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Spatial ecology of the southern hagfish *Myxine australis* (Myxiniformes: Myxinidae) in central Patagonia, Southwestern Atlantic

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This study presents the first analysis of the spatial distribution of a hagfish species in the Southwestern Atlantic, estimating density and probability of occurrence in relation to depth and latitude. Data were collected during bottom-trawl net surveys conducted between 43–47°S and 45–104 m depth, in an area located between two Biogeographic Provinces. *Myxine australis* was recorded at 51% of the sampling stations. Estimated densities ranged from 0 to 4,000 ind./km², with mean value of 510 ind./km². Frequency of occurrence increased with depth, reaching maximum values at depths greater than 80 m. Generalized linear models indicated that both depth and latitude had positive and significant effects on the probability of occurrence. Within the study area, the probability of encountering individuals increased by approximately 3% per additional meter and by 69% per degree of latitude southward. Density increased toward higher southern latitudes and with bottom salinity, with expected increases of approximately 53% per degree south and 57% per 0.1 PSU. Overall, the results show an increase in the abundance of *M. australis* southward, suggesting a preference for cold waters and a Magellanic distribution. This study provides the first spatial-ecological framework for this species and establishes a baseline for future biological and biogeographic analyses.

Keywords: Demersal, Density estimation, Distribution pattern, Jawless, San Jorge Gulf.

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Este estudio presenta el primer análisis de la distribución espacial de una especie de mixin en el Atlántico sudoccidental, estimando la densidad y la probabilidad de ocurrencia en relación con la profundidad y la latitud. Los datos se colectaron durante estudios con redes de arrastre de fondo realizados entre 43–47° S y 45–104 m de profundidad, en una zona situada entre dos provincias biogeográficas. Se registró la presencia de *Myxine australis* en el 51% de las estaciones de muestreo. Las densidades estimadas oscilaron entre 0 y 4000 ind./km², con un valor medio de 510 ind./km². La frecuencia de ocurrencia aumentó con la profundidad, alcanzando valores máximos a profundidades superiores a 80 m. Los modelos lineales generalizados indicaron que tanto la profundidad como la latitud tenían efectos positivos y significativos sobre la probabilidad de ocurrencia. Dentro del área de estudio, la probabilidad de encontrar individuos aumentó aproximadamente un 3% por cada metro adicional de profundidad y un 69% por cada grado de latitud hacia el sur. La densidad también mostró una relación positiva con la latitud y la salinidad de fondo, con un aumento esperado del 53% por cada grado hacia el sur y 57% por cada 0,1 PSU. En general, los resultados muestran un aumento de la abundancia de *M. australis* hacia el sur, lo que sugiere una preferencia por aguas más frías y una distribución magallánica. Este estudio proporciona el primer marco espacial-ecológico para esta especie y establece una base para futuros análisis biológicos y biogeográficos.

Palabras clave: Demersal, Densidad estimada, Golfo San Jorge, Patrones de distribución, Sin mandíbulas.

INTRODUCTION

Hagfish (Myxiniformes) are an ancient group of fish that inhabit marine benthic ecosystems. These fishes play the ecological role of scavengers and opportunistic predators, contributing to the recycling of organic matter in the oceans (Martini, 1998). Despite their functional importance, knowledge about the biology and ecology of most species in the group is scarce worldwide, especially in the southernmost region of South America (Knapp *et al*., 2011).

Interest in hagfish lies not only in their ecological function, but also in their potential as an emerging fishery resource (Ellis *et al*., 2015). In various regions of the world, they are targeted by fisheries that supply the Asian market for gastronomic and peltry purposes (Gorbman *et al*., 1990; Ellis *et al*., 2015). In this context, there are reports of fishing ground collapses (Gorbman *et al*., 1990), highlighting the vulnerability of these fisheries.

Eleven hagfish species have been reported for the Southwestern Atlantic (Norman, 1937; Nani, Gneri, 1951; Wisner, McMillan, 1995; Góngora *et al*., 2009; Mincarone, 2000, 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). Within this region, *Myxine australis* exhibits the widest known latitudinal range, with records along the continental shelf from 33° S off southern Brazil (Mincarone, Soto, 2001) to 55° S near Cape Horn (Friedlander *et al*., 2018), it has also been recorded in the Southeastern

Pacific (Chile) (Norman, 1937; Wisner, McMillan, 1995), as well as a single record from South Shetland Island (Norman, 1937). In central Patagonia (42°–47° S), *M. australis* shows a low frequency of occurrence (F%) in the bycatch of industrial bottom-trawl fisheries targeting Argentine hake *Merluccius hubbsi* and Patagonian shrimp *Pleoticus muelleri* (Góngora *et al*., 2012; Bovcon *et al*., 2013; Góngora *et al*., 2023). Differences in the number of records have been observed between the type of gear used in these fisheries, with fewer occurrences reported in the Argentine hake fishery (Jacobi, 2021). Central Patagonia is an area of bio-geographical importance as transitional zone between the Argentine Province, characterized by warm-temperate waters, and the Magellanic Province, distinguished by cold waters (López, 1963, 1964; Balech, Ehrlich, 2008; Cousseau *et al*., 2019). In this region, there are records that suggest an influx of species from warmer waters, a trend consistent with an emerging pattern of tropicalization (Galván *et al*., 2022).

The objective of this study is to analyze the frequency of occurrence of *M. australis* in central Patagonia and to estimate its density in the area. Spatial patterns were explored by examining the influence of depth, bottom salinity, bottom temperature, and latitude on the probability of occurrence and density estimates within the study area. Latitude and bottom temperature were analyzed as related variables: the former serves as a proxy for the spatial pattern of mean annual temperature, whereas the latter represents short-term variability. This work represents the first assessment of density estimation and spatial pattern analysis for a hagfish species in the Southwestern Atlantic.

MATERIAL AND METHODS

The data analyzed here were collected during two research cruises aboard the R/V *Puerto Deseado* within the monitoring program for the San Jorge Gulf of the "Pampa Azul" initiative (http://www.pampazul.gob.ar/). The sampling followed a regular grid design, comprising 53 sampling stations in November 2016 and 40 sampling stations in October 2017 (Fig. 1). Surveys were conducted in waters of the San Jorge Gulf and along the coast of Chubut Province in central Patagonia, Southwestern Atlantic, between 43°S and 47°S of latitude, at depths ranging from 45 and 104 m (Fig. **S1**). At each station a bottom-trawl with a 10 mm mesh size and a 4.50 m horizontal opening was deployed, towed at a speed ranging from 2 to 2.5 Kt. Geographic position, depth, tow duration, bottom temperature (measured 5 m above the seabed), bottom salinity (measured 5 m above the seabed) and the number of specimens captured were recorded at every station. Since in the laboratory all collected specimens were identified to the species level following Wisner, McMillan (1995) and Figueroa (2019). In the specific case of *M. australis*, specimens were identified based on a combination of morphological characters, including two fused cusps (multicups) in both the anterior and posterior sets, 30–38 total cusps, 86–118 total slime pores, and a whitish ventral band extending above the trunk pore line (Wisner, McMillan, 1995; Figueroa, 2019). Sex and sexual maturity were determined macroscopically based on the presence or absence, development, and size of the gonads, following the method described by Jacobi (2021), which is analogous to that used for *Eptatretus cirrhatus* (Martini *et al*., 2013).

From the collected data, the relative density estimation (individuals per km²) was calculated following the method of Alverson, Pereira (1969):

$$Dx = Cx / (Ax \times q)$$

Where the density of individuals (Dx) is expressed in terms of the number of individuals caught in haul x (Cx). The area covered (Ax) is expressed in square kilometers (km²) and is measured in haul x. The catchability coefficient (q) is assumed to be equal to 1.

Frequency of occurrence (F%) was computed for each year and for 20-m bathymetric intervals as: F% = (hauls in which the species was recorded/total hauls) X 100.

In order to identify trends in the spatial patterns of occurrence of *M. australis*, generalized linear mixed models (GLMM) were fitted. Firstly, the presence or absence of the species was modelled using bottom temperature, bottom salinity, latitude and depth as explanatory variables. The fitted model assumed an error with binomial distribution, and using the logit link function. Secondly, positive densities (values > 0) were analyzed in relation to the same explanatory variables by fitting a GLMM assuming an error with gamma distribution and using the log link function. Given that the data were derived from two distinct samplings (2016 and 2017), both analyses incorporated the year as a random variable to account for potential temporal dependencies between observations. Prior to the implementation of the models, an exploratory analysis of the data was conducted in accordance with the protocol recommended by Zuur *et al.* (2010). The procedure included evaluating collinearity among predictors through correlation analysis and calculating the variance inflation factor (VIF) to identify redundant variables.

In order to select the most parsimonious model, a backward elimination procedure was applied (Zuur *et al*., 2009). Initially, a complete model incorporating all non-collinear predictors was fitted, and models with and without the random effect "Year" were compared using Akaike Information Criterion (AIC) values to ascertain the necessity of its inclusion. Subsequently, non-significant predictors ($P > 0.05$) were sequentially eliminated. The significance of each variable was determined by comparing residual deviations between models using likelihood ratio tests (Zuur *et al*., 2009).

The models were fitted using the lme4 package (Bates *et al*., 2015) in R (R Development Core Team, 2025). Finally, the assumptions of the GLMM (*i.e*., adequacy of the specified error distribution, the independence of residuals, and the presence of over- or under-dispersion of the residuals) were verified on the selected models using the DHARMa package (Hartig, 2022).

RESULTS

During the research cruises, four hagfish species were recorded (*Myxine affinis*, *M. australis*, *M. knappi*, and *Notomyxine tridentiger*). However, only *M. australis* was commonly recorded, as the other species were rare and represented by very few records (n = 1 for *M. affinis* and *M. knappi*, and n = 2 for *N. tridentiger*), which precluded reliable population density estimates. The occurrence of *M. affinis* and *M. knappi* in the study area had already been previously reported by Jacobi *et al.* (2023). The presence of *M.*

australis was recorded in both sampling years. In 2016, the species was present in 57% of the 53 surveyed stations, with a total of 102 specimens recorded (range = 0–12; mean = 1.92 individuals per station). In 2017, it was detected in 47% of the 40 stations, with a total of 51 specimens recorded (range = 0–13; mean = 1.27 individuals per station). Of the total specimens collected, females accounted for 79.7%, hermaphrodites for 15.0%, and 5.2% showed no macroscopically visible gonads. The proportion of mature individuals was 83.6% in females and 60.8% in hermaphrodites.

The density estimations for 2016 ranged from 0 to 4,000 individuals per km² (ind. / km²), with a mean of 617 ind./km² (± 847.8). In 2017, density values ranged from 0 to 2,924 ind./km², with a mean of 317 ind./km² (± 646.6). When only stations at which specimens were captured were considered, a marked increase in mean density values was observed, resulting in 1,090 ind./km² (± 868.97) for 2016 and 845 ind./km² (± 748.02) for 2017.

For both years, the highest density values were observed in the southern region and at the mouth of the San Jorge Gulf (Fig. 1), between 45.5° and 46.8° S, at depths ranging from 70 to 100 m (Fig. 2). A visual analysis of the data, encompassing both the map (Fig. 1) and the bubble plot (Fig. 2), appears to indicate a downward trend towards the north and at shallower depths. The areas of highest and lowest density coincided spatially between the two years analyzed (Fig. 1).

In 2016, F% was high across all bathymetric ranges, with values equal to or exceeding 50%. The highest F% values were recorded at depths greater than 80 m, and at depths greater than 100 m F% reached 100% (Fig. 3). Conversely, in 2017, F% was observed to exceed 50% only within the 80–100 m range, while values in all other intervals were ≤20% (Fig. 3). Overall, the highest values of F% values in both years occurred at depths of greater than 80 m, whereas the lowest values were recorded at depths shallower than 40 m.

Data exploration of the full dataset revealed strong collinearity between bottom temperature and the other explanatory variables (*i.e.*, VIF values > 2). Therefore, the explanatory variables for the probability of occurrence were latitude, depth and bottom salinity. The model selection analyses for species occurrence indicated that there was no significant difference between the two years, as the model without the random effect Year had the lower AIC value (Tab. **S2**). Subsequent selection of the most parsimonious model revealed significant effects of depth and latitude, whilst bottom salinity and the interactions terms between variables were not significant (Tab. **S2**). The analysis revealed a positive and significant effect of depth (OR = 1.03; 95% CI = 1.00–1.07; p = 0.028), indicating that the odds of encountering individuals increase with depth. In a similar way, Latitude also showed a positive and significant effect (OR = 1.69; 95% CI = 1.07–2.80; p = 0.031), indicating that the probability of occurrence increases southward. Shallow and northerly regions exhibited low probabilities (less than 0.3), whereas the deepest and most southerly sectors exhibited probabilities greater than 0.8, indicating a distinct preference for more southerly and deep-water environments (Fig. 4). The diagnostic plots and tests performed did not reveal significant violations of the model assumptions (Fig. **S3**).

Exploratory data analyses for density indicated that there was no redundancy among the latitude, depth, bottom temperature and bottom salinity variables (VIF < 2); therefore, the four variables were evaluated in the model selection. Again, no

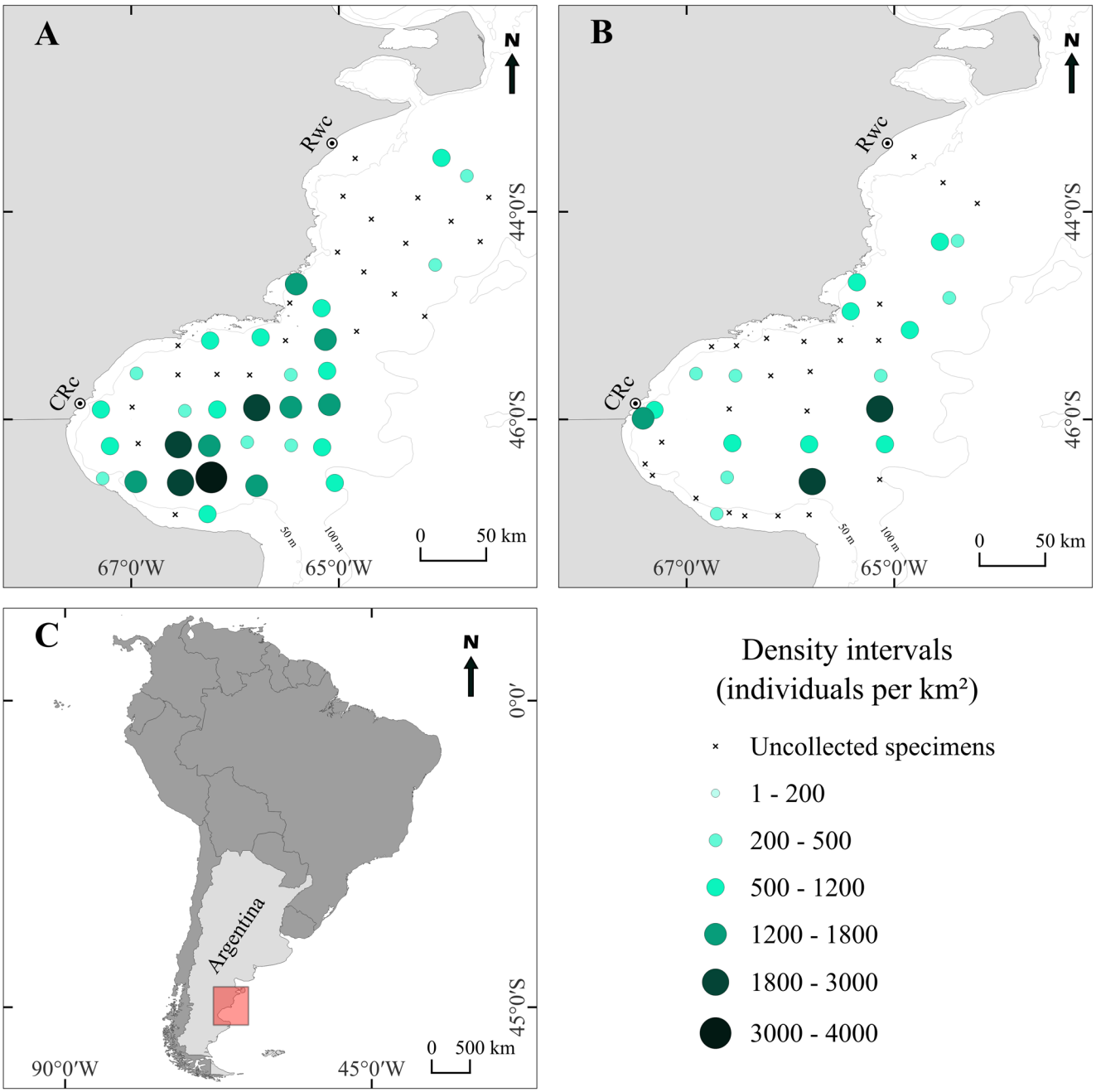

FIGURE 1 | Sampling stations surveyed in 2016 (**A**) and 2017 (**B**). Circle size indicates the estimated density of *Myxine australis* (individuals per km²) at each station, while. 'x' marks indicate stations where no specimens were recorded. Bathymetric isolines at 50 m and 100 m are included for environmental reference. (**C**) Geographic location of the study area (highlighted in red) in Southwestern Atlantic. CRc = Comodoro Rivadavia city, Rwc = Rawson city.

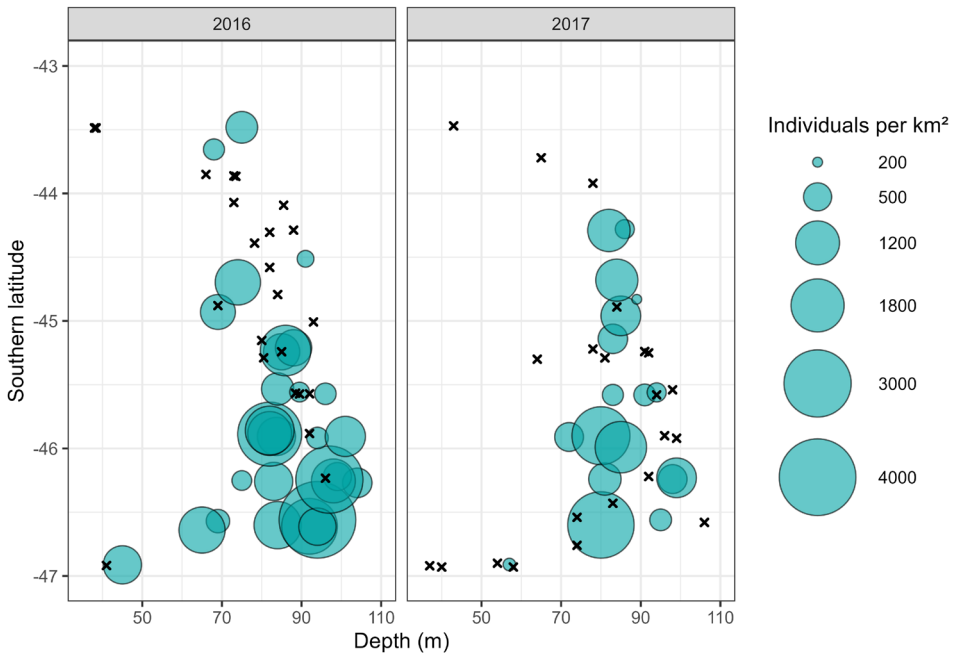

FIGURE 2 | Latitudinal and bathymetric distribution of the sampling stations in 2016 (left) and 2017 (right). Each point represents a sampling station and the circle size indicates the estimated density of *Myxine australis* (individuals per km^2). Stations where no specimens were recorded are marked with an 'x'.

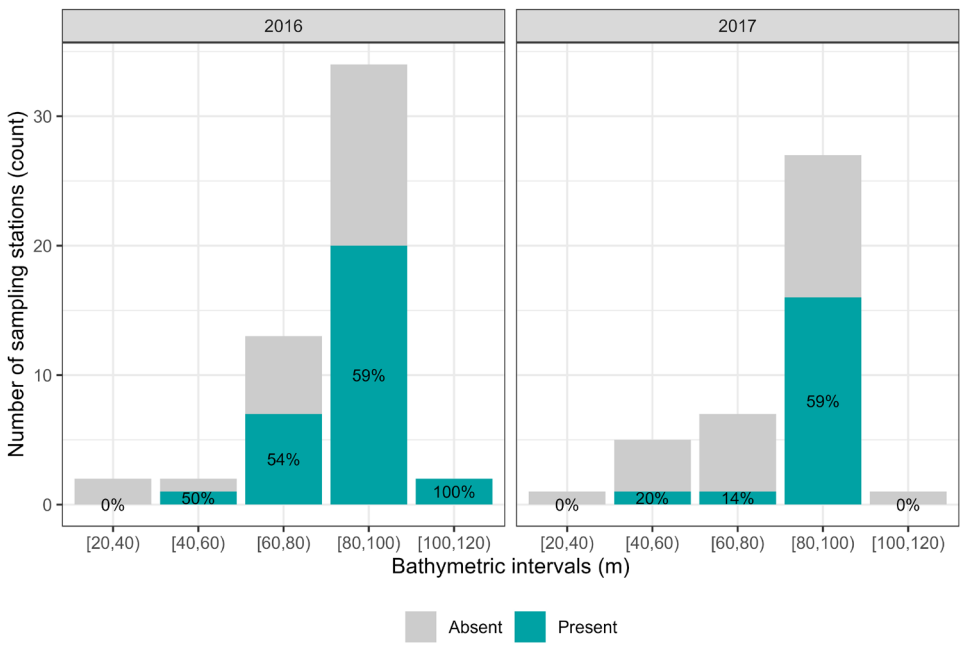

FIGURE 3 | Frequency of occurrence (F%) of *Myxine australis* according to bathymetric intervals in 2016 (left) and 2017 (right). Bars indicate the number of stations at which the species was present (green) or absent (grey) within each depth interval. Percentages indicate the proportion of stations with species presence in each depth interval.

significant differences were detected between sampling years (Tab. **S4**). In addition, the model selection protocol showed that depth and bottom temperature were not significant predictors (Tab. **S4**). The final model revealed a significant positive effect of increasing bottom salinity ($\beta = 4.530 \pm 1.832$, $p = 0.0173$) and latitude (further south; $\beta = -0.423 \pm 0.137$, $p = 0.0035$). These results statistically support the progressive increase in estimated density toward higher latitudes that had been previously observed through visual inspection (Figs. 1, 2, 5). However, the explanatory power of the model was limited, as pseudo-R^2 values ranged from 0.15 to 0.22 depending on the approximation used. This suggests that other oceanographic variables not considered here may also be influencing the density of *M. australis*. The diagnostic plots and tests performed did not reveal significant violations of the model assumptions (Fig. **S5**).

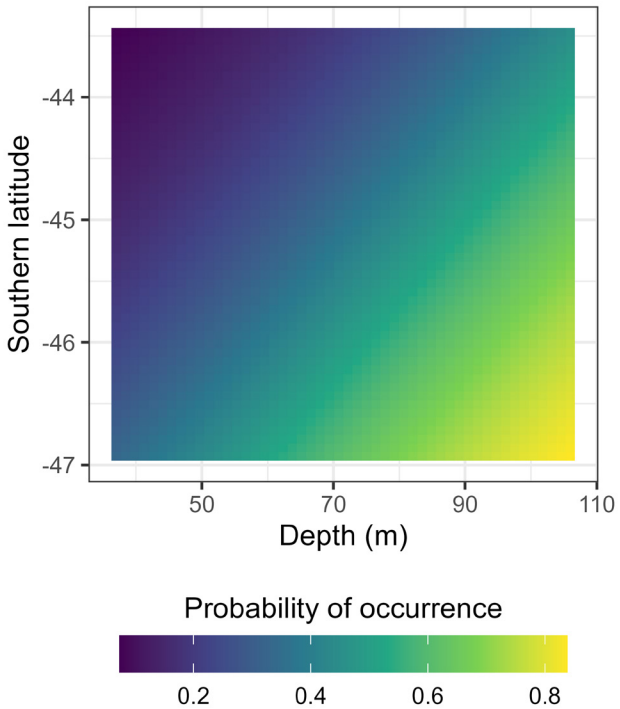

FIGURE 4 | Predicted probability of occurrence as a function of depth and latitude. The color scale indicates the estimated probability of *Myxine australis* presence, with purple tones representing low probability and yellow tones representing high probability.

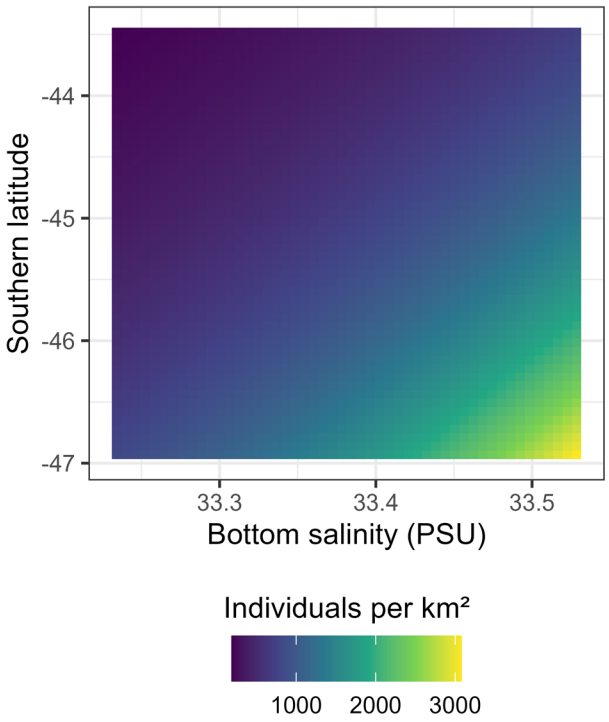

FIGURE 5 | Relationship between the estimated density of *Myxine australis* (individuals per km²), southern latitude, and bottom salinity. The color scale represents estimated density, with purple tones indicating low density and yellow tones indicating high density.

DISCUSSION

The F% obtained for *M. australis* in this study were 57% and 47% for 2016 and 2017, respectively. Conversely, analyses of bycatch from industrial fisheries in the region have reported F% below 4% (Góngora *et al*., 2009; Bovcon *et al*., 2013; Góngora *et al*., 2023). This discrepancy can be attributed primarily to contrasts in both the objectives and the fishing gear used. Research cruises are designed to document biodiversity, whereas fisheries operations aim to maximize the catch of the target species. In this study, a bottom-trawl net with a 10 mm mesh size was utilized, and the catch was subjected to a comprehensive examination. In contrast, commercial fisheries employ bottom-trawl nets with mesh sizes ranging from 45 to 120 mm. This mesh size has the potential to facilitate the escape of smaller fish and invertebrates. Accordingly, it can be assumed that previous fishery-dependent records likely underestimate the true occurrence of hagfishes.

The mean densities of *M. australis* in western central Patagonia reached 617 and 317 ind./km² in 2016 and 2017, respectively. These values are considerably lower than those reported for other species, including 176,300 ind./km² for *Eptatretus deani* (Wakefield, 1990), 59,700 ind./km² for *Myxine limosa* (Martini, 1998), and 16,465 ind./km² for *Myxine glutinosa* (Catchpole *et al*., 2006). These differences may be attributed to the sampling methodologies employed, given that the present study utilized bottom-trawl, whereas the aforementioned studies employed baited traps and visual censuses through camera surveys. In this context, it is probable that the reported densities are

underestimated, as our estimates reflect only the proportion of the population susceptible to bottom-trawl. This interpretation is supported by the fossorial lifestyle of these fishes, as described by Martini (1998).

Increases in hagfish density have been reported in association with anthropogenic activities, particularly fisheries (Martini, 1998). In the present study, the sampling stations closest to Comodoro Rivadavia city (Fig. 1) exhibited higher density values compared with adjacent stations of similar depths, a pattern that was more pronounced during the second year of sampling. In this context, it is plausible that urban discharges enhance the availability of organic matter in surrounding benthic substrates, potentially favoring the presence of *M. australis* by increasing trophic resources. However, the available evidence is insufficient to establish a direct link between these activities and the observed patterns. Conversely, no records were obtained in the area adjacent to Rawson city (Fig. 1). The influence of anthropogenic inputs of organic matter on the density and distribution of *M. australis* should therefore be further investigated in future studies. Other food sources, such as fishery bycatch or whale-fall, could influence the local density of the species. However, in the area near Comodoro Rivadavia, it is highly unlikely that fishery discards played a relevant role. No fishing activity occurs in this sector as since 2015, the shrimp fishing season has not been opened in the San Jorge Gulf, and in 2018 it was officially closed (CFP Resolution N° 7/2018); and, consequently, no local discards were generated. Fishing operations are restricted to the northern sector of the San Jorge Gulf, several hundred kilometers away, and the fishing season had ended approximately three months before sampling. This spatial and temporal separation makes any direct influence of fishery discards on the observed abundances unlikely. Whale-fall, on the other hand, are known to locally increase hagfish densities (Dahlgren *et al*., 2006). Nevertheless, such events are rare, spatially dispersed, unpredictable, and there was no evidence of recent comparable events in the area that could account for the observed patterns. In this context, the available evidence remains insufficient to assess the relative contribution of these potential sources to the observed density patterns.

The density estimates for *M. australis* allow for a discussion regarding its potential as a fishery resource in the region, within the context of the global expansion of hagfish-directed fisheries (Ellis *et al*., 2015). In central Patagonia, these densities were lower than those reported for species that are currently being exploited (Wakefield, 1990; Martini, 1998; Catchpole *et al*., 2006). Furthermore, *M. australis* exhibits relatively small body sizes, ranging from 91–394 mm (Wisner, McMillan, 1995). In contrast, *Eptatretus cirrhatus*, a target species in New Zealand, ranges from 225–812 mm with an average of 486 mm (Martini *et al*., 2013), whereas *M. limosa* in the Northwestern Atlantic reaches lengths of 195–638 mm and has a minimum commercial size of 410 mm (Grant, 2006). These differences in body size, in addition with the differences in density estimations, give rise to questions regarding the economic viability of fishing activities targeting *M. australis*. In this regard, it is imperative to employ other fishing gear in order to advance density estimations, and to enhance our understanding of the species' reproductive biology, so as to evaluate economic and ecological viability of a potential fishery.

The logistic model fitted for the probability of species occurrence indicated a positive and significant effect of both depth and latitude. The model parameters indicate that, within the study area, for each additional meter of depth, the odds of presence increase by 3%, while for each degree southward the odds increase by 69%. It should

be emphasized that variations in the odds do not necessarily correspond to equivalent or constant increments in the probability of occurrence, as the relationship between these variables may be non-linear in larger areas than the modeled here. However, our results do confirm an increase in the probability of finding individuals at greater depths in the continental shelf and in more southerly areas within the Southwestern Atlantic. Furthermore, our results indicated a positive and significant relationship with bottom salinity and with more southern latitudes. According to the fitted model, holding salinity constant, a 1° southward shift was associated with an approximate 53% increase in expected density. Likewise, small increases in bottom salinity (0.1 PSU) were associated with increases of approximately 57% in density.

One of the primary ecological factors contributing to the distribution limitations of hagfish is low temperature (Martini, 1998). In this regard, the permanent presence of cold waters from the Patagonian Current, which extends across the Patagonian Shelf (Piola, Rivas, 1997), and the associated Southern Patagonian Frontal System, which stretches from the Strait of Magellan to the southern sector of the San Jorge Gulf (Guerrero, Piola, 1997), provide the environmental conditions that could sustain the higher relative densities of *M. australis* recorded in the southernmost part of the study area and at the mouth of the San Jorge Gulf. However, the statistical analyses do not appear to directly reflect these patterns. In both models, temperature was not retained in the final formulation. Nevertheless, the lack of statistical significance should not be interpreted as ecological irrelevance. The variables analyzed correspond to point measurements obtained with a CTD, which represent short-term environmental conditions and likely do not adequately capture the thermal gradients structuring distribution at broader spatial scales. In this context, geographic variables such as latitude and depth may be acting as proxies for average environmental conditions, integrating broader temporal thermal gradients. Assuming a relatively small home range, hagfish are unlikely to respond to short-term thermal variability, and are more likely adapted to broader latitudinal and bathymetric thermal gradients.

To better discuss the model outputs, it is important to adopt a biogeographic perspective. The Argentine Continental Shelf, situated between 35° and 55° S, has been divided into two regions: the Argentine Province, characterized by warm-temperate waters, and the Magellanic Province, distinguished by cold waters (Balech, Ehrlich, 2008; Cousseau *et al*., 2019). According to Balech, Ehrlich (2008), the boundary between these provinces is diffuse. The Magellanic Province extends from Cape Horn to 42° S, where it moves offshore and continues northward to approximately 34° S, and is bounded to the east by the Brazil Current, which characterizes the Argentine Province (López, 1963, 1964). The geographical area under consideration in this study encompasses a section of the transitional zone between the aforementioned biogeographic provinces, a factor that may be responsible for the pronounced effect of latitude on both the probability of occurrence and the mean density. The latitudinal effect is consistent with a predominantly Magellanic distribution, with affinity for cold sub-Antarctic waters. The biogeographic context under discussion helps to explain the higher probability of occurrence and density estimation recorded at higher latitudes, where the oceanographic conditions characteristic of the Magellanic Province become dominant. Concurrently, the Magellanic Province's extension to approximately 34° S in deep waters of the shelf, provides a biogeographic foundation for the northernmost documented occurrences of the species as reported by Mincarone, Soto (2001).

In summary, this study provides the first assessment of the density and spatial patterns of a hagfish species in the southwestern Atlantic. The results indicate that *M. australis* exhibits a wide distribution pattern, though at lower densities compared to other species within the group. Given the fishing gear used, these values likely represent minimum estimates and should be complemented with traps or other targeted gear. The species showed a clear association with higher latitudes and deeper areas within the study region, consistent with a distribution aligned with the Magellanic Province and its cold sub-Antarctic waters.

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