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First Report on the Diet of the Angolan Flying Squid (*Todarodes angolensis*) in New Zealand Waters

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ABSTRACT

The Angolan flying squid (*Todarodes angolensis*) is a southerly distributed, large-bodied ommastrephid preyed upon by many large marine vertebrates such as the southern elephant seal and deep-sea squalid sharks. Here, we report its diet in New Zealand waters for the first time, identifying prey items from the stomach contents of 58 adults using morphology and DNA barcoding. Most of the 32 observed prey taxa occurred only once, and many stomachs contained only one observed prey taxon. Fishes, particularly myctophids (eight species), were the most frequently occurring and abundant prey class; the largest prey item was a javelin fish (*Lepidorhynchus denticulatus*), with a calculated length of 50 cm based on otolith measurements. Cephalopods were the second most common prey class, with the rough-skinned clubhook squid (*Moroteuthopsis ingens*) occurring most frequently and jewelled squids (*Histioteuthis* spp.) having the highest number of individuals ($n = 13$). No crustaceans were observed, but Tam O'shanter sea urchins (Echinothurioidea) were identified twice, perhaps representing secondary prey items or net feeding. Most of the squid contained anisakids, including *Skrjabinisakis physeteris*, which uses physeterid and kogiid cetaceans as its final host. Together, these findings indicate that *T. angolensis* is a highly active, opportunistic carnivore that also serves as a vector for anisakid parasites to cetacean apex predators.

1 | Introduction

Squids are obligate carnivorous molluscs and are an important part of nutrient cycling in marine ecosystems. Many squid species, particularly oceanic species in the family Ommastrephidae ('flying' squids, the main group targeted by commercial fisheries worldwide), have high abundances and complete their life cycle in 12–18 months, which is coupled with a high turnover rate sustained by voracious carnivory (Jereb and Roper 2010). Many ommastrephids are highly active throughout their life cycles, migrating to entirely different habitats with their own physical regimes as they develop, making squid responsive to environmental changes throughout their life cycle (Vidal and Shea 2023). From the 1980s until recently, some rapid growth in global squid populations was observed, attributed to climate change making the environment more suitable, combined with the decline in competing fish communities brought about by overfishing (Doubleday et al. 2016). However, not all squid populations are expected to benefit from environmental change; tropical habitats may become unsuitable for squid with ocean warming and acidification (Zakroff et al. 2019). Some tropical species are commercially important, such as chokka squid (*Loligo reynaudii*), and declining fishery stocks would make the industry unviable (Guerreiro et al. 2023). Together, the important role of squids in marine food webs is expected to change in the future, but not uniformly.

Another understudied facet of cephalopod biology is their role in parasite transmission networks. This area is important because parasites are known to exert a negative influence on fishery

species (Shinn et al. 2015), including cephalopods, where repeated infection of the hosts can negatively impact their health (Mladineo and Bočina 2007). Additionally, some parasite taxa, like anisakid nematodes, are transmitted through diet to their final host (Aibinu et al. 2019). Finding trophically transmitted parasites in cephalopods and apex predators provides evidence of a trophic link (Bennett et al. 2024). Finally, marine parasites comprise a significant portion of marine biomass, being reported to have a biomass similar to apex predators. Some also have a free-living stage where they can be a food source for animals that are not infected as a result (Kuris et al. 2008; Thieltges et al. 2013). Despite the influential role of parasites in ecosystems and their usefulness in understanding food webs, less than 1% of all invertebrates that could be infected by parasites have records of such infections in the literature (Bennett et al. 2022a). Therefore, documenting parasites in deep-sea cephalopods will help us understand not only the trophic linkages of cephalopods but also the transmission networks of the marine parasites themselves.

Despite their key role in many marine food webs and parasite transmission networks, the diets of roughly 90% of all cephalopod species remain unreported (Ibáñez et al. 2021). This knowledge gap in marine ecosystems is problematic because effective fisheries management and conservation of marine megafauna require an understanding of the different parts of the ecosystem. Reconstructing cephalopod diets is challenging for several reasons. In situ observations of the feeding behaviour of many marine species remain rare, so alternative methods are needed. Post-mortem examination of gut contents can be informative, but squid beaks masticate prey into morphologically unidentifiable fragments, and digestion is rapid, leaving few remains to identify (Ibáñez et al. 2021). There is also a lack of focus on many of the non-commercial species, so fewer samples are collected and many non-target specimens are discarded. The deep-sea habitat of many cephalopod species requires specialised equipment to access, further limiting scientific understanding of cephalopod trophic ecology. While direct observation of cephalopod dietary behaviour and morphological identification of gut contents have their limitations in understanding their trophic ecology, modern molecular methods can complement and augment these traditional analyses, recovering many additional prey taxa (Braid et al. 2012; McBride et al. 2023; Hu et al. 2026, this volume).

Ommastrephid squid diets are of particular interest due to their global commercial importance. Some, like the Humboldt squid, are known to exert a strong predation effect on local prey populations (Ehrhardt 1991). The same may be true for other species, particularly those reaching relatively large sizes, such as *Todarodes filippovae*, which can weigh 4.5 kg or more (Kojadinovic et al. 2011; New Zealand Ministry for Primary Industries, unpubl. data). Within the waters around Aotearoa New Zealand (hereafter NZ), the Angolan flying squid (*T. angolensis*) – another relatively large species, reaching >3 kg – has a southerly distribution that overlaps with that of the southern flying squid (*T. filippovae*) (Voss et al. 1998). Both are also reported in the waters around South Africa (Roeleveld et al. 1992; Villanueva and Sanchez 1989; Voss et al. 1998), where *T. angolensis* has been reported in the diets of squalid sharks, and also in fur seals inhabiting the Namibian Coast (de Bruyn et al. 2005; Ebert et al. 1992). Cherel (2020) suggested that, given the predominance of *T. angolensis* over *T. filippovae* in Kerguelen waters, it is likely that most of *Todarodes* sp. beaks reported in the diets of Kerguelen albatrosses (Family: Diomedeidae) and southern elephant seals (*Mirounga leonina*) belonged to *T. angolensis* (Cherel et al. 2000, 2002, 2008, 2017). Published reports on the diet of *T. angolensis* are presently limited to two studies on juvenile-maturing specimens from South Africa, which concluded that *T. angolensis* is primarily a predator of small myctophid fishes and macrozooplankton (Lipiński 1992; Kremer et al. 2025).

As a diel vertical migrator (Roeleveld et al. 1992), *T. angolensis* likely interacts with a range of prey taxa in different depth strata. A study on the interannual growth differences of *T. angolensis* cohorts reported that the juveniles were characterised by rapid growth rates, which decrease considerably with the onset of sexual maturity at around 8 months of age (Villanueva 1992). One cohort appeared to grow faster after a sudden influx of cold Antarctic water flowing into the local Benguela current, and the following year's cohort had reduced growth when water temperatures rose (Villanueva 1992). These two observations suggest that *T. angolensis* thrives under colder conditions; its life cycle may therefore be highly sensitive to climate change, and by extension, its influence within marine food webs could change drastically under future ocean-warming scenarios. Such changes cannot be monitored without baseline data, however. This study, therefore, aimed to describe the contents of *T. angolensis* in NZ waters for the first time. To maximise prey item identification, gut contents were analysed using a combination of morphology and DNA barcoding. Parasites were also collected and identified from the stomach tissues of NZ *T. angolensis*, providing an indirect understanding of the species food web.

2 | Methods

2.1 | Sample Collection

Specimens of *T. angolensis* ($n = 58$) were collected by Earth Sciences New Zealand (ESNZ), on the following surveys on *RV Tangaroa*: Sub-Antarctic Ecosystems Voyage (TAN1908), Sub-Antarctic Trawl Surveys (TAN2014, TAN2215, TAN2413), and a Chatham Rise Trawl Survey (TAN2401) (Figure 1). For each specimen, dorsal mantle length (ML), body weight and sex were recorded by ESNZ and AUT scientists onboard the vessel, and the specimens were stored at −20 °C until stomach content analysis. ML and total weight were lost for one specimen, which was not included in the average ML and body weight calculations. The ML range of the remaining 57 specimens was 300–550 mm (mean 439 mm), and the range of their body weight (g) was 620–3500 g (mean 1750 g). Females (N = 48) averaged 444 mm ML and 1810 g, whereas males (N = 9) averaged 410 mm ML and 1432 g.

2.2 | Gut Content Analysis

Stomachs were defrosted at room temperature for 10 minutes prior to dissection, and the stomach contents were examined under a dissecting microscope. The stomachs' digestion and fullness were scored according to a six-stage subjective scale

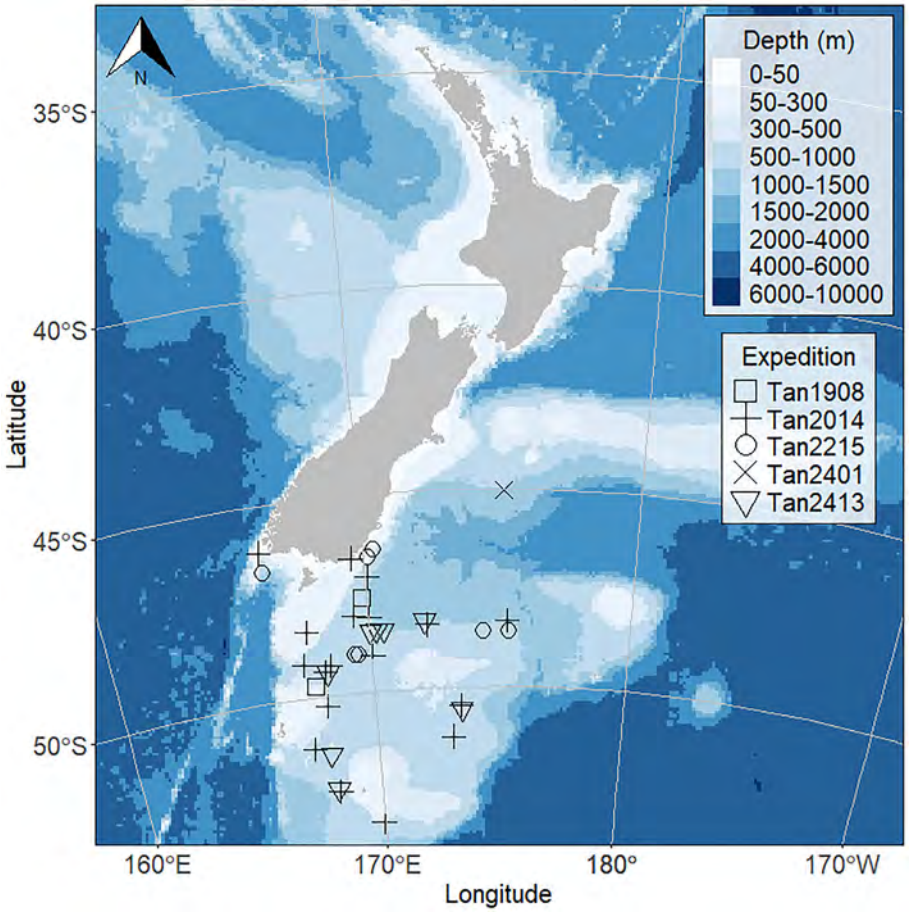

FIGURE 1 | Map of Aotearoa New Zealand showing the sample locations of the 58 *T. angolensis* specimens examined in this study.

(Jackson et al. 1998). Understanding the distribution of the sample population's digestion and fullness scores was done by calculating the sum and range of each digestion and fullness score.

After cutting open the stomach, the inner lining of the stomach was separated from the stomach wall with fine forceps. Both parts were inspected for parasites, which were sampled and preserved in 95% ethanol.

Stomach contents were rinsed with fresh water through a 0.3-mm-mesh sieve, and prey remains were categorised into soft tissue and hard tissue. Soft tissue remains were sampled, placed in Eppendorf tubes and refrozen at −20 °C for subsequent DNA barcoding. Hard tissue remains were sampled and stored in Eppendorf tubes for further morphological analysis: calcareous structures were stored dry, and chitinous/keratinous structures were preserved in 70% ethanol.

2.3 | Morphology

Hard-tissue remains were examined and identified under a light microscope, using species keys from the literature (O'Shea 1999; Ibanez and Jawad 2018; Xavier and Cherel 2021; Smale and Watson 2024; Stevens et al. 2024). A conservative count of individual prey based on sagittae (hereafter otoliths), eye lenses and cephalopod beaks was calculated by dividing the number of items found by two and rounding down. Any macro/microplastics were recorded and photographed (Figure 2).

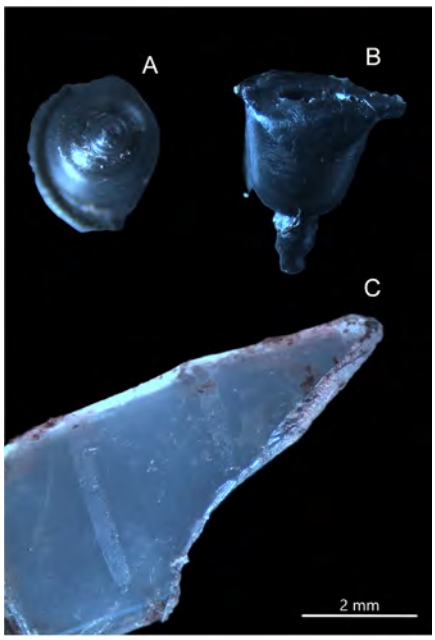

FIGURE 2 | Macroplastic fragments recovered from stomach contents of *T. angolensis*. Anterior (A) and lateral views (B) of black fragment; lateral view of clear fragment (C). Scale bar = 2 mm.

2.4 | DNA Barcoding

DNA lysis and extraction from soft-tissue samples followed the manufacturer's protocols for the DNeasy Blood & Tissue Kit (QIAGEN), and polymerase chain reaction (PCR) conditions followed those given by Braid et al. (2012), which amplifies the LCO1490 and HCO2198 primer pair (Folmer et al. 1994). After the DNA was amplified, PCR products were visualised on a 1% agarose gel, and samples showing a clear band were sent to Macrogen in Korea to be sequenced. Sequence editing was carried out in CodonCode Aligner (CodonCodeCorporation, Dedham, MA, USA), with low-quality sequences (Phred score > 200) being automatically removed from the analysis. Following editing and alignment in Codon Code Aligner (CodonCodeCorporation, Deham, Ma, USA), prey sequences were identified using the identification engine on the Barcode of Life Database (BOLD) version 3 in 2023 and then version 5 in 2024–2025. The criteria for attributing prey sequences to a known taxon were at least ≥85% match for the family level, 90%–95% match for genus and >95% for species. If the BOLD and BLAST sequence searches returned conflicting taxa at a similar % match, then the sequence's identification was resolved to the next highest level (e.g., genus, where records for two congeneric species matched the sequence in question). If conflicting species identifications were returned, but one of these taxa was not known to occur locally, the locally occurring taxon was given priority as a likely identification. Finally, the presence of identified hard tissues was also considered when assigning species to barcodes. Further information on the sequences can be found in the Appendix (Table S1).

2.5 | Parasite Identification

Parasites encysted in the stomach tissue were counted and stored separately in 70% ethanol for molecular characterisation. We identified both nematodes and cestodes, and selected representatives of each for DNA sequencing. Five nematodes and one cestode (unsuccessful, potentially due to poor specimen quality or PCR conditions) were extracted using the same protocols as diet items. For nematodes, the small subunit (18S rDNA) and internal transcribed spacer 1 (ITS1) genes were amplified using Nem18SF and Nem18 SR (Wood et al. 2013) and SS1 and N13R (Shamsi and Suthar 2016) primer pairs, respectively, and followed PCR conditions of Bennett et al. (2022b). Sequences were cleaned using EXOSAP Express PCR Product Cleanup Reagent (USB Corporation, USA) following manufacturer's instructions. Sanger sequencing by capillary electrophoresis was performed by the Genetic Analysis Service, Department of Anatomy, University of Otago (Dunedin, NZ). Resulting sequences were imported to Geneious Primev2.1, manually trimmed and compared on NCBI's BLASTn database for close matches to genus or species level for the lowest taxonomic identification possible. Attempts to sequence a single cestode specimen were made but were unsuccessful.

2.6 | Descriptive Statistics of Dietary Results

All prey items were collated together, but prey items that could not be identified to family level were aggregated by their class. Once all the prey items were categorised, the total number of each prey category (N), its percent numerical importance (%), the number of stomachs it occurred in (F) and its percent frequency of occurrence (% FO) were calculated (Table 1). Assessment of sample effort was done using the specaccum command from Vegan (version 2.6–6.1; Oksanen et al. 2024) in R Studio (version 4.4.3; R Core Team 2024) and the random method was selected. To avoid overestimating sampling effort, only the terminal nodes of identified prey taxa for the squid were counted.

Prey sizes were calculated from otolith length (fishes) and upper or lower rostral length (LRL) (cephalopods) using mainly published formulae, when available (Table 2). Where no formula was available for an exact species, a formula for a closely related species was substituted. The median length for each prey category was calculated using otoliths and beaks from *T. angolensis* stomach contents. A Kruskal–Wallis test was used to determine whether the median prey sizes were significantly different among three *T. angolensis* size ML (mm) groups (<40; 40–45; and >45 ML mm) for all prey, fishes and cephalopods separately.

The prevalence of parasitism in the sample population was calculated to determine the proportion of infected to uninfected specimens. The total, the mean and the range of parasite individuals infecting each squid were calculated to understand the distribution of parasite numbers in the 58 specimens. The number of parasites for squid with parasites ≤5 and more than >5 parasites was counted to determine whether the burden of infection had a uniform or patchy distribution.

3 | Results

3.1 | Digestion and Fullness

Out of 58 stomachs examined, 45 contained remains, of which 34 stomachs had a low to moderate fullness score (1–3). Only five specimens had a fullness score of 5 (extremely full), one of which was filled with large pieces of half-digested (stage 3) tissue from a rough-skinned clubhook squid (*Moroteuthopsis ingens*). Another full stomach contained half-digested tissue from several species, representing the greatest diversity of taxa of any stomach: three squids (another large *M. ingens*; jewelled squid, *Histioteuthis atlantica*; 'glass'/cranchiid squid, *Liguriella* sp.), plus two fishes (smooth oreo, *Pseudocyttus maculatus*; southern blacktip lanternfish, *Gymnoscopelus piabilis*). Another stomach that was extremely full had two pieces of macroplastics among soft tissues that were identified as hoki (*Macruronus novaezelandiae*) and *H. atlantica*, alongside otoliths belonging to the blackhead lanternfish (*Lampichthys procerus*) and the austral lanternfish (*Lampanyctus australis*). The stomachs investigated had a wide range of digestion stages, with the contents of 37 stomachs being heavily to nearly digested (scores 4–5), and eight slightly to half digested (scores 2–3). No stomach contents were considered to be freshly eaten (digestion stage 1).

3.2 | Prey Taxa of *T. angolensis*

Only 38 of the 58 stomachs examined had items (N = 81) that could be identified to at least a taxonomic class. Of these, 28

stomachs contained prey items (N = 66) that could be identified below the class level, and 26 of these stomachs contained prey items (N = 54) that could be identified to 29 terminal taxa (Table 1). Seventeen unique prey taxa were only recovered using morphology, 11 were only identified through DNA barcoding (N = 53 sequences), one was recovered from the same stomach using both methods, and another was recovered using morphology or DNA, but only from different stomachs. COI sequences for prey items and parasites are available in BOLD Systems in the public project titled 'Angolan flying squid diet' (project code: TAGNZ) and on GenBank (Accession range: PZ338786-PZ338838).

TABLE 1 | Total number of prey individuals detected (N) using either method, percentage of total prey items (%); number of stomachs containing the prey taxon and its percent frequency of occurrence across all stomachs with identifiable remains (% FO).

Prey	N, %	Stomachs, % FO
Echinoidea (Sea urchins)	**2 (2.49%)**	**2 (5.26%)**
Tam o'shanter urchins (Echinothurioidea)	2 (2.49%)	2 (5.26%)
Cephalopoda	**31 (38.27%)**	**19 (50%)**
Unidentified cephalopods	7 (8.64%)	7 (18.42%)
Amphitretidae		
Telescope octopus (*Amphitretus* sp.)	1 (1.23%)	1 (2.63%)
Cranchiidae		
Glass squid (*Liguriella* sp.)	1 (1.23%)	1 (2.63%)
Histioteuthidae		
Histioteuthis sp.	9 (10.84%)	3 (7.89%)
Atlantic jewel squid (*Histioteuthis atlantica*)	3 (3.7%)	3 (7.89%)
H. aff. *atlantica* (sensu Braid and Bolstad 2019)	1 (1.23%)	1 (2.63 %)
Onychoteuthidae		
Rough-skinned clubhook squid (*Moroteuthopsis ingens*)	4 (4.49%)	4 (10.52%)
Ommastrephidae		
Unidentified ommastrephid	2 (2.46%)	2 (5.26%)
Angolan flying squid (*Todarodes angolensis*)	1 (1.23%)	1 (2.63%)
Southern flying squid (*T. filippovae*)	1 (1.23%)	1 (2.63%)
Flying squids (*Todarodes* sp.)	1 (1.23%)	1 (2.63%)
Actinopterygii (Ray-finned fishes)	**48 (59.25%)**	**29 (76.31%)**
Unidentified fishes	8 (9.87%)	8 (21.05%)
Serrivomeridae		
Common sawtooth eel (*Serrivomer samoensis*)	1 (1.23%)	1 (2.63%)
Gempylidae		
False frostfish (*Paradiplospinus gracilis*)	1 (1.23%)	1 (2.63%)
Macrouridae		
Banded rattail (*Coelorinchus fasciatus*)	1 (1.23%)	1 (2.63%)
Four-ray rattail (*Coryphaenoides subserrulatus*)	2 (2.46%)	2 (5.26%)
Javelinfish (*Lepidorhynchus denticulatus*)	1 (1.23%)	1 (2.63%)
Merluccidae		
Hoki (*Macruronus novaezelandiae*)	3 (3.7%)	3 (7.89%)
Microstomatidae		
Pencil smelt (*Nansenia* sp.)	2 (2.49%)	2 (5.26%)
Moridae		
Johnson's cod (*Halargyreus johnsonii*)	1 (1.23%)	1 (2.63%)
Myctophidae		
Rough lanternfish (*Electrona subaspera*)	1 (1.23%)	1 (2.63%)

(Continues)

TABLE 1 | (Continued)

Prey	N, %	Stomachs, % FO
Carlberg's lanternfish (*E. carlsbergi*)	1 (1.23%)	1 (2.63%)
Southern blacktip lanternfish (*Gymnoscopelus piabilis*)	4 (4.93%)	4 (10.52%)
Austral lanternfish (*Lampanyctus australis*)	4 (4.93%)	4 (10.52%)
Hector's lanternfish (*Lampanyctodes hectoris*)	7 (8.64%)	1 (2.63%)
Blackhead lanternfish (*Lampichthys procerus*)	3 (3.7%)	2 (5.26%)
Protomyctophum sp.	1 (1.23%)	1 (2.63%)
Oreosomatidae		
Smooth oreo (*Pseudocyttus maculatus*)	1 (1.23%)	1 (2.63%)
Paralepididae		
Barracudina (*Magnisudis* sp.)	1 (1.23%)	1 (2.63%)
Phosichthyidae		
Lighthouse fish (*Phosichthys argenteus*)	2 (2.49%)	2 (5.26%)
Platytroctidae		
Common tubeshoulder (*Persparsia kopua*)	1 (1.23%)	1 (2.63%)
Trichiurdae		
Scabbard fish (*Benthodesmus elongatus*)	1 (1.23%)	1 (2.63%)
Trachichthyidae		
Orange roughy (*Hoplostethus atlanticus*)	1 (1.23%)	1 (2.63%)

Fishes were the most common and diverse prey class, with 21 unique taxa identified, representing 13 families (Table 1). Cephalopods were also important, with eight species from six families, while sea urchins (Class: Echinoidea) comprised only one unique family.

While fishes and cephalopods were identified in at least half of all stomachs containing identifiable prey (fishes 76.31 % FO, cephalopods 50 % FO), the highest occurrence for any individual prey species was for the rough-skinned clubhook squid (*M. ingens*) (10.52 % FO). Many prey taxa ($n = 23$; 60%) were identified from a single stomach caecum/individual. This included the prey species that occurred in the highest overall abundance (*Lampanyctodes hectoris*), with the remains of at least seven individuals in a single stomach but no others identified in other stomachs (Figure 3).

Individual stomachs contained between one and five prey taxa, with a mean of two prey taxa, although 75% of stomachs contained two or fewer taxa (Figure 4). The number of reported unique taxa did not reach an asymptote from the 26 stomachs that contained food items identifiable to lower taxa (Figure 4).

3.3 | Calculated Prey Sizes of *T. angolensis*

Based on otolith length, the longest individual fish consumed was *Lepidorhynchus denticulatus* (calculated at 50 cm), and the smallest a 3.2 cm long *Protomyctophum* sp. (Table 2). Based on beak LRL, the largest individual cephalopod was an 8.9 cm ML *Histioteuthis* sp., and the smallest a 5.3 cm ML *Histioteuthis* sp. (Table 2).

TABLE 2 | Fish and cephalopod prey taxa identified in *Todarodes angolensis* stomachs, and the median item and estimated prey size, along with the range.

Prey taxon	Stomachs	Median item size, mm	Median prey size, cm	Source
Otoliths	—	—	—	—
*Paradiplospinus gracilis**	1	3.5 OL	9.8 SL	Reid (1996)
*Electrona carlsbergi**	1	2.1 OL	4.6 SL	Stevens et al. (2024)
Protomyctophum sp.*	1	1.3 OL	3.2 SL[A]	Stevens et al. (2024)
Gymnoscopelus piabilis	4	3.8 (3.6–4) OL	7.8 (6.55–8.2) SL	Stevens et al. (2024)
Lampanyctus australis	4	3.1 (1.9–3.4) OL	11.7 (7.11–11.7) SL	Stevens et al. (2024)
Lampanyctodes hectoris	1	2.6 (2.5–2.9) OL	7.1 (6.7–7.51) SL	Stevens et al. (2024)
Lampichthys procerus	3	2.5 (2.4–3.7) OL	5.8 (5.5–8.8) SL	Stevens et al. (2024)
*Phosichthys argenteus**	1	2.2 OL	7.7 TL	Smale and Watson (2024)

(Continues)

TABLE 2 | (Continued)

Prey taxon	Stomachs	Median item size, mm	Median prey size, cm	Source
*Serrivomer samoensis**	1	1.2 OL	45 SL[B]	Quigley et al. (2023)
*Persparsia kopua**	1	4.0 OL	17.6 SL	Based on $y = 60.921x^{0.6566}$, $n = 26$, $r^2 = 0.8326$ (D Stevens, unpubl. Data)
*Benthodesmus elongatus**	1	4.3 OL	46.4 SL	Xavier et al. (2010)
Nansenia sp.	1	2.8	4.9 SL[C]	Battaglia et al. (2010)
Lepidorhynchus denticulatus	1	12.5 OL	50 TL	(D Stevens, unpubl. Data)
Cephalopod beaks	—	—	—	—
Histioteuthis sp.	3	3.5 (2.5–4.3) LRL	7.9 (5.3–8.9) ML[D]	Xavier and Cherel (2021)
Amphitretus sp.*	1	0.9 URL	5.8 ML[E]	Schwarz et al. (2020)

Note: Prey taxa that were represented by a single individual are indicated with an asterisk (*).
Abbreviations: A, estimation based on sub-Antarctic *P. bolini;* B, estimation is based on *S. beanii*; C, estimation based on *N. oblita*; D, estimation based on *H. atlantica*; E, estimation based on *Japetella diaphana*; LRL, lower rostral length; ML, mantle length (cephalopods); OL, otolith length; SL, standard length (fishes); TL, total length; URL, upper rostral length.

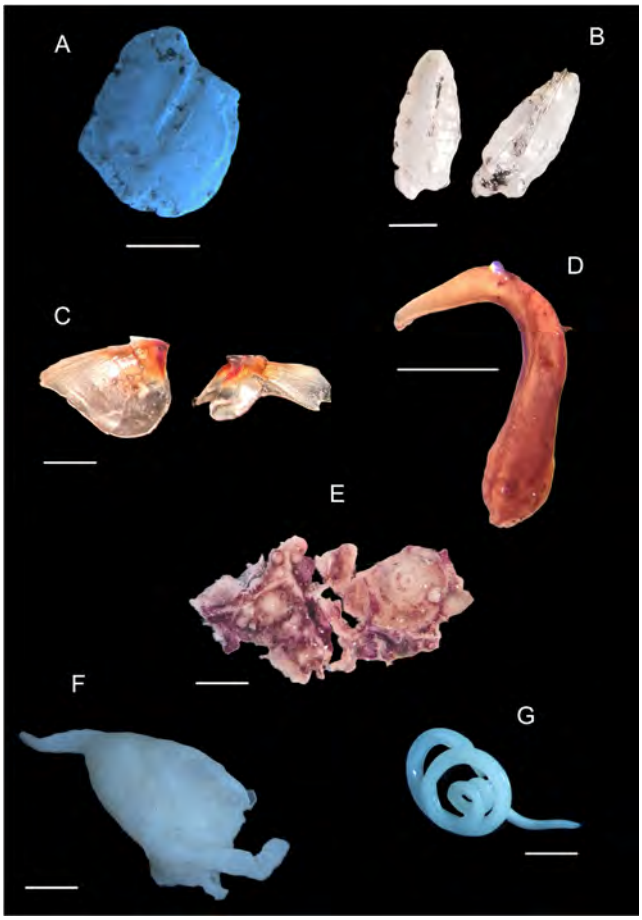

FIGURE 3 | Selected prey items and parasites identified in the gut contents of *Todarodes angolensis* from southern Aotearoa New Zealand waters. Otoliths of *Phosichthys argenteus* (A) and *Paradiplospinus gracilis* (B); Pelagic octopus (*Amphitretus*) beaks (C), tentacle club hook from an onychoteuthid squid (D); Echinothurioid urchin plate (E); Cestode (F); Anisakid nematode (G). Scale bar = 1 mm (A–C, E–G), 0.5 mm (D).

Moderate differences in median prey lengths for fish and cephalopod prey were observed for *T. angolensis* in all three size categories (ML < 40 cm, 40–45 cm, and >45 cm), but these differences were not statistically significant ($H = 1.07$, $df = 2$, $p = 0.5857$) (Figure 5). For cephalopod prey, the median prey size was 6.7 cm ML (for *T. angolensis* specimens < 40 cm ML) and 7.6 cm ML (specimens > 45 ML) ($H = 1.1579$, $df = 1$, $p = 0.2819$). For fish prey, the median estimated length was 9.8 cm (for *T. angolensis* individuals < 40 ML), 7.1 cm (individuals 40–45 cm ML) and 8.2 cm (individuals > 45 cm ML) ($H = 1.5972$, $df = 2$, $p = 0.4499$).

3.4 | Parasitism

Parasites were observed in 53 out of 58 (89%) of the squid examined. Parasite loads were relatively low for most individual squid; 50% of squid had ≤5 observed parasites, and only 39% had >5 parasites (a maximum of 34 observed in a single host, a female of ML 483 mm). A total of 332 parasites were found (318 anisakids, with nine identified as *Skrjabinisakis physeteris*) and nine cestodes (Figure 3).

4 | Discussion

This study aimed to describe the trophic ecology of *Todarodes angolensis* by analysing the stomach contents using morphological identification and DNA barcoding of prey tissues. This is the first study to investigate the diet of *T. angolensis* within Aotearoa New Zealand waters and to use a combination of morphology and DNA barcoding to identify prey of this species; past studies from South Africa have only used visual identification (Kremer et al. 2025; Lipiński 1992). The most frequently occurring prey genus was the jewelled squid (*Histioteuthis* sp.), and the most frequently occurring and speciose family was lanternfishes (Myctophidae, eight species). The prey taxa of *T. angolensis* observed in this study inhabit many depth strata and trophic levels, with deep-water carnivores being the most common prey type, and epipelagic, zooplanktivorous prey being the second most common.

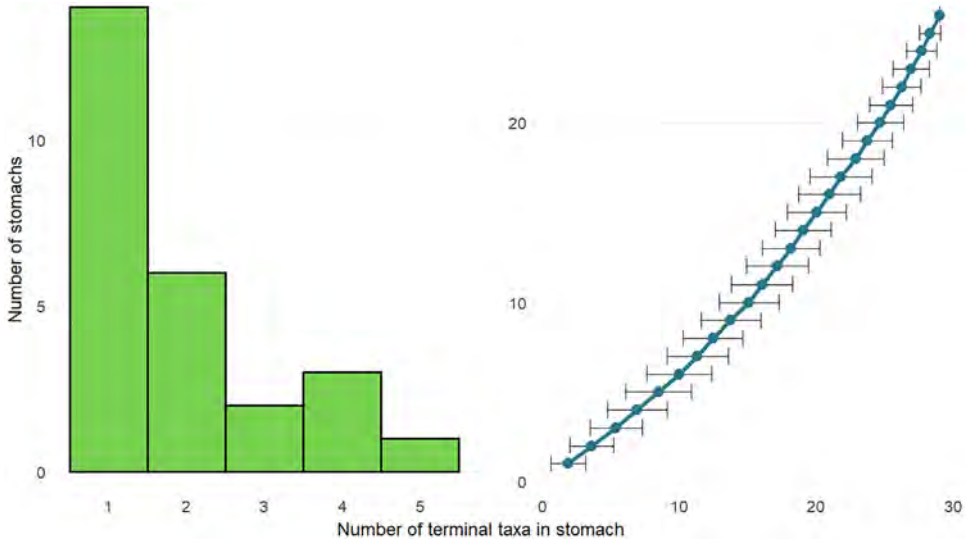

FIGURE 4 | Left: Histogram of dietary diversity observed in 28 specimens of *Todarodes angolensis*. Right: Rarefaction curve of the 28 sampled specimens with standard error bars.

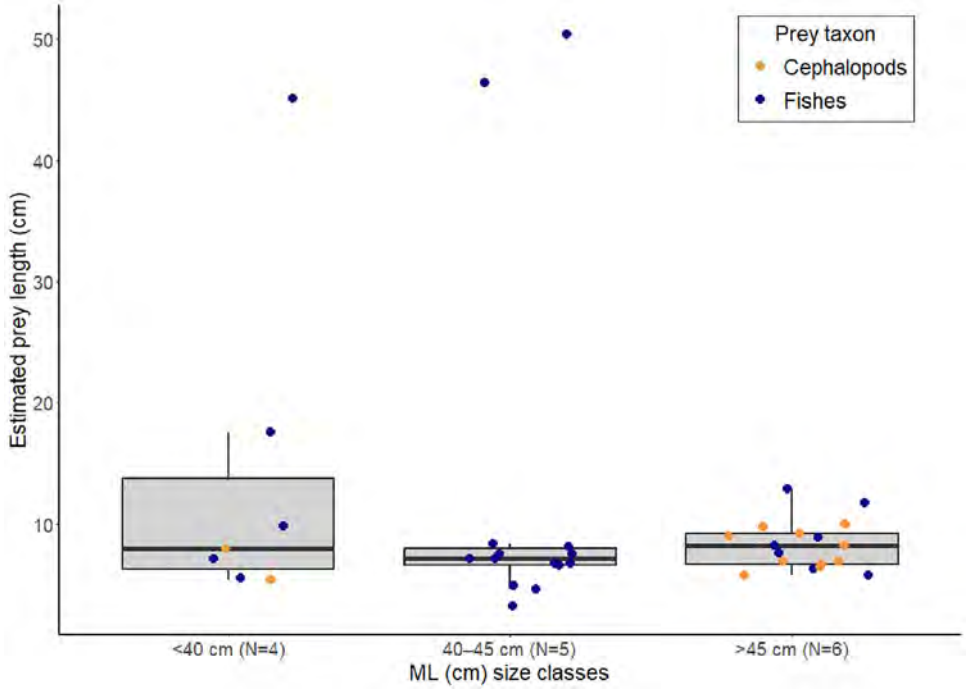

FIGURE 5 | Boxplots of estimated prey lengths from New Zealand *T. angolensis* stomach contents, with the estimated lengths for each prey item represented by individual points.

4.1 | Reported Prey Items of *T. angolensis*

4.1.1 | *Fishes*

Small zooplanktivorous species were the most common type of fish prey observed in NZ *T. angolensis*. *Lampanyctodes hectoris* was the most abundant fish prey taxon, although all seven individuals were identified from the same stomach, in contrast to results from South Africa, where it occurred in 50%–64% of *T. angolensis* specimens (Lipiński 1992). The most frequently occurring myctophid species in this study, at 10.52% FO each, were *Lampanyctus australis* (also reported by Kremer et al. 2025) and *Lampichthys procerus*. All three of these species are circumglobally distributed in the Southern Ocean and are associated with the continental slope environment (Young et al. 1996, 1988; Williams et al. 2001). During summer, when the specimens of *T. angolensis* in this study were caught, seasonal upwelling of nutrient-rich waters onto the continental shelf is known to influence zooplanktivorous fish populations due to increased zooplankton abundance (Williams et al. 2001).

This could indicate that *T. angolensis* follows aggregations of zooplanktivorous fishes due to seasonal upwelling, meaning that *T. angolensis* is a highly active carnivore.

One of the more frequently occurring was hoki (*M. novaezelandiae*). Although this appears to be a novel finding, Lipiński (1992) reported other merluccids (such as *Merluccius* sp.) in the diet of South African *T. angolensis*. As an adult, *M. novaezelandiae* feeds mainly on euphausiids, mesopelagic fishes and natant decapods (Connell et al. 2010). All *M. novaezelandiae* samples were identified only by barcoding, which is not surprising given that *M. novaezelandiae* can grow to more than 100 cm long (McMillan and Struthers et al. 2019) and squid are known to avoid consuming the cranial elements of larger fish, including the otoliths (e.g., Dawe et al. 1997; Jackson et al. 1998). This would make *M. novaezelandiae* hard to detect morphologically in the diet of *T. angolensis* through a morphology-only approach and highlights the importance of using an integrated approach to dietary studies of cephalopods.

Deep-sea demersal fishes, all of which are first-report prey items for *T. angolensis* in this study, were quite common. Of these, rattails (Family: Macrouridae) were the most diverse; while three of the species observed as prey are known to feed in the water column, they rarely occur more than 200 m off the seafloor (Stevens et al. 2020) and are understood to predate other demersal and benthic animals. These species have unique trophic ecologies, with *C. fasciatus* being understood to feed benthopelagically on hyperiid and gammarid amphipods (Stevens et al. 2020; Stevens and Dunn 2011). *Lepidorhynchus denticulatus* is known to prey on mesopelagic crustaceans, overlapping with *C. subserrulatus,* which is reportedly a predator of calanoids (Stevens and Dunn 2011; Jones 2008).

Todarodes angolensis preys on species that inhabit the mid-continental slope (this study; Kremer et al. 2025). In the current study, we reported orange roughy (*Hoplostethus atlanticus*) and Johnson's cod (*Halargyreus johnsonii*), which feed on mesopelagic fishes (Francis et al. 2002; Forman et al. 2016). In addition, we found remains of the smooth oreo (*Pseudocyttus maculatus*), which is known to prey on gelatinous zooplankton in local waters (Francis et al. 2002; Forman et al. 2016). Sloane's viperfish (*Chauliodus sloanii*), a mid-slope fish species (*fide* Kremer et al. 2025), has also been reported in the diet of South African *T. angolensis* specimens (Williams et al. 2001). The presence of mid-slope fish species as prey in both South Africa and NZ indicates that *T. angolensis* is a consistent visitor to the mid-slope habitat. The frequent occurrence of demersal fishes indicates that while *T. angolensis* is largely feeding in the mesopelagic region, it may also descend into the demersal community to feed. Thus, *T. angolensis* could be an important trophic link between deep-sea demersal communities and pelagic communities. Given the prevalence of *T. angolensis* in NZ sub-Antarctic waters (Stevens et al. 2022), effective modelling of *T. angolensis* within local nutrient cycles would be productive for future ecosystem modelling approaches to the management of local marine ecosystems.

Shallow-water and inshore fishes were absent in the diet of the *T. angolensis* specimens analysed in this study. This contrasts with Kremer et al. (2025), who identified numerous inshore fish taxa as prey. The squid analysed by Kremer et al. (2025) were likely juvenile to subadults, whereas the specimens studied here were mature, indicating a potential developmental shift in *T. angolensis's* diet. This ontogenetic dietary change in *T. angolensis* would be consistent with what is known about other deep-sea squid species, such as *M. ingens* (Phillips et al. 2003). Future dietary studies from local waters should include *T. angolensis* from different life stages to investigate ontogenetic shifts in diet.

4.1.2 | *Invertebrates*

Cephalopods were the second most abundant and diverse prey group, with remains found in half of the stomachs that contained identifiable prey items. Two small, gelatinous species were found (the glass squid *Liguriella* sp. and the telescope octopod *Amphitretus* sp.); Kremer et al. (2025) also identified beaks from a juvenile colossal squid, *Mesonychoteuthis hamiltoni*, a gelatinous cephalopod species during its early life stages. However, muscular, active cephalopods, such as the rough-skinned clubhook squid (*M. ingens*) and southern arrow squid (*N. sloanii*), were a more common component of *T. angolensis* diet in this study. These taxa co-occurred with other prey types, such as one stomach containing remains from the squids *M. ingens*, *H. atlantica* and *Liguriella* sp., and the fishes *P. maculatus* and *G. piabilis*. High dietary diversity in some *T. angolensis* individuals was also observed by Kremer et al. (2025), who identified the squids *Histioteuthis* sp., *M. hamiltoni*, *Brachioteuthis* sp., cf. *Todaropsis eblanae* and the fishes *E. machnata* and *Myctophum spinosum* within a single specimen. These ecologically diverse prey taxa suggest that *T. angolensis* is an opportunistic generalist, predating on small zooplanktivorous fishes, demersal fishes, muscular squids and small gelatinous cephalopods.

Among the cephalopod prey genetically identified from *T. angolensis* stomach contents, one conspecific sequence was recovered. Without more detailed analysis, such as the use of microsatellites, potential *T. angolensis* prey DNA cannot be distinguished from that of the host specimen, so cannibalism cannot be confirmed as a feeding strategy of NZ *T. angolensis*. However, there is morphological evidence of cannibalism in South African *T. angolensis* specimens (Lipiński 1992; Kremer et al. 2025). Cannibalism also occurs in other deep-sea cephalopod species such as *T. filippovae* and *M. ingens* (Phillips et al. 2003; Pethybridge et al. 2013).

One unexpected result was the occurrence of Tam o'shanter urchin remains (Order: Echinothurioidea) in two stomachs. These animals are generally found on soft sediments with patches of rocky nodules, at depths greater than 500 m (Rowden et al. 2013), and are likely detritivores, although their exact role in deep-sea food webs is poorly understood. Urchins are rare but not unheard-of prey for cephalopods (Golikov et al. 2019; Pierce et al. 1994). Experiments with tethered sea urchins within neritic waters off South-Eastern Australia revealed predation by the peachy octopus *Octopus tetricus* and the giant cuttlefish *Ascarosepion apama* (Day et al. 2023). The presence of deep-sea demersal fishes within several *T. angolensis* stomachs suggests feeding near the seafloor, so the urchins may be a natural prey item, although net feeding is also a possibility. Other echinoderms consumed by ommastrephids have been hypothesised as incidental ingestion alongside other prey items (Dunn 2009). We consider this unlikely given the advanced state

of digestion of the urchin prey remains, although it is possible that digestion may have continued during storage. The urchin fragments may also have been secondary prey items, although one of the other prey items reported with the urchin, *H. johnsonii*, is not known to be a predator of sea urchins. Prey remains thought to represent secondary consumption have previously been observed in ommastrephids, although these have tended to be small items such as pteropod shells (Chantheran 2022; Lordan et al. 1998).

One group reported by previous studies, but not identified among the present stomach contents, was macroplanktonic crustaceans (Lipiński 1992; Kremer et al. 2025). If present, these remains should have been visually discernible, as they were identified by eye in earlier studies (Lipiński 1992; Kremer et al. 2025). It is possible that further sampling would reveal their presence, but given their prevalence observed by previous authors, we hypothesise that this disparity is more likely due to dietary differences across life stages and/or the seasonal availability of macroplankton. Crustaceans are known to form more integral components of the diet in the earlier stages of several deep-sea squid species such as *Dosidicus gigas*, *Moroteuthopsis ingens* and *Illex argentinus* (Ivanovic and Brunetti 1994; Nigmatullin et al. 2001; Phillips et al. 2003), with a shift towards fish and cephalopod prey as they mature. Macroplanktonic crustacean abundances are also influenced by seasonal upwelling during the spring as plankton densities increase, and then gradually decline during the summer (Pinkerton et al. 2020). Our specimens were collected during the summer, whereas those sampled by Kremer et al. (2025) were collected during the spring, perhaps indicating that *T. angolensis* diet is opportunistic, feeding on whatever is available at the time.

4.1.3 | *Diversity of Diet*

The species accumulation curve did not reach an asymptote in the present study (Figure 4). Therefore, the present results do not represent the full dietary diversity of *T. angolensis*, and future studies will require a larger sample size to effectively characterise *T. angolensis* dietary diversity. The trend of high digestion and low fullness scores of most stomachs has been reported in other deep-sea oegopsid squids, which may indicate either a long interval since their last feeding event, rapid digestion or ongoing digestion during sample storage since some specimens were sampled in 2019 (Hu 2026; McBride et al. 2023; Pethybridge et al. 2013; Rosas-Luis et al. 2014; Omura and Endo 2016). In the future, for 'empty' or highly digested samples, next-generation sequencing technologies could be attempted on squid stomach liquids to determine whether additional prey DNA can be recovered.

4.2 | Demographic in Variation *T. angolensis*

The dietary differences found between the present and previous studies (Lipiński 1992; Kremer et al. 2025) could have been impacted by season and specimen maturity. The specimens examined here were sampled only during the austral summer, whereas the previous South African studies on *T. angolensis* collectively sampled from all of the seasons (Kremer et al. 2025; Lipiński 1992; Roeleveld et al. 1992; Villanueva and Sanchez 1989; Villanueva 1992). Our specimens were also larger (both longer and heavier) than in the aforementioned South African studies and had an ML more comparable to *T. angolensis* specimens caught in Tasman and Coral seas, which had a maximum ML of 59 cm (Voss et al. 1998). Using the non-linear correlation between ML and statolith increment number (Villanueva 1992), it is possible to infer the approximate the age of the specimens examined here, which were likely 11–13 months old at the time of capture. Lipiński (1992) stated that his specimens were subadult to adults in his study, and those examined by Kremer et al. (2025) were on average 6–8 months old. If *T. angolensis* is similar to other *Todarodes* species, such as *T. filippovae* and *T. pacificus*, it is likely that *T. angolensis* matures in 7–8 months and lives for approximately a year. Given that, it is likely that our specimens were well into maturity when captured, whereas the specimens examined by Kremer et al. (2025) were subadults.

4.3 | Parasitism in Aotearoa New Zealand *T. angolensis*

The overall prevalence of parasitism was very high, but most specimens had a low parasite intensity, with most of the parasites being found in a few individuals of the sample population. Five nematodes were identified as *Skrjabinisakis physeteris,* but due to the taxonomic uncertainty of *Skrjabinisakis* sp., it was prudent not to classify the remaining majority of nematodes without further study. A more detailed taxonomic treatment of *Todarodes angolensis* parasites will be presented as part of a wider study on deep-sea squid parasites (Li et al. 2026, this volume).

4.4 | Comparison to Other Squid Species

The prevalence of anisakid nematodes in sampled *T. angolensis* specimens likely relates to the generalist diet of the squid and the life cycle of anisakids. Anisakid nematode life stage 2 (L2) stages occur in planktivorous crustaceans, which then develop into L3 larvae as they are transferred to their intermediate hosts, such as myctophid fishes (Aibinu et al. 2019). The L3 larvae are stenoxenous and are highly likely to pass through several paratenic hosts before reaching their final, marine mammal hosts (Aibinu et al. 2019). A voracious, carnivorous generalist like *T. angolensis* can become serially infected with anisakid L3 larvae through the consumption of infected prey items as it ages.

The uneven distribution in parasite load in the sample population has been reported in other ommastrephid species such as *T. filippovae* and *Nototodarus gouldi* (Pethybridge et al. 2013; Hu 2026; Gibson and Jones 1993). This indicates that parasite infection does not occur randomly in *T. angolensis* but happens in clusters. This clustering effect could be explained by geographic variation in parasite density (a location effect on parasite numbers). For example, Pethybridge et al. (2013) observed no parasites in Tasmanian *T. filippovae* stomach tissues at one of the sample sites, which they believed to be a result of the marine mammal hosts being uncommon at that location. It is possible that a similar process is occurring in NZ, given the high local diversity of reported, albeit infrequent, visiting marine mammal species (Clement et al. 2021). However, the visiting marine mammal hosts'

contribution to local parasite densities within the broader marine food of NZ is not well known.

Another expression of the clustering effect on parasite intensity is that certain prey species might be more susceptible to infection than others due to their diet (Gonzalez et al. 2003; Anderson and Gordon 1982). For example, in a study on the diet of five Californian rockfish species (*Sebastes* spp.), *S. mystinus* reportedly had no anisakid nematodes infecting it despite its sister species being commonly infected (Moser and Sakanari 1986). This is because *S. mystinus* is known to feed on mostly algae and epifaunal bryozoans, which are not the intermediate hosts of anisakids (Roberts 1979). In comparison, the other rockfish species predated on gammarid amphipods, isopods and polychaetes, taxa that are known to be the intermediate hosts of anisakid nematodes (Roberts 1979). While there is no report of adult *T. angolensis* feeding on these crustaceans and polychaetes, they do consume myctophid fishes, which do feed on these prey groups (Williams et al. 2001). It is very likely that *T. angolensis* could become repeatedly infected by predating on infected myctophids, potentially explaining why some specimens had very high infection intensities.

Skrjabinisakis physeteris is known to infect cetaceans as their final host, particularly sperm whales (Family: Physeteridae), and dwarf and pygmy sperm whales (Family: Kogiidae) (Klimpel et al. 2010), demonstrating that *T. angolensis* serves as an intermediate or paratenic host for *S. physeteris*. Several of the reported prey items, such as histioteuthid squid and myctophid fish, are also known to serve as intermediate hosts for *A. physeteris* (Gaglio et al. 2018; Palomba et al. 2021; Li et al. 2026, this volume). Two other prey species, the southern arrow squid *N. sloanii* and rough-skinned clubhook squid *M. ingens*, are intermediate hosts for *Skrjabinisakis* sp. (Bennett et al. 2022c; Li et al. 2026, this volume), and *A. simplex* has been reported in the latter cephalopod species (Bennett et al. 2022c). *Skrjabinisakis simplex* has a similar lifecycle to *A. physeteris,* but its life cycle is more strongly associated with delphinid cetaceans (Klimpel et al. 2010). Understanding that *T. angolensis* predates on intermediate hosts for *A. physeteris* and *A. simplex* reveals an infection pathway for both nematode species to their own respective final hosts.

5 | Conclusion

This study is the first paper to report on the diet of large, adult *Todarodes angolensis* and for specimens from the South Pacific. This is especially noteworthy as previous studies on *T. angolensis* diet were based on juvenile/subadult specimens from South Africa (Lipiński 1992; Kremer et al. 2025). We identified 32 unique fish and cephalopod taxa, as well as sea urchins, but the prey taxon accumulation curve did not reach an asymptote, suggesting that future studies on *T. angolensis* diet with greater sample sizes would help to characterise the full dietary richness of this species. Overall, fish were the most common prey, and cephalopods were the second most common prey class, although most of the identified prey items were only observed once. Dietary evidence suggests that *T. angolensis* is an active, generalist carnivore that preys on a wide range of prey sizes throughout the water column. It is likely that *T. angolensis* undergoes an ontogenetic change in diet, consuming fewer myctophids and more cephalopods with maturity. However, previous studies were conducted in South Africa (Lipiński 1992; Kremer et al. 2025), so location may also influence dietary differences. Sampling a greater range of *T. angolensis* age groups in the same geographic locale will enable future ecologists to determine the extent of spatial variation in diet with development. Most of the *T. angolensis* specimens analysed were encysted with parasites, primarily anisakids, including *S. physeteris*, which is known to infect several of the prey items that were also observed in this study. As this nematode infects physeterid and kogiid cetaceans as its final host, its presence in *T. angolensis* makes this squid a likely vector for *S. physeteris* to these cetacean taxa. The voracious carnivory of *T. angolensis* allows the squid to become repeatedly infected with anisakid parasites, making *T. angolensis* a potent vector of parasites to marine mammal apex predators in Aotearoa, New Zealand.

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Ethical Approval

All the applicable national and international guidelines for the use of animals were followed by the authors.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All sequence data used in this study are available for download from GenBank and in BOLD under the project titled 'Angolan flying squid diet'.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Sequenced prey items from the *T. angolensis* stomachs. Taxa ID with * means that hard tissues of the final, assigned taxon were present in the stomach, and P represents non-local taxa. Tissue codes are F for fish sequences and C for cephalopod sequences.