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The Battle of Helminths Deep: Molecular Insights Into Oegopsid Squid Parasites in Aotearoa New Zealand

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ABSTRACT

Cephalopods play crucial roles in marine ecosystems due to their diverse and indispensable contributions to trophic webs. However, parasitological research on cephalopods remains limited in Aotearoa New Zealand (NZ), despite the commercial significance of certain squid species and the zoonotic potential of the parasites within them. This study aimed to enhance our understanding of parasitic infections in NZ deep-sea squid species. We examined 11 squid species, including the commercially harvested 'arrow' squids (*Nototodarus sloanii* and *N. gouldi*), alongside 5 additional large-bodied species: giant squid (*Architeuthis dux*), 'hooked' squids (*Moroteuthopsis ingens* and *Onykia* spp.), 'flying' squids (*Todarodes angolensis* and *T. filippovae*), Dana octopus squid (*Taningia danae*), and *Pholidoteuthis* sp., as well as a smaller-bodied glass squid (*Teuthowenia pellucida*), and cock-eyed squid (*Histioteuthis* sp.). Squid specimens were opportunistically collected during research surveys between 2016 and 2024. Their helminth parasites were sampled and sequenced for 28S rRNA, 18S rRNA, ITS1 and/or ITS2 rDNA. We identified 6 nematode taxa (*Anisakis berlandi*, *A. pegreffi*, *Anisakis* sp., *Skrjabinisakis physeteris*, *Lappetascaris* sp., and *Crassicauda* sp.), 3 cestode taxa (*Tentacularia coryphaenae*, *Hepatoxylon trichiuri*, and *Clistobothrium* sp.), and 1 trematode Accacoeliidae gen. sp. Furthermore, the genetic diversity of *Anisakis* spp. was analysed to explore potential influences of host geographic and phylogenetic patterns on parasite infections. This study contributes important baseline data to improve our understanding of parasite diversity in NZ cephalopods, with implications for ecological research and ecosystem management.

1 | Introduction

Documenting the presence, diversity and distribution of species at a given time point is fundamental for assessing ecological change. In an era where most of the world's ecosystems are experiencing some degree of change (Butchart et al. 2010; IPCC 2023), it is crucial to document biodiversity before it is lost. Although invertebrates comprise the vast majority of biodiversity on Earth, research efforts have disproportionately focused on vertebrates (Titley et al. 2017). This bias extends to parasitology, where parasites of vertebrates are far better studied than those infecting invertebrates (Poulin et al. 2023), despite the fact that parasites, particularly helminths, utilise both invertebrate and vertebrate hosts at different stages of their complex life cycles (Bennett et al. 2022). Parasitic helminths are not only invertebrates themselves but are also significant contributors to overall biodiversity in all ecosystems (Lafferty et al. 2006; Dobson et al. 2008; Bennett et al. 2024), and play important roles in structuring and maintaining healthy ecosystems (Dunne et al. 2013; Wood and Johnson 2015). Comprehensive documentation of parasites across a broad range of hosts, especially invertebrates, is essential for predicting

changes in parasite diversity and distribution under future environmental scenarios.

Cephalopods are a diverse and ecologically (and economically) important group of marine invertebrates whose parasitic fauna remains notably understudied (Roumbedakis et al. 2018; Tedesco et al. 2020; Purkayastha and Furuya 2025). Despite this knowledge gap, it is known that cephalopods can serve as intermediate, paratenic, or definitive hosts for a wide range of parasites with varied life cycle strategies (Roumbedakis et al. 2018; Tedesco et al. 2020). Cephalopods are also a vital food source for many top marine predators (Cherel 2020) and are of growing economic importance in global fisheries (Ainsworth et al. 2023).

Aotearoa New Zealand (hereafter NZ) hosts a rich diversity of cephalopods, with over 85 squid species recorded (Wassilieff and O'Shea 2025). However, parasite records exist for only a small fraction of these species (e.g. (Smith et al. 1981; Wharton et al. 1999; Mattiucci et al. 2009; Mattiucci et al. 2018; Bennett et al. 2022; Bennett et al. 2023). While the logistical challenges of accessing and sampling deep-sea organisms may partly explain this gap, it is still surprising given the commercial significance of several cephalopods species to NZ fisheries. For example, arrow squids (*Nototodarus* spp.) have supported one of the largest commercial fisheries in NZ since the 1970s (Fishery New Zealand 2025), with a peak annual value of approximately $140 million as of 2020, although the total annual catch has since halved (New Zealand Ministry for Primary Industries [MPI] 2025). In addition to their economic and ecological roles, squids are known vectors of zoonotic parasites such as *Anisakis* spp., which pose a risk to human health (Fujisawa et al. 2025). Therefore, it is important to investigate the diversity of parasites infecting NZ squid species, to inventory marine parasite biodiversity, to determine baseline data on parasites that can be monitored for change over time, and to assess potential zoonotic risk for species that are consumed by humans.

This study aimed to characterise the diversity of parasitic helminths infecting various oegopsid squids in NZ waters. We opportunistically collected parasitic helminths from eleven oegopsid squid species between 2016 and 2024 across multiple locations within the NZ Exclusive Economic Zone (EEZ). Parasites were identified using DNA sequencing. This research expands current knowledge of parasitic helminth diversity in NZ cephalopods, including various new host records. We also highlighted the widespread occurrence of *Anisakis* spp. across nearly all squid species examined.

2 | Materials and Methods

2.1 | Sample Collection

Parasites recovered from opportunistically collected squids between 2016 and 2024 from three locations (West Coast South Island, Chatham Rise, and Sub-Antarctic) within the NZ EEZ (see Figure 1) on scientific trawl surveys by Earth Sciences New Zealand (ESNZ, formerly known as the National Institute of Water and Atmospheric Research, Ltd [NIWA]). The examined squids include 'arrow' squids (*Nototodarus sloanii* ($n = 5$) and *N. gouldi* ($n = 4$)), giant squid (*Architeuthis dux* ($n = 1$)), 'hooked' squids [*Moroteuthopsis ingens* ($n = 13$)] and *Onykia* spp. ($n = 8$) [noting that *Onykia* '*robsoni*' is a species complex (Bolstad et al. 2018), with at least two species represented in our samples, herein referred to as *Onykia* spp.]), 'flying' squids (*Todarodes* (*To.*) *angolensis* ($n = 7$) and *Todarodes filippovae* ($n = 5$)), Dana octopus squid (*Taningia* (*Ta.*) *danae* ($n = 1$)), *Pholidoteuthis* sp. ($n = 2$), glass squid (*Teuthowenia* (*Te.*) *pellucida* ($n = 1$)), and cock-eyed squid (*Histioteuthis* sp. ($n = 3$)). Squid specimens were frozen at sea at −20°C and thawed before parasites were sampled, which were then preserved in 70% ethanol. Supplemental Table 1 lists each squid specimen's identity, geographic location, and sampling year.

2.2 | Parasite Identification and Phylogenetic Analysis

Representatives of parasites collected from each squid host, when numbers and condition allowed, were selected for molecular analysis. Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), following the manufacturer's protocol. Several genetic markers were targeted to facilitate species identification to the lowest taxonomic level possible. For nematodes in the first instance, we obtained 18S ribosomal RNA gene (18S) using primers Nem18SF and Nem18SR (Wood et al. 2013). For further insights (depending on availability of comparative sequences on NCBI GenBank https://www.ncbi.nlm.nih.gov/), and for the recovered trematode parasites, we amplified the 28S ribosomal RNA gene (28S) using primers T16 and T30 (Harper and Saunders 2001) and/or internal transcribed spacer regions (ITS1 and ITS2) using primers SS1/NC13R and SS2/NC2 (Shamsi and Suthar 2016). Polymerase chain reaction (PCR) protocols for 18S included the following conditions: 94°C for 5 min, 35 cycles of 94°C for 30 sec, 54°C for 30 sec and 72°C for 1 min, and 72°C for 10 min. PCR protocols for 28S consisted of 94°C for 5 min, 38 cycles of 94°C for 30 s, 45°C for 30 s and 72°C for 2 min, and 72°C for 7 min. Lastly, PCR protocols for ITS1 and 2 consisted of 94°C for 5 min, 30 cycles of 94°C for 30 s, 55°C for 30 s and 72°C for 30 s, and 72°C for 5 min. Following amplification, PCR products identified as positive with a 1% agarose gel were cleaned using EXOSAP Express PCR Product Cleanup Reagent (USB Corporation, Cleveland, OH, USA) and sequenced with their respective PCR primers using Sanger sequencing by the Genetic Analysis Service, Department of Anatomy, University of Otago (Dunedin, NZ).

Raw sequences were imported to Geneious Prime version 2025.2.2, trimmed using the trim function with default parameters and manually edited for incorrect or ambiguous base pairs. Each sequence went through screening using BLASTn (Basic Local Alignment Search Tool for nucleotides) from NCBI (https://blast.ncbi.nlm.nih.gov/) to compare percentage identity to relatives and allow for family, genus or species level identifications. To illustrate the positioning of our species amongst other closely related species and to support our identifications, we used Bayesian inference to produce phylogenetic trees for some lesser-known species. We created alignments for three new

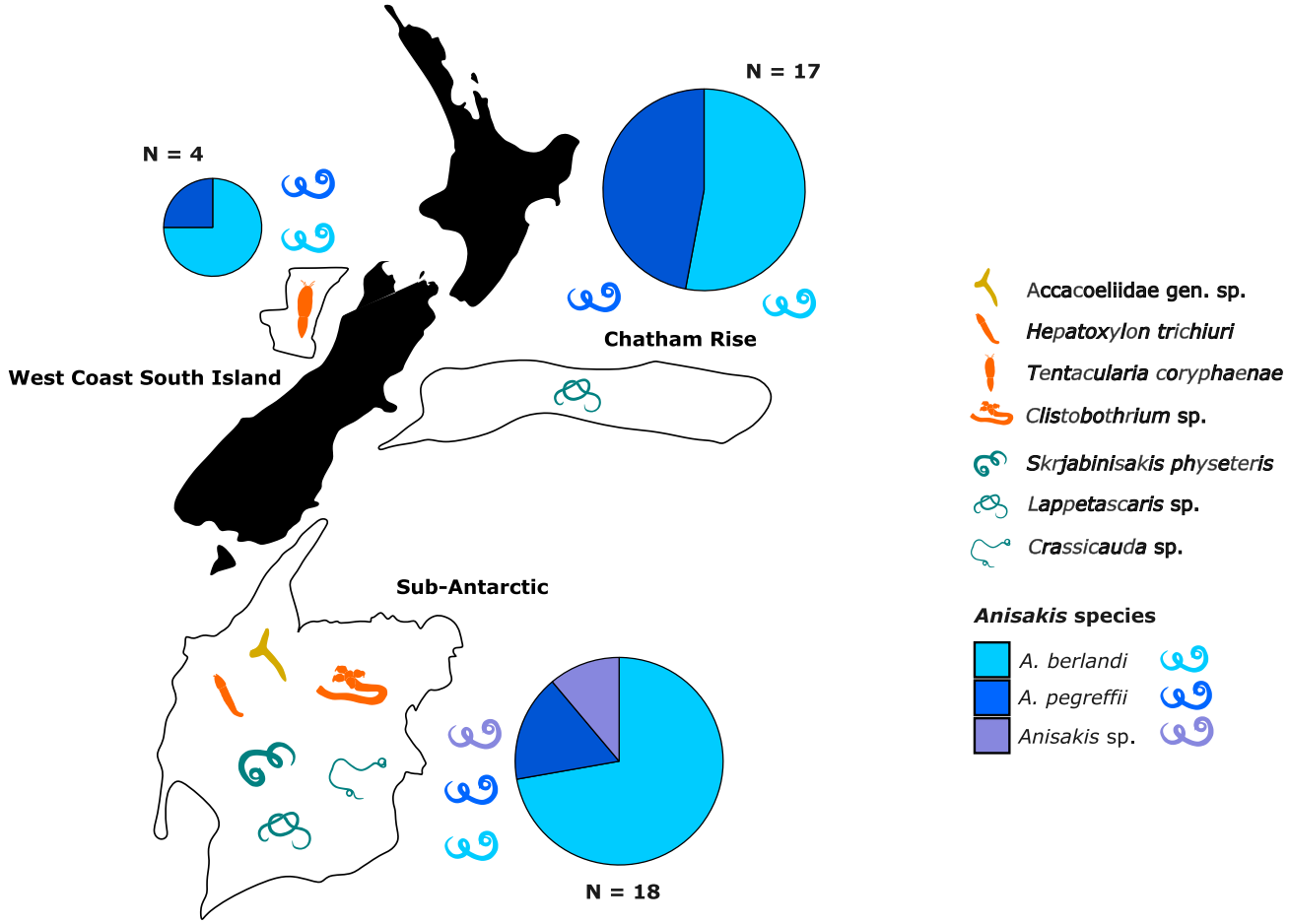

FIGURE 1 | Parasites recovered from squids in three locations: West Coast South Island, Chatham Rise, and sub-Antarctic. Pie charts depict the composition of *Anisakis* species in each location, with colours representing the three *Anisakis* taxa identified and pie size proportional to the number of *Anisakis* samples per location.

representative species recovered, including for nematodes Raphidascaridae (28S) and Tetrameridae (18S) and trematode family Accacoeliidae (28S). Each alignment was created together with sequences of closest relatives downloaded from GenBank following BLASTn searches. All new sequences, even those not included in phylogenetic analyses, are available on GenBank under accession numbers PZ105766-PZ105821. Bayesian inference was conducted for each alignment using the Geneious Prime MrBayes plugin v2.2.4 (Huelsenbeck and Ronquist 2001). The analyses performed have random starting trees for two runs (each with one cold and three heated chains), running for 1,000,000 generations using a Markov Chain Monte Carlo (MCMC) approach. The model was set at GTR with invgamma rates and heating temperature was set to 0.02 and we set burnin to first 25% of trees. The final phylogenies were summarised as 50% majority-rule consensus trees, with clade credibility support values (Bayesian posterior probability, BPP) and branch length information. A BPP higher than 0.8 was considered moderately supported and greater than 0.95 was considered high nodal support. Uncorrected pairwise genetic distances were calculated using MEGA version 11 (Tamura et al. 2021).

To investigate the genetic structure of *Anisakis* spp., we constructed a haplotype network based on aligned ITS2 sequence data. Some sequences were shorter in bp length compared to others but still included in the haplotype network with the assumption that they matched 100% to longer bp haplotype representatives. Sequences were aligned using the ClustalW algorithm implemented in the msa package (version 1.38.0) (Bodenhofer et al. 2015) within R Statistical Software (version 4.2.2; R Core Team 2022). The haplotype network was constructed using the pegas package (version 1.3) (Paradis 2010) to visualise genetic relationships among haplotypes.

3 | Results

We identified 10 parasite species from the 11 oegopsid squid taxa collected across three locations in New Zealand waters: six nematode, three cestode and one trematode (Figure 1 and Table 1). Nine of the 10 parasite taxa were recovered from squids sampled in sub-Antarctic waters, with five species found exclusively in this region.

Anisakis spp. were the most frequently recovered parasites, present in nearly all squid species examined except for the googly-eyed glass squid, *Te. pellucida* (Table 1). Three distinct taxa of *Anisakis* were identified: *A. pegreffii*, *A. berlandi*, and *Anisakis* sp. (Table 1 and Figure 2). The ITS1 sequence of our *A. pegreffii* specimens showed 100% match with numerous *A. pegreffii*

TABLE 1 | Parasite taxa recovered from New Zealand squid hosts collected from 2016–2024.

Parasite	Host	Location	Year
Trematode			
Accacoeliidae gen. sp.	*Teuthowenia pellucida*[NR]	Sub-Antarctic	2024
Cestode			
Hepatoxylon trichiuri	*Architeuthis dux*[NL, NR], *Moroteuthopsis ingens*[NR]	Sub-Antarctic	2018
Tentacularia coryphaenae	*Onykia* spp.[NR], *Taningia danae*[NL, NR], *Pholidoteuthis* sp.[NR]	West Coast South Island	2021, 2024
Clistobothrium sp.	*Histioteuthis* sp.[NR]	Sub-Antarctic	2024
Nematode			
Anisakis berlandi	*Architeuthis dux*[NL,NR], *Nototodarus sloanii*[NR], *Moroteuthopsis ingens*[NR], *Onykia* spp.[NR], *Todarodes angolensis*, *Todarodes filippovae*[NR], *Pholidoteuthis* sp.[NR], *Histioteuthis* sp.[NR]	Chatham Rise, Sub-Antarctic, West Coast South Island	2016, 2018–2022, 2024
Anisakis pegreffii	*Nototodarus gouldi*[NL, NR], *Nototodarus sloanii*, *Moroteuthopsis ingens*[NR], *Onykia* spp.[NR], *Todarodes filippovae*[NR]	Chatham Rise, Sub-Antarctic, West Coast South Island	2016, 2019, 2020, 2024
Anisakis sp.	*Todarodes angolensis*[NR], *Taningia danae*[NL, NR]	Sub-Antarctic	2020
Skrjabinisakis physeteris	*Todarodes angolensis*[NR]	Sub-Antarctic	2020
Lappetascaris sp.	*Todarodes filippovae*[NR]	Chatham Rise, Sub-Antarctic	2024
Crassicauda sp.	*Histioteuthis* sp.[NR]	Sub-Antarctic	2024

Abbrevations: NL, No location information; NR, New records of host-parasite associations.

GenBank entries, such as accession MT791094 from snapper *Chrysophrys auratus* in Australia and NZ waters (Hossen et al. 2021). Similarly, ITS1 sequences of *A. berlandi* and *Anisakis* sp. matched 100% to multiple *A. berlandi* sequences on GenBank (e.g., *A. berlandi* from the whale *Kogia breviceps* in Australia; accession MK325192; Shamsi et al. 2019). Given the higher variability in ITS2, we used ITS2 sequences to construct our haplotype network. The analysis revealed that *A. berlandi* and *Anisakis* sp. differed by two base pairs, while *A. pegreffii* was also two base pairs away from *Anisakis* sp. (Figure 2), leading us to refrain from categorising *Anisakis* sp. to species level. Both *A. berlandi* and *A. pegreffii* were found in squids from all three sampling locations, with *A. berlandi* being more commonly recovered (Figure 1), especially from the two onychoteuthid squid taxa, *Moroteuthopsis ingens* and *Onykia* spp.

In addition to *Anisakis*, three other nematode species were identified. The ITS1 sequence of *Skrjabinisakis physeteris* matched 100% to various GenBank entries (e.g., accession EU327691 from a *Sotalia fluviatilis* dolphin in Brazil; Iniguez et al. 2009). Two *Lappetascaris* sp. nematodes isolated from *To. filippovae* from the Chatham Rise and sub-Antarctic were also found. The *Lappetascaris* sp. sequence formed a highly supported clade within the Raphidascarididae family (BPP ≥ 0.95) based on partial 28S rDNA (Figure 3), and showed 99.5% similarity to *Lappetascaris* sp. from a coastal loliginid squid (*Uroteuthis duvaucelii*) from Bangladesh (accession ON117609; Bao et al. 2022). Another nematode recovered from *Histioteuthis* sp. (cock-eyed squid) nested within the genus *Crassicauda* based on partial 18S rDNA data (Figure 3). Our sequence matched 100% to *Crassicauda anthonyi* from a Cuvier's beaked whale (*Ziphius cavirostris*) in Brazil (accessions MZ362866, MZ362867; Febronio et al. 2021) and *Crassicauda giliakiana* from a firefly squid (*Watasenia scintillans*) in Japan (accession LC700444), and 99.9% to *Crassicauda magna* from a pygmy sperm whale (*K. breviceps*) off the coast of Australia (accession KM233410; Jabbar et al. 2015) and *Crassicauda boopis* from a fin whale (*Balaenoptera physalus*) off the Belgian coast (accession KY263809; Lempereur et al. 2017).

The only trematode recovered from *T. pellucida* was identified based on partial 28S rDNA as clustering within the family Accacoeliidae (Figure 4). Our sequence showed 94.2% identity to *Accacoelim contortum* from an oceanic sunfish (*Mola mola*) in Spain (accession KT005303; Ahuir-Baraja et al. 2015) and the United Kingdom (accession AY222190; Olson et al. 2003), a violet snail (*Janthina janthina*) and a Portguese man o' war (*Physalia physalis*) from Australia (accession OR814153, OR814154; Louvard et al. 2024). However, our trematode did not nest within any described genus in the family, suggesting it may represent a novel lineage within Accacoeliidae.

Three cestode species were identified based on the 28S rDNA sequences. Two belonged to the order Trypanorhyncha: *Tentacularia coryphaenae* Bosc, 1802 (Family Tentaculariidae), and *Hepatoxylon trichiuri* (Holten, 1802) Dollfus, 1942 (Family Sphyriocephalidae). *Tentacularia coryphaenae* was recovered from *Ta. danae*, *Onykia* spp., and *Pholidoteuthis* sp. off the West Coast of South Island, while *H. trichiuri* was found in *A. dux* and *M. ingens* from sub-Antarctic waters (Figure 1 and

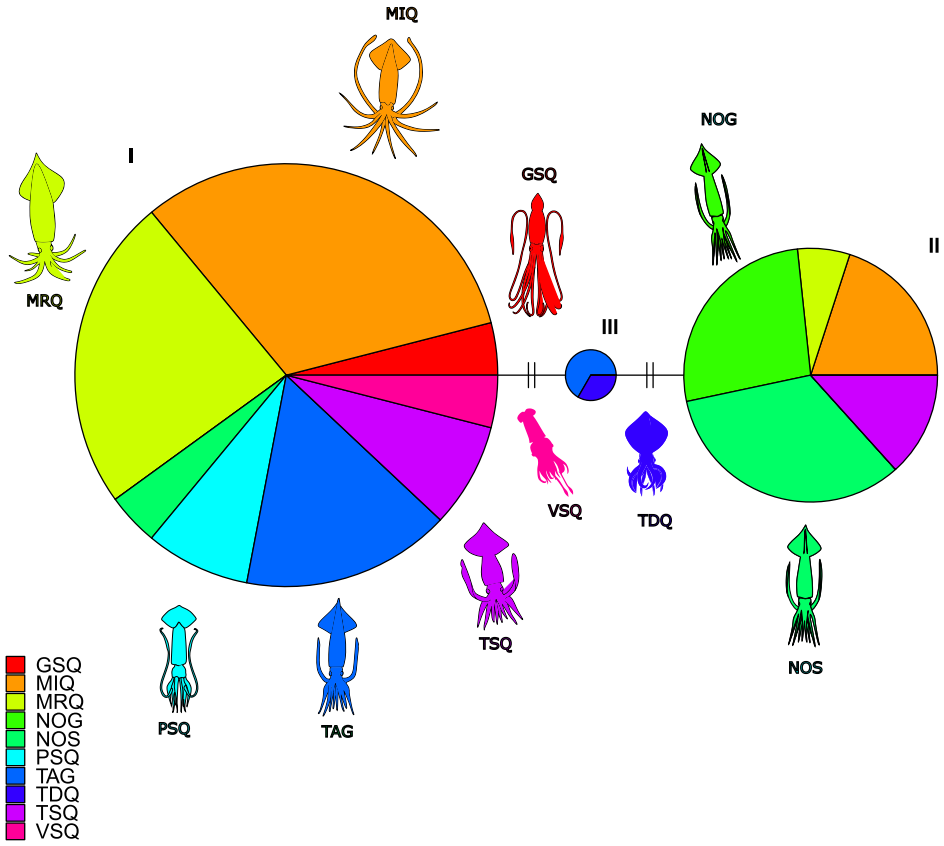

FIGURE 2 | Haplotype network of *Anisakis* spp. nematodes (*A. berlandi*, *A. pegreffii*, and *Anisakis* sp.) recovered from squid hosts. Node colour indicates squid species; node size reflects the number of samples per haplotype. Squid species codes: NOG = *Nototodarus gouldi*, NOS = *Nototodarus sloanii*, MIQ = *Moroteuthopsis ingens*, MRQ = *Onykia* spp., TAG = *Todarodes angolensis*, TDQ = *Taningia danae*, TSQ = *Todarodes filippovae*, GSQ = *Architeuthis dux*, PSQ = *Pholidoteuthis* sp., VSQ = *Histioteuthis* sp.

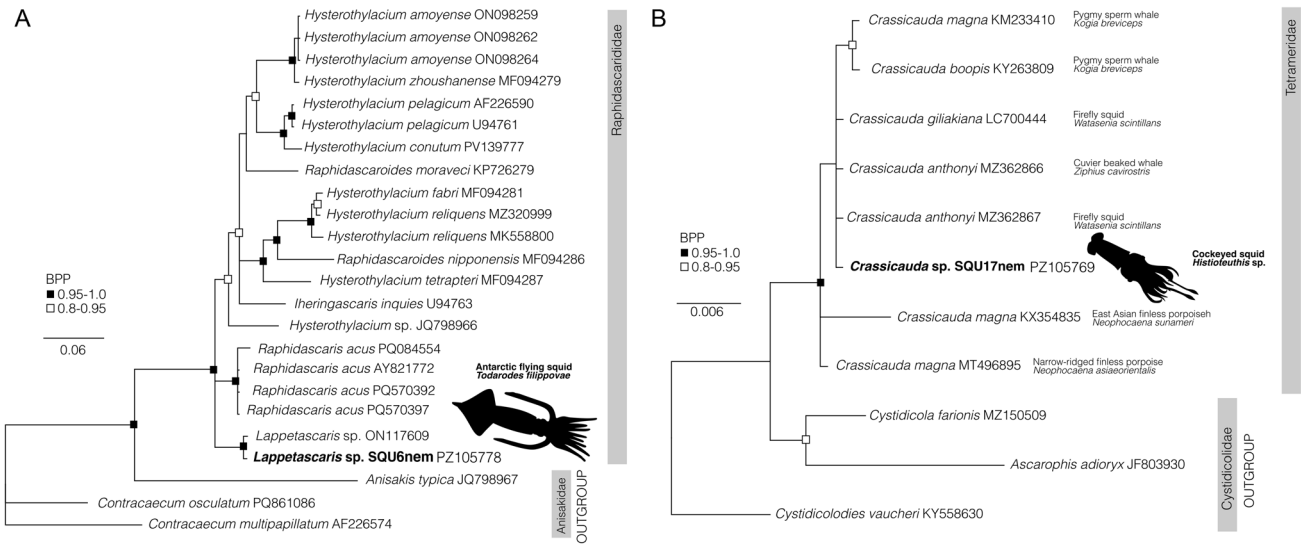

FIGURE 3 | Bayesian phylogenetic inference of nematodes from (A) Family Raphidascarididae based on partial 28S rDNA and (B) Family Tetrameridae based on partial 18S rDNA data. Scale represents substitutions per base. Bayesian posterior probability (BPP) is denoted by black (BPP > 0.95) and black with white filled (0.95 > BPP > 0.8) squares. The bolded sequences are new representatives from this study (Raphidascarididae gen. sp. infecting *Todarodes fillipovae* and *Crassicauda* sp. infecting cockeyed squid *Histoteuthis* sp.).

Table 1). Our *T. coryphaenae* and *H. trichiuri* 28S sequences conformed to plerocercoid representatives of the species, *T. coryphanae* from various bentho- and pelagic fish from Indonesia and Hawaii (accessions EF095265-9; Palm et al. 2007), and plerocercoids of *H. trichiuri* from a blue shark (*Prionace glauca*) off the Atlantic coast of USA (Olson et al. 2001), silver scabbard fish

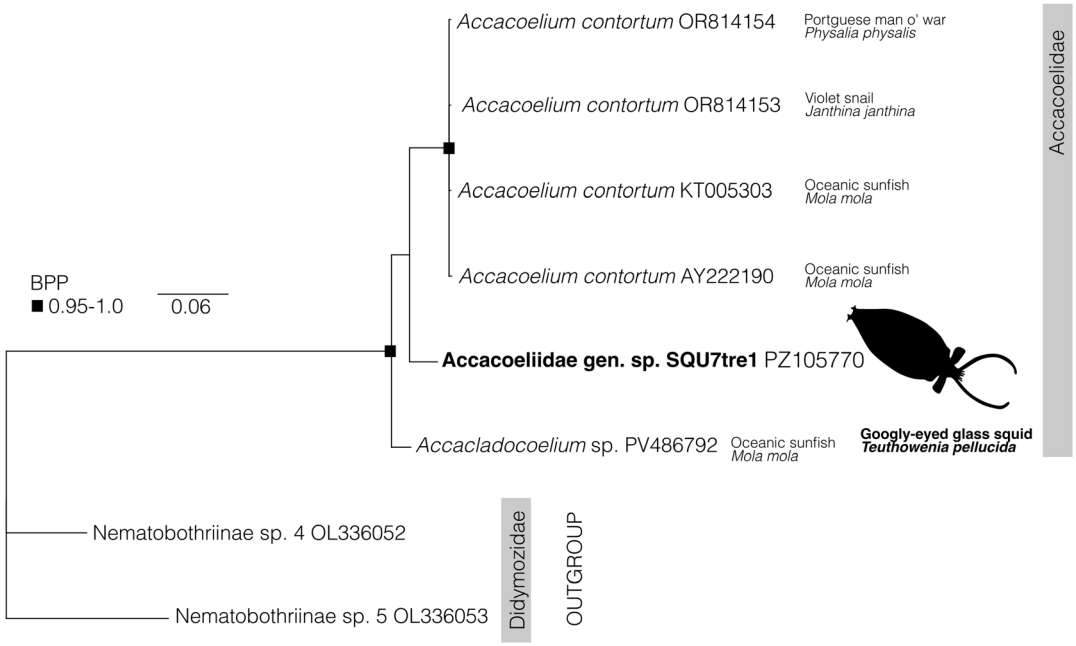

FIGURE 4 | Bayesian phylogenetic inference of trematodes from Family Accacoeliidae based on partial 28S rDNA data. Scale represents substitutions per base. Bayesian posterior probability (BPP) denoted by black squares. The bolded sequence is a new representative from *Teuthowenia pellucida*, googly-eyed glass squid (Family Cranchiidae).

(*Lepidopus caudatus*) in Central Mediterranean Sea (Palomba et al. 2021b), pomfret (*Taractes rubescens*) in Indonesia (Palm et al. 2007) and arrow squid (*N. sloanii*) in NZ (Bennett et al. 2022). The third cestode taxon recovered from *Histioteuthis* sp. in the Sub-Antarctic matched 100% to *Clistobothrium* sp. from *M. ingens* from the Chatham Rise (accession ON661310; Bennett et al. 2022), a coastal loliginid squid (*Doryteuthis pealeii*) from Italy (accession MT584207; Guardone et al. 2020), a porbeagle shark (*Lamna nasus*) from the Falkland Islands (JF436969; Randhawa and Brickle 2011), and another coastal loliginid squid (*D. gahi*) from the Falkland Islands (AF382072; Brickle et al. 2001) on GenBank. It also showed 99.85% identity to *Clistobothrium* sp. n. 1 from a porbeagle shark (*L. nasus*) from the Atlantic Ocean (accession MT732133; Caira et al. 2020).

4 | Discussion

This study contributes greatly to our knowledge of parasites living in association with deep-sea squid hosts in NZ waters. Worldwide, most cephalopod–parasite observations have been made in the Mediterranean Sea, the Northeast Atlantic, and the Northwest Pacific (Tedesco et al. 2020). Here, we have identified 10 parasitic helminths species from 11 NZ oegopsid squid species, yielding 23 new host-parasite associations among 25 total records. The most frequently recovered parasites were nematodes of the genus *Anisakis*, specifically *A. berlandi* and *A. pegreffii*, which were recovered across all three sampling regions and from 10 of our 11 oegopsid hosts.

The Sub-Antarctic region yielded the highest parasite diversity, with nine of the ten parasite species recovered from squids sampled there, including five species found exclusively in that region. This could be explained by the fact that higher sample size of parasites from this region simply reflects their larger species recovery. Alternatively sub-Antarctic waters may harbour richer or more distinct parasite assemblages, potentially due to ecological factors such as host availability, food web complexity, and environmental conditions (Amundsen et al. 2009; Vanstreels et al. 2020). Historical records also note that fish caught in sub-Antarctic waters, including around Antipodes and Auckland Islands in the early 1900s, frequently harboured heavy parasite burdens, with some specimens reported to have their entire lateral muscles filled with roundworms (Waite 1916). These findings highlight the importance of including remote and offshore habitats in biodiversity surveys, as they may serve as reservoirs of cryptic or novel parasite diversity that remains undetected in more accessible coastal systems (Danovaro et al. 2014).

The presence of *Anisakis* spp., especially since some were found in the mantle tissue, is of public health concern due to the risk of anisakiasis, a zoonotic disease that humans may contract through consumption of raw or undercooked seafood containing larval nematodes (Mattiucci et al. 2018). While fish are well-documented sources of human infection (Bao et al. 2017; Shamsi and Sheorey 2018), squid are also increasingly recognised as significant vectors (Fujisawa et al. 2025). Moreover, global consumption of cephalopods, especially ommastrephid (or 'flying') squids, has risen markedly over the past three decades (Vieites et al. 2019). The *Anisakis* life cycle involves marine mammals (primarily cetaceans) as definitive hosts, crustaceans as first intermediate hosts, and fish and cephalopods as intermediate or paratenic (Mattiucci et al. 2018); more recent studies have also identified seabirds and sea snakes harbouring larval stages (Shamsi et al. 2017). Humans are considered accidental hosts (Mattiucci et al. 2018).

Among the *Anisakis* taxa identified, *A. pegreffii* is known to cause invasive anisakiasis, where the larva penetrates the gut wall, leading to symptoms such as abdominal pain, nausea, and allergic reactions (Mattiucci et al. 2018). *Skrjabinisakis physeteris* (previously known as *Anisakis physeteris*) may also pose similar risks, while *A. berlandi* has not yet been definitively linked to human disease (Mattiucci et al. 2018). In our study, *A. berlandi* was the dominant species found, especially in the commercially important arrow squids *N. gouldi* and *N. sloanii*, suggesting a potentially lower risk of anisakiasis from these squids. However, anisakiasis may be underdiagnosed due to its nonspecific and highly variable symptoms, which can include bleeding, headache, intestinal obstruction, anaemia, and, in severe cases, respiratory arrest, as summarised in a recent global cases review (Shamsi and Barton 2023). Misidentification of causative species also remains common (Bao et al. 2017; Fujisawa et al. 2025). Furthermore, allergic reactions to *Anisakis* antigens can occur even after consuming dead larvae in cooked or canned seafood (Audicana et al. 2002), underscoring the need for surveillance.

Despite their commercial significance, *N. sloanii* and *N. gouldi* have received limited parasitological investigation until recently. Bennett et al. (2022, 2023) documented a diverse parasite fauna in *N. sloanii* from coastal Otago waters, including cestodes and nematodes totalling 11 species. In contrast, our samples from Chatham Rise and West Coast South Island yield only *A. pegreffii* and a single *A. berlandi*, suggesting that geographic location and ecological niche may influence parasite diversity and abundance. González et al. (2003) showed that the ecological niche of cephalopod hosts is the main factor shaping their parasite species composition, and geographic factors may also play a significant role (Bower and Miyahara 2005). Expanding parasite surveys across habitats, depth ranges, and seasons will be critical for understanding what governs parasite communities and for predicting infection responses to environmental change.

Beyond *Anisakis*, our recovery of *S. physeteris*, *Lappetascaris* sp., and *Crassicauda* sp. expands the known nematode fauna of NZ cephalopods. The 28S sequence of our larval *Lappetascaris* sp. specimens recovered from *T. filippovae* in both Chatham Rise and Sub-Antarctic regions closely matched *Lappetascaris* sp. (99.5% similarity) from a coastal squid, *U. duvaucelii*, in Bangladesh waters (Bao et al. 2022). *Lappetascaris* larvae are commonly found in cephalopods and have been reported from a wide range of squid species globally, including *Histioteuthis* spp. in the Mediterranean Sea (Palomba et al. 2021a), *Todarodes pacificus* in Japan (Takahara and Sakurai 2010), and several squids in the North Pacific (*Thysanoteuthis rhombus*, *Ommastrephes bartramii*, *Onychoteuthis borealijaponica*, and *Gonatopsis borealis*) (Nagasawa and Moravec 2002). Although generally considered nonzoonotic, *Lappetascaris* may still possess pathological potential (Bao et al. 2022). Its lifecycle remains unresolved, but top predator teleost fish were thought to be the definitive host based on the phylogenetic relationship between *Lappetascaris* and *Hysterothylacium* (Palomba et al. 2021a). The *Crassicauda* sp. nematode recovered from the cockeyed squid (*Histioteuthis* sp.) clustered within the *Crassicauda* clade based on partial 18S rDNA. Our sequence matched 100% to sequences identified as *C. anthonyi* and *C. giliakiana*, and 99.9% to sequences identified as *C. magna* and *C. boopis*, all previously recovered from squids and whales (Jabbar et al. 2015; Lempereur et al. 2017; Febronio et al. 2021). The high sequence similarity across species highlights the conserved nature of the 18S rRNA gene in this group, limiting species-level resolution without additional markers. However, the presence of *Crassicauda* sp. in the Southern Ocean highlights health concerns for whales that act as definitive hosts due to *Crassicauda* spp. associations with severe, even fatal respiratory, renal or gastrointestinal lesions (Febronio et al. 2021), including in NZ (Duignan 2003; Lehnert et al. 2019). While large mammal hosts are not always able to be sampled for parasitological investigations, monitoring the presence of problematic parasites, such as *Crassicauda*, through second intermediate or paratenic hosts, such as cephalopods, may provide an appropriate alternative.

The discovery of a potentially novel trematode lineage in the glass squid *Te. pellucida* further emphasises the hidden diversity of offshore parasite communities. The trematode specimen resembled an immature adult, suggesting that *T. pellucida* may serve as a second intermediate, paratenic, accidental, or even definitive host (if specimens were recently acquired). Our 28S sequence likely represents a genus not yet represented on GenBank, with only 94.2% similarity to *Accacoelium contortum*, which infects the oropharyngeal chamber of ocean sunfish (*M. mola*) as its definitive host (Ahuir-Baraja et al. 2015). Little is known about the life cycles of accacoeliids, although the second intermediate hosts for *A. contortum* were recently reported as oceanic pleuston, the violet snail (*J. janthina*) and the Portuguese man o' war (*P. physalis*) (Louvard et al. 2024). *Teuthowenia pellucida* spends its paralarval and juvenile stages in epipelagic waters (above 200 m) before ontogenetically descending to habitats as deep as 2000 m (Evans 2013), making it feasible that this squid could consume appropriate infected prey during its shallower early life stages.

All the cestodes identified in this study represent new host–parasite records. These include *H. trichiuri* from *A. dux* and *M. ingens*; *T. coryphaenae* from *Onykia* spp., *T. danae*, and *Pholidoteuthis* sp.; and *Clistobothrium* sp. from *Histioteuthis* sp. The trypanorhynch cestodes *H. trichiuri* and *T. coryphaenae* use sharks as definitive hosts, crustaceans as first intermediate hosts, and fish and squids as second intermediate or paratenic hosts (Palm and Caira 2008; Alves et al. 2017). *Heptoxylon trichiuri* has been reported in fish from many regions (Tiralongo et al. 2020), including NZ (Sin et al. 1992), and in jumbo squid (*Dosidicus gigas*) off central Chile, where it reached 70% prevalence (Pardo-Gandarillas et al. 2009). It was also previously recovered from *N. sloanii* in Otago, where it likely plays a role in transmitting the parasite to large sharks (Bennett et al. 2022; Bennett et al. 2023). *Tentacularia coryphaenae* has been reported from *Todarodes* and *Sthenoteuthis* squids in Indian waters (Purkayastha and Furuya 2025). The *Clistobothrium* sp. (order Phyllobothriidea) found in *Histioteuthis* sp. matched sequences obtained from the hooked squid *M. ingens* from the Chatham Rise (Bennett et al. 2022), *D. pealeii* in Northwest Atlantic (Guardone et al. 2020), and porbeagle sharks (*Lamna nasus*) from the Atlantic Ocean (Randhawa and Brickle 2011; Caira et al. 2020), suggesting a wide geographic distribution. The plerocercoid larvae infect squids, oarfish, and a variety of small sharks, with adult stages found in porbeagle sharks (Randhawa and Brickle 2011; Caira et al. 2020). The numerous and diverse cestodes recovered from various squids and their

exclusive maturing in elasmobranchs, points towards the ecological role of cephalopods as prey for elasmobranchs in the Southern Ocean (Palm and Caira 2008; Caira et al. 2020; Cherel 2020).

Trophically transmitted parasites can serve as valuable indicators of predator–prey relationships (Valtonen et al. 2010; Bennett et al. 2019). Our findings highlight some predator–prey dynamics involving NZ squids and offer insights into their ecological roles. For example, *Histioteuthis* spp. have previously been identified as prey for marine birds such as albatrosses (Cherel 2020) and porbeagle sharks (Cherel and Duhamel 2004). The presence of *Clistobothrium* sp. pleurocercoid larvae infecting *Histioteuthis* spp. and presence of *Clistobothrium* sp. adult forms infecting porbeagle sharks supports the conclusion that this shark species preys upon these squid species in NZ waters and thereby becomes infected with *Clistobothrium* sp. Similarly, the detection of *H. trichiuri* or *T. coryphaenae* in *A. dux*, *M. ingens*, *Onykia* spp., *T. danae*, and *Pholidoteuthis* sp. indicates that these squids form part of the diet of sharks that act as definitive hosts, consistent with previous diet studies (Dunn et al. 2010; Dunn et al. 2013; van der Vyver et al. 2015; Cherel 2020). However, such transmission patterns do not necessarily reflect active prey selection by predators and may instead arise when parasitised prey exhibit increased vulnerability to capture, for example, through impaired escape responses (Timi and Poulin 2020). Combined, this data suggests that squid play important roles as prey for pelagic sharks in the Southern Ocean, underscoring the value of incorporating parasitological data into ecological toolkits to better understand marine trophic interactions.

This study presents an opportunistic survey of parasitic helminths recovered from oegopsid squids collected in southern NZ waters. As such, we report only the presence of parasites observed in the sampled individuals through visual examination. Quantitative data on parasite intensity and prevalence were not collected and, therefore, cannot be assessed. These squid species likely host additional parasite taxa not detected in this study, particularly those with seasonal or life-stage-specific infection patterns. Parasites are increasingly being used as stock discriminators for squid and fish populations for commercial management (Catalano et al. 2014; Mattiucci et al. 2015; Poulin and Kamiya 2015; Timi and Buchmann 2023; Gutiérrez et al. 2024; Marcotegui et al. 2024; Braicovich et al. 2025). The diversity of parasites recovered in this study illustrates the large scope for future targeted sampling to assess infection dynamics across populations and regions.

In an era of accelerating ecological change, documenting parasite diversity in marine invertebrates is not only a matter of scientific curiosity but a necessity for understanding ecosystem health and resilience. This study provides foundational data on helminth parasites of NZ cephalopods, revealing both widespread zoonotic taxa and new host–parasite records. The presence of *Anisakis* spp. in commercially valuable squid species may have implications for seafood safety, and the discovery of previously unrecorded parasite associations enriches our understanding of host–parasite networks in the Southern Ocean. Future research would include studies quantifying parasite prevalence, abundance, and distribution across cephalopod population, and integrating parasitological data into fisheries management and public health frameworks.

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Conflicts of Interest

No potential conflict of interest was reported by the authors.

Data Availability Statement

All genetic data produced in this study are available to download from GenBank under accessions PZ105766-PZ105821.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Parasite taxa recovered from opsegoid squid collected at three New Zealand locations (2016–2024), with corresponding isolate identifiers, Earth Sciences New Zealand National Invertebrate Collection catalogue numbers (NIWA catalogue numbers), and GenBank accession numbers.