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Towards unlocking the trophic roles of rarely encountered squid: Opportunistic samples of *Taningia danae* and a *Chiroteuthis* aff. *veranii* reveal that the Southern Ocean top predators are nutrient links connecting deep-sea and shelf-slope environments

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Deep-sea squids are presumably vital components of largely undescribed marine ecosystems, yet limited access to specimens has hampered efforts to detail their ecological roles as predators and preys. Biochemical techniques such as stable isotope analyses, fatty acid analyses, and bomb calorimetry are increasingly recognized for their ability to infer trophic ecology and dietary information from small quantities of tissue. This study used five opportunistically collected *Taningia danae* specimens and one *Chiroteuthis* aff. *veranii* specimen retrieved from the Great Australian Bight, South Australia, to detail the trophic ecology of these poorly understood squids. Four body tissue types (i.e., arm, buccal mass, mantle, and digestive gland) were assessed for their utility in stable isotope (SI) and fatty acid (FA) analyses, and we found that the arm, buccal mass, and mantle tissues had similar SI and FA profiles, suggesting that they can be used interchangeably when the entire specimen is unavailable. δ^{13}C, δ^{15}N, and fatty acid data suggests that the *T. danae* and *C.* aff. *veranii* specimens lived in the Southern Ocean and were high-trophic-level predators, feeding on deep-sea fishes and small squids, while also taking advantage of the summer upwelling region of the Great Australian Bight. The fatty acid analysis and bomb calorimetry results indicate that these squids might be important reservoirs of essential FAs (EPA and DHA) for Southern Ocean predators and that the whole-body energy content of *T. danae* individuals can reach up to 362,250 kJ. Our findings indicate that these squids may be contributing greatly to the transport of nutrients and energy between the Southern Ocean deep-sea and the Great Australian Bight shelf–slope environments. In addition to building our understanding of the trophic ecology of two poorly understood deep-sea squids, these findings also highlight the utility of partial specimens and demonstrate the important ecological information that can be obtained from few samples that may be opportunistically collected.

KEYWORDS

deep-sea squid, trophic ecology, stable isotope analysis, fatty acid analysis, energy content, *Taningia danae*, *Chiroteuthis* aff. *veranii*

1 Introduction

Squids are vital components of marine ecosystems globally, occupying a broad range of ecological roles owing to their diverse morphology, habitat, behavior, and diet (Jereb and Roper, 2010; Coll et al., 2013). The 300 known species of squid range from low-trophic-level species in nearshore reefs to top predators in deep-sea and pelagic ecosystems (Navarro et al., 2013). Most squids are mesopredators feeding on small fishes and crustaceans and shunting key nutrients to large fishes, cetaceans, sharks, pinnipeds, and seabirds (De La Chesnais et al., 2019). Thus, squids are vital ecosystem members that facilitate energy and nutrient transfer in food webs (Merten et al., 2021) and can exert both top-down (i.e., predator influencing prey) and bottom-up (i.e., prey influencing predator) controls on a multitude of important marine species (De La Chesnais et al., 2019). The Southern Ocean alone is home to 42 different squid species, ranging in size from 5.7 cm (*Abraliopsis gilchristi*) to greater than 2 m (*Mesonychoteuthis hamiltoni* and *Architeuthis dux*) (Cherel, 2020). Furthermore, there is evidence to suggest that 12–24 million tonnes of cephalopods (primarily squids) might be consumed in the Southern Ocean annually (Santos et al., 2001) by at least 45 diverse predator species, showcasing the importance of squid as energy and nutrient resources in pelagic environments (Rodhouse, 2013). Additionally, global squid catches and abundances have both increased in recent decades (Doubleday et al., 2016), and their rapid growth and ability to adapt to environmental changes may make squid an especially ecologically and economically important taxa in changing ecosystems (Xavier et al., 2015).

Despite a global distribution and their increasingly important ecological roles, little is known about many squid species, with substantial knowledge gaps regarding diet, behavior, reproduction, distribution, physiology, and genetics (Albertin et al., 2012; Xavier et al., 2015; Xavier et al., 2018; Cherel, 2020; Ibáñez et al., 2021; Sato, 2021). The most researched are species that are commercially important, such as Humboldt squid (*Dosidicus gigas*) in the eastern Pacific Ocean or those that are easy to keep in aquaria (Roper and Shea, 2013). Comparatively little research effort has been applied to deep-sea and large-bodied squid species (Roper and Shea, 2013), owing to the myriad of difficulties associated with sampling animals occupying these mysterious habitats (Cherel et al., 2009b). Trawling often yields mixed and unreliable capture success (Roper and Shea, 2013), as large and fast squid are able to avoid trawl capture (Judkins et al., 2017), while trawls are known to damage delicate deep-sea specimens (Braid et al., 2014). Direct sightings of elusive species are becoming more common as camera technology becomes more affordable and accessible (O'Brien et al., 2018), but rarely do these provide information other than distribution, external morphology, and a snapshot of behavior (Kubodera et al., 2007; Gomes-Pereira and Tojeira, 2014; Hoving et al., 2014; Robinson et al., 2021). Much of the current genetic, physiological, and ecological data available on deep-sea and large squids has come from opportunistically retrieved carcasses, and beaks recovered from squid predators (Bolstad and O'Shea, 2004; Cherel and Hobson, 2005; Rosa et al., 2005). Research of large, deep-sea, or rarely sighted squids must be conducted whenever opportunities arise, and as they are abundant predators and preys, understanding their trophic interactions may be key for understanding food webs, nutrient dynamics, and ecosystems that are otherwise difficult to research and monitor.

Trophic ecology research aims to understand predator–prey interactions using methods such as direct observations, images or video recordings of predation events, gut content analyses, or molecular analyses of fatty acids (FAs) and stable isotopes (SIs) (Guerreiro et al., 2015; Da Silveira et al., 2020). Unfortunately, many of these methods are difficult to apply to inconspicuous marine species, especially large and deep-sea squids. Direct observation or image evidence of feeding events is difficult to attain due to the high cost and low success of these sampling methods (Robinson et al., 2021). Much of our understanding of large-bodied and deep-sea squids has instead come from investigations of deceased, opportunistically obtained specimens (see González et al., 2003; Rosa et al., 2005). In these cases, gut content analysis has varied success, typically requiring large sample sizes due to the frequency of empty stomachs, and the results are limited to identifiable prey items, which only represent the most recent feeding events (Braley et al., 2010; Rodhouse, 2013). Squids also have fast rates of digestion and a narrow esophagus that travels directly through the center of the brain, meaning that preys are thoroughly macerated with the beak and radula, reducing the incidence of identifiable stomach contents (Ibáñez et al., 2021).

Stable isotope analysis for trophic ecology primarily uses ratios of carbon-13 to carbon-12, and nitrogen-15 to nitrogen-14 isotopes in biological tissues (referred to as δ^{13}C and δ^{15}N) to infer foraging area and trophic level, respectively. δ^{13}C varies predictably with latitude and is depleted in pelagic food webs *vs.* coastal and benthic zones (Cherel et al., 2000), while $\delta^{15}N$ enriches as it travels up food webs with each successive link from prey to predator (Kelly, 2000). The use of these isotopes has been applied to studying the trophic ecology of squids and has also more recently been expanded into studies of ontogenic shifts in diet and species migrations (Merten et al., 2017; Golikov et al., 2019; Queirós et al., 2019). Stable isotope analysis is commonly used on cephalopod beaks, as these are undigestible hard parts readily found in the stomachs of their predators, including sperm whales (Cherel and Hobson, 2005). However, as SI analysis can be applied to any body tissue, it is an ideal tool for detailing the trophic ecology of opportunistically sampled animals, where only limited tissue types might be available (Jackson et al., 2007). Similar to $\delta^{13}C$, FAs differ at the base of the food web, as primary producers synthesize and retain unique FAs (Dalsgaard et al., 2003; Parrish, 2013). These FAs are assimilated in predators with minimal modification from prey items and thus can be used to infer a predator's diet and trace nutrient pathways to basal food webs (e.g., pelagic zooplankton vs. diatoms vs. coastal macroalgae) (Desforges et al., 2022). Additionally, FAs can be used to explore the availability of key nutrients within an ecosystem and can indicate the potential role or importance of species as prey items (Parzanini et al., 2018). As with SIs, FAs can be measured from most body tissues, although the different physiological roles of varying tissues mean that they preferentially retain different FAs (Phillips et al., 2002), eliminating the possibility of cross-tissue comparisons. Regardless, FA analyses are an ideal tool for trophic ecologists working with rare and opportunistically collected samples, and multiple tissues should be collected to fully capitalize on these occasions.

The Great Australian Bight (GAB), located off the southern coast of Australia, is a site of high productivity, driven by the convergence of the warm eastward flowing Leeuwin current and the cold westward flowing Flinders current as well as annual summer upwelling events (Van Ruth et al., 2018). The GAB includes the shallow continental shelf area around the southern coast, including Kangaroo Island, as well as the continental slope and the abyssal plains, which exceed 5,000-m depth (Rogers et al., 2013). Over the past decade, efforts to improve our understanding of the deep-sea ecosystem of the GAB have increased substantially (e.g., the GAB Research Program and GAB Deepwater Survey by CSIRO). From 2013 to 2017, 304 survey operations were conducted from 200- to 5,000-m depths in the GAB. Of the 1,267 invertebrate species recorded, almost one quarter (401 species) of these were previously undescribed (MacIntosh et al., 2018), indicating how poorly understood the diversity of the benthic and abyssal depths are in this region.

The present study was developed from the opportunistic recovery of five large squid carcasses from the ocean surface in the eastern GAB in March of 2019. The largest of these specimens measured approximately 120 cm in mantle length, and all five of these specimens were identified as *Taningia danae*. *Taningia danae* is a globally distributed and abundant, but rarely seen or researched, species of deep-sea squid, with no tentacles (i.e., only has arms present) and two large photophores on the tips of two arms (Quetglas et al., 2006). In December of 2021, an additional smaller squid specimen, identified as *Chiroteuthis* aff. *veranii*, was retrieved from a similar location and included in the study due to its rarity and unknown diet and trophic role. The aim of this study was to use $\delta^{13}C$ and $\delta^{15}N$ SIs, FAs, and energy content to determine the ecological role of these elusive deep-sea squids in the GAB with reference to other cephalopod species encompassing global, southern temperate, and polar squid distributions. Two libraries of published SI and FA data were compiled for comparison with the data collected from the squids in this study. One dataset consisted of global squid data and was a source of comparison to other squid species that may have similar diets, trophic roles, and physiology. The second dataset included multi-taxa marine species (e.g., cetaceans, fishes, crustaceans, etc.) from the GAB and southeast Australia, the Southern Ocean, New Zealand, and the Antarctic (Supplementary Figure S1) and was used to assess potential trophic interactions between the squids and other local species. The specific objectives of this study were to (a) assess the utility of different body sections for trophic ecology by comparing SI, FA, and energy density data from four different body parts (arms, buccal mass, mantle, and digestive gland); (b) determine the foraging habitat and trophic role of *Taningia danae* and *Chiroteuthis* aff. *veranii* with comparison to published data from squid globally; and (c) describe the roles of these squids and potential trophic interactions within their identified food webs with comparison of published data collected from multi-taxa marine species across the southern hemisphere.

2 Materials and methods

2.1 Specimen collection and identification

The six squid specimens analyzed in this study ("GAB squids"; five *Taningia danae* and one *Chiroteuthis* aff. *veranii*) were opportunistically collected from the eastern GAB, from 34-39°S and 135-139°E (Supplementary Figure S1) between 2019 and 2021 by Australian Fishing Enterprises. The deceased squids were initially spotted floating on the ocean surface by commercial tuna fishery spotter planes and subsequently collected by tuna fishing vessels. The squids were generally in good condition, with evidence of only minor post-mortem scavenging (eyes missing from seabird predation) and decomposition only on specimen Td3 (Supplementary Figure S2). The specimens were frozen onboard the vessels and transported to the Australian Fishing Enterprises facility in Port Lincoln, South Australia, where they were stored at −20°C until transport to Flinders University for subsampling. The specimens were thawed only sufficiently to be measured (e.g., mantle length, and arm length), described (i.e., noting distinguishing features such as arm and tentacle morphology and mantle and fin shape), and subsampled (Supplementary Table S1). Approximately 5 g of tissue from the mantle, arms, buccal mass, and digestive gland was sampled from each individual, cutting from the central portions of the tissues to avoid contamination, and immediately refrozen at −20°C for subsequent analyses. Approximately 3 g of each tissue type for each specimen was freeze-dried at −88°C for 72 h and then manually homogenized into a fine powder using a mortar and pestle.

2.2 Stable isotope analysis

Although squid mantle and arms have low lipid content (<2% wet weight, Phillips et al., 2002), making lipid removal not explicitly necessary for these tissues, the digestive gland has a high lipid content, which is variable both between and within squid species (6–55% wet weight; Phillips et al., 2002; Phillips et al., 2003; Pethybridge et al., 2012; Moovendhan et al., 2019). Therefore, lipid extraction was performed on all samples to ensure consistency across the study and to allow for comparisons with SI data available in the scientific literature, most of which have been chemically lipid extracted. Following a modified Bligh and Dyer (1959) protocol, lipids were removed by soaking the samples in 10 mL of 2:1 dichloromethane/methanol solution for 24 h. The delipidated samples were filtered and oven-dried at 60°C for 48 h to remove the remaining solvent. For each tissue type in each individual squid, one sample of approximately 1.50 mg (± 10%) of homogenized, delipidated tissue was weighed and placed into a tin capsule. The samples were analyzed in triplicate to confirm analytical precision.

Stable carbon and nitrogen isotope ratios were measured using an Isoprime GC5 continuous flow isotope ratio mass spectrometer with a vario ISOTOPE cube elemental analyzer (Elementar Australia Pty Ltd) at Flinders University Chemical Analysis Services. Blank tin capsules and standards were run throughout the analysis to measure analytical precision and correct for isotopic drift. The standards used were L-glutamic acid enriched in light C and N isotopes (^{12}C and ^{14}N) (USGS40) and heavy C and N isotopes (^{13}C and ^{15}N) (USGS41) (Sercon Ltd., UK). Stable isotope results were exported using the IonVantage software from Elementar and expressed in a standard notation as follows:

$$\delta X = [\frac{Rsample}{Rstandard} - 1] * 1000$$

where X is ^{15}N or ^{13}C and R is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C in the sample, following the international standards of Pee Dee Belemnite for CO_2, and atmospheric nitrogen for N_2.

2.3 Fatty acid analysis

Three replicates of approximately 0.025 g per tissue type per individual squid specimen were weighed into 20-mL glass test tubes for FA extraction by direct transmethylation (Parrish et al., 2015). To separate the FAs from their glycerol backbones, tissue was soaked in 3 mL of 10:1:1 methanol/dichloromethane/hydrochloric acid solution at 80°C for 2 h. At the completion of the 2-h solvent soak, the samples were removed from heat and cooled to ambient temperature before the addition of 1 mL of milli-Q water and 1.8 mL of 2:1 hexane/dichloromethane solution, followed by vortex mixing and centrifuging at 2,000 rpm for 5 min. The upper layer containing the FA methyl esters (FAMEs) was removed and placed into 2-mL glass vials. The vials were placed under nitrogen gas streams to evaporate the solvent, leaving only pure FAMEs. The addition of 1.8 mL of hexane/dichloromethane solution and dehydration with nitrogen gas was repeated three times, maximizing the FA retention. The FAMEs were suspended in 1 mL of dichloromethane for subsequent quantification. Fatty acid methyl esters were identified and quantified using gas chromatography mass spectrophotometry (GCMS) analysis with Agilent Technologies 5975C Series GC/MSD (Agilent Technologies, Inc., USA) equipped with Triple-Axis HED-EM Detector, SGE Analytical Science (Ringwood, Victoria, Australia) BP21 capillary column (15 m length, 0.25 mm internal diameter, and 0.25 µm film thickness), Agilent 7683B Series Injector, and Agilent/HP 7683 automatic liquid sampler. Quality checks were performed throughout the analysis with a blank sample containing 1 mL dichloromethane at the start of each run, plus an internal FA standard (C4–C24) (Sigma-Aldrich, USA). The output was analyzed and processed using MassHunter Qualitative Analysis software and the National Institute of Standards and Technology (https://www.nist.gov) database of FA compounds. Individual FA values were reported as percentage of the total FAs per sample analyzed so that contributions to FA profiles could be established. Fatty acids contributing<0.1% across the 45 samples were removed, leaving 21 FAs for tissue and species comparisons within the GAB squids (Supplementary Table S2).

2.4 Energy content (GAB *Taningia danae*)

One sample of each *T. danae* tissue type was combusted in a bomb calorimeter (Parr 6200 Isoperibol with semi-micro bomb) to obtain the energy content of the tissues. Before measuring the samples, a standard of benzoic acid was run. For each *T. danae* sample, approximately 0.025 g of freeze-dried, homogenized tissue was pressed into a pellet, packed into a crucible, and ignited in the bomb calorimeter. The heat released was measured and converted to kilojoules per gram wet weight.

2.5 Data analysis (GAB squids)

The isotopic compositions and FA profiles of the GAB squids alone were analyzed using PRIMER 7 + PERMANOVA (Anderson et al., 2008; Clarke and Gorley, 2015). To visually compare the isotopic composition across tissue types and species, a $\delta^{13}C$ and $\delta^{15}N$ biplot was created. Multivariate data visualization was used to assess if and how FA profiles differed across tissue type and species. Fatty acid data was square-root-transformed, and a resemblance matrix was generated using a Bray–Curtis measure of similarity. The data was visualized using a principal coordinates ordination (PCO) plot, and vectors were overlaid showing FAs with Pearson correlations >0.8 to indicate the direction and magnitude of the correlation with individual FAs. Similarity of Percentages (SIMPER) analyses were conducted using the previously generated resemblance matrices on factors of tissue type and species to determine the percentage dissimilarities between groups and the FAs contributing to the between-group differences.

The whole-body energy density of *T. danae* was roughly estimated using the energy density results for the mantle, arm, and digestive gland tissues. These were multiplied by the body weight proportions of *T. danae* given in Kelly (2019), wherein fins comprised 61% of body mass, mantle 14%, head and arms 23%, and viscera 4% (the digestive gland being 0.88%). Mantle energy density was multiplied by the fins + mantle proportions (0.75), arm energy density was multiplied by head and arms proportions (0.23), and digestive gland energy density was multiplied by the digestive gland proportion (0.0088). These were summed to provide an estimate of the whole animal energy density of *T. danae* tissues.

2.6 Collection, filtering, and refinement of published data

Additional SI and FA data were collected from published literature and legacy datasets (Nichols et al., 2023), enabling for the determination of the feeding ecology and trophic role of the GAB squids (available in Supplementary Tables S8–S12). Data were collected for (a) any squid species globally and (b) any marine species found in the southeast Australia, New Zealand, the Southern Ocean, and the Antarctica marine regions (henceforth referred to as southern marine species; Supplementary Figure S1).

Stable isotope data as mean δ^{13}C and δ^{15}N and associated metadata including species, location (sea or ocean sampled), and tissue type were collated from published literature. In total, 155 SI datapoints were used from the muscle and beak analyses of squid globally, and 293 data points were used from any tissue of multi-taxa southern marine species, including groups such as crustaceans, fishes, seabirds, and marine mammals. Beaks are commonly used for SI research of cephalopods but are comprised of chitin, which is known to be enriched in in 14-nitrogen, resulting in δ^{15}N values lower than that of muscle tissues from the same animal. In previous works, the δ^{15}N values of beaks have been adjusted for comparison to muscle samples by adding between 3.5‰ and 4.8‰ (Cherel and Hobson, 2005; Navarro et al., 2013; Guerreiro et al., 2015). Thus, we adjusted all beak δ^{15}N data that were not already corrected in the source publication by + 3.5‰ to allow more reliable comparisons with our GAB squids. The triplicate SI ratios generated for each tissue type across the GAB squids were condensed to the mean muscle-specific isotope ratio per specimen. The isotope ratios in the digestive gland were depleted in both δ^{13}C and δ^{15}N and so were excluded from the muscle-specific mean. A δ^{13}C and δ^{15}N biplot was created to qualitatively compare the trophic ecology of the six specimens in this study with squid globally and to assess the role that these squids play within local food webs.

Fatty acid profiles were recorded as the percent contribution of each FA to the total FA quantity. For each profile, metadata including the species, taxon type (cephalopod, fish, chondrichthyan, etc.), location (sea or ocean sampled), and tissue type were recorded, as well as other information such as sex and maturity status, if available. If multiple FA profiles were reported within a single source for the same species, location, and tissue type, the mean FA profile across all samples was calculated for use. In total, 116 and 298 FA profiles were used from tissues of squids globally and tissues of multi-taxa southern marine species, respectively (metadata and citations can be found in the Supplementary Material).

Fatty acid data are reported differently throughout the literature. Up to 60 different FAs are often measurable on the GCMS; however, only those exceeding 2%, 1%, 0.2%, or 0.1% or simply those deemed “of interest” by the authors tend to be reported in the literature. Thus, depending on the author, the means of analysis, and tissue types, FA profiles may not be directly comparable. As this study combined FA data from a wide range of sources, many FAs needed to be grouped together to minimize the effects of differing sources. Firstly, FA profiles were standardized to sum up to 100%, eliminating the influence of minor FAs that were not measured or reported in many profiles. Secondly, FAs were filtered to further minimize any confounding effects of data source. For the global squid dataset, FAs reported in fewer than 50 samples and those with a mean of less than 0.5% across all samples were removed. For the southern marine species dataset, the mean percentage of each FA was calculated across each separate taxa group (cephalopods, fishes, chondrichthyes, etc.), and FAs with a mean of less than 2% within all taxa groups were removed. This ensured that any FAs important to only one taxon group were retained for analysis rather than be removed due to their lack of contribution in other taxon groups. This standardization process followed Meyer et al. (2019) and resulted in a 15 FA global squid dataset and a 12 FA southern marine, multi-taxon species dataset (Supplementary Table S2).

The triplicate FA profiles generated for each tissue type across the GAB squids were averaged to one profile per tissue type, per specimen, and included in the final FA datasets. The comparison of the six specimens within this study to squid globally was divided into two datasets: muscular tissue profiles (unspecified soft tissues, mantle, buccal mass, arm, and fin) and digestive tissue profiles (digestive gland, stomach, stomach fluid, cecum oil, and whole homogenized individuals). These datasets warranted a separate analysis, as the two tissue types have distinct FA profiles that are not directly comparable. Bray–Curtis similarity matrices were generated from the square-root-transformed data. The data were visualized using a PCO plot, and vectors were overlaid showing FAs with Pearson correlations >0.5. Similarity of Percentages (SIMPER) analyses were conducted using the previously generated resemblance matrices on factors of tissue type and location to determine the percentage dissimilarities between groups and the FAs contributing to the between-group differences.

Energy density data, as kilojoules per gram wet weight, were collected and analyzed for southern mid-trophic marine species (squids and fishes). In instances wherein one species had several differing energy densities available, the greatest kilojoules per gram value was retained for analysis. Additionally, body mass data were collected of all species included in the energy density analyses so that the approximate energy content per individual could be calculated. "As reported body masses can vary greatly; the greatest published body masses were used for analysis. This was so that the energy contents calculated per individual were more likely overestimations than underestimations, and thus comparisons made to *T. danae* energy content would be viable. *Taningia danae* whole-body energy density was multiplied by both the greatest individual body mass recorded, 161 kg, and a more conservative body mass, 60 kg (Roper and Jereb, 2010), to provide two points of comparison with the other southern marine species.

3 Results

3.1 GAB squids

Stable isotope ratios differed between individual specimen, species, and tissue type (Table 1; Figure 1), with the highest δ^{15}N found in the mantle and the lowest in the buccal mass. Digestive gland tissues were depleted in δ^{13}C and δ^{15}N *versus* the muscle tissues (mantle, arm, and buccal mass) (Figure 1). The carbon-to-nitrogen (C:N) ratio of all muscle tissues in all squid specimens ranged from 2.83 to 3.14, and the C:N ratio of the digestive gland was higher than that of the muscle tissues (Table 1).

In *T. danae* and *C.* aff. *veranii*, saturated fatty acids (SFAs) and polyunsaturated fatty acids (PUFAs) were most abundant in the muscle tissues, while monounsaturated fatty acids (MUFAs) were most abundant in the digestive gland (Table 2). In muscles, the most abundant individual FAs were 16:0, 22:6ω3, and 20:5ω3, whereas in the digestive glands the most abundant were 16:0, 18:0, and 20:1ω9 (Table 2). The fatty acid profiles were differentiated primarily by tissue type (digestive gland or muscle tissue), followed by species (Figure 2), as the digestive gland FA profiles of *T. danae* were 19.09–20.10% dissimilar from the muscle FA profiles (Supplementary Table S3). This dissimilarity was influenced by higher proportions of 18:1ω9, 20:1ω9, and 24:1ω9 and lower proportions of 22:6ω3, 20:5ω3, and 16:0 in the digestive gland (Figure 2). The muscle tissues were all<10% dissimilar within each species (Supplementary Table S4). The muscle tissues of the *T. danae* specimens were 9.92–11.80% dissimilar to the muscles of the *C.* aff. *veranii* specimen (Supplementary Table S5). In total, 59% of this dissimilarity was influenced by the *C.* aff. *veranii* tissues having higher proportions of 16:1ω7*t*, 18:2ω6, and 20:5ω3 and lower proportions of 22:6ω3, 20:3ω3, and 24:0 *versus* the *T. danae* tissues.

The digestive gland of *T. danae* had a greater energy content (5.94 kJ/g) than the muscular tissues which ranged from 2.53 kJ/g for the mantle tissue to only 0.50 kJ/g for the buccal mass (Table 3). Using the body part proportions given for *T. danae* in Kelly (2019), the whole-body energy density of *T. danae* is estimated at approximately 2.25 kJ/g.

3.2 GAB squids vs. global squids

Globally, squids had a δ^{13}C range from -25.80‰ to -15.10‰ and a δ^{15}N range from 6.30‰ to 17.90‰ (Figure 3). The GAB squids were comparatively depleted in δ^{13}C, and most aligned with squid species collected from the Southern Ocean (Figure 3; Supplementary Figure S3). The GAB squids were also enriched in δ^{15}N, with few squids from the Southern Ocean, southeast Australia, and New Zealand areas having higher δ^{15}N in comparison (Figure 3; Supplementary Figure S4). Four specimens of *T. danae* (Td) from the Southern Ocean and southeast Australia had similarly enriched δ^{15}N values compared to the GAB *T. danae* specimens (Figure 3). In contrast, one *T. danae* specimen from the Southern Ocean was considerably enriched in δ^{15}N than the GAB specimens, at 15.30‰ (Figure 3). *Chiroteuthis* sp. and *C. veranii* specimens (two and three samples, respectively) had δ^{15}N values ranging from 11.50‰ to 12.90‰ and δ^{13}C values ranging from -20.00‰ to -16.50‰ (Figure 3).

The SIMPER analysis revealed a 23.30% dissimilarity between the FA profiles of digestive gland and mantle muscle tissues from squids sampled globally. In total, 47% of this dissimilarity between tissue types was due to higher proportions of MUFAs (18:1, 20:1, 22:1, 16:1, and 24:1) in the digestive gland tissue, and 27.00% was attributed to higher proportions of 22:6ω3, 20:5ω3, and 16:0 in mantle tissue.

TABLE 1 δ^{13}C and δ^{15}N (‰) composition and carbon-to-nitrogen ratio (C:N) of arm (A), buccal mass (B), mantle (M), and digestive gland (DG) from *Taningia danae* (Td) and *Chiroteuthis* aff. *veranii* (Cav) specimens collected from the eastern Great Australian Bight.

		Td1	Td2	Td3	Td4	Td5	Cav1
δ^{13}C	A	-21.29 ± 0.14	-20.94 ± 0.18	-20.59 ± 0.31			-21.71 ± 0.29
	B	-22.37 ± 0.18	-20.70 ± 0.35	-20.04 ± 0.12			-21.35 ± 0.34
	M	-21.41 ± 0.03		-20.76 ± 0.14	-21.51 ± 0.19	-21.78 ± 0.15	-22.37 ± 0.40
	DG	-23.80 ± 0.22		-22.15 ± 0.17			
δ^{15}N	A	10.37 ± 0.16	10.48 ± 0.15	11.49 ± 0.21			10.10 ± 0.08
	B	11.01 ± 0.10		12.80 ± 0.08	12.03 ± 0.10	12.23 ± 0.06	11.23 ± 0.05
	M	10.77 ± 0.21	10.98 ± 0.16	12.08 ± 0.47			9.94 ± 0.11
	DG	9.57 ± 0.29		10.78 ± 0.13			
C:N	A	2.96 ± 0.02	2.87 ± 0.05	2.95 ± 0.06			2.91 ± 0.27
	B	3.08 ± 0.03	2.98 ± 0.01	2.83 ± 0.03			2.83 ± 0.04
	M	2.99 ± 0.03		2.99 ± 0.03	3.11 ± 0.02	3.14 ± 0.04	3.03 ± 0.06
	DG	3.98 ± 0.02		3.37 ± 0.05			

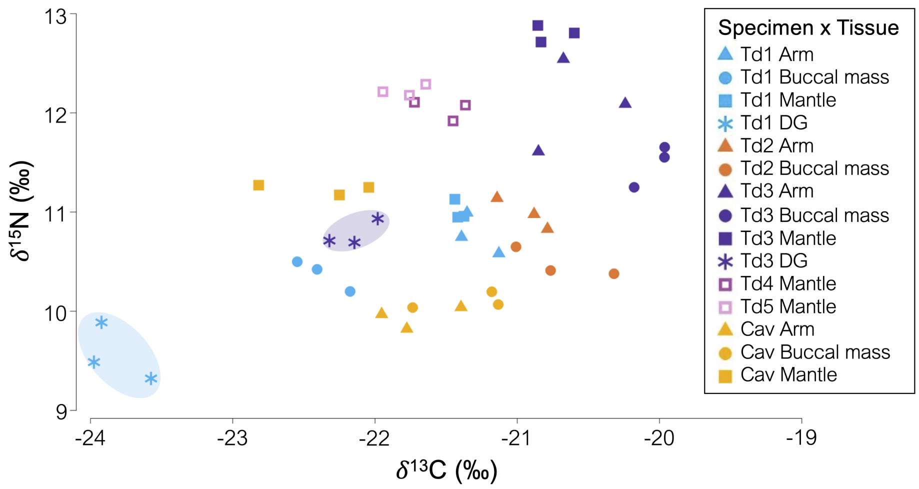

FIGURE 1
δ^{13}C and δ^{15}N (‰) composition of mantle, arm, buccal mass, and digestive gland from *Taningia danae* and *Chiroteuthis* aff. *veranii* collected from the eastern Great Australian Bight. Ellipses are drawn to illustrate the separation between muscle tissues and the digestive gland.

Globally, squid muscle tissue FA profiles were well separated by sampling area (Figure 4A), with GAB *T. danae* and GAB *C.* aff. *veranii* being least dissimilar to the squid samples taken from the northeast Atlantic (12.26% and 13.52% dissimilar, respectively) and southeast Australia (12.25% and 13.57% dissimilar, respectively; Supplementary Table S6). The GAB squid samples grouped closely with southeast Australian samples including *Todarodes filippovae* (Tf), *Idioteuthis cordiformis* (Ics), and *Ommastrephes brevimanus* (Omb) (Figure 4A). Two *Architeuthis dux* (Ad) samples were also similar in FAs, with one from eastern Australia and the other from the northeast Atlantic Ocean. The southeast Australia and Southern Ocean samples were differentiated from other areas by higher proportions of FAs 16:0, 20:1, 22:1, and 24:1. The Southern Ocean samples were differentiated from southeast Australia samples by higher proportions of FAs 16:1, 18:1, and 22:5ω3, while the southeast Australian samples, including the samples from this study, had higher 18:0. There were two samples taken from chiroteuthids, a *C. veranii* (Cv) sample from the northwestern Atlantic and a *Chiroteuthis* sp. (Cx) from southeast Australia. Both samples had lower proportions of FA 18:0 and higher proportions of 18:1 in the mantle *versus* the GAB *C.* aff. *veranii*. Zero *Taningia* spp. were found for comparison.

The fatty acid profiles from the digestive parts of squids (including whole squids, digestive glands, stomachs, stomach fluid, or cecum oil) showed less grouping by sampling area than was evident in the muscle tissues (Figure 4B). The Southern Ocean squid species remain characterized by MUFAs including 16:1, 18:1, and 24:1, as with the muscle FA profiles of Southern Ocean squid. The GAB *T. danae* was least dissimilar (19.30%) to the southeast Australian samples (Supplementary Table S7) and clustered close to several whole squid samples of *Octopoteuthis megaptera* (Ome), *Lycoteuthis lorigera* (Ll), *Histioteuthis atlantica* (Ha), *Mastigoteuthis* sp. (Max), *Ancistrocheirus lesueurii* (Ale), and *O. bartramii* (Omb), plus a digestive gland sample of *Nototodarus gouldi* (Ng). These samples were characterized by lower proportions of 14:0, 16:1, and 18:1 and higher proportions of 18:0 and 20:1. When filtering the dataset to include only the digestive gland samples and re-generating the PCO plot, the digestive gland samples of the GAB *T. danae* were distinct from all but one sample; *Nototodarus gouldi* (Ng) from southeast Australia (Supplementary Figure S5). No *Taningia* spp. FA samples were available for comparison.

3.3 GAB squids vs. southern marine species

The isotopic ratios of the marine species from southeast Australia, New Zealand, the Southern Ocean and Antarctica were well grouped by sample area along the δ^{13}C axis, with samples with δ^{13}C lower than -20‰ almost entirely Southern Ocean and Antarctic species (Figure 5). The GAB squids' δ^{13}C values (from -20.59‰ through -21.71‰) were most similar to taxa from the Southern Ocean. Overall, the southeast Australian samples were more enriched in δ^{15}N over the Southern Ocean species but had a slightly smaller range, from 6.00‰ to 16.10‰ in the southeast Australian samples, versus 5.00‰ to 17.80‰ in Southern Ocean samples (Figure 5). The GAB squids had δ^{15}N values similar to intermediate trophic level species such as fishes among the samples from southeast Australian taxa or similar to high-trophic-level species, such as seabirds, among the samples from Southern Ocean taxa.

The fatty acid profiles of the multi-taxon species sampled in this study were best grouped by taxon, with most variation occurring along the PCO1 axis (Figure 6). Squid FA profiles had higher proportions of 22:6ω3, 20:5ω3, 18:0, and 16:0 than other southeast Australia, New Zealand, Southern Ocean, and Antarctic taxa. The GAB squids were closely grouped and characterized by these same FAs, although they had relatively higher proportions of these FAs than most published squid samples (Supplementary Figure S6). The digestive gland profiles from GAB *T. danae* specimens Td1 and Td3 had higher proportions of MUFA and lower 22:6ω3 and 20:5ω3

TABLE 2 Percentage contribution of specific fatty acids to total FAs as mean ± standard deviation in the mantle, arm, buccal mass, and digestive gland tissues of *Taningia danae* and *Chiroteuthis* aff. *veranii* collected from the eastern Great Australian Bight.

	Taningia danae				*Chiroteuthis* aff. *veranii*		
	Arm	Buccal mass	Mantle	Digestive gland	Arm	Buccal mass	Mantle
	n = 3	*n* = 3	*n* = 4	*n* = 2	*n* = 1	*n* = 1	*n* = 1
12:0	0.00 ± 0.0	0.06 ± 0.2	0.27 ± 0.8	0.00 ± 0.0	0.05 ± 0.1	0.58 ± 1.0	0.00 ± 0.0
14:0	1.60 ± 0.3	1.22 ± 0.4	1.80 ± 0.3	2.12 ± 0.4	2.97 ± 0.9	1.78 ± 0.4	1.28 ± 0.1
15:0	0.26 ± 0.1	0.24 ± 0.1	0.27 ± 0.1	0.41 ± 0.1	0.44 ± 0.2	0.32 ± 0.1	0.43 ± 0.2
16:0	25.58 ± 1.0	25.95 ± 1.8	26.71 ± 2.0	21.52 ± 3.9	26.7 ± 3.0	27.62 ± 0.7	28.67 ± 1.4
17:0	1.07 ± 0.0	1.19 ± 0.1	1.12 ± 0.1	1.76 ± 0.6	1.02 ± 0.1	1.20 ± 0.0	1.09 ± 0.0
18:0	11.91 ± 1.6	12.69 ± 1.5	11.06 ± 2.8	18.04 ± 3.9	10.65 ± 1.8	12.29 ± 0.6	11.95 ± 0.8
20:0	0.42 ± 0.0	0.49 ± 0.2	0.31 ± 0.1	0.61 ± 0.1	0.26 ± 0.1	0.30 ± 0.1	0.25 ± 0.0
24:0	0.72 ± 0.3	0.50 ± 0.4	0.51 ± 0.3	0.06 ± 0.1	0.35 ± 0.3	0.11 ± 0.2	0.30 ± 0.3
ai-17:0	0.06 ± 0.1	0.06 ± 0.1	0.04 ± 0.1	0.61 ± 0.1	0.33 ± 0.1	0.26 ± 0.0	0.27 ± 0.0
Σ SFA	41.64 ± 2.1	42.41 ± 2.5	42.09 ± 4.3	45.12 ± 8.9	42.79 ± 4.4	44.47 ± 0.5	44.24 ± 2.2
16:1ω7c	0.22 ± 0.1	0.19 ± 0.1	0.29 ± 0.0	0.61 ± 0.2	0.65 ± 0.2	0.32 ± 0. 0	0.35 ± 0.0
16:1ω7t	0.02 ± 0.1	0.00 ± 0.0	0.05 ± 0.1	0.23 ± 0.1	0.81 ± 0.3	0.82 ± 0.0	1.01 ± 0.0
18:1ω9c	2.14 ± 0.3	2.47 ± 0.8	2.39 ± 0.6	11.54 ± 5.8	2.55 ± 0.5	1.35 ± 1.0	2.21 ± 0.1
20:1ω9c	7.97 ± 0.3	8.85 ± 0.5	7.76 ± 1.6	16.35 ± 0.9	6.95 ± 0.4	8.41 ± 1.5	7.36 ± 0.1
22:1ω9c	3.04 ± 0.4	3.01 ± 0.9	2.90 ± 0.4	4.11 ± 0.9	3.21 ± 0.0	2.40 ± 0.4	3.79 ± 0.3
24:1ω9c	0.72 ± 0.1	0.81 ± 0.3	0.67 ± 0.2	2.23 ± 0.2	0.78 ± 0.2	0.72 ± 0.1	0.54 ± 0.5
Σ MUFA	14.11 ± 0.9	15.34 ± 2.1	14.06 ± 2.7	35.06 ± 6	14.95 ± 0.4	14.04 ± 0.1	15.26 ± 0.2
18:2ω6t	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.26 ± 0.0	0.94 ± 0.5	0.30 ± 0.0	0.38 ± 0.0
20:2ω6c	0.36 ± 0.1	0.26 ± 0.0	0.33 ± 0.1	0.97 ± 0.2	0.41 ± 0.1	0.46 ± 0.3	0.33 ± 0.0
20:3ω3c	0.93 ± 0.3	0.39 ± 0.4	0.50 ± 0.4	0.28 ± 0.1	0.28 ± 0.1	1.27 ± 0.9	0.00 ± 0.0
20:4ω6c	1.46 ± 0.2	2.09 ± 1.0	1.34 ± 0.4	2.35 ± 0.2	1.81 ± 0.1	1.66 ± 0.4	2.20 ± 0.1
20:5ω3c	13.47 ± 1.1	13.86 ± 1.5	13.77 ± 1.4	9.01 ± 1.3	16.51 ± 0.7	19.16 ± 0.6	16.86 ± 0.6
22:6ω3c	28.03 ± 1.2	25.65 ± 2.8	27.91 ± 4.4	6.94 ± 2.1	22.31 ± 3.1	18.65 ± 0.8	20.74 ± 1.6
Σ PUFA	44.25 ± 1.8	42.25 ± 3.8	43.86 ± 5.3	19.81 ± 3.6	42.26 ± 4.0	41.50 ± 0.5	40.50 ± 2.3

FAs<0.1% were excluded.

SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids.

than the other GAB squid muscle samples and were clustered closely to FA profiles from four fish species; *Epigonus lenimen* (Ele), *E. carlsbergi* (Ec), *Lepidorhynchus denticulatus* (Ld), and *Nemichthys* sp. (Nmx) (Figure 6).

The whole-animal energy density per gram of *T. danae* is lower than all other southern marine squid and fish species that could be found in published literature (Figure 7; Supplementary Table S8). However, as *T. danae* is a large-bodied squid species, the whole-animal energy content of even the moderately sized individuals can surpass 130,000 kJ, which is higher than all species analyzed except for the toothfishes (*Dissostichus* spp.). The largest *T. danae* individual reliably measured, weighing 161 kg (Roper and Jereb, 2010), might contain an energy content of up to 362,250 kJ (Figure 7), greater than all other squids and fishes analyzed except for Antarctic toothfish, *Dissostichus mawsoni.*

4 Discussion

Deep-sea squids are presumably vital components of these largely undescribed marine ecosystems, yet limited access to specimens has hampered efforts to detail their ecological roles as predators and prey. The opportunistic collection of five *Taningia danae* specimens and one *Chiroteuthis* aff. *veranii* specimen from the GAB enabled the comparison of FAs and SIs across four body tissue types showcasing that muscular tissues can be used interchangeably in the absence of entire specimens. It also suggested that the digestive gland offers insights into the foraging habitats of squids as predators while also being the key site of nutrient storage and indicating which nutrients are gained by the predators feeding on them. The SIs and FAs suggested that the *T. danae* and *C.* aff. *veranii* specimens probably lived in the Southern

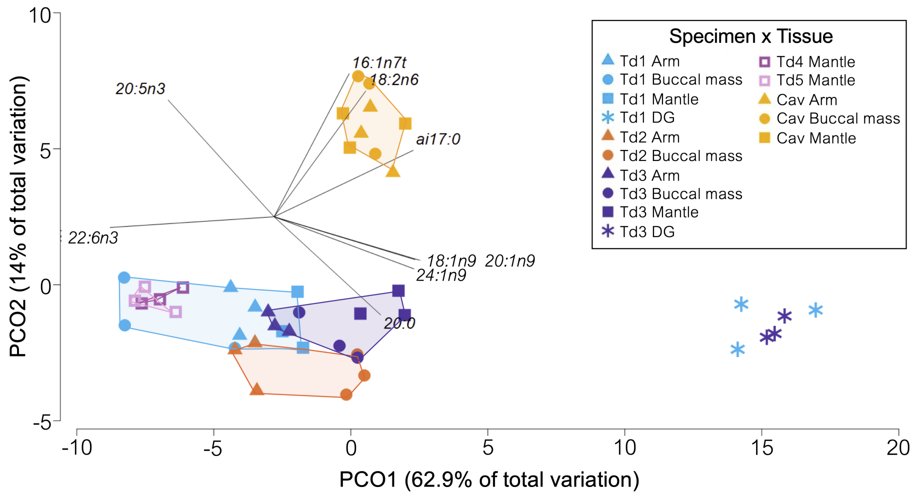

FIGURE 2
Principal coordinates ordination plot of fatty acid (FA) profiles from *Taningia danae* and *Chiroteuthis* aff. *veranii* collected from the eastern Great Australian Bight. A vector showing Pearson correlations >0.8 is overlaid, indicating the FAs contributing to differences between samples, and polygons are drawn to show the grouping of muscle tissue profiles by specimen.

Ocean and were high-trophic-level predators likely consuming deep-sea fishes and small squids and are sources of essential FAs (EPA and DHA) and calories for Southern Ocean predators.

4.1 Limitations

As this study was entirely opportunistic with regard to the GAB squid specimens, there are several limitations. These limitations may cause variation in both the stable isotope values recorded and the fatty acid results as well as affect the reliability of the results due to the small sample size. This should be considered when reading the hypotheses and conclusions presented here. In SI analysis, squid beaks are a commonly sampled tissue as they are retrieved frequently in predator stomachs (Hoving et al., 2014). Beaks contain chitin, which causes depletion in $\delta^{15}N$ values, and there is tissue accumulation, rather than turnover, across an organism's lifetime (Cherel and Hobson, 2005). Newly synthesized areas of the beak, such as the lower wing, have less chitin and can more reliably show recent dietary signatures, while the rostrum and whole homogenized beaks compress an entire lifetime of ecological information into a single isotopic ratio (Cherel and Hobson, 2005). There is some uncertainty when comparing beaks to muscle tissues, and therefore comparing the GAB squids data to published squid beak data may impact the comparison with squid globally. Correction values of +3.5‰ (Navarro et al., 2013) and +4.8‰ $\delta^{15}N$ (Guerreiro et al., 2015) have been applied to beak isotopic ratios to make them more comparable to muscle tissues. However, different correction factors would be required for beak samples taken from the wing, rostrum, or whole beak, which has not, to the best of our knowledge, been developed yet. In this study, we applied a single, conservative correction factor of +3.5‰ to any beak samples taken from the literature that were not already corrected in the source publication. We did this so that these samples could be more reliably compared with the muscle samples taken from the GAB squids, but we are aware that applying a single-correction factor may have caused over- or under-corrections of particular samples, potentially impacting conclusions made here.

TABLE 3 Energy density of *Taningia danae* (n = 1) tissues as measured through bomb calorimetry.

Tissue type	Energy content (kJ/g wet weight)
Arm	1.31
Buccal mass	0.50
Mantle	2.53
Digestive gland	5.94
Whole[a]	2.25

[a]Whole-body energy density estimated using body part proportions given in Kelly (2019).

Additionally, *Taningia danae* is an ammoniacal squid, which means that their tissues contain elevated levels of ammonia, which helps the animal achieve neutral buoyancy and reduce energy costs (Clarke et al., 1979). Ammonia in the muscle tissues of elasmobranchs can have effects on SI values, and studies have suggested that rinsing samples in deionized water can remove the urea (Li et al., 2016). When comparing shark muscle samples with lipids extracted *versus* samples that were both lipid-extracted and deionized-water-rinsed, the urea extracted samples had $\delta^{15}N$ values increased by just under 1.0‰ and $\delta^{13}C$ values decreased by just under 1.0‰ (Martin and Jaquemet, 2019). To our knowledge, this method has not been tested in ammoniacal squid tissues and is not currently standard among SIA of squid muscle.

Comparisons among beak data, lipid extracted muscle data, and urea removed muscle data will likely require the development of a set of correction factors that could be applied to allow for better use of published data, which is a convenient way of utilizing opportunistic sampling events, regardless of how small sample sizes are.

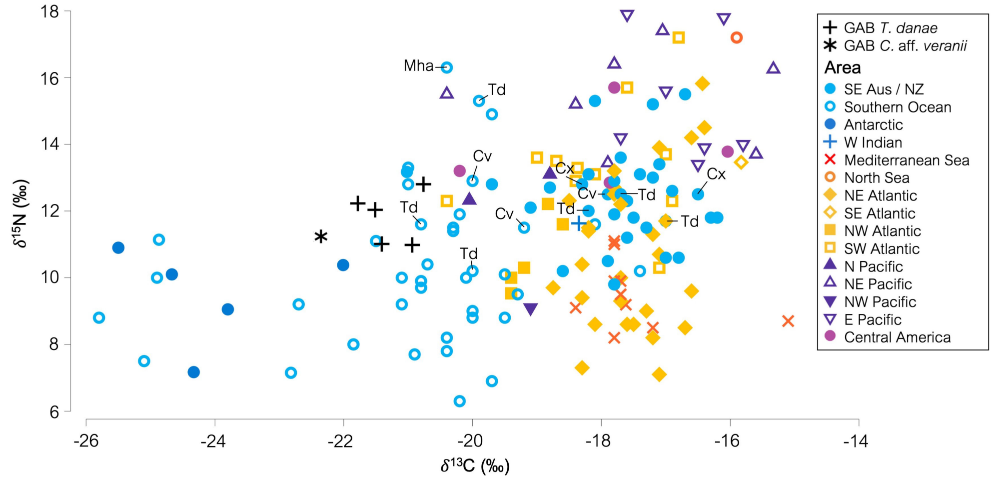

FIGURE 3
Biplot of $\delta^{13}C$ and $\delta^{15}N$ (‰) from global squid studies. Great Australian Bight squid data used is mean muscle $\delta^{13}C$ and $\delta^{15}N$. The data points referred to in the text are labeled with species abbreviation. GAB Td, *Taningia danae* from the eastern Great Australian Bight; GAB Cav, *Chiroteuthis* aff. *veranii* from the eastern Great Australian Bight; Mha, *Mesonychoteuthis hamiltoni*; Td, *Taningia danae*; Ln, *Loliolus noctiluca*; Cv, *Chiroteuthis veranii*; Cx, *Chiroteuthis* sp.

In FA analysis, both decomposition and frozen storage are known to cause the degradation of PUFAs over time (Budge et al., 2006; Atayeter and Ercoşkun, 2011; Meyer et al., 2017). The GAB squid specimens were potentially decomposing in the environment for an unknown amount of time before retrieval and then were frozen for at least 3 years before samples were taken and processed for SI analysis and FA analysis. In another study, squid mantle frozen for 12 months at -20°C had proportions of PUFAs (especially 22:6ω3) decrease by approximately 10% and SFAs (especially 16:0 and 18:0) increase by approximately 10% *versus* fresh tissue (Atayeter and Ercoşkun, 2011). The GAB squids in this study were found to have relatively high 16:0 and 18:0 and low PUFAs in their tissues *versus* other squid samples, which may be an artefact of extended frozen storage or decomposition. Additionally, with the collection and use of published data, the storage period of many of those samples or levels of decomposition by the time of retrieval is unknown. Thus, we suggest that detailed tissue information is provided in future studies that use opportunistically collected specimens.

4.2 Body part utility

The clustering of the GAB squid muscle tissues (arm, buccal mass, and mantle) and the distinctiveness of the digestive glands

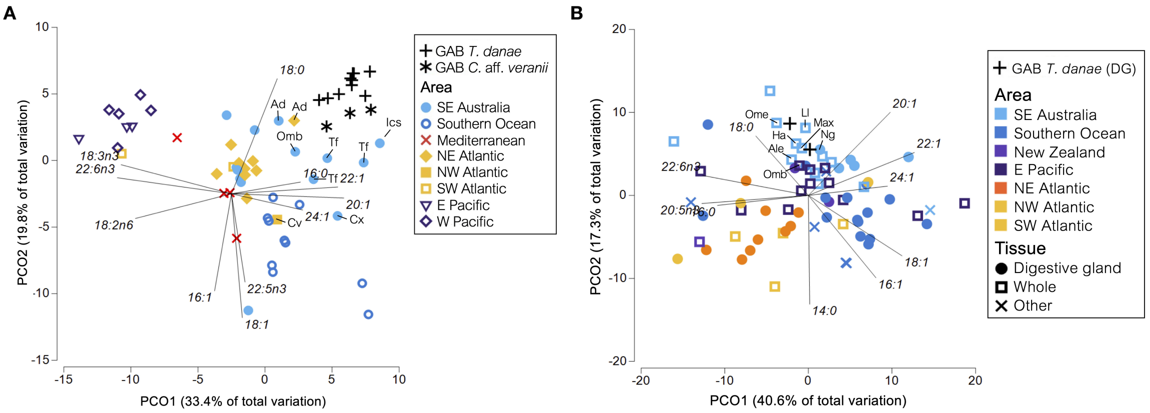

FIGURE 4
Principal coordinates ordination plots of fatty acid (FA) profiles of **(A)** squid muscle tissues (unspecified muscle, mantle, arms, fins, and buccal mass) and **(B)** squid digestive parts (digestive gland, whole squid, stomach, stomach fluid, and cecum oil) in studies conducted globally. Only FAs with a mean proportion of >0.5% across the global squid dataset and present in >50 of the samples were retained. A vector overlay showing Pearson correlations >0.5 indicates the individual FAs contributing to differences between samples. GAB, Great Australian Bight. Only samples referred to in the text are labeled with species abbreviation. Ad, *Architeuthis dux*; Omb, *Ommastrephes bartramii*; Tf, *Todarodes filippovae*; Cv, *Chiroteuthis veranii*; Cx, *Chiroteuthis* sp.; Ics, *Idioteuthis cordiformis*; Ome, *Octopoteuthis megaptera*; Ale, *Ancistrocheirus lesueurii*; Ha, *Histioteuthis atlantica*; Ll, *Lycoteuthis lorigera*; Max, *Mastigoteuthis* sp.; Ng, *Nototodarus gouldi*.

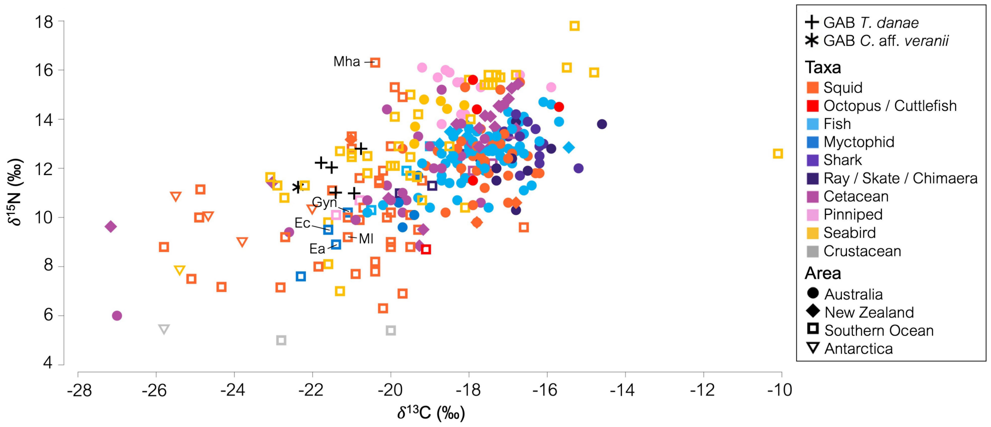

FIGURE 5
Biplot of $\delta^{13}C$ and $\delta^{15}N$ (‰) from marine species sampled from southeast Australia, New Zealand, the Southern Ocean, and Antarctica. GAB squid data used is mean muscle $\delta^{13}C$ and $\delta^{15}N$. GAB, Great Australian Bight. The data points referred to in the text are labeled with species abbreviation. Ec, *Electrona carlsbergi*; Ea, *Electrona antarctica*; Gyn, *Gymnoscopelus nicholsi*; Ml, *Moroteuthopsis longimana*; Mha, *Mesonychoteuthis hamiltoni*; Ln, *Loliolus noctiluca*.

suggest that the three muscle tissues could be used mostly equivalently, with similar SI and FA profiles. Often in opportunistic sampling of squid only a portion of the animal is retrieved, so being able to sample any of these muscle tissues and gain similar, useable results is vital for describing deep-sea and continental shelf food webs.

There are minor and variable isotopic differences among muscle tissue types, such as mantle being the most enriched in $\delta^{15}N$ and buccal mass the least enriched, but these are likely due to the minor differences in protein content between the three tissue types (Shulman et al., 2002; Hobson and Cherel, 2006). Due to the limited number of squids with all three muscle tissue types available (three individuals across the two species), this could not be explored further within this study. However, these relatively minor isotopic differences should not preclude the interchangeable use of muscle tissues when equivalent tissues are unavailable across specimens, as the differences among these tissues do not exceed the differences among individuals of the same species. The digestive gland samples were relatively depleted in both $\delta^{13}C$ and $\delta^{15}N$ and increased in C:N ratio compared to the other tissues analyzed, which is likely due to the high oil content (Cherel et al., 2009a; Ruiz-Cooley et al., 2011; Svensson et al., 2016). Studies using SIs to

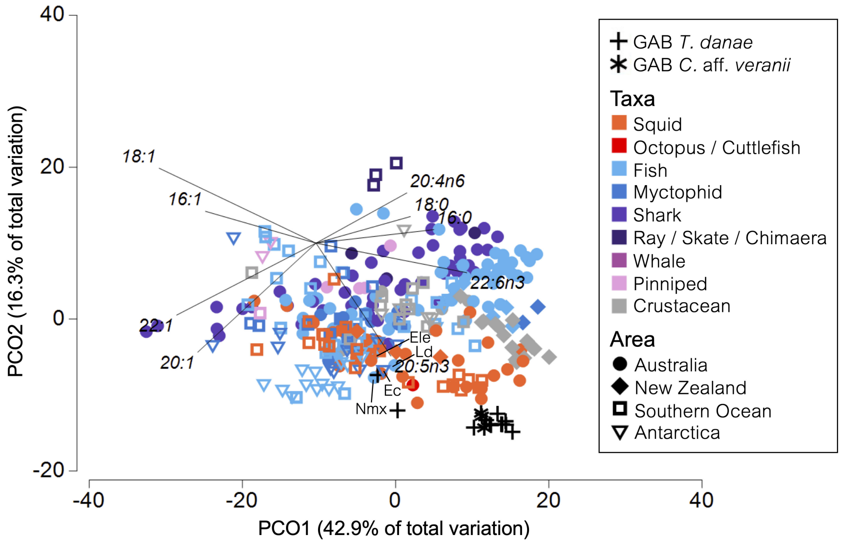

FIGURE 6
Principal coordinates ordination plot of published fatty acid (FA) profiles of marine species collected in southeast Australia, New Zealand, the Southern Ocean, and Antarctica. Only FAs with a mean proportion >2% in all taxa groups were retained. A vector showing Pearson correlations >0.5 has been overlaid, indicating the individual FAs contributing to differences between samples. GAB: Great Australian Bight. The data points referred to in the text are labeled with species abbreviation. Nmx, *Nemichthys* sp.; Ele, *Epigonus lenimen*; Ec, *Electrona carlsbergi*; Ld, *Lepidorhynchus denticulatus*.

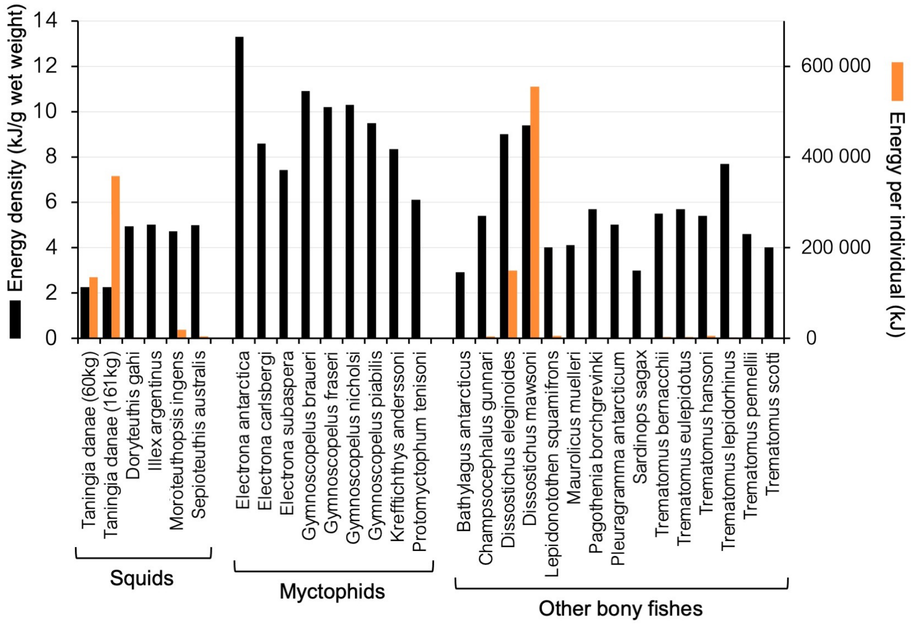

FIGURE 7
Energy content of Southern Ocean fishes and squids as found in published literature. Whole-body energy densities, as kilojoules per gram wet weight, are shown with black columns. An estimate of the whole-animal energy content is shown with orange columns and was determined by multiplying the greatest recorded whole-body energy density by the greatest recorded whole-animal body mass.

examine the trophic ecology of squids will either need to limit comparisons to within digestive glands or develop mathematical correction factors as has been done with beaks and other tissues.

The digestive gland of squid has been the preferred source tissue for diet determination using FAs, as it is the primary lipid storage organ, incorporating FAs from the diet across the previous 10 days with minimal biomodification (Phillips et al., 2001; Stowasser et al., 2006). Additionally, the digestive gland has greater lipid content (13–54% wet weight) compared to muscle tissues (<2% wet weight) (Phillips et al., 2002; Shulman et al., 2002; Phillips et al., 2003) with phospholipids, which are involved in tissue structure, comprising much of this observed differences (20:5ω3, 22:6ω3, 16:0; Rosa et al., 2005). Squid digestive glands typically contain lower proportions of these phospholipid PUFAs and higher levels of key MUFAs (Phillips et al., 2001; Zhukova, 2019). The GAB squid results were consistent with data from previous Australian and Southern Ocean oegopsid studies, where the proportion of PUFA in the muscles was 42.40–58.10% *versus* 17.30–32.40% in the digestive gland, and the proportion of MUFA in the muscles was 13.60–21.80% *versus* 47.00–66.10% in the digestive gland (Phillips et al., 2001; Phillips et al., 2002; Pethybridge et al., 2013). However, the suite of FAs contributing to clustering of FA data by area appeared to be similar between muscle and digestive tissues—for example, the southeast Australian squid samples including the GAB squids were differentiated from the rest of the samples by higher proportions of 16:0, 18:0, and 22:1 in both plots, while the Southern Ocean samples were differentiated by higher proportions of 16:1, 18:1, and 24:1. Digestive gland tissue is not often available from opportunistically collected squid, but these results indicate that similar dietary information and ecological inferences may instead be attainable from muscle tissues.

In the future, multi-species comparisons of squid tissues through controlled feeding studies should aim to determine how SIs and dietary FAs incorporate into squid muscle and digestive gland tissues to understand the molecular processes unique to squids. The differences across tissue types observed in this study indicate that this is an important area of future work that should be undertaken on more easily accessible squid species, such as southern calamari *Sepioteuthis australis*.

4.3 Foraging grounds

δ^{13}C from squid muscle tissues between -22.90‰ and -19.50‰ are classified as “subantarctic” (Guerreiro et al., 2015), a finding that fits well with both the global squids and southern multi-taxa SI data compiled here. The GAB squids, retrieved from latitudes of approximately 39-34°S, had δ^{13}C ranging from -23.80‰ to -20.04‰, similar to SI ratios recorded in samples from the Kerguelen Plateau (49°S), Marion Island (47°S), Macquarie Island (55°S), and South Georgia (55°S). Therefore, the GAB squids having "subantarctic" carbon ratios might indicate that they lived further south than where they were collected and may have been moved to the GAB post-mortem, perhaps by a predator such as a sperm whale.

Alternatively, the GAB squids might have migrated from their subantarctic range north toward the GAB to feed in the high-productivity, cold-water upwelling food web that exists along the continental slope each austral summer (Van Ruth et al., 2018). The copepod FA biomarkers 20:1ω9 and 22:1ω9 (Parrish et al., 2005; Stowasser et al., 2009) are referenced frequently in FA studies of deep-sea and Southern Ocean squids, with several authors suggesting the presence of a copepod–myctophid–squid higher-order predator food chain within the Southern Ocean (Rodhouse et al., 1992; Phillips et al., 2001; Pethybridge et al., 2013). The GAB squids had high proportions of these FAs within their digestive glands and muscles, suggesting that the GAB squids likely feed within this food chain. The GAB *T. danae* and southeast Australian squids also had higher proportions of these two FAs in their digestive glands *versus* other Southern Ocean squids. Copepods are abundant in the eastern GAB (Van Ruth and Ward, 2009) and can significantly increase in population size in times of upwelling (Weikert, 1977; Jemi and Hatha, 2019), so it is possible that the GAB squids may have moved north to the continental slope to opportunistically forage upon fish schools that follow copepods around these upwelling regions. The rate of FA incorporation and isotopic turnover of squid muscle has yet to be determined, although studies on fishes have suggested a FA incorporation time of a few days or weeks, while the isotopes turnover was at a rate of several months (Young et al., 2010). This might further explain why the FA profiles of the GAB squids reflect more recent GAB feeding, while δ^{13}C reflects a long-term subantarctic range.

If movements between the Southern Ocean and the GAB are regular for these squid species, whether for foraging or some other cause such as spawning, they may be previously unrecognized vectors of nutrient and energy transport between these environments. The role these squids play in linking the nutrient-rich shelf–slope environment of the GAB to the nutrient-poor Southern Ocean deep-sea may be important to the trophic functioning of both environments.

4.4 Trophic role and diet

Squids in the Southern Ocean and southeast Australia occupy a broad range of trophic levels, with δ^{15}N values ranging from 5.00‰ to 17.80‰—equating to four or five trophic levels (assuming an average trophic enrichment factor of approximately 2.75‰ δ^{15}N per trophic level; Caut et al., 2009). The GAB squids with high δ^{15}N values were at the second highest trophic level, just below the colossal squid *Mesonychoteuthis hamiltoni* from the Southern Ocean. *Mesonychoteuthis hamiltoni* is the heaviest known invertebrate (Rosa et al., 2017) and is thought to consume Antarctic toothfish (*Dissostichus mawsoni*, Remeslo et al., 2015), which, in turn, are high-trophic-level predators of mid- to large-sized cephalopods and fishes (Queirós et al., 2021). Additionally, the similarities between the GAB squid FAs and FA profiles from other large, actively predatory squid species including giant squid *Architeuthis dux*, Antarctic flying squid *Todarodes filippovae*, flying squid *Ommastrephes bartramii*, whiplash squid *Idioteuthis cordiformis*, and arrow squid *Nototodarus gouldi* suggest roles as active pelagic predators. When comparing the GAB squids' δ^{15}N to other taxa from the southern ecosystems, it appears that the GAB squids occupied a similar trophic level to a broader range of Southern Ocean top predators including seabirds, cetaceans, and other large squids. Thus, it is suggested that the GAB *T. danae* and *C.* aff. *veranii* were high-trophic-level predators within the Southern Ocean ecosystem.

Little is known of the diet of most deep-sea animals in general, and only a few opportunistic records of identifiable prey items have been recorded from the stomachs of large-bodied squids. Fortunately, some items have been identified from the stomach contents of two *T. danae* retrieved off the coast of Spain, consisting of a few blue whiting (*Micromesistius poutassou*) vertebrae, *Gonatus* sp. tentacle hooks, and integuments from crustaceans (González et al., 2003). These results are far from a comprehensive analysis of *T. danae* diet but do provide some evidence that *T. danae* is capable of feeding on active, pelagic fish and squid species as well as crustaceans. *Chiroteuthis* aff. *veranii* diet has not been described, although other chiroteuthids are known to feed on crustaceans, molluscs, and fish (Kubota et al., 1981). However, the *C.* aff. *veranii* specimen from this study is substantially larger than most previously studied *Chiroteuthis veranii* specimens [approximately 400 mm mantle length *versus* 50–297 mm in Rodhouse and Lu (1998); Mensch (2010), and Guerra et al. (2011)]. Therefore, the diet and general trophic ecology of the GAB *C.* aff. *veranii* specimen may be very different from what has previously been described for *C. veranii* globally.

Using the global mean trophic enrichment factors (2.75‰ for δ^{15}N and 0.75‰ for δ^{13}C; Caut et al., 2009), the predicted prey items of the GAB squids include *Gymnoscopelus nicholsi*, *Electrona carlsbergi*, and *Electrona antarctica*, three deep-sea myctophids abundant in the Southern Ocean (Kozlov, 1995), and *Moroteuthopsis longimana*, an Antarctic deep-sea squid. The maximum prey length suggested for squid are prey that measure between half to two thirds of the squid's mantle length (Bidder, 1966), which would be 50–80 and 20–30 cm for *T. danae* and *C* aff. *veranii*, respectively. The myctophid species are small in length, with total length less than 20 cm (Collins et al., 2012), placing them within the GAB squids' prey size range, but *M. longimana* can attain mantle lengths of up to 1 m (Laptikhovsky et al., 2013), which is out of this range.

The *T. danae* digestive gland FA profiles in this study further suggest deep-sea fish and squid predation. The *T. danae* digestive gland samples were similar in FA profile to whole homogenized fish samples and whole homogenized squid samples (Figure 6). The whole deep-sea fishes that were similar to the GAB *T. danae* digestive gland samples (and might represent potential prey species) were *E. carlsbergi*, *Epigonus lenimen*, *Lepidorhynchus denticulatus*, and *Nemichthys* sp. With the exception of *Nemichthys* sp., these species are within the size range of *T. danae* prey (<50 cm, Meynier et al., 2008; Pethybridge et al., 2013; Froese and Pauly, 2022) and are abundant in the deep-sea and continental slope communities of the Southern Ocean and southeast Australia (May and Blaber, 1989; Kozlov, 1995). The whole squid profiles and therefore possible squid prey species grouped closely to *T. danae* digestive glands were *Octopoteuthis megaptera*, *Lycoteuthis lorigera*, *Histioteuthis atlantica*, *Mastigoteuthis* sp., and *Ancistrocheirus lesueurii*. Comparatively less is known about the abundance of these species *versus* the potential fish prey, but they are all deep-sea and pelagic ones (SeaLifeBase 2022). In addition, apart from *A. lesueurii* which grows to 54 cm in mantle length (Hoving and Lipinski, 2015), these squid species are all classified as small with mantle lengths less than 25 cm (Lipiński, 1993; Hoving et al., 2007; Pethybridge et al., 2010; Kelly, 2019), again fitting within the suggested maximum prey size of *T. danae*.

The GAB squid had high proportions of EPA 20:5ω3 and DHA 22:6ω3 within their muscle tissues, even compared to other squids. This could be due to these FAs being taken in by the GAB squids through their diet and may be further evidence for a diet consisting of squid, as EPA and DHA are common in squid muscle tissues (Ozogul et al., 2008), and research has shown that fish that are fed squid diets have increased levels of these FAs in their tissues (Turner and Rooker, 2005; Sun et al., 2018). Additionally, dietary EPA and DHA have been linked to higher growth rates in fish (Lutfi et al., 2022), and therefore a diet rich in these two FAs may be necessary for the maintenance of muscle tissue synthesis in large squids such as the GAB squids in this study.

EPA and DHA are physiologically important for all omnivorous organisms, including humans (Gladyshev et al., 2013), and have been linked with a variety of important processes including anti-inflammatory processes, stress resistance, neural development, and behavior (Parrish, 2013; Zhukova, 2019). The high levels of these FAs in the tissues of the GAB squids may mean that these are important sources of dietary EPA and DHA for their known predator species including sperm whales (*Physeter macrocephalus*), northern elephant seals (*Mirounga angustirostris*), and seabirds (Cherel et al., 2009b; Guerreiro et al., 2015; Yoshino et al., 2020). *Chiroteuthis* aff. *veranii* could be especially important, as its similar proportions of EPA and DHA, but smaller body size, may make it an important source of these FAs for smaller predators such as swordfishes (e.g., *Xiphias gladius*), toothfishes (*Dissostichus* spp.) (Cherel and Hobson, 2005; Young et al., 2010), and deep-sea-foraging Southern Ocean cetaceans such as the pygmy sperm whale (*Kogia breviceps*) (Dos Santos and Haimovici, 2001).

4.5 Energy content

Squids are generally less energy-dense than fishes, primarily due to lower levels of lipid and protein in their tissues (Croxall and Prince, 1982). This is reflected in the energy content of *T. danae* tissues, which was lower than the calorie content of all other deep-sea fishes and squids. The digestive gland, with a higher lipid content than the other tissues, also had a greater energy density. Many deep-sea squids, including *T. danae*, are considered ammoniacal. This results in a reduced energy density of muscle tissues, and a previous study estimates that ammoniacal squids have a whole-body energy density of 2.3 kJ/g (Clarke et al., 1985), which supports the *T. danae* whole-body energy density estimate made in this study.

Taningia danae has been noted in the diets of many marine predators globally, forming minor components of the diets of seabirds (Clarke et al., 1981; Guerreiro et al., 2015), marine mammals (Condit and Le Boeuf, 1984; MacLeod et al., 2003; Cherel et al., 2009b; Yoshino et al., 2020), sharks (Smale and Cliff, 1998; Mendonça, 2009; Ménard et al., 2013), and predatory fishes (Tsuchiya et al., 1998; Cherel et al., 2004; Potier et al., 2007; Ménard et al., 2013) and significant components of the diets of both sperm whales and sleeper sharks (identified in source as *Somnoisus cf.* microcephalus, likely *Somniosus antarcticus*) in the Southern Ocean (Cherel et al., 2004, Evans and Hindell, 2004). While *T. danae* is not densely calorific when compared to smaller Southern Ocean fish and squid species, their large body size means that, per individual, they are the second most calorie-rich mid-trophic species in the Southern Ocean. One *T. danae* individual might provide as many calories as several dozens of smaller prey items, with the added benefit of reducing the foraging costs for the predator (Evans and Hindell, 2004; Goldbogen et al., 2019). A previous study by Aoki et al. (2012) suggested that foraging on large squids may provide sperm whales with a high caloric intake for reduced energetic expenditure, especially given that the bursts of speed required to catch these squids can be highly costly (Aoki et al., 2012).

4.6 Conclusions

In the biodiverse and economically important areas of the Southern Ocean and the GAB, there is a need to fully understand the trophic interactions of higher-order predators such as large squids. The use of opportunistic sampling events is critical for studying elusive species in deep-sea areas, and this study has shown that even remnants of large squid muscle tissues floating on the sea surface can provide useful ecological information. Squid digestive glands are widely acknowledged to be effective in FA analysis to provide additional evidence of diet, but in this study, we found that muscle tissues can also be used. Researchers who intend to use opportunistic samples of squid in trophic ecology studies should collect any biological tissues that they have access to (e.g., arm, mantle, and buccal mass) for both SI analysis and FA analysis to gain information regarding potential diet, food chains, geographic origin, and trophic role. For the GAB squids, the comparison of multiple tissue types helped us determine that they were most likely living in the Southern Ocean and had a broad diet of deep-sea fishes and other squids. We also found that the GAB squids might play a role in providing important nutrients to other higher-order predators and could have an additional role in facilitating nutrient and energy transport between the Southern Ocean deep-sea and the GAB shelf–slope environments. Despite the small sample sizes, the lower quality of the GAB squids due to opportunistic sampling, and the other discussed limitations, this study has highlighted the types of ecological information that can be obtained from small and degraded biological samples, which can be important in building knowledge of trophic ecology in deep-sea squid research.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because the samples used were already deceased naturally upon collection.

Author contributions

BJ: Conceptualization, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. RB: Conceptualization, Funding acquisition, Supervision, Writing - original draft, Writing - review & editing. MD: Conceptualization, Funding acquisition, Supervision, Writing - review & editing. JH: Formal Analysis, Methodology, Supervision, Writing - review & editing. BM: Formal analysis, Investigation, Resources, Validation, Writing – review & editing. KR: Conceptualization, Resources, Writing – review & editing. LM: Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Writing - original draft, Writing - review & editing.

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Conflict of interest

Author KR is employed by Australian Southern Bluefin Tuna Industry Association.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1254461/full#supplementary-material

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