus denticulatus	Javelinfish		100%	1 (1.43%)	1	2 (2.86%)	2012, 2013
Merlucciidae								
	Merluccius australis	Hake	✓	100%	2 (2.86%)	—	—	2015

(Continues)

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TABLE 2 | (Continued)

Taxon	Common name	First report	DNA barcode ID % Match	DNA barcode ID NC (FO%)	Morphological ID Ind	Morphological ID NC (FO%)	Sample year
Macruronus novaezelandiae	Hoki	✓	100%	2 (2.86%)	1	**1 (1.43%)**	2013
Moridae							
Pseudophycis bachus	Red cod	✓	100%	1 (1.43%)	1	**1 (1.43%)**	2013
Myctophidae							
Lampanyctodes hectoris	Hector's lanternfish		—	—	4	1 (1.43%)	2013
Symbolophorus boops	Bogue lanternfish	✓	—	—	1	1 (1.43%)	2013
Symbolophorus sp.	Lanternfish		99.8%–99.82%	2 (2.86%)	—	—	2013
Paraulopidae							
Paraulopus nigripinnis	Cucumber fish	✓	100%	1 (1.43%)	—	—	2015
Percophidae							
Hemerocoetes cf. *artus*	Narrow opalfish	✓	—	—	2	3 (4.29%)	2013
Hemerocoetes sp.	Opalfish		94.75%–95.33%	4 (5.71%)	1	**2 (2.86%)**	2013, 2015
Sternoptychidae							
Maurolicus walvisensis	Pearlside		100%	1 (1.43%)	—	—	2012
Unidentified fish			—	—	—	20 (28.57)	2012, 2013, 2015
Mollusca							
Mastigoteuthidae							
Idioteuthis cordiformis	Love-heart squid	✓	100%	1 (1.43%)	—	—	2012
Ommastrephidae							
Nototodarus gouldi	Gould's arrow squid		99.81%–100%	12 (17.14)	—	—	2012, 2013, 2015
Nototodarus sloanii	Southern arrow squid	✓	100%	1 (1.43%)	—	—	2012
Sepiolidae							
Stoloteuthis maoria	Bobtail squid	✓	100%	1 (1.43%)	1	1 (1.43%)	2012
Unidentified cephalopod			—	—	—	16 (22.86%)	2012, 2013, 2015
Rhodophyta							
Bangiophyceae	Red algae	✓	99.36%	1 (1.43%)		—	—
Foraminifera							
Unidentified foraminiferan		✓	—	—	1	1 (1.43%)	2013

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encountered most frequently were *Nototodarus gouldi* (FO 17.14%), opalfish (*Hemerocoetes* sp.; FO 10%), and red rock crab (*Guinusia chabrus*; FO 5.72%). At least nine stomachs contained two or more prey items (Table 2). Based on the 99% threshold for species identifications defined in the Methods section, 48 sequences were identified to species level, while 11 additional sequences were identified to higher taxa (Table 2). The nematode parasite *Anisakis* sp. was only observed embedded within the wall of the stomach caecum and is not included as a prey item.

3.1 | Morphological Identification

A total of 15 prey species were morphologically identified across five phyla (Table 2; Figures 2 and 3), including five taxa that were not recovered through DNA barcoding. Prey remains examined from stomach 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.

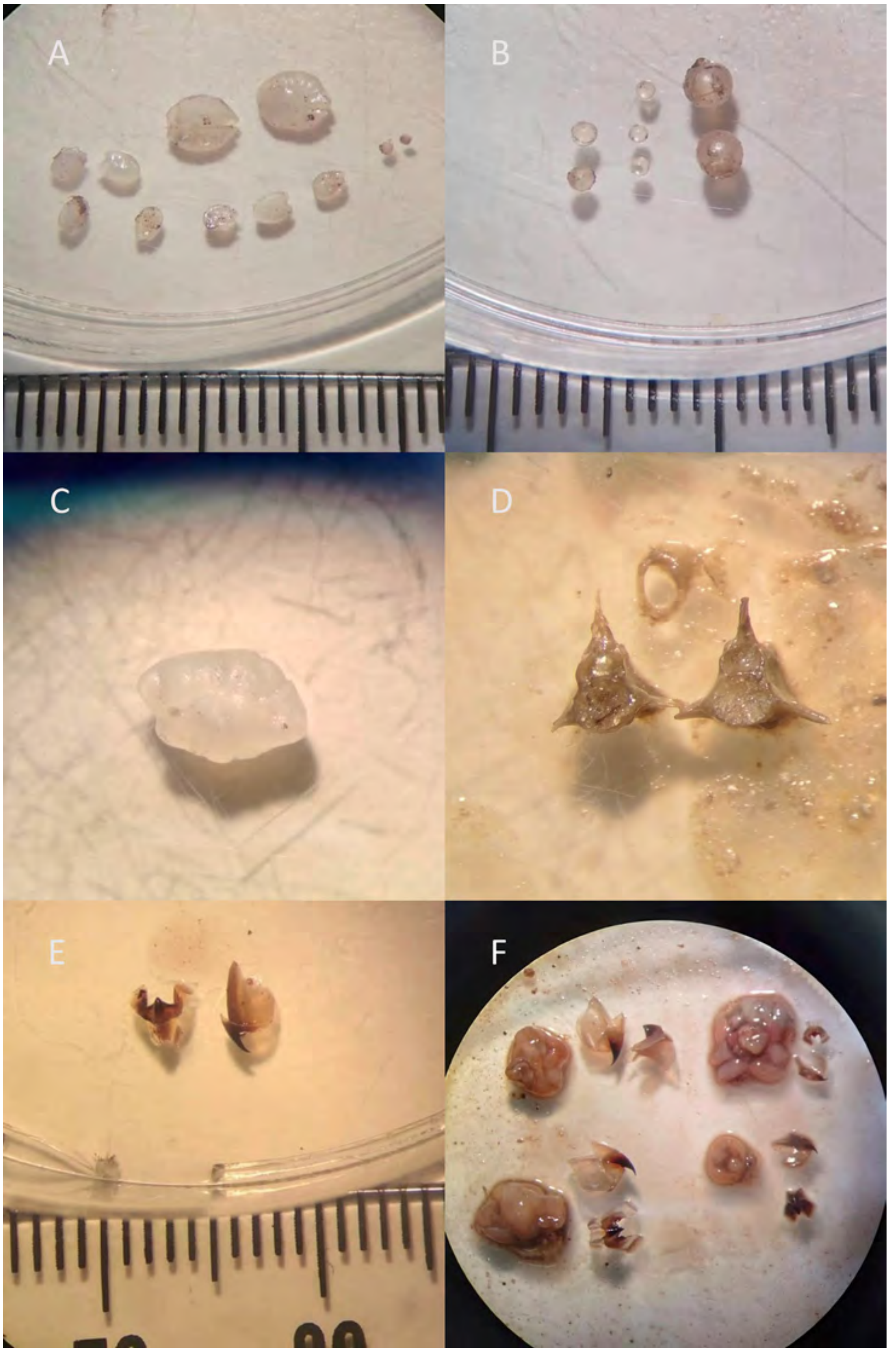

FIGURE 2 | Characteristic hard parts and associated soft tissues from *Nototodarus gouldi* gut contents. (A) Otoliths of *Symbolophorus boops* (large) and *Lampanyctodes hectoris* (small); (B) Fish eye lenses; (C) Otolith of *Gnathophis* sp.; (D) Vertebrae of *Gnathophis* sp. with soft tissue; (E) *Stoloteuthis maoria* beak; and (F) *N. gouldi* beaks (right) beside the associated buccal mass (left). Scale bar with 1 mm increments.

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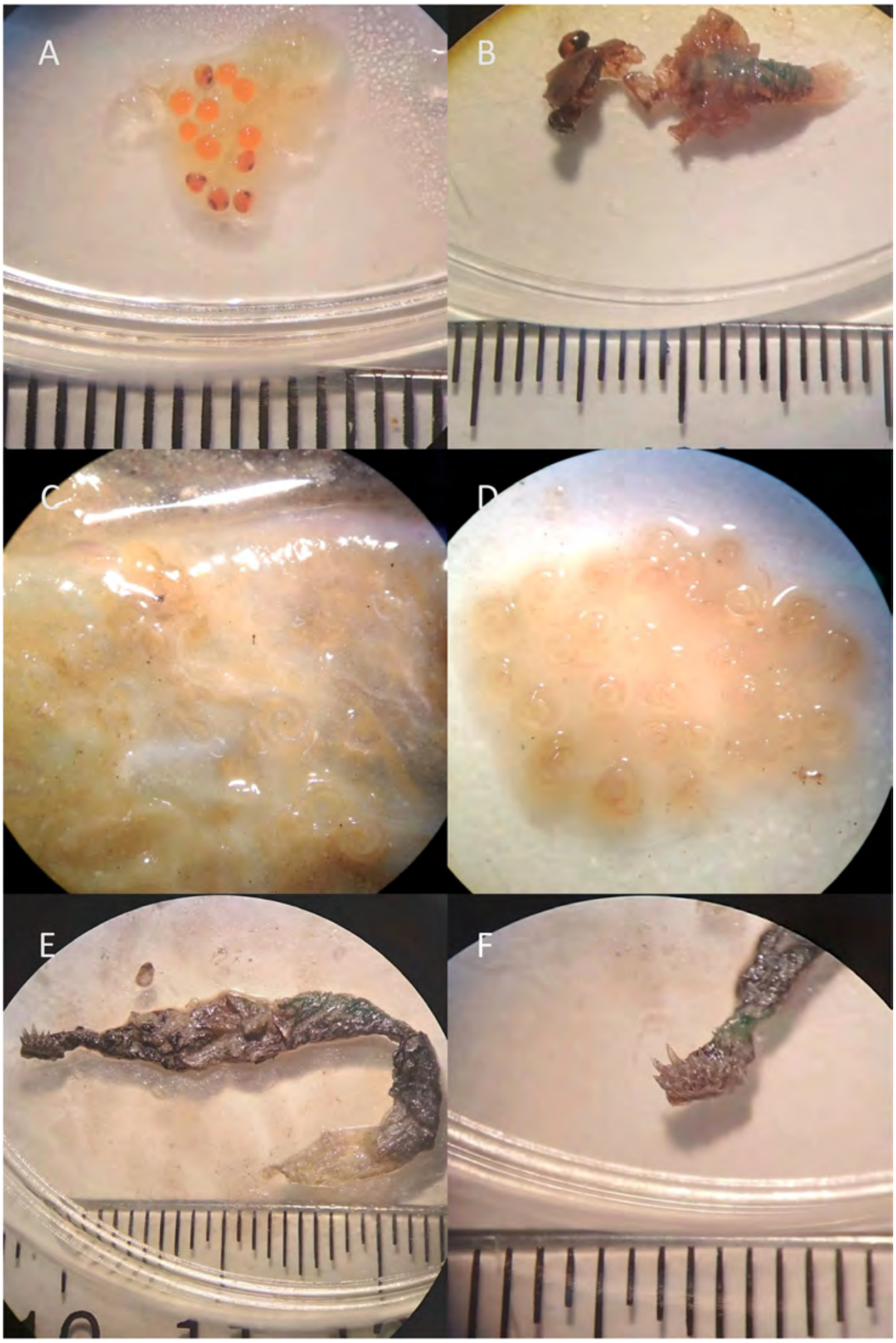

FIGURE 3 | Prey remains and parasites from *Nototodarus gouldi* gut contents. (A) *Ibacus alticrenatus* mid-stage eggs; (B) *Guinusia chabrus* megalopa head, abdomen, and telson; (C) *Anisakis* sp. embedded in the stomach caecum lining; (D) *Anisakis* sp. parasites dissected out of caecum lining; (E) unidentified annelid; and (F) head of unidentified annelid. Scale bar with 1 mm increments.

Crustacean remains (hard parts, such as shells, chelipeds, sternum, and peduncles) were found in 38.6% of caeca ($n = 27$). Hard parts were used to identify a brachyuran megalopa, but a more precise identification was not possible through morphological examination.

A total of 39 fish otoliths were found across 15 stomach caeca. Based on otolith morphology, eight fish species were identified (Table 2). Five stomach caeca contained opalfish (*Hemerocoetes* sp.; 153–156 mm SL), which were also identified through DNA barcoding. The stomach caecum that contained the greatest number of myctophids had at least four individuals of Hector's lanternfish (*Lampanyctodes hectoris*; 46.3–57.4 mm SL) and one bogue lanternfish (*Symbolophorus boops*; 92.6 mm SL). Two sagittae were found in a single stomach caecum that were identified as a juvenile hoki (*Macruronus novaezelandiae*); unfortunately, because both sagittae were broken, an accurate size estimate could not be made. One sagitta could not be identified to species.

Cephalopod remains were identified in some stomach caeca, with beaks present in the guts of 15 individuals, seven of which

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had flesh or buccal mass attached (Figure 2F). Four small beaks (< 1mm lower rostral length) with intact buccal bulbs were recovered but were too small to identify morphologically. These specimens are estimated to have been <100 mm ML.

Other prey included an unidentified annelid (Figure 3E), which has morphological features consistent with *Chaetopterus* sp. but with hard parts that could suggest *Glycinde* sp., and a calcareous spiral was also found and was tentatively identified as a foraminiferan (Retaria).

3.2 | DNA Barcoding

Out of 77 soft tissue samples that were extracted, 60 sequences were recovered and identified (Table 2), while 17 sequences were contaminated or failed to sequence. Of the successful sequences, 46 could be attributed to species (similarity of 99% or above), with a total of 22 unique prey species represented, of which 12 were only identified through DNA barcoding and not recovered in the morphological analysis of prey remains. Fishes were the most diverse prey group (14 species from 14 genera in 11 families) and were identified from 17 individuals (24% FO), followed by Mollusca and Arthropoda (four species each). Two taxa were identified to genus because sequences could not be identified to the species level: opalfish (*Hemerocoetes* sp.) and a nematode (*Hysterothylacium* sp.). Four cephalopod species were identified from the stomach caeca of 15 individuals: *N. gouldi* ($n = 12$), *Nototodarus sloanii* ($n = 1$), *Idioteuthis* cf. *cordiformis* ($n = 1$), and *Stoloteuthis maoria* ($n = 1$).

Top recurring prey species identified in stomach caeca using DNA included Gould's arrow squid, *N. gouldi* ($n = 14$); opalfish, *Hemerocoetes* sp. ($n = 4$); and red rock crab, *Guinusia chabrus* ($n = 4$). Red cod (*Pseudophycis bachus*), conger eel (*Gnathophis* sp.), and opalfish (*Hemerocoetes* sp.) were initially identified by both DNA barcoding and morphological identification of otoliths. Based on DNA results, six stomach caecum samples contained two or more prey items. Of the stomach caeca with multiple prey items, the contents contained either both squid and fish, or multiple fish species.

3.3 | Parasites

Two parasite taxa were identified in *N. gouldi*. Nematodes from three individuals from 2015 identified as *Anisakis pegreffii* by Li et al. (this volume) were extracted from the caecum lining. Nematodes were observed in 48 out of the 70 stomachs (68.6%), with up to 30 nematodes in a single stomach caecum (which was observed in two individuals) (Figure 3C,D). Individual nematodes varied in in length and width; all appeared translucent and did not show any macroscopic visual character differences that would allow us to differentiate them into different morphotypes. Three caeca also contained free-floating nematodes identified through DNA barcoding as *Hysterothylacium* sp. (BOLD Process IDs GCNGA021-26, GCNGA056-26, and GCNGA060-26; GenBank IDs PZ407916-PZ407918).

4 | Discussion

This study presents the first data on the feeding ecology of Gould's arrow squid, *Nototodarus gouldi*, from Aotearoa New Zealand waters. An integrative approach was used (combining morphological identification, DNA barcoding, and parasite identification) to maximize our trophic understanding of this species. Although the majority of the stomach caeca analyzed contained highly digested prey remains, a diverse array of prey was identified, comprising 29 taxa across seven phyla. Of these, 17 species and four phyla were reported for the first time in the diet of *N. gouldi*. Our results suggest that this squid is a generalist, likely opportunist, predator with prey items including fish, cephalopods, and crustaceans. The wide variety of prey spanning pelagic to benthic environments (e.g., red rock crab, slipper lobster, and opalfish) indicates that *N. gouldi* feeds throughout the water column. In addition, the two parasite species that were recovered (*Anisakis pegreffii* and *Hysterothylacium* sp.) have implications for fisheries because they can be associated with human disease (Shamsi et al. 2023) and can also provide additional information about trophic links in this system.

4.1 | Fish Prey

Five species of fishes that are managed under the NZ QMS were found in the diet of *N. gouldi* in the present study. Previous studies also reported pilchard (*Sardinops sagax*) as a prey item for this species (O'Sullivan et al. 1983; Braley et al. 2010; Pethybridge et al. 2012), while the other four species are reported here for the first time. We also confirmed the presence of hoki (*Macruronus novaezelandiae*) through both DNA and otoliths. This species has also been recently reported from the diet of another ommastrephid, *Todarodes angolensis* (Clough et al. this volume). DNA of the endemic dark ghost shark (*Hydrolagus novaezealandiae*) was recovered from the stomach caecum from a single individual from the Chatham Rise and represents the first report of an elasmobranch in the diet of *N. gouldi*. Although elasmobranchs are unexpected as prey item for squids, *Deania calcea* has previously been reported in the gut contents of the love-heart squid (*Idioteuthis cordiformis*) in NZ waters (Braid et al. 2014). A single individual from 2013 contained red cod (*Pseudophycis bachus*), which was detected through DNA and supported by a broken otolith. Although DNA was used to detect hake (*Merluccius australis*), otoliths were not recovered from the stomach caeca, which could indicate that the squid had preferentially consumed only the soft body tissue of the fish, and supports an integrative approach to dietary analyses (Clough et al. this volume).

Myctophids were found in the present study, which is consistent with the diet of *N. gouldi* from Australia, where fatty acid analysis of *N. gouldi* and its prey have revealed that myctophids have the most closely related profile (Pethybridge et al. 2012). Hector's lanternfish (*Lampanyctodes hectoris*) was the most numerous species consumed (four individuals) among the remains we examined, but was only found in the gut contents of a single squid; this species is also preyed upon by *N. gouldi* in Australia (Pethybridge et al. 2012). We report *Symbolophorus boops* in the diet of *N. gouldi* for the first time.

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Opalfish (*Hemerocoetes* spp.) were also important, with otoliths recovered from five individuals from the west coast of the South Island in the present study. Intact otoliths were identified as *Hemerocoetes* cf. *artus*, while eroded otoliths could not be identified below the genus level. This result is supported by DNA, but the sequences recovered had a match of only 94.75%–95.33% to *Hemerocoetes artus*, which suggests that they likely represent a different species in the genus. There are five accepted species in this genus (WoRMS Editorial Board et al. 2025), but only two species (*Hemerocoetes artus* and *Hemerocoetes morelandi*) have sequences available on BOLD, and although *Hemerocoetes morelandi* has a southern distribution in NZ waters, the other four species also likely occur in this area (Roberts et al. 2015). This highlights the importance of using complete reference databases for high prey resolution in dietary studies that rely on genetics.

4.2 | Cephalopod Prey

Ommastrephids have previously been reported in the diet of *N. gouldi* (O'Sullivan et al. 1983; Braley et al. 2010) and were also found herein. We found four beaks with intact buccal bulbs attached, which were identified as *N. gouldi* using genetics. Although contamination from the predator stomach cannot be ruled out, true cannibalism is supported by the squid beaks attached to the soft tissues that returned *N. gouldi* sequences (e.g., Figure 2F), and is consistent with previous studies (O'Sullivan et al. 1983; Braley et al. 2010). This suggests that adults were preying on juvenile individuals, which has also been reported in another ommastrephid, the Humboldt squid (*Dosidicus gigas*; Nigmatullin et al. 2001). We also report *Nototodarus sloanii* as a new prey taxon; it was identified from samples collected from the northern Chatham Rise in the present study, where both species are known to co-occur (Smith et al. 1987). Future dietary studies that focus on cannibalism in *Nototodarus* should include morphology so that the frequency of occurrence of adults and juveniles in their diet can be determined.

Two additional cephalopods are reported as new prey records in *N. gouldi* from Chatham Rise. *Idioteuthis cordiformis* is an unexpected prey record for *N. gouldi*. The maximum depth that specimens were retrieved from in this study was 397 m, while *I. cordiormis* is known to inhabit waters of 750–1500 m (Braid et al. 2015). However, their geographic distributions do overlap and *I. cordiformis* is known to undertake diel vertical migrations (Jereb and Roper 2010). Although *I. cordiformis* can reach a very large size (at least 930 mm mantle length; Braid et al. 2015), it is likely that a juvenile was targeted. In contrast, a very small pelagic bobtail squid species, *Stoloteuthis maoria*, was also found as a prey item. Beak fragments were morphologically consistent with this species, and this was supported by genetic evidence. Both *S. maoria* and *I. cordiformis* are infrequently encountered on the Chatham Rise, but our understanding of the cephalopod diversity in this area has increased with dedicated efforts for their identification (Stevens et al. 2017).

4.3 | Crustacean Prey

Crustaceans were expected prey items based on previous studies of *N. gouldi* (O'Sullivan et al. 1983; Braley et al. 2010; Pethybridge et al. 2012), but the presence of a gooseneck barnacle (*Lepas australis*) was not. This species was recovered from two individuals from the same station from the west coast of South Island. One individual's stomach caecum contained soft tissue attached to a white shell that was morphologically identified as a gooseneck barnacle; DNA confirmed this identification. A second individual did not have obvious barnacle remains, but one of the soft tissue pieces sequenced also matched *L. australis*. This barnacle is sessile and disperses on drifting kelp (*Durvillaea antarctica*, *Macrocystis pyrifera*), so its presence as a prey item may reflect feeding on macroalgal detritus or colonized floating matter (Fraser et al. 2018; Avila et al. 2020). Although net contamination cannot be ruled out, the absence of kelp debris suggests potential opportunistic foraging on sinking rafts or associated fauna.

4.4 | Additional Prey

Annelids had been previously reported from the diet of *N. gouldi* (Braley et al. 2010). The unidentified annelid from the present study had morphological features that could represent either *Chaetopterus* sp. or *Glycinde* sp. (Figure 3E,F) and therefore could not be identified below phylum. Unfortunately, several attempts to amplify DNA extracted from this specimen failed. Braley et al. (2010) also recovered an annelid from *N. gouldi*, a nereid polychaete, which failed to amplify as well. This prey item was recovered from a single specimen from the west coast of the South Island, while an unidentified worm from a different phylum (Chaetognatha) was recovered as a prey item from *N. sloanii* from the Chatham Rise (Dunn et al. 2009). Worms are rarely recovered as prey for *Nototodarus* (Dunn et al. 2009; Braley et al. 2010), and these records likely indicate opportunistic feeding.

The detection of two of the new prey items likely represents secondary predation. The identification of red algae (class Bangiophyceae) in one individual was unexpected because squids are carnivorous. Unanticipated items, such as plant matter, have previously been found in gut contents of *D. gigas*, which may have consumed them due to stress (Braid et al. 2012). However, because no large fragments of algae were found in the stomach (the identification was based on genetics), the red algae found in *N. gouldi* likely represents secondary ingestion. The detection of secondary predation is likely in DNA-based studies, and it cannot be distinguished from primary predation (Sheppard et al. 2005). The stomach caecum of this individual also contained fish bones, which could have been from a herbivorous or generalist fish. A calcareous spiral, which likely represented a foraminiferan, was present in the stomach caecum of one individual in the present study. Jones (2012) found foraminifera in the diet of javelinfish (*Lepidorhynchus denticulatus*) and silverside (*Argentina elongata*), which were both found as prey items for *N. gouldi* in the present study. Although secondary predation would not represent a feeding event, it provides important information about energy flow in this system.

4.5 | Parasites

Anisakis sp. larvae were found encysted in the stomach caecum lining in most (68.8%) of the *N. gouldi* individuals in the present study. Similarly, Pethybridge et al. (2012) found *Anisakis* spp. in the stomach walls in *N. gouldi* from Australian waters, and

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Li et al. (this volume) identified parasites from our specimens as *A. pegreffii*. Consuming raw or undercooked seafood that contains *Anisakis* spp. larvae can cause anisakiasis in humans (Sakanari et al. 1989). Pethybridge et al. (2012) found that parasite loading varied with season, with a peak occurring in August and September. Our sample size is too low to determine any significant trends, but parasites were regularly found in specimens from most sample sets (~77% excluding the lowest sample set), but very low (~36% occurrence) in samples from Te Tai-o-Aorere Tasman Bay in March/April of 2015. Pethybridge et al. (2012) suggested that seasonal changes in diet may impact parasite loading and that *N. gouldi* is an important vector in the transmission of *Anisakis* to its predators, which is supported by the current results. *Anisakis* larvae were previously identified in red cod (*Pseudophycis bachus*) and *Nototodarus sloanii* from NZ waters (Wharton et al. 1999), which were both recovered as prey items for *N. gouldi* in the present study, which could indicate a transmission pathway. However, future studies are needed to evaluate the impact of seasons on parasite loading in this species in NZ.

Hysterothylacium sp. were identified in *N. gouldi* for the first time in the present study. This roundworm was identified through DNA barcoding from parasites found in the gut contents of three individuals collected off the west coast of the South Island, and in Cook Strait. In the present study, red cod (*Pseudophycis bachus*), and opalfish (*Hemerocoetes* sp.) were found as prey items for *N. gouldi*, and *Hysterothylacium aduncum* uses red cod as a definitive host (Bennett et al. 2023) and opalfish (*Hemerocoetes monopterygius*) as an intermediate host (Bennett, Poulin, and Presswell 2022). However, the sequences recovered for this roundworm did not match closely with *Hysterothylacium aduncum* sequences in BOLD but two were closer (>97.2% match) to "*Hysterothylacium* sp. 1 EB" from Patagonia, near the Port of Rawson (BOLD Process ID: DPDP419-16) and one with a closest match (89.42%) to *Hysterothylacium deardorffoversteetorum* from the coast of South Carolina (GenBank accession MF663227). It is possible the species recovered in the present study is one of the 92 accepted species in this genus (WoRMS Editorial Board et al. 2025) that has not been sequenced yet, because only 10 taxa have DNA barcodes on BOLD. A better understanding of the parasitic helminths in marine food webs in Aotearoa New Zealand is needed (Bennett, Presswell, and Poulin 2022).

5 | Limitations

In addition to the limitations discussed above regarding sample size and the potential for prey fragments to be overlooked, we acknowledge that gut content analyses can only provide a brief snapshot of the focus species' prey spectrum. The highly digested prey remains found in the majority of the stomach caeca could have been impacted by collection time, sample age, and storage duration. Squid digestion rates are rapid; Lipiński (1987) reported that for the myopsid "chokka" squid *Loligo reynaudii* in South Africa, prey remains were mostly undigested within the first 3 h after ingestion and then rapidly digested between 4 and 7 h, and the stomach was totally cleared after ten hours. If *N. gouldi* in New Zealand waters actively feeds at night as found by O'Sullivan and Cullen (1983) in Bass Strait, then squids collected during the day may have had more digested gut contents. Unfortunately, the specific collection time was only available for TAN1201 and KAH1503, so it is not possible to determine whether the time of sample collection impacted the digestion stage. Future studies dietary studies for *N. gouldi* focused on stomach caecum contents should consider collection time.

Longer-term dietary trends could also be assessed in future through several potential methods, such as analyzing stable isotopes of the muscular tissue (e.g., Braid et al. 2014) or beaks (e.g., Cherel et al. 2005). Fatty acid analysis could provide another line of evidence; their use by Pethybridge et al. (2012) supported morphological results, corroborating that fish and cephalopods were important prey for *N. gouldi*.

6 | Conclusion

This study constitutes the first report of the diet of *N. gouldi* in Aotearoa New Zealand waters. Although most of the prey recovered were in alignment with what has been previously found in Australian waters (O'Sullivan et al. 1983; Braley et al. 2010; Pethybridge et al. 2012), some unexpected items were also uncovered, such as red algae, foraminifera, and gooseneck barnacles. The present study was restricted to opportunistically collected samples; we recommend that future studies compare the diet and parasites of *N. gouldi* from different locations throughout its distribution to determine whether population-level differences can be observed. Morphology and genetics should be used as complementary identification methods whenever possible because each method identified prey items that would have been missed by the other. The impacts of season on parasite loading should also be investigated. Because *N. gouldi* supports an important commercial fishery, the detection and identification of parasites is essential for mitigating associated diseases in humans. Understanding the trophic role that *N. gouldi* plays in the local marine ecosystem is an essential step in establishing an ecosystem-based fisheries management approach—as has been highlighted for other commercially harvested species (e.g., Thrush et al. 2010)—particularly since it consumes other species that are economically important, or may become so in the future (such as myctophids; see, e.g., Shaviklo 2020).

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Data Availability Statement

All sequences are posted on the Barcode of Life Data Systems (BOLD) in the public project Gut Contents of *Nototodarus gouldi* from Aotearoa (project code: GCNGA) and available on GenBank (PZ407899-PZ407958).

References

Avila, C., C. Angulo-Preckler, R. P. Martín-Martín, B. Figuerola, H. J. Griffiths, and C. L. Waller. 2020. "Invasive Marine Species Discovered on Non-native Kelp Rafts in the Warmest Antarctic Island." *Scientific Reports* 10, no. 1: 1–9. https://doi.org/10.1038/s41598-020-58561-y.

Beatson, E., and S. O'Shea. 2009. "Stomach Contents of Long-Finned Pilot Whales, *Globicephala melas*, Mass-Stranded on Farewell Spit, Golden Bay in 2005 and 2008." *New Zealand Journal of Zoology* 36, no. 1: 47–58. https://doi.org/10.1080/03014220909510139.

Beatson, E., S. O'Shea, and M. Ogle. 2007. "First Report on the Stomach Contents of Long-Finned Pilot Whales, *Globicephala melas*, Stranded in New Zealand." *New Zealand Journal of Zoology* 34, no. 1: 51–56. https://doi.org/10.1080/03014220709510063.

Beatson, E., S. O'Shea, C. Stone, and T. Shortland. 2007. "Notes on New Zealand mammals 6. Second Report on the Stomach Contents of Long-Finned Pilot Whales, *Globicephala melas*." *New Zealand Journal of Zoology* 34, no. 4: 359–362. https://doi.org/10.1080/03014220709510095.

Bennett, J., B. Presswell, and R. Poulin. 2022. "Biodiversity of Marine Helminth Parasites in New Zealand: What Don't We Know?." *New Zealand Journal of Marine and Freshwater Research* 56, no. 2: 175–190. https://doi.org/10.1080/00288330.2021.1914689.

Bennett, J., B. Presswell, and R. Poulin. 2023. "Tracking Life Cycles of Parasites across a Broad Taxonomic Scale in a Marine Ecosystem." *International Journal for Parasitology* 53, no. 5-6: 285–303. https://doi.org/10.1016/j.ijpara.2023.02.004.

Bennett, J., R. Poulin, and B. Presswell. 2022. "Large-Scale Genetic Investigation of Nematode Diversity and Their Phylogenetic Patterns in New Zealand's Marine Animals." *Parasitology* 149, no. 13: 1794–1809. https://doi.org/10.1017/S003118202200138X.

Braid, H. E., and K. S. R. Bolstad. 2014. "Feeding Ecology of the Largest Mastigoteuthid Squid Species, *Idioteuthis cordiformis* (Cephalopoda, Mastigoteuthidae." *Marine Ecology Progress Series* 515: 275–279. https://doi.org/10.3354/meps11008.

Braid, H. E., and K. S. R. Bolstad. 2015. "Systematics of the Mastigoteuthidae Verrill, 1881. (Cephalopoda: Oegopsida) from New Zealand Waters." *New Zealand Journal of Zoology* 42, no. 3: 187–256. https://doi.org/10.1080/03014223.2015.1063516.

Braid, H. E., and K. S. R. Bolstad. 2019. "Cephalopod Biodiversity of the Kermadec Islands: Implications for Conservation and Some Future Taxonomic Priorities." *Invertebrate Systematics* 33, no. 2: 402–425. https://doi.org/10.1071/IS18041.

Braid, H. E., J. Deeds, S. L. DeGrasse, J. J. Wilson, J. Osborne, and R. H. Hanner. 2012. "Preying on Commercial Fisheries and Accumulating Paralytic Shellfish Toxins: A Dietary Analysis of Invasive *Dosidicus gigas* (Cephalopoda Ommastrephidae) Stranded in Pacific Canada." *Marine Biology* 159: 25–31. https://doi.org/10.1007/s00227-011-1786-4.

Braley, M., S. D. Goldsworthy, B. Page, M. Steer, and J. J. Austin. 2010. "Assessing Morphological and DNA-Based Diet Analysis Techniques in a Generalist Predator, the Arrow Squid *Nototodarus gouldi*." *Molecular Ecology Resources* 10, no. 3: 466–474. https://doi.org/10.1111/j.1755-0998.2009.02767.x.

Brodziak, J., and J. Link. 2002. "Ecosystem-Based Fishery Management: What Is It and How Can We Do It?" *Bulletin of Marine Science* 70, no. 2: 589–611.

Chantheran, N. G. 2022. "A Multi-Method Assessment of Southern Arrow Squid (Nototodarus sloanii) Diet in New Zealand Waters." MSc Thesis. Auckland University of Technology.

Cherel, Y., and K. A. Hobson. 2005. "Stable Isotopes, Beaks and Predators: A New Tool to Study the Trophic Ecology of Cephalopods, including Giant and Colossal Squids." *Proceedings of the Royal Society B: Biological Sciences* 272, no. 1572: 1601–1607. https://doi.org/10.1098/rspb.2005.3115.

Clough, S., E. Fitzgerald, D. Stevens, J. Bennett, H. Braid, and K. Bolstad. This volume. "First Report on the Diet of the Angolan Flying Squid (Todarodes angolensis) in New Zealand Waters." *New Zealand Journal of Zoology*.

Department of Conservation. 2020. "Te Mana o Te Taiao – Aotearoa New Zealand Biodiversity Strategy." Accessed December 11th, 2025. https://www.doc.govt.nz/globalassets/documents/conservation/biodiversity/anzbs-2020.pdf.

Dunn, M. R. 2009. "Feeding Habits of the Ommastrephid Squid *Nototodarus sloanii* on the Chatham Rise, New Zealand." *New Zealand Journal of Marine and Freshwater Research* 43, no. 5: 1103–1113. https://doi.org/10.1080/00288330.2009.9626533.

Folmer, R., M. Nilges, P. Folkers, R. Konings, and C. Hilbers. 1994. "A Model of the Complex Between Single-Stranded DNA and the Single-Stranded DNA Binding Protein Encoded by Gene V of Filamentous Bacteriophage M13." *Journal of Molecular Biology* 240, no. 4: 341–357. https://doi.org/10.1006/jmbi.1994.1449.

Fraser, C. I., A. K. Morrison, A. M. Hogg, et al. 2018. "Antarctica's Ecological Isolation Will Be Broken by Storm-Driven Dispersal and Warming." *Nature Climate Change* 8, no. 8: 704–708. https://doi.org/10.1038/s41558-018-0209-7.

Gray, J. E. 1849. *Catalogue of the Mollusca in the Collection of the British Museum I: Cephalopoda Antepedia*. 164. British Museum.

Ivanova, N. V., T. S. Zemlak, R. H. Hanner, and P. D. N. Hebert. 2007. "Universal Primer Cocktails for Fish DNA Barcoding." *Molecular Ecology Notes* 7, no. 4: 544–548. https://doi.org/10.1111/j.1471-8286.2007.01748.x.

Jackson, G., J. McKinnon, C. Lalas, R. Ardern, and N. Buxton. 1998. "Food Spectrum of the Deepwater Squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand Waters." *Polar Biology* 20, no. 1: 56–65. https://doi.org/10.1007/s003000050276.

Jereb, P. and C. F. E. Roper. 2010. "Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Volume 2. Myopsid and Oegopsid Squids." In *FAO Species Catalogue for Fishery Purposes*. 605. FAO.

Jones, M. R. L. 2012. "Diets and Feeding Relationships of Deep-Sea Fish from Central and Southern New Zealand." PhD thesis. Auckland University of Technology.

Li, C.-H., J. Bennett, H. Braid, et al. submitted, this volume. "The Battle of Helminths Deep: Molecular Insights into Oegopsid Squid Parasites in Aotearoa New Zealand." *New Zealand Journal of Zoology*.

Lipiński, M. R. 1987. "Food and Feeding of *Loligo vulgaris reynaudii* from St Francis Bay, South Africa." *South African Journal of Marine Science* 5, no. 1: 557–564. https:doi.org/10.2989/025776187784522513.

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Lischka, A., D. W. Stevens, S. N. van Dijk, et al. In review. "The Diet of the Glacial Squid *Psychroteuthis glacialis* in the Ross Sea Region, Antarctica." *Marine Ecology Progress Series*.

McBride, L. E., H. E. Braid, D. W. Stevens, and K. S. R. Bolstad. 2023. "Trophic Ecology of the Deep-Sea Squid *Moroteuthopsis ingens* (Cephalopoda: Onychoteuthidae) from the Chatham Rise, Aotearoa New Zealand." *New Zealand Journal of Marine and Freshwater Research* 57, no. 4: 582–596. https://doi.org/10.1080/00288330.2022.2086268.

McCoy, F. 1888. "*Ommastrephes gouldi* (McCoy)." *Natural History of Victoria: Prodromus of the Zoology of Victoria* 17: 255–257.

Meynier, L., K. A. Stockin, M. K. H. Bando, and P. J. Duignan. 2008. "Stomach Contents of Common Dolphin (*Delphinus* sp.) from New Zealand Waters." *New Zealand Journal of Marine and Freshwater Research* 42, no. 2: 257–268. https://doi.org/10.1080/00288330809509952.

Ministry for Primary Industries. 2025. "Arrow Squid (SQU) Plenary Report." Accessed December 11th, 2025. https://www.mpi.govt.nz/dmsdocument/69681-Fisheries-Assessment-Plenary-May-2025-Volume-1-ARROW-SQUID-SQU.

Nigmatullin, C. M., K. N. Nesis, and A. I. Arkhipkin. 2001. "A Review of the Biology of the Jumbo Squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae)." *Fisheries Research* 54, no. 1: 9–19. https://doi.org/10.1016/S0165-7836(01)00371-X.

O'Sullivan, D., and J. Cullen. 1983. "Food of the Squid *Nototodarus gouldi* in Bass Strait." *Marine and Freshwater Research* 34, no. 2: 261–285. https://doi.org/10.1071/MF9830261.

Pethybridge, H., P. Virtue, R. Casper, et al. 2012. "Seasonal Variations in Diet of Arrow Squid (*Nototodarus gouldi*): Stomach Content and Signature Fatty Acid Analysis." *Journal of the Marine Biological Association of the United Kingdom* 92, no. 1: 187–196. https://doi.org/10.1017/s0025315411000841.

Pikitch, E. K., C. Santora, E. A. Babcock, et al. 2004. "Ecosystem-Based Fishery Management." *Science* 305, no. 5682: 346–347. https://doi.org/10.1126/science.1098222.

Ratnasingham, S., C. Wei, D. Chan, et al. 2024. "BOLD v4: A Centralized Bioinformatics Platform for DNA-Based Biodiversity Data." In *DNA Barcoding: Methods and Protocols*. 403–441. Springer US.

Roberts, C. D., A. L. Stewart, and C. D. Struthers, eds. 2015. "The Fishes of New Zealand." In *4 Volumes*. 2008. Te Papa Press.

Sakanari, J. A., and J. H. McKerrow. 1989. "Anisakiasis." *Clinical Microbiology Reviews* 2, no. 3: 278–284. https://doi.org/10.1128/cmr.2.3.278.

Shamsi, S., and D. P. Barton. 2023. "A Critical Review of Anisakidosis Cases Occurring Globally." *Parasitology Research* 122: 1733–1745. https://doi.org/10.1007/s00436-023-07881-9.

Shaviklo, A. R. 2020. "A Comprehensive Review on Animal Feed, Human Food and Industrial Application of Lanternfishes; from Prototypes to Products." *Turkish Journal of Fisheries and Aquatic Sciences* 20, no. 11: 827–843. https://doi.org/10.4194/1303-2712-v20_11_06.

Sheppard, S. K., J. Bell, K. D. Sunderland, J. Fenlon, D. Skervin, and W. O. C. Symondson. 2005. "Detection of Secondary Predation by PCR Analyses of the Gut Contents of Invertebrate Generalist Predators." *Molecular Ecology* 14, no. 14: 4461–4468. https://doi.org/10.1111/j.1365-294X.2005.02742.x.

Smale, M. J., and G. Watson. 2024. *Otolith Atlas of Marine Fishes of Southern Africa and Adjacent Oceans*. 2nd ed. NISC Ltd.

Smith, P., R. Mattlin, M. Roeleveld, and T. Okutanp. 1987. "Arrow Squids of the Genus *Nototodarus* in New Zealand Waters: Systematics, Biology, and Fisheries." *New Zealand Journal of Marine and Freshwater Research* 21, no. 2: 315–326. https://doi.org/10.1080/00288330.1987.9516227.

Stevens, D. W., H. E. Braid, L. Meynier, et al. 2024. "A Guide to the Otoliths of Southern Ocean Lanternfishes (Myctophidae)." *Polar Biology* 47: 1543–1558. https://doi.org/10.1007/s00300-024-03312-2.

Stevens, D. W., R. L. O'Driscoll, S. L. Ballara, and Y. Ladroit. 2017. "Trawl Survey of Hoki and Middle-Depth Species on the Chatham Rise, January 2016 (TAN1601)." New Zealand Fisheries Assessment Report 2017/08.131.

Thrush, S. F., and P. K. Dayton. 2010. "What Can Ecology Contribute to Ecosystem-Based Management?" *Annual Review of Marine Science* 2: 419–441. https://doi.org/10.1146/annurev-marine-120308-081129.

Tuck, I., R. Cole, and J. Devine. 2009. *Ecosystem Indicators for New Zealand Fisheries*. 188. New Zealand Aquatic Environment and Biodiversity Report No. 42.

Uozumi, Y. 1998. "Fishery Biology of Arrow Squids, *Nototodarus gouldi* and *N. sloanii*, in New Zealand Waters." *Bulletin National Research Institute of Far Seas Fisheries* 35: 1–111.

Wharton, D. A., M.-L. Hassall, and O. Aalders. 1999. "*Anisakis* (Nematoda) in Some New Zealand Inshore Fish." *New Zealand Journal of Marine and Freshwater Research* 33, no. 4: 643–648. https://doi.org/10.1080/00288330.1999.9516907.

Wong, E. H. K., and R. H. Hanner. 2008. "DNA Barcoding Detects Market Substitution in North American Seafood." *Food Research International* 41, no. 8: 828–837. https://doi.org/10.1016/j.foodres.2008.07.005.

WoRMS Editorial Board. 2025. "World Register of Marine Species." Accessed November 29, 2025. Available from https://www.marinespecies.orgatVLIZ.

Xavier, J., and Y. Cherel. 2021. *Cephalopod Beak Guide for the Southern Ocean: An Update on Taxonomy (Revised Edition)*. 129. British Antarctic Survey.

11758821, 2026, 2, Downloaded from https://rsnz.onlinelibrary.wiley.com/doi/10.1002/njz2.70031 by Auckland University Of, Wiley Online Library on [01/06/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License