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Posted Date: 3 January 2024

doi: 10.20944/preprints202401.0172.v1

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*Article*

# Southern Horse Mackerel (*Trachurus trachurus*) Distribution Patterns Based on Fine Scale Resolution Data

**Hugo Mendes [1,*], Cristina Silva [1] and Manuela Azevedo [1]**

[1] Instituto Português do Mar e da Atmosfera, Rua Prof. Doutor Alfredo Magalhães Ramalho, 6, 1495-165 Algés, Portugal

* Correspondence: hmendes@ipma.pt.; Tel.: + 351 213027000

**Abstract:** In this study, the distribution patterns of southern horse mackerel are examined using commercial fine-scale resolution data. Using landings by size category and VMS data from the Portuguese commercial bottom trawl fishery, which consistently targets horse mackerel, this study provides a comprehensive analysis of horse mackerel age distributions spanning a decade (2010-2020). Importantly, the study addresses potential biases in commercial effort data and establishes the usefulness of commercial bottom-trawl gear as a suitable method for sampling and evaluate southern horse mackerel stock dynamics. Ordered regression models were applied to allow for the modelling of the distribution of multiple age categories and investigate spatio-temporal migrations off the Portuguese coast. Southern horse mackerel shows a widespread age distribution range and stable abundance with indications of seasonal and spatial patterns in the distribution of specific age groups. The insights derived from this research contribute valuable knowledge for understanding the dynamics and distribution patterns of fish populations.

**Keywords:** commercial fine-scale resolution data; distribution patterns; southern horse mackerel;

**Key Contribution:** distribution patterns of fish populations based on commercial fine scale resolution data

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## 1. Introduction

In fisheries science, understanding and identifying fish habitats is crucial for improving fisheries management. Each marine species exhibits distinct habitat requirements throughout various life history stages, shaped by species-specific traits and ontogeny.

The quantification of patterns of fish distribution can be influenced by the scale at which the observations are made and how data are collected and compiled. Population and community dynamics may show different spatial and temporal structures when the data are observed in different scales. The choice of an appropriate spatial and time scale is key to correctly predict shifts in fish distribution. Processes occurring at smaller temporal or local spatial scales may be unnoticed when relying on data and observations conducted at larger scales. Conversely, processes operating at a larger scale may display gradual variations and be perceived as constant when examined through data and observations at smaller scales [1,2]. In practical terms, the scale of time and space for data is typically established because of the limited fund constraints and currently, understanding of the life history and distribution of many marine organisms in Iberian waters is mostly based on intermittent "snapshots" of species presence, abundance, and distribution, most commonly based on available survey data [3,4,5].

The horse mackerel, *Trachurus trachurus* (Linnaeus, 1758) is one such fish species that plays an important role in the fisheries and ecosystem dynamics of the Northeast Atlantic. While the distribution and movement of horse mackerel has been investigated in previous studies a comprehensive study to describe the distribution based on fine scale temporal and spatial scale data has yet to be completed. The geographical distribution of the horse mackerel covers the whole platform and slope of the European and African coasts from Norway to the Gulf of Guinea, and the Mediterranean and Black Sea [6]. The southern stock population exhibits a geographic distribution spanning the Western Atlantic coastline of the Iberian Peninsula, from the Strait of Gibraltar to Cape Finisterre in Galician waters in the northwestern region of Spain. This stock off the west and southern coast of the Iberian Peninsula has several genetic, phenotypic and distributional characteristics that distinguish them from the rest of the stocks in the northeast Atlantic [7]. The Portuguese area represents 87% of the total coverage of the stock area and is where the majority of the catches are taken. Moreover, previous studies also indicate that all life stages are present in the Portuguese area supporting the current stock area definition [8,9].

Figure 1 illustrates the Portuguese area, delineating oceanographic zones based on specific geographic and physical attributes. These attributes correspond to distinct oceanographic conditions with the presence of deep canyons creating natural boundaries. These physical features contribute to unique behaviors observed in the biological communities within the designated areas [10,11]. Previous studies based on spring and autumn scientific survey data, have suggested the presence of diverse migratory patterns within the stock population. During the autumn season, coinciding with the recruitment period, juvenile horse mackerel are most commonly found in the northwestern region with a wider continental shelf. Conversely, during the spring season, the highest concentration of juvenile individuals is observed in the southern region. Adults are typically distributed uniformly along the entire coastline, with their greatest aggregations occurring in the winter and spring, notably within the southwestern and southern zones [12,13].

Murta (2008) [8] analyzing autumn groundfish survey data, suggested the existence of ontogenic migrations in horse mackerel along the Iberian Atlantic coast, involving two migration paths along the coastline at various depths. Along the Portuguese coast, most year classes initially cluster in the northwest, shifting southward, and occasionally returning to northern waters after reaching seven years of age. The author hypothesized that the migratory movements of horse mackerel were driven by feeding and spawning requirements.

The previous studies were all based on snapshot data from scientific research surveys. However, since the introduction from the European Commission (EC) of legislation [14,15] to monitor European fishing vessels using satellite-based vessel monitoring systems (VMS), the expanding time-series VMS is enabling fisheries scientists to consider the fine-scale spatial and temporal dimensions in commercial fisheries data. VMS allows for the real-time tracking and monitoring of fishing vessels, providing information on their location, speed, and activity. This represents a significant advance in fisheries research.

Vessel monitoring systems are now widely available across Europe for scientific purposes and several studies highlight the potential of VMS for accurately collecting georeferenced effort data and linking it to logbook and/or observer catch data. However, there are several difficulties associated with the use of commercial data for estimating abundance since commercial fishing vessels tend to target specific areas [16,17] as well as other challenges as overestimation and synchronization that still need to be addressed 18,19,20]. Data from the VMS can offer a comprehensive set of indicators to improve inputs for stock assessments, enable real-time distinction of fishing grounds and facilitate the assessment of regulatory measures. It could also be used to evaluate the effectiveness of marine protected areas and to inform the design of spatial management measures [21] and to support the development of ecosystem-based fisheries management [22,23]

Azevedo and Silva (2020) [24] combined VMS data with species sales notes by commercial size category and biological information from onshore sampling to investigate the potential of this fine scale spatio-temporal resolution in biological, fishery and effort data to assess horse mackerel distribution patterns by life-stage. This study expands the temporal scope of this work to analyze age specific patterns of seasonal and inter-area migrations and to assess both intra- and inter-annual fluctuations in horse mackerel species distribution from VMS and bottom trawl fishery data. The commercial bottom trawl fishery provides a valuable source of data for understanding the dynamics of southern horse mackerel populations. The fine-scale resolution data obtained from this study offers insights into the spatial and temporal distribution patterns of the species, as well as the fishing effort exerted to capture them. In addition to the fishing effort, the catch-at-age composition of southern horse mackerel provide valuable insights into the population structure and dynamics.

By understanding the dynamics and distribution patterns of fish populations, fisheries managers can make informed decisions about sustainable fishing practices and conservation efforts. The framework used has the potential to provide valuable background for the management and conservation of commercially exploited fish stocks in the Northeast Atlantic.

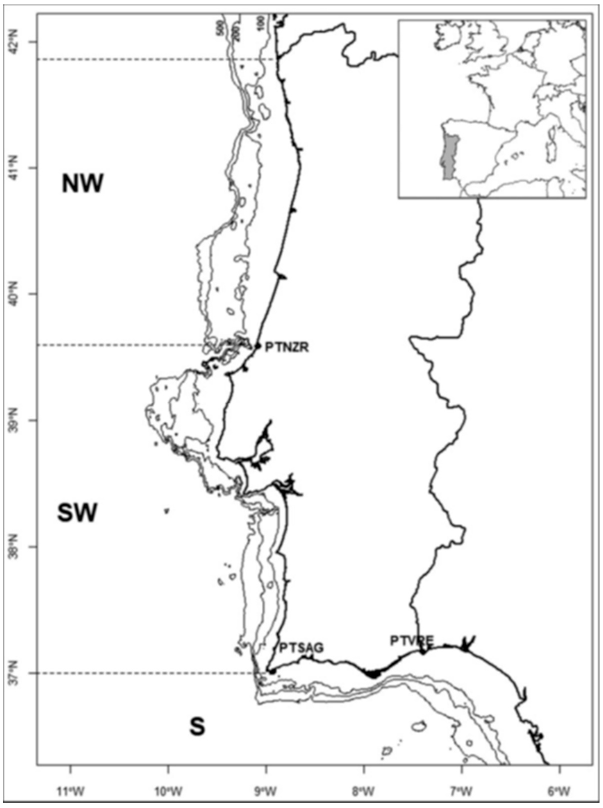


**Figure 1.** Study area. Portuguese Iberian Peninsula, showing depths isobaths and the three distinct geographic areas defined by noticeable geomorphological features.

## 2. Materials and Methods

### *2.1. Data exploration*

Horse mackerel is the main target species of the Portuguese bottom trawl fishery. From 2010-2020 bottom trawling consistently constituted the dominant gear for harvesting this species. The landings of horse mackerel in Portuguese auctions are performed by size categories, following EU regulation [25] and the landings distribution by size-category from 2010-2020 is primarily among the size categories ranging from T3 to the T5. However, in certain years we observed substantial landings of the smaller size-category T6 and the larger T2. The mean length of horse mackerel across different size categories exhibited notable stability throughout the period from 2010 to 2020. This consistency is indicative of economic reasons, as maintaining stability in length aligns with economic interests, especially given the significant variations in the price of horse mackerel by size categories. A detailed description of the landings distribution by fishing gear, size-category and mean length of horse mackerel across different size categories from 2010-2020 can be found in Supplementary material (Figures S1 to S4).

Discards are estimated by Portugal since 2014 from national at-sea sampling programmes on board commercial vessels operating in the area. Discards are usually very low and not frequent thus being considered negligible [26]. For the purposes of this study, we will use the terms landings and catch interchangeably in reference to the data.

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To describe the spatial and seasonal patterns of this fishery, horse mackerel catch length composition along the Portuguese coast was estimated by fishing trip using the estimated length composition by size-category obtained from the onshore sampling scheme and following the raising methodology detailed in Azevedo et al. (2020, 2021) [24,27]. Horse mackerel bottom trawl landings and size-category were coupled with the corresponding bottom trawl VMS trip records to characterize the spatial distribution of the landed size categories along the Portuguese coast (Table 1). Bottom trawl effort was estimated by applying vessel-speed criteria between 2 and 5 knots [28] to identify VMS records that correspond to fishing activity. Catch data by trip are assigned to the trip VMS positions based on the sales date recorded at auction and the assigned landing date. The total landings by size-category assigned to each trip were uniformly distributed by all VMS fishing records of the trip, proportionally to the effort in each point. To correctly allocate bottom trawl trip landings to each area, only single-area trips were considered, accounting for 77% to 87% of horse mackerel bottom trawl catches between 2010 to 2020. Depth information of fishing activity locations was added to the VMS records by overlaying them on a 1-min depth grid layer obtained from the website Satellite Geodesy (Global Topography, Measured and Estimated Seafloor Topography, https://topex.ucsd.edu/cgibin/get_data.cgi). Duplicate records and spurious values in position, speed, effort and catch were identified along the process and removed from the subsequent analysis. The catch-at-length composition by trip was subsequently converted into catch-at-age, based on information collected within the National Biological Sampling Programme, in which individual fish ages are determined counting the growth bands in otoliths following the guidelines from the ICES age reading workshops [29]. Since, according to the birth date convention, the youngest fish caught in the second semester are aged "zero" [30,31], semester Age-Length Keys (ALKs) were computed and applied to the estimated catch-at-length in the corresponding semester. Fish of 11 years and older were pooled into age 11+ as used for stock assessment purposes [26]. By converting the catch-at-length composition into catch-at-age data, this study aims to unravel the age composition patterns of the species. The analysis of age groups and their seasonal and depth patterns can offer a deeper understanding of the life history and behavior of southern horse mackerel, shedding light on their spawning seasons, migration patterns, and habitat preferences.

**Table 1.** Description of data (type, resolution and data basis) applied in the period 2010-2020.

| Type | Time | Space | Basis |
|---|---|---|---|
| Catch-at-length (number) | Trip | 0.05º x 0.05º | Landings (weight) by trip recorded at auction by size-category * length-weight relationship |
| Catch-at-age (number) | Trip | 0.05º x 0.05º | Catch-at-length by trip * semester Age-Length Keys |
| Effort (hours trawling * kW) | Daily | 0.05º x 0.05º | VMS data (time by trawling fishing positions) * vessel power information (from EU Fleet Register) |
| Depth (meters) | | 0.05º x 0.05º | Satellite Global Topography |

Table 2 presents the final set of data used in this study with key information about the fishing activity from 2010 to 2020 including the number of boats, total trips, trawl hours, average engine power (measured in kilowatts, kW), and average depth (meters). Analyzing this data provides insights into how fishing operations have evolved during this time. The number of active vessels has remained relatively stable, fluctuating between 34 and 43. This stability is reflected in both the total number of trips and trawl hours. While the average engine power shows a slight decline over the analyzed period, the average trawling depth remains close to 100 meters. The absence of noticeable trends or significant changes in these factors suggests a consistent fishing intensity and strategies. The lack of substantial shifts in the data has important implications for interpreting catch data, indicating a certain stability in fishing practices over the studied period

**Table 2.** Summary of data (vessels, effort, depth and catch) in the period 2010-2020.

| Year | Number of vessels | Total number of trips | Total trawl hours | Average engine power (kW) | Average depth (m) |
|---|---|---|---|---|---|
| 2010 | 38 | 4352 | 53683.1 | 538.9 | 97.6 |
| 2011 | 35 | 3842 | 52479.5 | 529.1 | 99 |
| 2012 | 37 | 4412 | 54449.0 | 529.3 | 107.5 |
| 2013 | 34 | 4093 | 46158.2 | 523.8 | 114.1 |
| 2014 | 36 | 4279 | 53240.3 | 526.8 | 119 |
| 2015 | 43 | 4537 | 59361.8 | 519.6 | 111.8 |
| 2016 | 43 | 4778 | 52682.5 | 516.7 | 114.4 |
| 2017 | 39 | 4577 | 61092.6 | 515.3 | 110.9 |
| 2018 | 42 | 4511 | 64709.4 | 514.1 | 102.3 |
| 2019 | 43 | 4721 | 65473.4 | 495.5 | 94.9 |
| 2020 | 42 | 4736 | 68020.0 | 465.1 | 100.9 |

### *2.2. Effort data distribution*

Indices of relative abundance and composition data representing the proportions of the sampled population within different age, length, sex, or weight categories directly inform trends in population biomass [32]. Catch-per-unit effort (CPUE) is a measure of the amount of fish caught per unit of fishing effort, such as the number of fish caught per hour of fishing and is often used as an index of abundance in stock assessment models. Fishery-dependent indices are subject to various factors that can challenge the assumption of proportionality to abundance [33]. One of the major challenges when utilizing these indices is that fishing effort is not uniformly distributed in time and across the stock area. Instead, it tends to concentrate in regions where fish abundance is higher and when market demand is higher. To address these issues, exploratory analysis was performed on the spatial distribution of daily fishing effort measured in trawling engine power*hours (kW*hour). The exploratory analysis also aimed to assess potential changes in fishing effort and targeting strategies that could affect the fishery catchability from 2010 to 2020. A detailed description on fishing effort distribution and selectivity can be found in Supplementary material (Figures S5 to S8).

Results show that fishing effort was stable over the analyzed period, with no significant trend observed (Figure S5). Catches of horse mackerel have remained relatively stable over time. Despite the increasing fishing opportunities for this stock, the fishing industry has maintained a consistent effort level towards horse mackerel in order to stabilize its commercial value [34]. Commercial fishing vessels often concentrate their efforts in specific target areas where fish are abundant. Target fishing grounds for trawlers are also conditioned by morphological traits and protection legislation, such as operation restrictions in areas near the shoreline, which can lead to overestimation of abundance in some areas and underestimation in other areas and/or ages. Although age 0 individuals do not seem to be well recruited in the trawl fishery, overall, the total catch by age of horse mackerel trawl fishery has not changed significantly from 2010-2020 with a consistent pattern of catches and most occurring between ages 1 and older (Figure S7). This could indicate a lack of significant changes in factors affecting fishery catchability, such as changes in the fishing gear and targeting strategies. This is important as a varying selectivity for different sizes of fish can introduce bias in our estimates of abundance, whether measured by length or age [32].

Figure 2 shows the auto-correlation function (ACF) and partial auto-correlation function (PACF) between the fishing effort and the preceding observations on various days. Autocorrelation measures the correlation between the amount of effort and its lagged values, while partial autocorrelation focuses on the unique correlation between the variable and a specific lag, excluding the influence of intermediate lags. In the context of this analysis, the fishing effort exhibits a notable autocorrelation, particularly in consecutive days, indicating a persistent relationship with its past values. Additionally, the strong weekly cycle observed in the autocorrelation function suggests a recurring pattern every seven days. This weekly cycle in fishing effort can be attributed to the economic weekly cycles of buyer's demand in the auction market that fishermen typically align their effort. Fishermen often strategically align their fishing efforts with these weekly demand fluctuations, resulting in the pattern observed in the autocorrelation function. The partial autocorrelation function further refines our understanding by isolating the direct influence of specific lagged observations. Together, these functions provide insights into the temporal dependencies within the fishing effort data.

Spatial distribution also showed to some degree a cyclic behavior evident in the distribution of effort by latitude depicted in Figure 3. The empirical variogram between all pairs of fishing locations shows a non-monotonic structure with a cyclic pattern (Figure S7). Although a large coverage of the spatial trawl effort is available, there are patterns in the total amount of effort exerted across the identified fishing grounds. For example, the fishing grounds among the defined geographic areas (NW, SW and S) are clearly divided by geomorphological traits where no effort is exerted. The number of vessels identified and consequently the effort in the South region was clearly inferior to the other areas (Figure 3). Moreover, horse mackerel fishery distribution in the Southern region is characterized by the widespread presence of adult fish ranging from coastal waters to over the slope [24]. We opted to exclude the South region from subsequent analyses because of the low effort and catches, and identified specific and narrow fishing grounds that could lead to inadequate coverage of this area. This exclusion was considered necessary to mitigate the potential introduction of significant bias to the age distribution within the study area.

As expected, there were several difficulties associated with using commercial effort data for estimating abundance. Time and spatial non-randomness were observed in our fishing effort data, characterized by a pronounced weekly cycle and under-sampled and/or unsampled grid cells. Using the complete spatial resolution of 0.05ºx0.05º for abundance estimation and including the South region in our analysis had the potential of introducing a substantial bias. Consequently, our analysis and framework concentrated on the two areas (NW, SW) with broader coverage of fishing effort.

Given the robust weekly pattern in fishing effort associated with market week cycles, effort values were averaged on Julian weeks and for each geographic area. Our simple average smoothing approach is expected to overcome the issues above referred and we considered it appropriate to standardize our effort data.

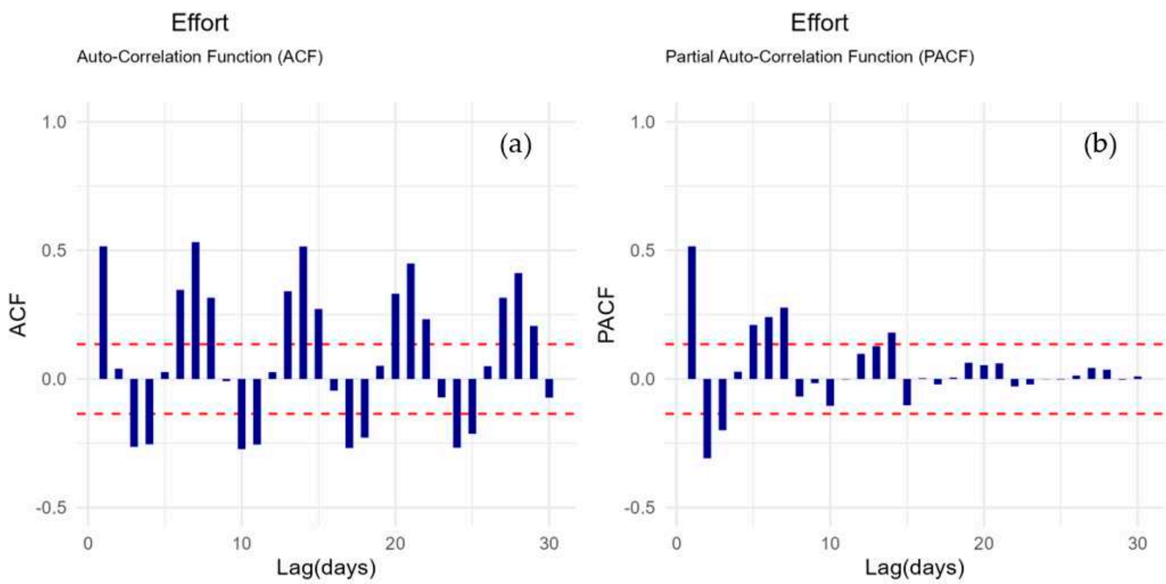


**Figure 2. (a)** Auto-correlation and **(b)** Partial auto-correlation function between fishing effort at different daily lags. Fishing effort is correlated each consecutive day and shows a strong weekly cycle.

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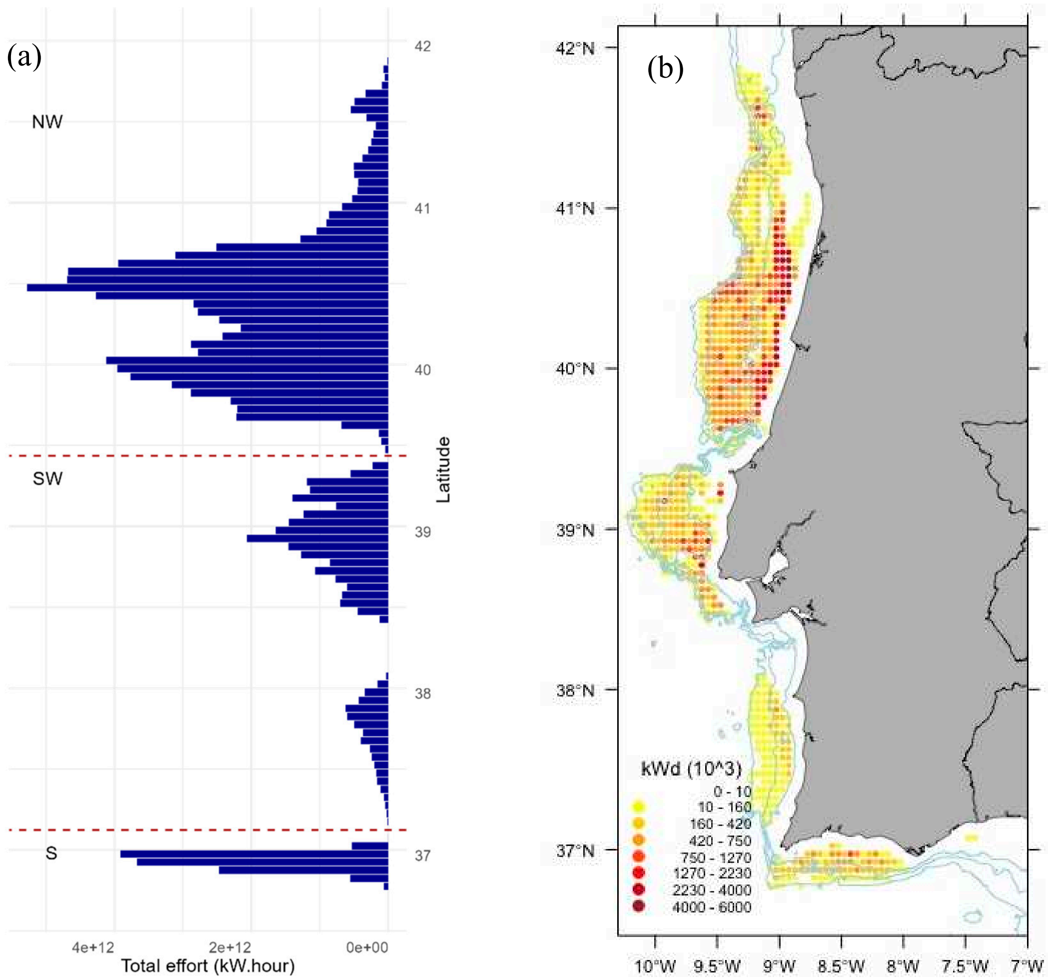


**Figure 3. (a)** Distribution of effort by latitude and **(b)** corresponding spatial distribution in 2010-2020 showing the 100m, 200m and 500m isobaths.

Integrating the VMS effort data with the onshore sampling scheme for horse mackerel, coupled with biological and commercial data, yielded spatial weekly catch-at-age abundance indices encompassing age groups from 0 to 11+. Subsequent analysis of this dataset aims to evaluate migratory patterns, as previously indicated in studies, and support the effectiveness of this framework in optimizing the use of high-resolution commercial data for improving fisheries management.

*2.3. Statistical analysis*

The age composition catch data from ages 0 to 11+ can be viewed as an ordered categorical response, comprising the count of individuals in each age group normalized by fishing effort to achieve a CPUE abundance index. If there are only two groups present (e.g. juvenile, adult), the response can be considered binary. In this scenario, standard logit transformation and modeling tools such as generalized linear models (GLM) or generalized additive models (GAM) can be applied, as previously tested by Azevedo and Silva, 2020 [24]. Conversely, in cases where more than two groups are present, the response is multinomial, and a standard logit transformation is unsuitable. In our study, the variation in multinomial catch-at-age data was performed by continuation-ratio logits. In the multinomial case, a response probability is described by multiple logits and a unique feature of continuation-ratio logits is that the various logits for a response can be viewed as logits for

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independent binomially distributed data [35]. Continuation-ratio logit models (CR model) have the advantage over other ordinal regression methods in that it is very easy to remove or loosen the proportional odds assumption. This allows for all covariates or some subset of covariates to be able to freely vary with every level of a category [36]. This is particularly useful since the proportional odds assumption is not accomplished for every age group derived from the trawl nets selectivity.

The response variable is the age group, $a$ = R…A, where $R$ denotes the recruitment age and $A$ the oldest age class category. The CR model is then well suited to model the distribution of ages through $A$ minus $R$ models for the conditional probability of being of age $a$ given that it is at least age $a$, $P(Y = a|Y \geq a)$. The continuation-ratio logits are then defined as [36]:

$$log\left(\frac{P_a}{P_a + \cdots + P_A}\right), a = R \ldots A - 1 \quad (1)$$

Continuation-ratio logits have the particular feature that the different logits for a response can be regarded as logits for independent binomially distributed data. Each logit can then be analyzed separately by means of a generalized linear model. This approach enables the application of generalized linear models separately to each level of the logits, facilitating the analysis of the variation in multiple age categories [37].

We combined CR models to generalized additive models, allowing for the analysis of ordered multinomial responses with separate linear or non-linear terms for each age category using Vector Generalized Additive Models family functions [39] for fitting VGAM models. A VGAM model was fitted using a logit link as a function of the discrete variable fishing *area* (Northwest and Southwest) and in this study we also describe how smooth functions of continuous variables *depth* and *Julian week* are suitable for describing each age distribution CR models.

Individual linear and non-linear effects on each combination of the response and predictor variables were performed to analyze the parallel assumption (*i.e.*, no input variable has a disproportionate effect on a specific age level). In instances where the parallel assumption was violated, a modification of the CR model was applied where a set of predictor coefficients was estimated for each individual age category. This flexibility is particularly useful when the parallel assumption is not met by accounting for potential differences in the predictor variable effects across different categories of the response variable but can be computational challenging [39]. Several combinations of predictor variables were tested on parallel, non-parallel or partial parallel models and the selected age distribution model was chosen based on the deviance explained and AIC values.

All analyses were carried out using the R software, version 4.3.2 [40] as well as the extension packages *VGAM* [39]. The spatial data were analyzed with the package *sp* [41] and the visualization performed with *ggplot2* [42].

## 3. Results

### *3.1. CPUE-at-age distribution*

The age selectivity of our sampling commercial vessels remained consistent between 2010-2020 and most catches occurred between ages 1 to 6 as these ages appear to be better represented in the catch-at-age data (Figure 4). There could be several factors contributing to this pattern, including the greater availability of these age groups for the specific fishing grounds and the gear used by the horse mackerel trawl fishing fleet. Still, the decreasing trend observed with ageing fish is to be expected by the increased mortality and lesser availability to the fishery and provides some confidence that our abundance indicator is able to follow horse mackerel cohorts. Notably, age-0 individuals do not seem to be well recruited in the trawl fishery, suggesting a potential gap in the abundance index for this specific age category.

Visual inspection on the mean catch per unit effort at different ages (CPUE-at-age) between 2010 and 2020 shows inter annual temporal variability (Figure 4a). The CPUE-at-age exhibits fluctuations across these years, with some values clearly above the average in successive years. This could suggest the presence of robust year classes, where certain age groups of the fish population exhibit notably higher catch rates over consecutive ages. Another key aspect revealed by the CPUE analysis is the

 doi:10.20944/preprints202401.0172.v1



existence of age specific seasonal patterns as shown by our aggregated data by Julian week. Variability in CPUE-at-age is evident over different weeks, suggesting age dependent seasonal variation (Figure 4b). The combined average catch per unit effort at different ages reveals distinct seasonal patterns for various age groups. Younger fish at age-0 and age-1 appear to be more available during the winter and autumn seasons. For age-2 and age-3, a less defined seasonal pattern is observed, with their occurrence primarily from the beginning of the year until early summer. In contrast, fish at age-4 and older exhibit increased mean abundance in the spring season, suggesting a potential association with their increased availability to fisheries during the spawning season. Although, this species is recognized as a multiple spawner with relatively extended spawning season (Gonçalves et al. (2008). The simple average smoothing method effectively eliminated the pronounced economic weekly cycle and associated variability. Mitigating this variability successfully identified some seasonal patterns and addressed a potential bias in using commercial effort data. This emphasizes the importance of considering temporal dynamics and filtering data with specific timeframes

The visual inspection of aggregated CPUE-at-age by geographic area already reveals some patterns. Notably, the NW area is characterized by a concentration of younger individuals, while a gradual shift in mean CPUE of older individuals is observed towards the SW area (Figure 4c). The CPUE-at-age over the three different depth strata provides some insights in the age distribution of horse mackerel individuals by depth, revealing the stratified nature of the population resulting from ontogenic migrations. Younger individuals predominantly occupy shallower strata, gradually shifting to deeper strata with age. However, even though older individuals (beyond age 5-6) prefer deeper waters, there are also occurrences of younger individuals in these deeper strata (Figure 4d). This feature adds some complexity in the distribution of this adaptable species and the need for a careful approach in assessing the habitat preferences of different age groups. The observed spatial and temporal distinctions and transitions highlight the importance of understanding the distribution of age classes, emphasizing the complexity of age-specific behavior across multiple areas and temporal periods.

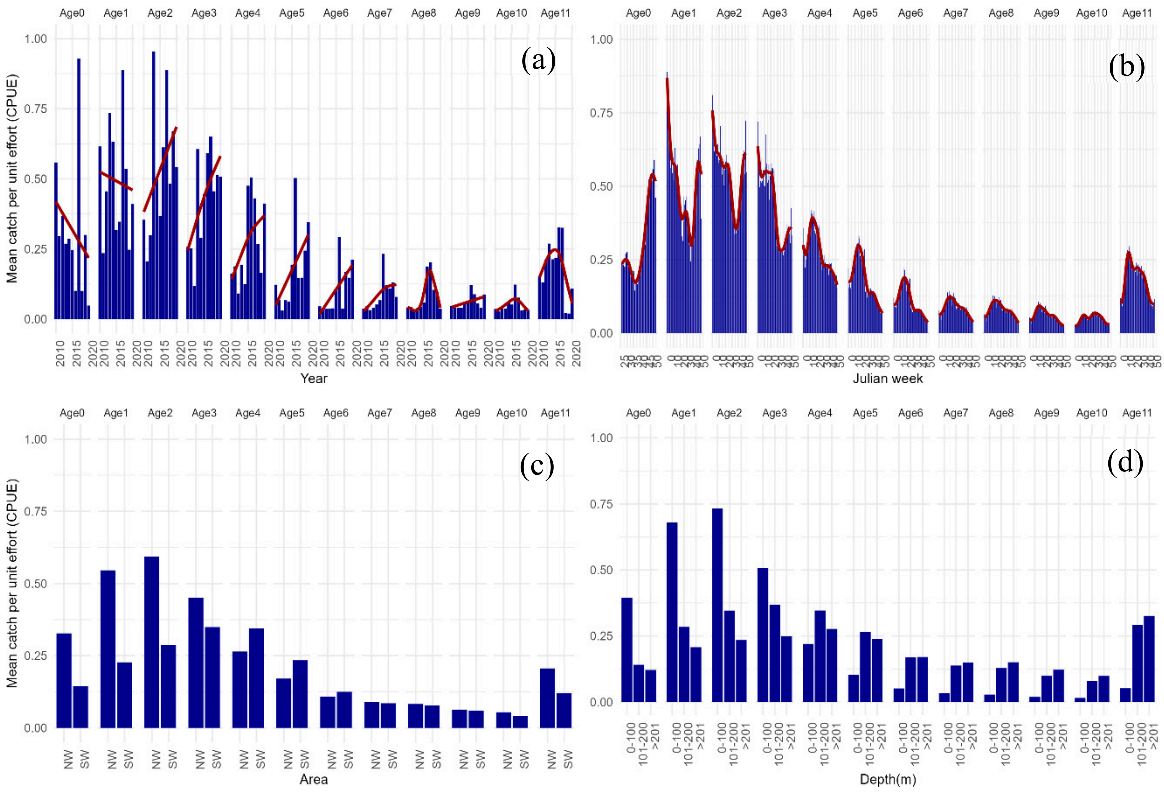


**Figure 4.** Mean catch per unit effort from age-0 to age-11+; **(a)** Large year variability between 2010-2020; **(b)** age seasonal variability by Julian week; **(c)** regional variability in NW and SW areas; **(d)** age

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vertical distribution by depth strata, 0-100m, 101-200m and >201m. Smoothed trends are represented by the red lines.

To further enhance our visual exploration of age-dependent migrations, Figure 5 illustrates the proportion of CPUE-at-age across Julian weeks for each year, categorized by depth levels, 0-100m, 101-200m and >201m and in the NW and SW geographic areas. By examining the diagonal panels in each age/year plot, we can effectively trace the proportion of each age/year class within spatial variables depth and area throughout the Julian weeks of each year and provide a more detailed illustration of the age specific distribution, without relying on the filtered aggregated mean abundances. This approach shows a more detailed depiction of how age distributions vary across both temporal and spatial dimensions. The plus group age 11+ was removed from the analysis because this group consists of surviving members from previous ages resulting in a combination of several cohorts in this group that could confound the analysis. Figure 5 also highlights the trajectory of the 2010 cohort, providing a representation of its path over time. Additionally, in Figure S9, we present the spatial distribution of the 2010 cohort, offering an illustration of this cohort geographical dispersion as an example.

Examining the distribution of age groups based on the proportion of abundance in the two studied geographic areas reveals some distinct patterns. Age-0 despite not being completely recruited in the trawl fishery and only available from the second semester, it is visible that the majority of age-0 are concentrated in the NW area. Age-1 and age-2 also exhibit higher availability in the NW region, with some concentrations observed in the SW area. Age-3 appears to have an equal distribution in both regions, showing a more pronounced seasonal pattern in the SW area, where the majority of this age class is prevalent in the mid-year. Older individuals demonstrate a higher prevalence in the SW region, although in specific age/year classes, they are also observed in the NW area. Analyzing the trajectory of each year class enables our hypothesis of younger ages in the northwest area that progressively move to south returning to north at older ages. Moreover, there appear to be consistent trends and patterns among the various age/year classes that suggest the presence of stable migratory behaviors.

Analyzing the proportion of age abundances in three depth strata, 0-100m, 101-200m and >201m shows that younger age groups, from age-0 to age-2, are primarily concentrated in the shallower strata, although there are observable occurrences in the deeper strata. Age-3, on the other hand, displays a more balanced distribution across all three strata, with some variability observed among different year classes. Age-4 and older individuals are much more frequent in the intermediate and deeper strata with minimal occurrences in the shallower strata throughout the year. The prevalence of older ages at deeper strata is evident supporting the hypothesis of ontogenic migration to deeper areas.

The visual representation of both aggregated and proportional age abundance indices has revealed consistent trends and patterns within different age/year classes. These observations indicate the existence of stable migratory behaviors along the western coast, extending to various depths.

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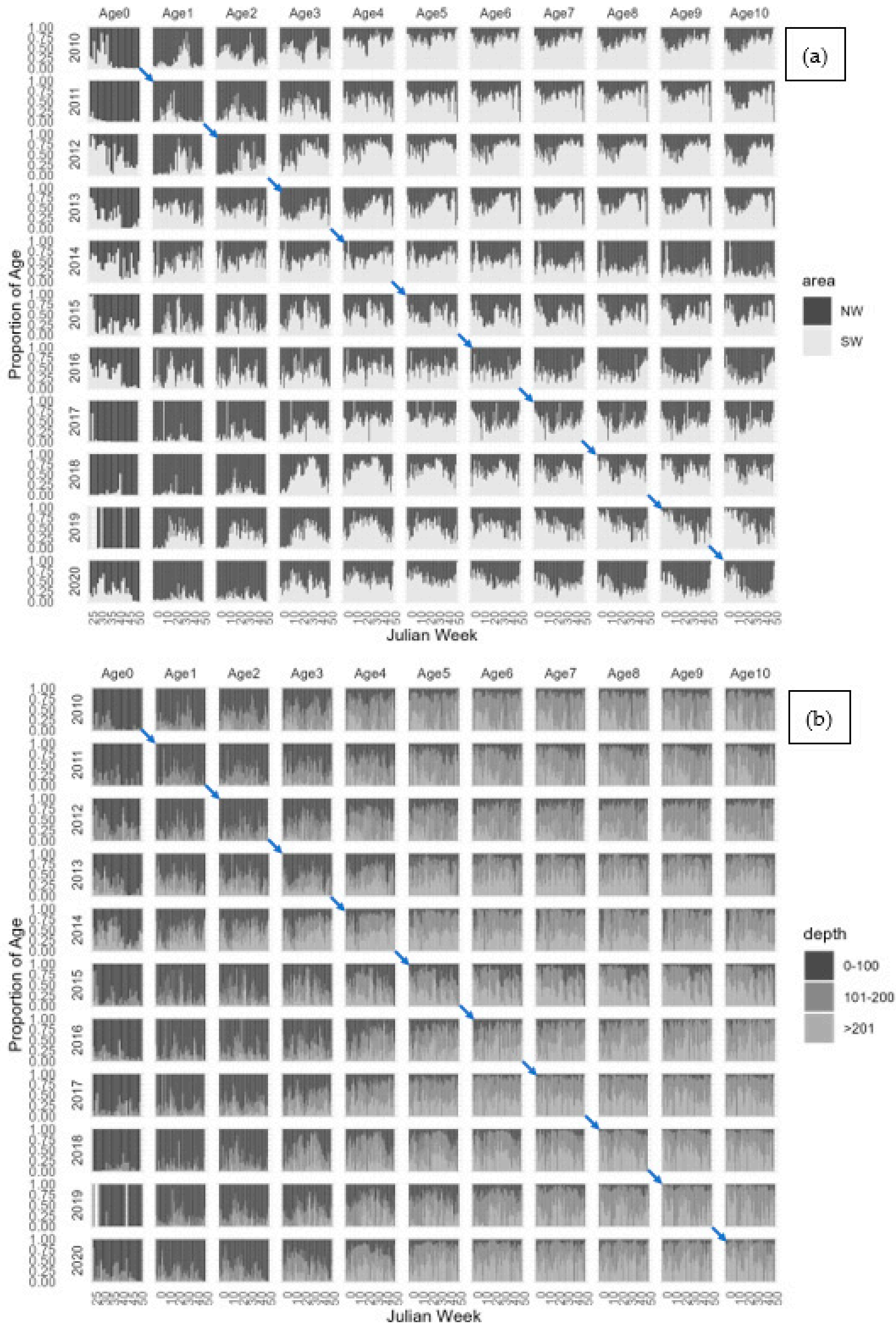


**Figure 5.** Weekly CPUE-at-age from 2010-2020 in **(a)** Northwest (NW) and Southwest (SW) Portuguese areas and by **(b)** depth levels, 0-100m, 101-200m and >201m. The diagonal panels in each age/year plot trace the proportion of each age for a given year class. Blue arrows represent the 2010 cohort trajectory from age-0 to age-10.

*3.2. Model results*

Using the CPUE-at-age as abundance indicator for horse mackerel we explored the age probability distribution of horse mackerel within the available cohorts in our data. Age-0 was

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removed from the CR models because this age class is not completely recruited to the trawl fleet. Parallelism or proportional assumptions were checked before proceeding with the CR model. Preliminary exploration suggested an intermediary model between the parallel and the non-parallel model where only some of the explanatory variables are parallel and others not. Detailed outputs of the VGAM function for the CR models tested including parameter estimates, significance and model diagnostics are available in Supplementary material (Tables S1, S2).

Several models were tested for age groups, a = 1…10 and the multiple logits of the conditional probabilities $P(Y = a|Y \geq a)$. The selected model chosen based on the improved AIC and deviance explained can be written as follows:

$$logit\ P(Y = a|Y \geq a) = \alpha_a + \beta_a area + s_a(Julian\ week) + s(depth), \quad (2)$$

where *s()* represents vector cubic smoothing splines for each age and the conditional probabilities are modeled as a function of categorical variable *area* and smooth terms for continuous variables *Julian week* and *depth*, treated as unparallel and parallel processes, respectively in the model. It states that *area* and *Julian week* variable effects should not be the same in all the categories as opposed to *depth* where the effect is the same across all the age categories.

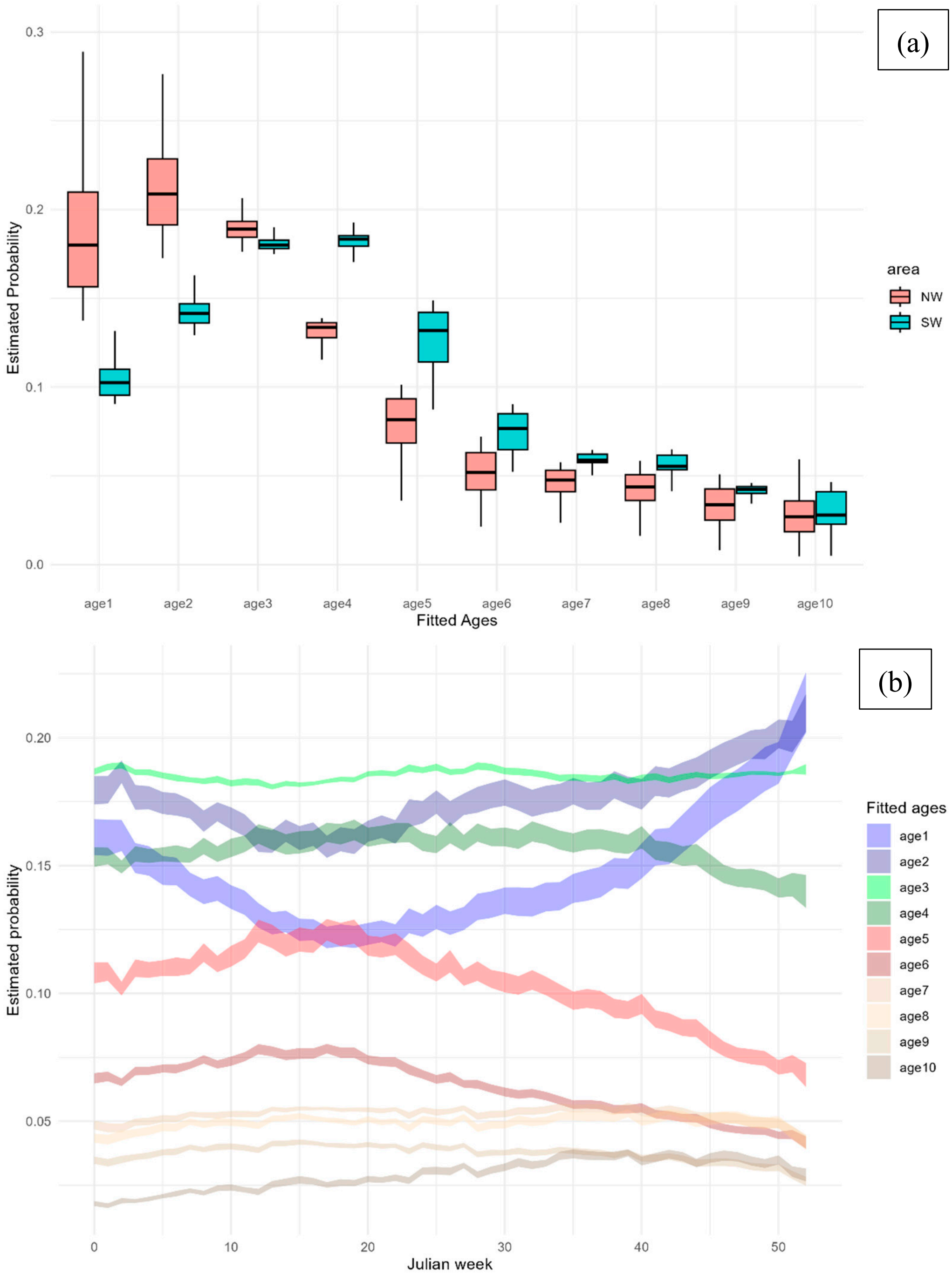
The CR model predictions revealed that age probabilities across geographical areas have distinct patterns. In the younger age groups (age-1 and age-2), a higher probability is observed in the Northwest (NW), age-3 has similar probabilities between areas while from age-4 to age-6 an area shift occurs, and these age groups become more prevalent in the Southwest (SW). Older age groups exhibit comparable probabilities in both areas (Figure 6a). A reliable indicator of age-dependent migrations is the increase or absence of decrease in the abundance of a specific age/year class within a given area, accompanied by a corresponding decrease of the same year class in an adjacent area.

Furthermore, the examination of age distribution across Julian weeks exposes some seasonality patterns. Age-1 and age-2 exhibit similar patterns, with a higher occurrence during autumn and winter. Age-3 and age-4 display a less pronounced seasonal pattern, with relatively uniform probabilities throughout the year. Age-5 and age-6 increase in the probability of occurrence from the beginning of the year until early summer. Older individuals exhibit a less pronounced seasonality pattern (Figure 6b).

Age distribution with respect to depth also reveals distinct patterns across different age groups. Age-1 and age-2 exhibit a similar pattern, characterized by higher abundance in shallow waters, gradually decreasing with depth until reaching 150 meters, although also occurring below this depth. Age-3, on the other hand, displays a relatively consistent occurrence across all depth levels. Ages-4 to age-6 share a common pattern, exhibiting reduced presence in shallow waters and a gradual increase in occurrence as depth increases, peaking around 125 meters. In contrast, older age groups demonstrate a predominant occurrence within the depth range of 100 to 150 meters, with a slight decline in abundance observed at greater depths (Figure 6c). Although the selected CR model was fitted assuming parallelism in the depth effect, a deviation from this effect is evident in the predicted estimated age probabilities. This distinct pattern, observed in the data, may be attributed to the combination of the several predictor variables included in the model.

 doi:10.20944/preprints202401.0172.v1





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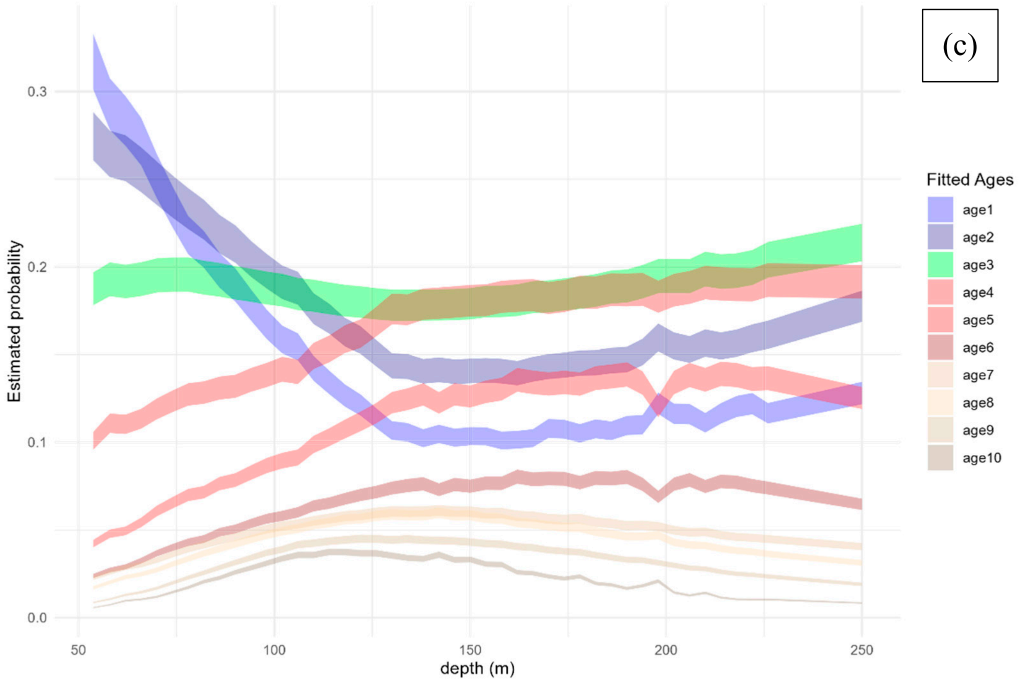


**Figure 6. (a)** Boxplots of predicted age probability of occurrence in each of the categorical area levels and average predicted probability with 95% confidence interval by (**b**) Julian week and **(c)** depth. (Outliers not shown in the boxplot).

## 4. Discussion

This study on the age distribution patterns of horse mackerel reveals important insights into the challenges associated with commercial fishery data collection. The study employs a fine-scale framework that exposes seasonal variations and patterns in the abundance of specific age groups, contributing to a comprehensive understanding of the spatial and temporal dynamics of age distributions in fish populations.

The continuation-ratio logit model proved to be a robust analytical tool for investigating age distributions. Specifically designed for analyzing ordinal categories, this model provides a practical framework for understanding sequential process where the response takes on successive stages over time [39]. Unlike other well recognized ordinal models such as cumulative models, these models do not encounter structural issues related to out-of-order cumulative probabilities or substantive dispersion effects [36]. Therefore, they could be applied effectively to our commercial trawl data, which is anticipated to contain some under-sampling of certain regions and depths and consequently age categories. The utilization of the continuation-ratio logit model combined with the flexibility of generalized additive modelling enabled the characterization of multiple age patterns, and various linear and non-linear relationships within the data. This combination showed a valuable and insightful approach for comprehensively analyzing age distributions and understanding the factors influencing the distribution of different age categories within the several cohorts available in our data. While some experiments were conducted involving interactions between time and spatial predictor variables this proved to be computational challenging in a model with already 50 parameters. However, it is important to note that further analysis should be undertaken to test the potential impact of interactions on the models predictions that can potentially improve the overall model fit.

The study acknowledges potential weaknesses, such as using horse mackerel effort and catch data from the bottom-trawl fishery and under-sampling of certain regions and depths. In fact, model fitting excluded horse mackerel data from the Southern area and from depth strata deeper than 500 m depth. It is noted, however, that horse mackerel catches from the Portuguese trawl fishery come mainly from the western coast (NW and SW areas) at depths <500 m and, also, that the analysis of the fishery strategy revealed a rather stable catchability over the analysed period. Moreover, while horse mackerel is commonly categorized as a pelagic fish, its behaviour on the Portuguese and Spanish coasts deviates from typical pelagic species. In these regions, it is primarily captured using bottom-trawl gear and assessed through scientific bottom trawl surveys, such as the ICES IBTS surveys. Research on the species distribution implies a demersal behaviour, especially during daylight hours, as observed in studies by Murta (2008) [8]. Dietary analyses further reinforce the species close association with the seabed as horse mackerel primarily consumes organisms likely obtained near the seabed, suggesting a stronger association with the sea floor compared to typical pelagic species [43]. Therefore, utilizing bottom-trawl for sampling horse mackerel was considered appropriate, without introducing significant bias to the data used in this study. The trawling fleet is the most important fishery for this species, nevertheless, catches are also obtained from other fleets operating in coastal areas (purse seine) and deeper areas (gillnets) [26] as fishing intensity can be distributed across a wide range of age groups. Enhancing the abundance index for younger age groups, particularly age-0, could be achieved by incorporating and applying the same framework used in this study to the purse seine fleet. Similarly, refining abundance indices for older age groups could be accomplished through the analysis of vessels employing gillnets that catch older and larger horse mackerel and enlarging the spatial scale to the northernmost and southernmost limits of the stock distribution. Still, the analysis of fine scale commercial data analysis has the potential to mitigate the shortcomings of scientific survey data, where a notable weakness lies in the uneven distribution of sampling across time, resulting in potential under-sampling of specific time periods.

Spatio-temporal analyses play a crucial role in accounting for variability in commercial sampling over space and time, since ensuring that the indices of abundance consider the spatial and temporal distribution of effort is essential for accurate abundance and composition estimates (Maunder et al). Using the whole spatial resolution of the data in the analysis can be problematic due to a small number of samples and missing data in particular areas, as commonly observed in commercial data. In addition to spatial variability, we also considered the temporal distribution of fishing effort. This study also revealed a strong week cycle of fishing effort related to auction market economic cycles. This is particularly important as fishing activity may fluctuate seasonally or over different time periods, leading to variations in abundance and age composition data. By accounting for these temporal dynamics, we can better understand the changes in abundance and composition over time. To mitigate this issue, a straightforward simple average smoothing method has been successfully implemented to reduce bias and deliver accurate information for the specific time (Julian week) and spatial scales (geographic areas) examined in this study. By incorporating these considerations, we provide a comprehensive framework for addressing the variability in effort, leading to more robust and accurate estimates of age abundance composition data for stock assessment purposes.

The study reveals a certain stability in horse mackerel age composition distribution, indicating a relatively constant population during the period 2010-2020, especially in the western Portuguese coast. Despite small variations, the analysis of catch-at-age per unit effort suggests seasonal patterns in the age composition, attributed to the horse mackerel behaviour and availability to fishing gears that could be related to the potential impact of spawning and feeding migrations on fishing yields. Geographical differences in the presence of juveniles and adults are observed, suggesting variations in the migratory behaviour across different areas. Ultimately, the findings suggest that horse mackerel may have a more continuous distribution throughout the year in the western area, with some regional variations and possible connections to migratory patterns to adjacent areas. Although the southern limit of the stock might be not adequately sampled, the observed complex age distribution patterns in the southern area may signal a mixed population structure, challenging the notion of a uniformly continuous stock in this region, as suggested by earlier studies. The southern limit of the southern horse mackerel stock is not as evident despite a previous study indicating that the populations off the north of Africa and the Iberian Peninsula are not part of a continuous stock [7].

The migratory patterns of horse mackerel stock in the region presently designated as the southern stock appear to be more intricate as outlined in the data analyzed in this study. Achieving a more detailed analysis of these behaviours is currently challenging, and this could be improved with increased temporal coverage and the incorporation of additional fleet information to enhance spatial coverage. The potential resolution of this limitation in the future involves integrating combined information from bottom-trawl, purse seine, and polyvalent fleets, offering a more comprehensive understanding of horse mackerel migrations along the Atlantic coast of the Iberian Peninsula. While tagging could also yield valuable insights into the movements of horse mackerel, it is worth noting that previous attempts have highlighted technical challenges in achieving an adequate survival rate for tagged individuals [7, 8]. Our analysis also reinforces horse mackerel ontogenic deepening with increasing size and age, suggested by Murta (2008) [8] using a time series of horse mackerel abundance from survey data and by Azevedo and Silva (2020) [24] by modelling the variation in the daily proportion of adult fish of the Portuguese bottom trawl catches in a single year of 2017. The latter study revealed interesting patterns in the distribution of adult and juvenile horse mackerel where the proportion of adult fish was found to increase from shallow waters up to a depth of approximately 220 meters, and then slightly decrease thereafter. Additionally, the proportion of adult fish increased from January to June, coinciding with the main spawning season of horse mackerel off the Portuguese coast.

A more detailed analysis of the age composition in this study revealed similar patterns with a finer examination of age groups. From the analysis of the predicted probabilities of the CR model, age-1 (entirely juvenile) and age-2 (64% juvenile) exhibit distinct seasonal and depth patterns, showing increased abundance in the autumn and winter seasons and a decline in abundance with depth until 150m. Age-3 lacks a clear pattern throughout the year and by depth, likely due to a mix of behaviours from both adult and juvenile (18%) individuals in this age category. Age-4, almost fully mature, follows a depth pattern similar to previous adult observations but lacks a discernible seasonal trend. For age-5 and older, the pattern aligns with findings from the prior study, indicating increased abundance with depth, a somewhat decreasing trend with depth in older ages and increased abundance from the beginning of the year until early summer also aligning with the spawning season of horse mackerel. The stratified nature of the population resulting from ontogenic migrations, with younger individuals predominantly occupying shallower strata and gradually shifting to deeper strata can be shown in age specific distribution.

This study revealed interesting insights into horse mackerel distribution range and age specific distribution from the Northwest (NW) area to the Southwest (SW) area. The findings indicate a pattern of age specific distribution, with the NW area characterized by a concentration of younger individuals, with a gradual shift in abundance observed towards the SW region from age-3 to age-6. Older individuals seem to balance in both regions and could indicate a return of older individuals to the NW area in the spawning season. There are indications that these older individuals are also more available in the northernmost distribution of the stock based on the Spanish IBTS survey in Galician waters and the catch profile of trawlers operating in the region [26]. The consistent trends and patterns observed across various year classes suggest the presence of migratory behaviours in horse mackerel.

Despite specific age related distribution patterns, there is also an evident ubiquitous presence of all age groups across different areas and depths, indicating a stable age composition distribution. This stability points to a relatively constant population during the period 2010-2020. Villamor et al. (1997) [44] similarly noted that horse mackerel fishery in the southernmost part of the Bay of Biscay occurs along the entire continental shelf throughout the year, with only slight spatial-seasonal variations in landings.

Horse mackerel, characterized by high genetic variability, possesses a broad foundation for adapting to various conditions and stressors. Additionally, the species notable vagility and gene flow indicates potential population connectivity and the ability to move about freely and migrate [7] which could also add to the species resilience in response to environmental and fishing pressures. Additionally, there is evidence of sustained reproductive capacity across the observed Spawning Stock Biomass (SSB) levels [26], with the species employing a multiple batch spawning strategy [45]. This strategy, distributing the risk to their offspring on a temporal and spatial scale as a more successful risk-spreading strategy, proves to be effective, especially in the context of diverse gear

 doi:10.20944/preprints202401.0172.v1



selection patterns [46]. In fact, this is the particular case of the southern horse mackerel stock which is explored by different gears with complementary size selection patterns [26]. These aspects collectively indicate the resilience of horse mackerel as a species, reflecting its ability to maintain recruitment, a widespread distribution and a rather stable abundance which could reflect in the absence of clearly defined age distribution patterns even in the presence of detailed fine scale resolution data.

There are several studies that collectively suggest that environmental factors can play a role in shaping the population dynamics and distribution of horse mackerel populations. The influence of several environmental factors, such as sea surface temperature (SST), wind components and oceanic transport indices can shape the distribution and spawning areas of this fish species [7][47][[48]. Growth and maturation can also be influenced by the photoperiod and winter upwelling along the Portuguese coast can negatively affect recruitment [49]. Our findings emphasize the need for further investigations to disentangle ecological factors influencing horse mackerel age distributions patterns and their implications for fisheries management. Furthermore, employing statistical analyses that incorporate multiple categories in the response variable, as in our analysis, is meaningful to identify the key aspects driving the dynamics of horse mackerel populations. The framework used in this study could enhance the importance of understanding the relationship between environmental variables and horse mackerel dynamics in the North Atlantic and Iberian waters, emphasizing the need to consider factors such as temperature, wind patterns, and oceanic circulation in future studies. The impact of these environmental variables on the mortality rates and distribution of the fish species could shed light on the complex interplay between climatic and oceanic conditions and the distribution and survival of life stages, notably early life stage, of this fish species.

Although our study focused on the age distribution patterns of horse mackerel, the method used for estimating time series of fishing-effort distributions from VMS data could have several potential applications in fisheries and environmental assessment and management. For example, it could be used to identify areas of high fishing effort and to assess the impact of fishing on the environment. It could also be used to evaluate the effectiveness of marine protected areas and to inform the design of spatial management measures. Additionally, the method could be used to compare fishing effort across different gears or over time, and to support the development of ecosystem-based fisheries management. There are implications of these findings for the management and conservation of horse mackerel populations in the Atlantic. The migrations of horse mackerel should be considered when designing management strategies, as well as the differences in recruitment patterns between different areas and depths. The study provides valuable information for understanding the ecology and dynamics of horse mackerel populations and could be used to inform future research on the species, ultimately contributing to a more informed fisheries management.

**Supplementary Materials:** The following supporting information can be downloaded at the website of this paper posted on Preprints.org, **Supplementary material_Data**: Figure S1 to S9 for exploratory data analysis on catch and effort; **Supplementary material_ Model**: Table S1, S2 and Figure S9 to S11 for vgam outputs of the Continuation Ratio Logit model results.

**Author Contributions:** Conceptualization, Hugo Mendes, Manuela Azevedo, Cristina Silva; data curation, Manuela Azevedo, Cristina Silva; formal analysis, Hugo Mendes; writing—original draft preparation, Hugo Mendes. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The data presented in this study are available on request from the corresponding author. The data underlying this article cannot be shared publicly due to VMS data provider confidentiality conditions. The data will be shared on reasonable request to the corresponding author.

**Acknowledgments:** We thank all the collaborators involved in the collection of biological data at the auction markets. We also like to thank the Portuguese Directorate of Fisheries (DGRM) for providing detailed landings and VMS data. This study was supported by the Portuguese National Biological Sampling Programme from the EU Data Collection Framework (PNAB/DCF).

**Conflicts of Interest:** The authors declare no conflict of interest.

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