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Trophic variation in the Southern hagfish Myxine australis under contrasting bottom- trawling scenarios

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Abstract

The trophic ecology of hagfishes remains one of the least understood among marine vertebrates, and the limited knowledge available has led them to be considered primarily scavengers. Consequently, an important role in the consumption of fisheries discards has been attributed to them. In this study, we analyzed, for the first time, the trophic ecology of a hagfish, *Myxine australis*, under contrasting bottom-trawling scenarios using gastrointestinal content analysis and stable isotope analysis of carbon and nitrogen. The results revealed a generalist and opportunistic feeding strategy based on the consumption of fish and invertebrates, with no evidence of ontogenetic changes in diet. The species also occupied a tertiary consumer position, with a marked dependence on benthic resources. In areas subjected to bottom trawling, the isotopic niche during the trawling period was approximately three times larger than that observed during the pre-trawling period. Differences in isotopic values and C:N ratios suggested periods of fasting followed by high food intake. Overall, these results indicate that *M. australis* exhibits trophic plasticity, shifting its feeding strategy according to resource availability, exploiting both natural resources and potential anthropogenic subsidies associated with fishing activity.

INTRODUCTION

Hagfishes are a group of jawless vertebrates (Ota et al. 2013) with an exclusive marine distribution and a benthic lifestyle (Fernholm 1998). At present, 92 species grouped into a single family are recognized (Fricke et al. 2026); however, knowledge of their trophic ecology remains limited and is restricted to a small number of species. Of the total number of recognized species, published information was found for only 15 (16.4%), while only eight species (8.7%) have been the subject of studies explicitly addressing some aspect of their trophic ecology (Table 1). Most studies describe hagfishes as scavengers, particularly those based on observations in baited traps (Martini et al. 1997; Catchpole et al. 2006; Yeh and Drazen 2011), underwater observations (Fernholm 1974; Wakefield 1990; Collins et al. 1999; Dahlgren et al. 2006), or associations with fishing activities (Fernholm 1974; Catchpole et al. 2006). In contrast, studies based on stable isotope and intestinal content analysis have reported evidence of predatory or opportunistic feeding habits in several species, including *Eptatretus cirrhatus*, *E. springeri*, *E. stoutii*, *Myxine glutinosa*, and *Neomyxine biniplicata* (Shelton 1978; Zintzen et al. 2013; Mickle 2016; Tabert et al. 2025). Likewise, in some species (*E. sheni*, *E. taiwanae*, and *E. yangi*), scavenging behavior has been assumed without direct trophic evidence (Luo et al. 2016).

Table 1

Summary of the available literature analyzing or mentioning aspects of the trophic ecology of species in the family Myxinidae. Authors and year of publication, species studied, methodology used to obtain trophic information, and whether the information was obtained directly or indirectly are indicated. It is also indicated whether trophic ecology was a primary goal of the study or whether the information was obtained as a secondary result or reported anecdotally.

Author & year	Species	Method	Description	Observation type
Fernholm (1974)	*Eptatretus burgeri*	Underwater observations	Scavenger	Direct primary
Luo et al. (2016)	*Eptatretus burgeri*	Parasitology	Scavenger	Indirect secondary
Yamaguchi (2025)	*Eptatretus burgeri*	Laboratory observations	Scavenger	Direct secondary
McLeod *et al.* (2007)	*Eptatretus cirrhatus*	C, N & S stable isotope	Opportunistic feeding	Indirect secondary
Zintzen et al. (2013)	*Eptatretus cirrhatus*	C & N stable isotope	Active predator & scavenger	Indirect primary
Wakefield (1990)	*Eptatretus deani*	Gut content	Possible predator	Direct secondary
Smith and Baco (2003)	*Eptatretus deani*	Underwater observations	Scavenger	Direct primary
Yeh and Drazen (2011)	*Eptatretus deani*	Underwater observations	Scavenger	Direct primary
Mickle (2016)	*Eptatretus minor*	C, N & S stable isotope	Opportunistic feeding	Indirect primary
Luo et al. (2016)	*Eptatretus sheni*	Parasitology	Scavenger	Indirect secondary
Zintzen et al. (2013)	*Eptatretus sp.*	C & N stable isotope	Scavenger	Indirect primary
Mickle (2016)	*Eptatretus springeri*	C, N & S stable isotope	Active predator	Indirect primary
Worthington (1905)	*Eptatretus stoutii*	Gut content & behavioral observations	Opportunistic feeding & cannibal	Direct primary
Tamburri and Barry (1999)	*Eptatretus stoutii*	Laboratory observations	Scavenger	Direct secondary
Yeh and Drazen (2011)	*Eptatretus stoutii*	Underwater observations	Scavenger	Direct primary
Tabert et al. (2025)	*Eptatretus stoutii*	C & N stable isotope	Active predator	indirect secondary

Author & year	Species	Method	Description	Observation type
Luo et al. (2016)	*Eptatretus taiwanae*	Parasitology	Scavenger	Indirect secondary
Luo et al. (2016)	*Eptatretus yangi*	Parasitology	Scavenger	Indirect secondary
Smith and Baco 2003)	*Myxine circifrons*	Underwater observations	Scavenger	Direct primary
Collins et al. (1999)	*Myxine cf. fernholmi*	Underwater observations	Scavenger	Direct primary
Shelton (1978)	*Myxine glutinosa*	Gut content	Active predator	Direct primary
Catchpole et al. (2006)	*Myxine glutinosa*	Baited traps	Scavenger	Direct primary
Dahlgren et al. (2006)	*Myxine glutinosa*	Underwater observations	Scavenger	Direct primary
Pace et al. (2016)	*Myxine glutinosa*	Unusual observation	Active predator	Direct anecdotical
Martini et al. (1997)	*Myxine limosa*	Baited traps	Opportunistic predator & scavenger	Direct primary
Auster *et al.* (2006)	*Myxine limosa*	Underwater observations	Opportunistic feeding	Direct anecdotical
Leigh et al. (2016)	*Myxine limosa*	Trap & bait preferences	Scavenger	Direct primary
Mickle (2016)	*Myxine mcmillanae*	C, N & S stable isotope	Scavenger	Indirect primary
Zintzen et al. (2013)	*Neomyxine biniplicata*	C & N stable isotope	Active predator	Indirect primary
Zintzen et al. (2011)	*Neomyxine sp.*	Underwater observations	Active predator	Direct anecdotical

Consequently, more than 90% of the species described lack information on their feeding habits. In addition, most of the available evidence is based on isolated or incidental observations, or was obtained from studies whose primary objective was not to describe diet (supplementary material; Table S1). This fragmentary information has linked hagfish to fishing activity, where they may act as important consumers of fishery discards (Fernholm 1974; Martini 1998; Catchpole et al. 2006). However, active predation and variability in their trophic strategies according to habitat and resource availability have also been documented (Shelton 1978; Zintzen et al. 2011, 2013; Mickle 2016). In this context, expanding

diet studies is necessary to better understand their trophic role in the local food webs and assess the influence of fishing activities on their trophic ecology.

In the southwestern Atlantic, 11 hagfish species have been recorded (Norman 1937; Nani and Gneri 1951; Wisner and McMillan 1995; Góngora et al. 2009; Mincarone 2001a,b; Knapp et al. 2011; Bovcon et al. 2013; Delpiani et al. 2020; Jacobi et al. 2023; Góngora et al. 2023; Mincarone et al. 2024; Mincarone et al. 2026). In this region, *Myxine australis* has the widest known latitudinal distribution, with records from different areas of the continental shelf, ranging from 55°S at Cape Horn (Friedlander et al. 2018) to 33°S off southern Brazil (Mincarone and Soto 2001). In addition, the species has been reported in the southeastern Pacific off the coast of Chile (Norman 1937; Wisner and McMillan 1995), and a single record is known from the South Shetland Islands (Norman 1938). Recently, *M. australis* was reported as the most abundant species of the group in the waters of central Patagonia (Jacobi *et al.* 2026). Despite its abundance, a marked information gap persists regarding aspects of its life history, with a complete lack of knowledge of its trophic ecology being particularly noteworthy (Rincón-Díaz et al. 2024).

Bottom trawl fisheries targeting mainly Argentine hake *Merluccius hubbsi*, and Patagonian red shrimp *Pleoticus muelleri*, operate on the continental shelf of central Patagonia, Argentina (Góngora et al. 2012; Bovcon et al. 2013; Góngora et al. 2023), with *M. australis* being incidentally captured in both fisheries (Góngora et al. 2023). The Patagonian red shrimp fishery constitutes the largest and most profitable crustacean fishery in the southwestern Atlantic (Góngora et al. 2012; de la Garza *et al.* 2018), with spatial management that has varied over time. Between 1996 and 2006, 75% of shrimp catches were recorded in the waters of the San Jorge gulf (Góngora et al. 2012). However, since 2015, the shrimp fishing season has not been authorized in the waters of the San Jorge gulf, and in 2018 the area was officially closed to this fishery (Fischbach and Bertuche 2017; Buratti et al. 2022). Currently, the fishery operates mainly in offshore waters, between 42° and 46°S (Cinti et al. 2024; Moriondo *et al.* 2025). These spatiotemporal changes in fishing effort generate contrasting scenarios of seabed disturbance and discard availability, which could alter the resource base available to benthic communities. In this regard, evidence of discard consumption from these fisheries has been reported in the area for chondrichthyans (*Bathyraja brachyurops*, Tschopp et al. 2020; *Mustelus schmitti*, Pasti et al. 2021; *Zearaja brevicauda*ta, Tschopp et al. 2024) and teleosts (*Acanthistius patachonicus* and *Pseudopercis semifasciata*, Funes et al. 2019).

Spatiotemporal changes in the development of the local bottom trawl fisheries provide an opportunity to assess the trophic responses of organisms in environments subjected to anthropogenic disturbance. In this context, stable isotope analysis constitutes a robust tool for estimating intraspecific variation in trophic niche (Bearhop et al. 2004; Sweeting et al. 2005). Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values provide a time-integrated signal of nutrient assimilation derived from an individual's diet (Hesslein et al. 1993); rather than providing only a snapshot of what has been consumed at a particular point in time (Pinnegar and Polunin 1999; Bearhop et al. 2004). This type of analysis is widely used to study trophic relationships in marine ecosystems (Logan and Lutcavage 2008; Majdi et al. 2018; Nielsen et al. 2018). In addition, trophic fractionation results in consumers being enriched in $\delta^{13}C$ and $\delta^{15}N$

relative to their food sources (Caut et al. 2009; Hussey et al. 2014). This allows $\delta^{13}C$ values to be used to identify the origin of primary production sources (pelagic or benthic) and $\delta^{15}N$ values to estimate relative trophic position (Post 2002). In addition, the C:N ratio is an indicator of lipid content in the analyzed tissue (Post et al. 2007; Hoffman and Sutton 2010), allowing intraspecific variation in energy reserves to be assessed and different trophic strategies to be inferred (Zintzen et al. 2013).

Within this framework, the present study analyzes, for the first time, the trophic ecology of a hagfish species by comparing scenarios with and without bottom-trawling activity targeting Patagonian red shrimp, *P. muelleri*. Based on the premise that bottom trawling can generate additional food resources through discards, incidental mortality, and seabed disturbance (Kaiser and Spencer 1994), we hypothesized that fishing activity modifies the availability and diversity of food resources for *M. australis*. To assess this possibility, stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) from the species were used to analyze potential changes in isotopic niche and C:N ratios as proxies for lipid content and nutritional condition associated with different bottom-trawling scenarios. Complementarily, intestinal contents were analyzed to characterize diet composition and explore the diversity of prey items consumed, while relative trophic position and benthopelagic dependence of *M. australis* were estimated from $\delta^{13}C$ and $\delta^{15}N$ values in specimens collected in the San Jorge gulf, Patagonia Argentina, Southwestern Atlantic.

MATERIALS AND METHODS

A total of 116 *M. australis* Jenyns, 1842 specimens were analyzed for intestinal contents, and 57 specimens were analyzed for stable isotope analyses. Specimens were collected from two sectors of the Argentine Continental Shelf in central Patagonia, which represent contrasting scenarios of bottom-trawling activity. On the one hand, 36 specimens were collected in offshore waters within the area where the Patagonian red shrimp fishery targeting *P. muelleri* is actively conducted. Of these, 19 individuals were obtained in April 2022, before the beginning of the fishing season (pre-trawling period), during a survey of the Patagonian king crab population, *Lithodes santolla*, coordinated by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). The other 17 specimens were incidentally captured by the trawling fleet in August 2023 during the active shrimp fishing season (trawling period) (Fig. 1). The remaining 21 specimens for stable isotope analyses were collected from the San Jorge gulf, an area closed to bottom-trawling targeting Patagonian red shrimp. These specimens were collected more than two years after the last shrimp trawling season, during research surveys conducted aboard the ARA Puerto Deseado in November 2016 (GSJ-2016) and October 2017 (GSJ-2017), within the framework of the Pampa Azul initiative (Fig. 1). During these surveys, a bottom-trawl net with a 4.5 m horizontal opening and a 10 mm mesh size was used. Herbivorous invertebrate samples were also collected during these surveys and used as isotopic baselines. To establish the pelagic baseline, zooplankton was collected using a double plankton net (standard MiniBongo; 0.3 m diameter, 1.5 m total length, and 200 μm mesh size). Bivalves were separated from the catch obtained with the same net used to collect *M. australis* specimens (see Funes et al. 2019 and Galván et al., 2024 for further details).

All specimens analyzed were identified to species level in the laboratory following the diagnostic characters proposed by Wisner and McMillan (1995) and Figueroa (2019). Total length was recorded for each individual, after which specimens were dissected to obtain a dorsal muscle sample for stable isotope determination and to remove the intestinal tract for diet characterization.

Diet description was based on the visual analysis of intestinal contents from 116 specimens. Of these, 87 specimens were captured at the sites described above in central Patagonia, while 29 specimens were collected during a survey of the Patagonian scallop *Zygochlamys patagonica*, bottom-trawl fishery were analyzed (Fig. 1). Prey items were identified to the lowest possible taxonomic level using a stereomicroscope and specialized literature (Boschi et al. 1992; Gosztony and Kuba 1996; Boschi 2016). Diet composition was quantified using occurrence frequency (%F), calculated as the proportion of intestinal contents in which each prey group or subgroup was recorded relative to the total number of intestinal contents containing food. %F was calculated for each site and for all specimens combined. The number or weight of prey items could not be quantified due to the characteristics of the contents encountered; nevertheless, %F is considered the most robust and interpretable indicator of diet composition in fishes (Baker et al. 2014).

Dorsal muscle samples were dried for 48–72 h at 40–50°C and subsequently ground into a homogeneous powder. From each sample, 1.0 ± 0.2 mg was weighed for the determination of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios, without applying any additional treatments. Analyses were performed at the Stable Isotopes Center of the University of New Mexico using continuous-flow isotope ratio mass spectrometry coupled to an elemental analyzer (Costech ECS 4010) connected to a ThermoFisher Scientific Delta V Advantage mass spectrometer through a CONFLO IV interface. Isotope ratios were expressed using standard delta (δ) notation relative to the V-AIR ($^{15}N/^{14}N$) and Vienna Pee Dee Belemnite (V-PDB; $^{13}C/^{12}C$) standards. Internal standards were analyzed at the beginning, between samples, and at the end of each analytical run. Results were normalized using standards calibrated against soy, tuna, whey protein, casein, IAEA N1, IAEA N2, USGS 42, and USGS 43. Mean standard deviations of the reference materials were 0.03‰ for $\delta^{13}C$ and 0.08‰ for $\delta^{15}N$. Since the C:N ratio obtained for several samples was greater than 3.5, $\delta^{13}C$ values were mathematically normalized using the following equation: $\mathbf{\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N}$ (Post et al., 2007).

To assess the occurrence of ontogenetic shifts in diet, the relationship between body size and isotopic composition was analyzed using linear regression. Independent models were fitted using total length as the predictor variable and $\delta^{15}N$ and $\delta^{13}C_{normalized}$ ($\delta^{13}C_n$) values as response variables. Specimens captured in the San Jorge gulf in 2016 were excluded because total length data were not available. Model assumptions were tested using the Shapiro–Wilk test for normality and by visually inspecting the residuals.

Based on $\delta^{15}N$ and $\delta^{13}C_n$ values, isotopic niches were evaluated by calculating the sample size-corrected standard ellipse area (SEAc) and Bayesian standard ellipse area distributions (SEAb) (Reid et al. 2016). These metrics were calculated for each site using the “SIBER” package (Jackson and Parnell, 2023) in R

software (R Core Team 2026). Posterior distributions of SEAb were estimated using a Markov chain Monte Carlo (MCMC) algorithm with 2×10^6 iterations, a burn-in of 10^3 iterations, thinning of 10, and two independent chains. Differences in ellipse size among groups were assessed by calculating the proportion of posterior iterations in which the SEAb of one group was larger than that of the other, interpreted as the posterior probability that one isotopic niche had a larger area than the other group. Values close to 1 indicated a high posterior probability that the isotopic niche area of one group was larger than that of the other.

Differences in lipid reserves among groups were assessed using a median difference test on C:N values based on bootstrap techniques, following the approach proposed by Johnston and Faulkner (2021). This method was appropriate because it does not assume normality or homogeneity of variances and is robust to small sample sizes. The analysis was implemented using the R code provided as supplementary material by Johnston and Faulkner (2021), with 10,000 bootstrap resamples. Additionally, to quantify the magnitude of the difference between groups, a bootstrap distribution of the difference in medians was generated, from which a 95% confidence interval was obtained.

In addition, trophic position (TP) and benthopelagic reliance were estimated using the “tRophicPosition” package (Quezada-Romegialli et al. 2022) in R software (R Core Team 2026), using two isotopic baselines: a pelagic baseline (zooplankton) and a benthic baseline (bivalves). Trophic position was estimated only for specimens captured in the San Jorge gulf, as primary consumer isotope data required to establish the baseline for these calculations were available only for this area. Given the temporal variability in the San Jorge gulf baseline (see Galván et al. 2024), each year was analyzed separately using the baseline specifically collected for that year. Generic Trophic Discrimination Factor (TDF) values corresponding to the review by Post (2002) were used in the model ($\Delta^{13}C = 0.39 \pm 1.3$; $\Delta^{15}N = 3.4 \pm 0.98$). Interannual differences in TP and benthopelagic reliance were assessed by comparing their posterior distributions, calculating the difference between posterior samples from the two years and the corresponding 95% credible interval (95% CrI).

RESULTS

Analysis of intestinal contents showed that 83.6% of the intestines contained food contents (Table 2). Among the intestines containing contents, 99% showed an advanced digestion, which in most cases prevented prey identification at low taxonomic levels. Only 19.6% of the intestines with contents presented hard parts or structures that allowed prey identification to the level of phylum (Bryozoa), subphylum (Crustacea), class (Polychaeta), order (Decapoda and Amphipoda), or family (Myxinidae) (Table 1). Structures of taxonomic interest were never abundant.

Except for amphipods, bryozoans, and hagfish eggs, the remaining prey items were never found intact. Fish occurrence was inferred from the presence of scales and bone fragments, whereas in a single individual, several “bites” of muscle tissue with remnants of integument were observed. Across all intestines analyzed, the most represented prey groups were fish and crustaceans (Table 2). However,

crustaceans were not recorded in specimens incidentally captured during the trawling period or in specimens collected during the *Z. patagonica* survey (Table 2). In addition, Polychaeta, Bryozoa, and Myxinidae were recorded only in specimens collected during the *Z. patagonica* survey (Table 2).

Table 2
Diet composition of *Myxine australis* determined through the analysis of intestinal contents and expressed as occurrence frequency (%F). Results are presented according to the site or period of capture, as well as for all specimens analyzed. Pre-trawling = specimens captured before the beginning of the fishing season; Trawling = specimens incidentally captured during the Patagonian red shrimp fishery; GSJ-2016 and GSJ-2017 = specimens captured during research surveys conducted in the San Jorge gulf in 2016 and 2017, respectively; Scallop = specimens incidentally captured during the Patagonian scallop fishery; Total = all specimens analyzed.

Intestine (n)	**Pre-trawling**	**Trawling**	**GSJ-2016**	**GSJ-2017**	**Scallop**	**Total**
	21	**20**	**23**	**23**	**29**	**116**
With contents (n)	18	19	15	18	27	97
Empty (n)	3	1	8	5	2	19
Food item (%F)						
Crustacea	22.2	–	20.0	11.1	–	9.3
Amphipoda	11.1	–	6.7	–	–	3.1
Decapoda	–	–	6.7	11.1	–	3.1
Undetermined crustacean	11.1	–	6.7	–	–	3.1
Polychaeta	–	–	–	–	7.4	2.1
Bryozoa	–	–	–	–	3.7	1.0
Fishes	16.7	15.8	13.3	–	7.4	10.3
Myxinidae	–	–	–	–	7.4	2.1
Undetermined fish	16.7	15.8	13.3	–	–	8.2

Examination of the available data for assessing ontogenetic shifts in diet showed no evidence of a relationship between body size and $\delta^{15}N$ and $\delta^{13}C_n$ values in *M. australis*. Linear regressions performed for sites where body size data were available showed slopes close to zero, low coefficients of determination ($R^2 < 0.09$), and were not significant ($p > 0.05$), indicating that the observed isotopic variation was not associated with individual body size (Supplementary Material, Table S1 and Fig. S2).

Isotopic niche size (SEAc) varied among sites and sampling periods (Fig. 2). The ellipses corresponding to the same site did not overlap between sampling periods (Fig. 2), indicating shifts in isotopic niche position. In offshore waters, differences were observed in isotopic niche size as described by SEAc

values. Before the beginning of the fishing season (pre-trawling), SEAc was 0.865, which was significantly lower ($p = 0.001$) than that observed during the trawling period (2.608). In addition, the ellipses did not overlap, and lower $\delta^{15}N$ values were observed during the trawling period (Fig. 2). In contrast, SEAc values in the San Jorge gulf were 1.295 and 1.680 in 2016 and 2017, respectively, with no significant differences in isotopic niche size ($p = 0.329$). However, the ellipses showed shifts along both isotopic axes (Fig. 2).

The C:N ratio values differed between the offshore groups but were similar between years in the San Jorge gulf (Fig. 3). The bootstrap test showed significant differences in offshore waters between pre-trawling and trawling periods ($p = 0.0001$; 95% CI of the p-value = 5.13×10^{-6}–5.66×10^{-4}). The median C:N ratio during the pre-trawling period was lower than during the trawling period, with a difference of -0.77 (95% CI = -1.3 – -0.4). A marked difference in the dispersion of the data was also observed (Fig. 3), with the greatest dispersion occurring during the trawling period. In contrast, C:N ratio values in the San Jorge gulf were similar between the years analyzed. The bootstrap test showed no significant differences between years ($p = 0.316$; 95% CI of the p-value = 0.307–0.325). The observed difference between the 2016 and 2017 medians was 0.11 (95% CI = -0.156–0.408), and the dispersion of the data was similar between years (Fig. 3).

Estimates of trophic position (TP) and the relative contribution of benthic (α) and pelagic trophic pathways for specimens captured in the San Jorge gulf (the only site where primary consumers were available to construct the isotopic baselines) indicated that *M. australis* occupies a tertiary consumer position with a strong reliance on benthic resources. In 2016, *M. australis* had an estimated trophic position of 3.66 ± 0.13 (95% CrI = 3.4–3.9), with a relative benthic contribution of $\alpha = 0.71 \pm 0.11$. In 2017, the estimated trophic position showed greater variability and was slightly higher (TP = 3.83 ± 0.38, 95% CrI = 2.95–4.53). The benthic contribution remained relatively similar ($\alpha = 0.69 \pm 0.19$). Despite the observed difference of ≈ 2.7‰ in $\delta^{15}N$ values between 2016 and 2017 (Fig. 2A), relative trophic levels and benthic reliance remained constant between years. Posterior comparisons between years showed no differences in trophic position or benthopelagic reliance. The posterior mean difference (2016 − 2017) was − 0.19 trophic levels (95% CrI: -1.11–0.66). The posterior mean difference (2016 − 2017) in benthic reliance was 0.015 (95% CrI: -0.39–0.49).

DISCUSSION

The analysis presented on the trophic ecology of *M. australis* not only provides relevant information on the diet of this species, for which knowledge was previously lacking (Rincón-Díaz et al. 2024), but also contributes to expanding our understanding of the diversity of trophic roles and feeding strategies present among hagfish species (Table 1). The intestinal content analyses presented in this study allowed the diversity of prey items to be characterized across sites and periods with different fishing histories. In this context, greater prey-item diversity was observed at the sites or during the periods corresponding to pre-trawling and GSJ-2016, whereas lower diversity was recorded during the trawling period and in GSJ-2017. Specimens from the scallop fishery showed an intermediate and distinct diet composition,

representing the only site where consumption of polychaetes, bryozoans, and hagfish eggs was recorded; moreover, none of the prey items observed at the other sites were shared with this group. It should also be noted that crustacean consumption was observed at sites or during periods with little or no bottom-trawling activity, whereas partial fish remains predominated in those with greater fishing activity (Table 2).

Overall, 83.6% of the intestines contained food contents. However, virtually all of these (99%) consisted of material in an advanced stage of digestion, making taxonomic identification of prey difficult due to the absence of identifiable hard structures. Most of the identifiable prey were highly fragmented, possibly due to the feeding behavior described for the group (Zintzen et al. 2011; Haney et al. 2019). Only small prey items, such as amphipods and hagfish eggs, were recorded intact. Consumption of hagfish eggs has previously been documented in other species, such as *M. glutinosa* (Shelton 1978) and *E. stoutii* (Worthington 1905). It should be noted that the coexistence of *M. australis* and *Notomyxine tridentiger* in the study area prevents determining the species-specific origin of the eggs observed. In *M. glutinosa*, the selective composition of intestinal contents, together with the presence of fragmented and torn fish and crustacean remains, has been interpreted as evidence of active benthic predation rather than predominantly scavenging (Shelton 1978). In the case of *M. australis*, the results obtained do not allow discrimination among the different feeding strategies proposed for the group; nevertheless, the diversity of prey items recorded is consistent with generalist and opportunistic feeding behavior. Likewise, the high proportion of highly digested contents highlights the need to incorporate complementary tools, such as metabarcoding, in future studies to increase the taxonomic resolution of the prey consumed.

Ontogenetic changes in diet are common and expected among fishes and are considered a fundamental component of their ecology, often reflecting changes in morphology, habitat use, prey availability, and energetic requirements throughout the life cycle (Mittelbach and Persson 1998; Sánchez-Hernández et al. 2018; Rios *et al.* 2019). However, Clark and Summers (2012) suggest that juveniles and adults of *E. stoutii* may not undergo ontogenetic changes in diet, consuming functionally equivalent prey, although adults may ingest proportionally larger food portions. In addition, Zintzen et al. (2013) found no significant relationship between body length and isotopic values in three hagfish species from New Zealand. The results of the present study provide indirect evidence for the absence of ontogenetic changes in the diet of *M. australis*. Taken together, these studies suggest that the absence of ontogenetic variation may represent a common characteristic in some hagfishes species, although the limited number of available studies prevents establishing this pattern at the family level. Alternatively, ontogenetic changes may not involve relevant modifications in the type of prey consumed, but rather variations in the amount of food ingested. The absence of a trend in $\delta^{15}N$ values with size is consistent with patterns reported for fish that consume small detritivores invertebrates or exhibit scavenging behavior (Rios *et al.* 2019), a pattern that agrees with what has been previously described for the hagfishes. On the other hand, as marine food webs are largely structured by body size (Arim et al. 2010) and gape size is a major constraint on the consumption of larger (Scharf et al. 2000) and, consequently, higher-trophic-level prey, it is generally expected that trophic level increases as carnivorous fish grow (e.g. Deudero et al. 2004). However, this general assumption may not apply to hagfishes because their

knotting behavior (Zintzen et al. 2011; Haney et al. 2019) reduces the importance of gape size as a constraint on prey size, potentially making trophic level independent of gape size.

The isotopic niche width of specimens from the San Jorge gulf did not differ significantly between years, although shifts along both isotopic axes were observed. This pattern is consistent with variations in isotopic baselines associated with the oceanographic dynamics of the gulf (Galván et al. 2024) and suggests that, despite temporal fluctuations in carbon and nitrogen sources, the diversity of resources exploited by the species remained constant. In contrast, isotopic niche width showed a marked difference under the bottom-trawling scenario. In offshore waters, SEAc during the trawling period was approximately three times larger than during the pre-trawling period, suggesting greater heterogeneity in the resources consumed by *M. australis* when the fishing fleet was operating. This could be associated with increased availability of resources derived from fishing activity, consistent with the findings of Funes et al. (2019), who reported a shift and increase in isotopic niche size in demersal fishes exposed to bottom trawling in Patagonia.

In addition, the isotopic shift in offshore waters occurred mainly along the $\delta^{15}N$ axis. Individuals captured during the pre-trawling period showed values approximately 2.7‰ in $\delta^{15}N$ values higher than those recorded during the trawling period. This result differs from that observed by Funes et al. (2019), who documented an increase in trophic position in organisms exposed to fishing activity, consistent with the consumption of prey at higher trophic levels. The higher $\delta^{15}N$ values observed during the pre-trawling period could be associated with the nutritional condition of hagfishes. Hagfishes species are known to be capable of withstanding prolonged periods of fasting (Zintzen et al. 2013; Mickle 2016), and starvation can produce $\delta^{15}N$ enrichment as a consequence of catabolic processes (Hertz et al. 2015; Doi et al. 2017). In this regard, individuals exhibiting the highest $\delta^{15}N$ values simultaneously showed lower C:N ratio values, indicating a lower proportion of lipids, which is indicative of lower energy reserves and a possible fasting state. Conversely, specimens captured during the trawling period showed the highest C:N ratio values, suggesting greater energy reserves, which could be associated with increased resource availability and voracious feeding. In contrast, C:N ratio values in the San Jorge gulf did not differ. Overall, these results suggest that nutritional condition is an important factor in the interpretation of isotopic signals in this species.

Although the influence of interannual variation in offshore waters cannot be completely ruled out; the combination of variation in isotopic niche width, the predominant shift along the $\delta^{15}N$ axis, and differences in C:N ratio supports the hypothesis of variation in nutritional condition, possibly linked to changes in food availability among sites and periods. However, the temporal separation of more than one year between the two sampling periods and the absence of direct measurements of resource availability preclude establishing a causal relationship between fishing activity and the observed pattern.

Despite the marked shift observed in $\delta^{15}N$ values between 2016 and 2017 in the San Jorge gulf (≈ 2.7‰), estimates of trophic position and relative benthopelagic reliance indicated stability in the trophic ecology of *M. australis* in the San Jorge gulf. Posterior comparisons revealed no differences in trophic position or

benthopelagic dependence between years, suggesting that the isotopic variations recorded mainly reflect changes in the ecosystem's isotopic baselines rather than modifications in the diet or resources exploited by the species. Overall, these results suggest that, despite the interannual oceanographic variability documented for the gulf (Galván et al. 2024), the species exhibits a conservative trophic strategy, occupying the role of a tertiary consumer with a strong reliance on the benthic resource pathway.

As previously mentioned, the behavior of a few species has historically been extrapolated to characterize the entire Myxinidae family, primarily as scavengers. However, the available evidence is not consistent. Some studies support this interpretation (Collins et al. 1999; Smith and Baco 2003; Catchpole et al. 2006), whereas others describe opportunistic feeding habits (McLeod *et al.* 2007; Zintzen et al. 2013; Mickle 2016) or document active predatory behavior (Zintzen et al. 2011). Our results do not rule out scavenging, but show that in the less disturbed environment, the species exhibited behavior more consistent with a diet combining continuous feeding and the consumption of both invertebrates and fish, although it cannot be established whether these were actively consumed or obtained as carrion. This is consistent with observations suggesting that hagfishes trophic strategies are more diverse than traditionally assumed, including variation associated with habitat and local food availability (Zintzen et al. 2013; Mickle 2016). Deep-water species, where food sources are limited, have a greater capacity for lipid storage, which would indicate an adaptation to withstand prolonged periods of fasting (Zintzen et al. 2013; Mickle 2016). Likewise, isotopic analyses indicate a strong dependence on pelagic primary production, consistent with a diet based mainly on the consumption of pelagic-derived carrion (Mickle 2016). In contrast, the coastal species *Neomyxine biniplicata* showed indirect evidence of active predation (Zintzen et al. 2013). In addition, sympatric species with overlapping spatial distributions have been observed to exhibit overlaps in their isotopic niches, although they differ in the degree of specialization of their feeding strategies (Mickle 2016). Although our results for *M. australis* cannot rule out carrion consumption, they clearly rule out reliance on pelagic-derived carrion as a major food source. This is consistent with the predominantly shelf-associated distribution of the species, which is recorded mainly at depths shallower than 120 m (Jacobi *et al.* 2026), which is consistent with the pattern of lower dependence on carrion and active consumption of benthic invertebrates, as previous evidence suggests that hagfish trophic strategies vary along depth gradients, with a tendency toward increasing scavenging with increasing depth (Yeh and Drazen 2011; Zintzen et al. 2013). Species inhabiting shallow environments show a greater tendency toward predatory behavior (Zintzen et al. 2013), whereas those occurring at intermediate depths exhibit opportunistic feeding habits (Zintzen et al. 2013; Mickle 2016), and deep-water species show a strong dependence on pelagic-derived carrion (Drazen et al. 2011; Zintzen et al. 2013; Mickle 2016).

Overall, the results obtained demonstrate that *M. australis* exhibits trophic plasticity and can exploit a wide variety of the benthic resources available in the environment, regardless of the scenario. The stability observed in trophic indicators in the San Jorge gulf contrasts with the greater variability recorded under bottom-trawling scenarios, where changes in isotopic niche width and the nutritional condition of individuals were observed. This pattern suggests that, although the species maintains a

relatively stable trophic position as a tertiary consumer with a strong dependence on benthic resources, it has the capacity to adjust its feeding strategy in response to changes in food availability. In this context, *M. australis* could benefit from both naturally derived resources, through the consumption of invertebrates and other benthic organisms, and anthropogenic subsidies associated with fishing activities. These results represent the first steps toward understanding the trophic ecology of a largely unknown species and highlight the need to incorporate environmental variability, nutritional condition, and the influence of human activities to understand the ecological role of hagfishes in marine ecosystems, elucidating whether they consume fishery discards opportunistically or actually play a central role in the recycling of this organic matter.

DECLARATIONS

Competing Interests

The authors declare that they have no competing interests that could have influenced the work reported in this manuscript.

Ethical Approval

Not applicable.

Consent to Participate

Not applicable.

Consent to Publish

Not applicable.

AI statements

The authors used artificial intelligence–based tools to assist with language editing and improvement of clarity in the manuscript. These tools were not used to generate data, perform analyses, or influence the interpretation of results. All scientific content, analyses, and conclusions are the sole responsibility of the authors, who reviewed and approved the final version of the manuscript.

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Author Contribution

Conceptualization: JKJ; BND; CPD; GDE. Methodology: JKJ; BND; CPD; GDE. Formal analysis and investigation: JKJ; GDE. Writing – original draft preparation: JKJ. Writing – review and editing: JKJ; BND; CPD; FCA; MAC; VM; GDE. Funding acquisition: GDE. Resources: BND; FCA; MAC; VM; GDE. Supervision: BND; GDE. Validation: JKJ; BND; CPD; GDE.

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Data Availability

The data supporting the findings of this study are available from the corresponding author, upon reasonable request.

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Figures

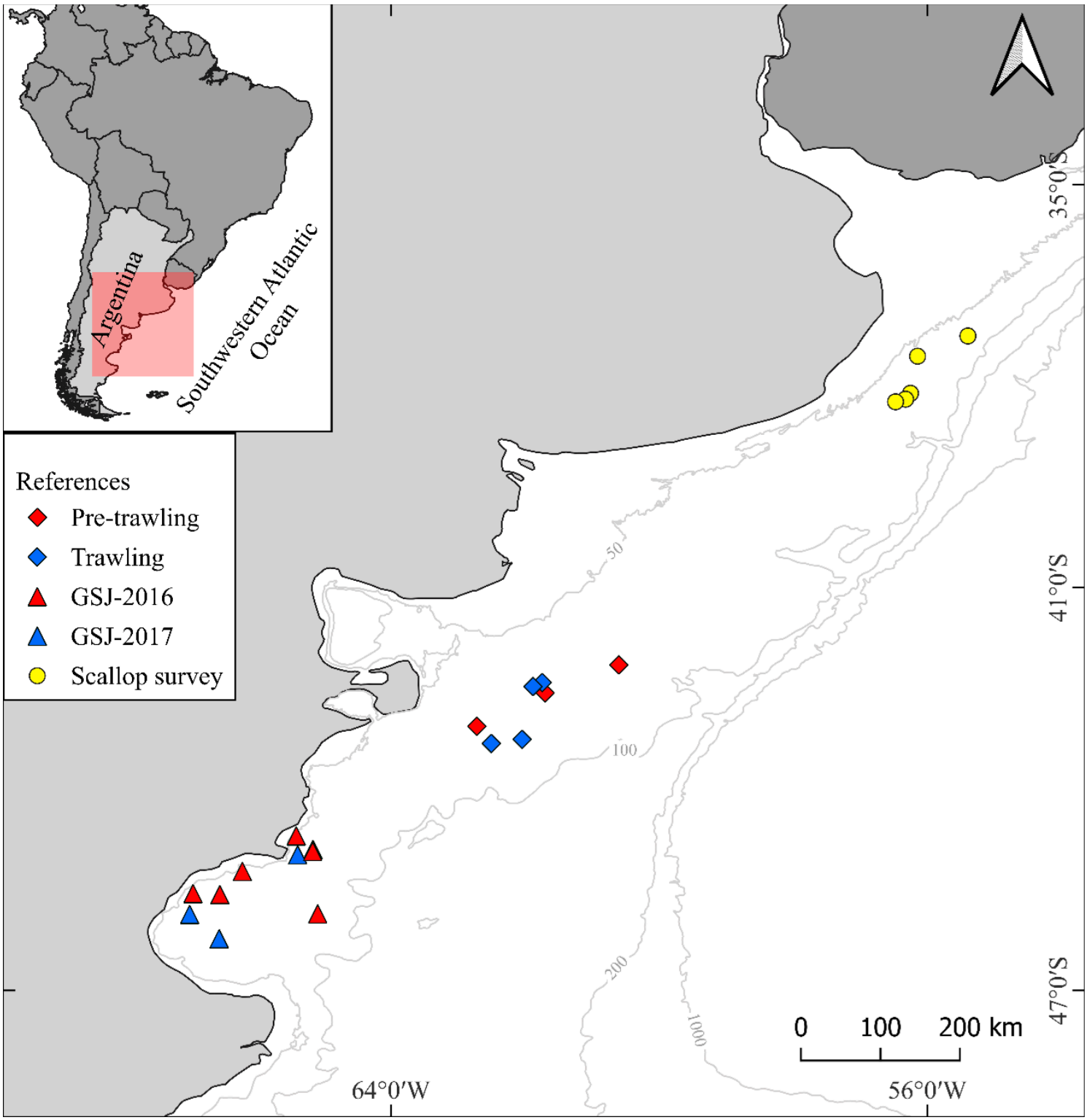


Figure 1

Map showing the location of the capture sites of the specimens analyzed. Diamonds indicate the sites within bottom-trawling areas before (red) and during (blue) the trawling period. Triangles indicate the specimen capture sites during research surveys in the San Jorge gulf (GSJ) in 2016 (red) and 2017 (blue). Yellow circles indicate the specimen capture sites during the Patagonian scallop survey. Isobaths at 50, 100, 200, and 1000 m are shown as an environmental reference.

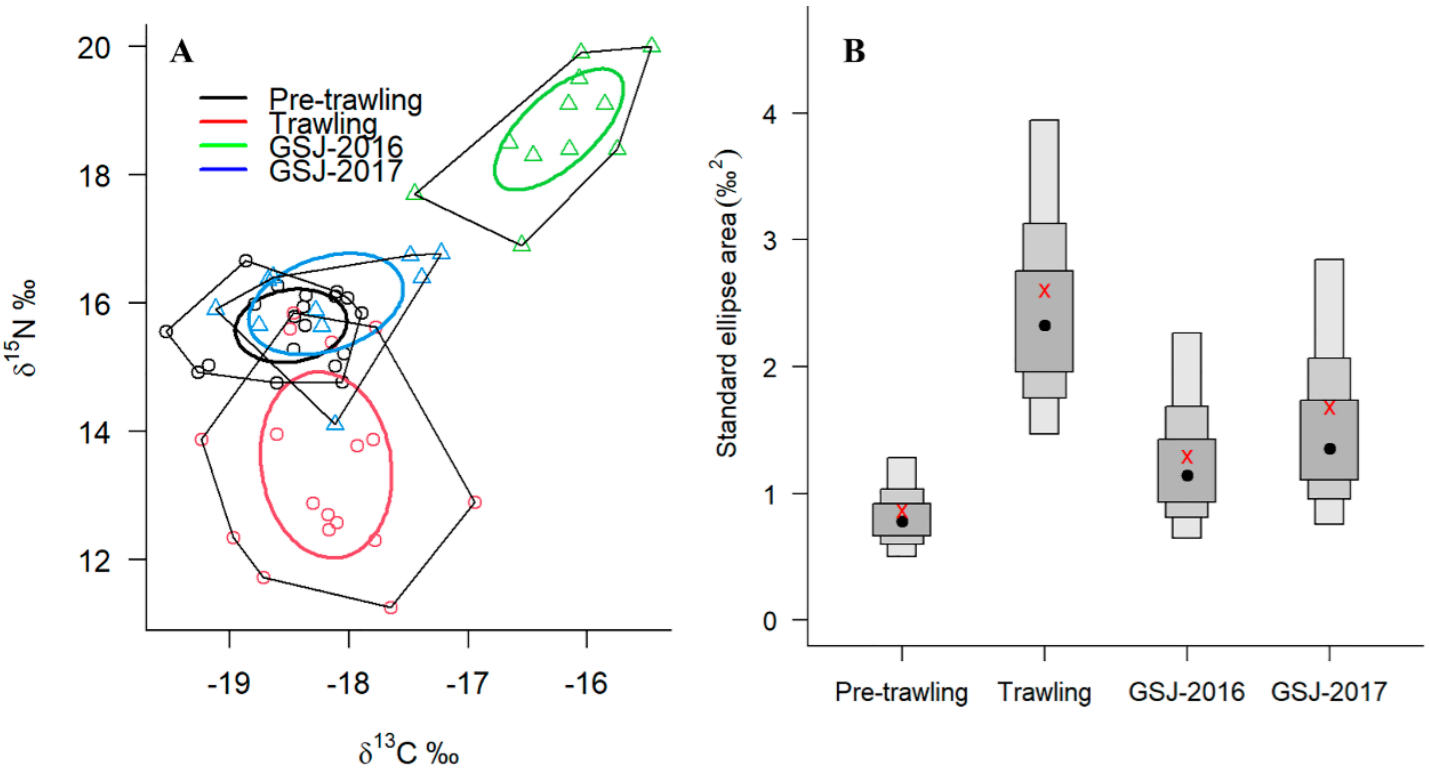


Figure 2

Panel A) δ¹⁵N and δ¹³C values of the hagfish specimens analyzed. Colors identify the different datasets, and lines represent their standard ellipses and convex hull area. Panel B) shows the posterior distributions of standard ellipse area; the black dot indicates the median and the red cross indicates the mean. Pre-trawling = specimens captured before the beginning of the fishing season; Trawling = specimens incidentally captured during the Patagonian red shrimp fishery; GSJ-2016 and GSJ-2017 = specimens captured during research surveys conducted in the San Jorge gulf in 2016 and 2017, respectively.

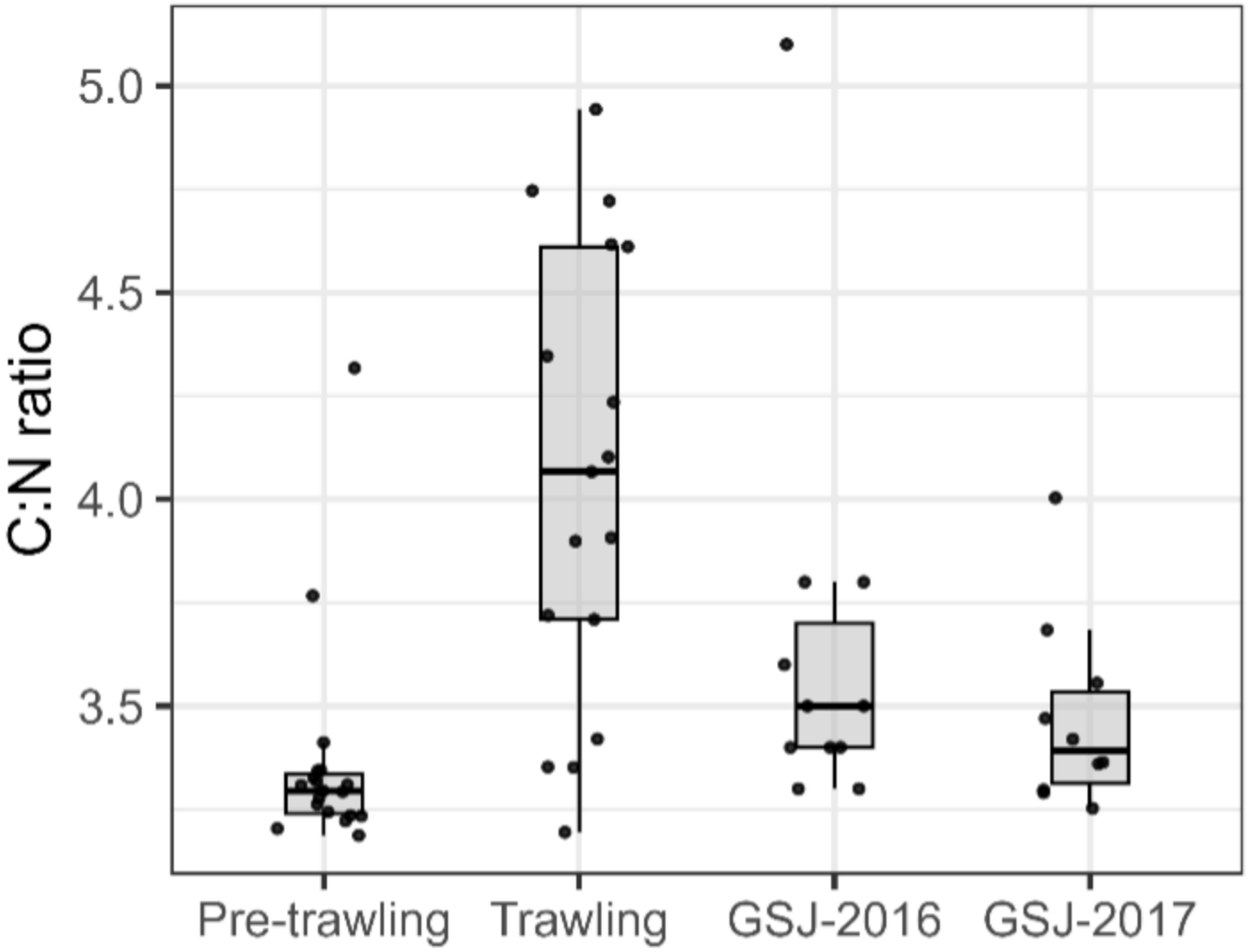


Figure 3

Distribution of C:N ratio values in the samples analyzed, discriminated by dataset. The median and distribution of values are shown using boxplots. Pre-trawling = specimens captured before the beginning of the fishing season; Trawling = specimens incidentally captured during the Patagonian red shrimp fishery; GSJ-2016 and GSJ-2017 = specimens captured during research surveys conducted in the San Jorge gulf in 2016 and 2017, respectively.

Supplementary Files

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- SupplementarymaterialTrophicvariationMaustralis.docx