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# Spatial heterogeneity of biological traits and effects on fisheries management based on the assumption of a single stock. The case of the common hake (*Merluccius gayi*) in Chile

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Understanding the spatial structure of fishing resource stocks is a fundamental aspect for the management and development of sustainable and productive fisheries. However, this aspect is usually simplified under the assumption of a stock unit, which assumes biologically similar and spatially homogeneous individuals, regardless of the real ranges and characteristics of their distribution. The persistence of geographic patterns in the biological traits of species suggests the spatial structuring of a population, a highly relevant aspect in stock assessment, calculation of Biological Reference Points (BRP), and management of fishing resources. In this work, the spatial heterogeneity of the biological traits of common hake (*Merluccius gayi*) from off-central Chile is modeled. Considering four reference zones, biological data collected over 26 years of monitoring fisheries and acoustic surveys is analyzed. The findings allow to biologically differentiate these areas whose main characteristics are the increase from north to south in the condition factor, gonad weight, and size at maturity. The Spawning Potential Ratio (SPR), fishing mortality, and BRP are calculated. Exploratorily, if these areas were considered closed subpopulations, results show that overexploitation is not a characteristic of all hake fishing areas, and that not considering the heterogeneity of biological traits causes the overestimation of the population condition in the main fishing areas. The aim of this research was to understand the spatial structuring of common hake based on the heterogeneity of biological attributes and its impact for fisheries management purposes.

## KEYWORDS

generalized linear mixed model, length-based pseudo-cohort analysis (LBPA), single stock, spatial biological traits, spatially structured population, spawning potential ratio

## 1 Introduction

Fisheries management has traditionally considered a single-stock hypothesis. This definition has often been based on administrative agreements, on historical fishing grounds, or for practical reasons. Current knowledge has shown that species with a limited spatial structure and which are genotypically and phenotypically homogeneous are an exception rather than the rule (e.g. Ames and Lichter, 2013; Ciannelli et al., 2013; Kerr et al., 2017; Gatti et al., 2020; Shackell et al., 2022). The common-pool assumption simplifies fish populations to a set of biologically similar and spatially homogeneous individuals, regardless of the actual ranges and characteristics of their distribution. The management and evaluation of stocks are often unaware of the spatial dynamics of the resources, arguing the lack of spatially explicit data (Guan et al., 2013). However, it is becoming increasingly difficult to support the stock unit hypothesis when examining the spatial heterogeneity shown by fishing data (Punt, 2019). Defining management units that are appropriate and consistent with spatial patterns is relevant for the sustainability of fisheries and the conservation of resources, even more so given that the number of overexploited populations has increased by 34% (FAO, 2020). Failure to recognize the spatial dynamics of a population in fisheries assessment and management could increase the number of overexploited resources (e.g. Frank and Brickman, 2000; Fu and Fanning, 2004; Cadrin and Secor, 2009) due to a high probability of estimating erroneous productivity levels and biased references. This may prevent reaching the established management objectives and affect the application of a stock assessment model, impacting the sustainability of the fishery, its profitability, and the resilience of the fishing communities (Kerr et al., 2017).

Trend differences between areas, as understood in the biological data series collected from fisheries, cannot be explained simply by selectivity effects (Punt, 2019). Rather, spatial heterogeneity in biological parameters (e.g. growth, fertility, maturity, and natural mortality) often provide evidence in favor of heterogeneous spatial structures in marine populations (e.g. Ciannelli et al., 2013; Canales et al., 2016; Canales et al., 2018; Shackell et al., 2019). In fact, the spatiotemporal patterns in the biological traits of a species (e.g. size and maturity) are characteristics typical of discrete populations with low levels of admixture (Cadrin, 2020). In this sense, spatiotemporal differences in environmental conditions are considered responsible both for the pattern of movement of individuals in a population (Keyl and Wolff, 2008) and for the distinction in individual biological traits. Notwithstanding assumptions of independent populations, several studies have shown evidence to support hypotheses of connected fish subpopulations under the metapopulation theory (e.g. Petitgas et al., 2010). Some examples are Atlantic cod (*Gadus morhua*) (Smedbol and Wroblewski, 2002), European anchovy (*Engraulis encrasicolus*) subpopulations (Traina et al., 2011); cyprinids (*Pogonichthys macrolepidotus*) in San Francisco estuaries (Feyrer et al., 2015), Atlantic herring (*Clupea harengus*) (McQuinn, 1997; Ware and Schweigert, 2001); European pilchard (*Sardina pilchardus*) in Galicia (Carrera and Porteiro, 2003); Chilean jack mackerel (*Trachurus murphyi*) in Chile

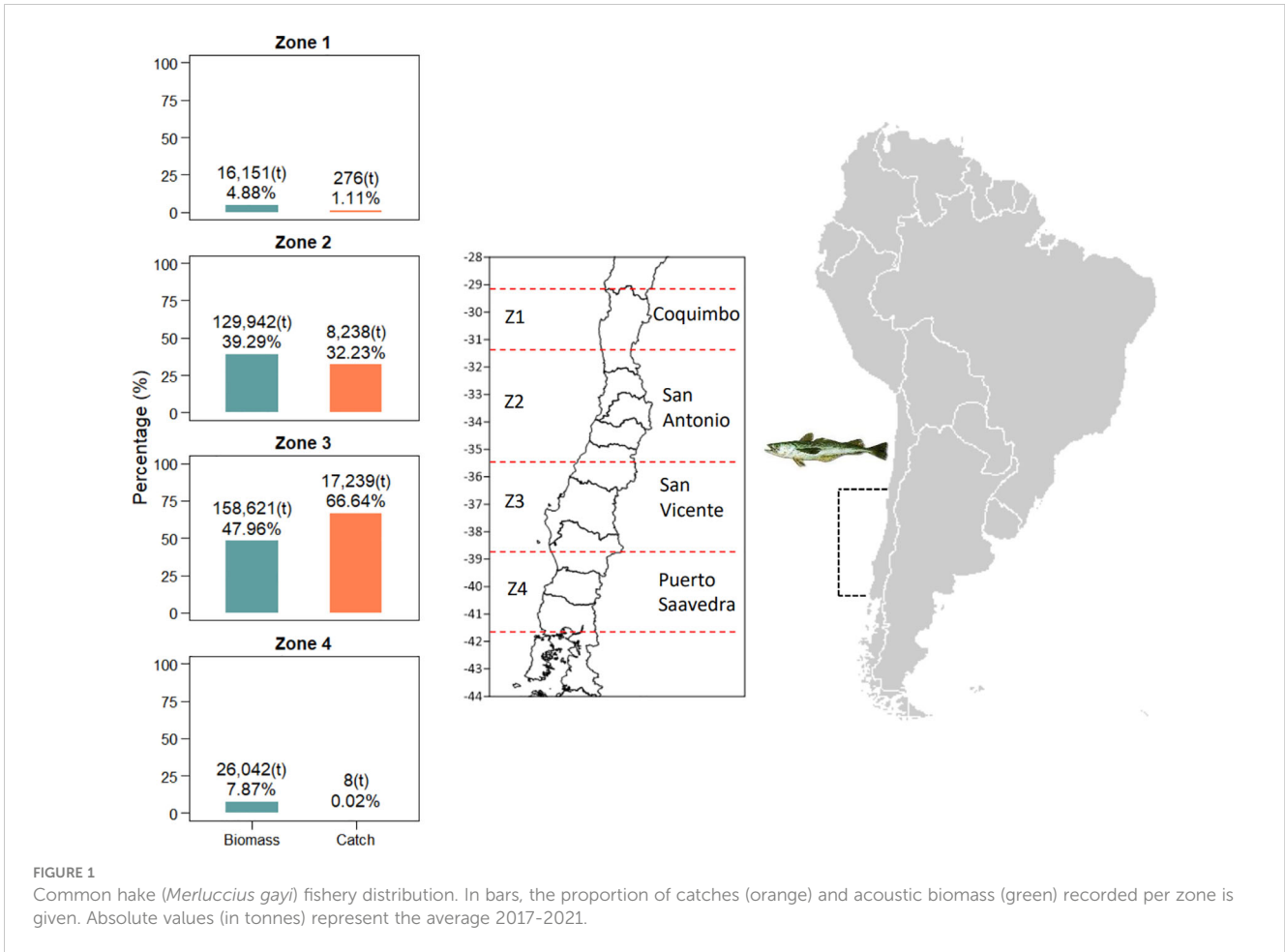
(Gerlotto et al., 2012); and anchoveta (*Engraulis ringens*) in the Chile-Peru Humboldt system (Canales et al., 2018).

From the fisheries management perspective, simulation exercises have shown that productivity estimates of fish populations improve substantially when the assessment models consider spatial structures (Hurtado-Ferro et al., 2014; Punt, 2019; Cadrin et al., 2020). Furthermore, while “traditional” population assessments view biological traits as invariant over time, studies have shown that environmental conditions explain the phenotypic expression of certain species. A phenotypic response to poor conditions (environmental and/or density-dependence) can be reflected in condition factor, inhibited growth rates, altered or modified physiology, changes in reproductive and ethological patterns (e.g. de Mérona et al., 2009; Van Beveren et al., 2014; Karjalainen et al., 2016) or due to fishing pressure (e.g. Engelhard and Heino, 2004; Sharpe and Hendry, 2009; Kuparinen et al., 2016). Evidence of this type of characteristics is recorded, for example, in the Fulton condition factor (weight) (e.g. Brosset et al., 2015; Canales et al., 2016) and in the maturity to size ratio (e.g. De Roos et al., 2006; Keck et al., 2014; Hunter et al., 2015; Brosset et al., 2016).

In Chile, one of the oldest and most important fishing populations is the common hake *Merluccius gayi* (Guichenot 1848), whose habitat is found in cold and poorly oxygenated coastal ecosystems off the coasts of Chile. It is distributed from 29°10'S to 42°00'S (Figure 1) at preferred depths between 100 and 200 m (Guevara-Carrasco and Leonart, 2008). The characteristics of the seabed off Chile and the dominant environmental variables in the hake distribution area are very distinctive and characteristic. The increased width of the continental shelf, particularly south of 35°S (Sobarzo et al., 2007), determines larval retention points (Payá et al., 1994), and favorable habitat conditions for the main prey that make up the diet of common hake, such as crustaceans, decapods, euphausiids, and clupeids (Arancibia and Fuentealba, 1993; Cubillos et al., 2003; San Martín et al., 2013). This species sustains an important fishery made up of an industrial bottom trawling fleet and an artisanal fleet operating with gillnets. The most recent annual landings reach an average of 25 thousand tons (SERNAPESCA, 2021) and, following biomass estimates reported by acoustic survey, they are mainly concentrated between 31°25'S and 38°39'S, corresponding to zones 2 and 3 (Figure 1).

Since the late 1970s, evidence of spatial heterogeneity of the biological attributes has been reported for this species. Among these, the work of Avilés et al. (1979) stands out, who, based on biological-fishing indices, migratory patterns, and monitoring of the reproductive process, propose the existence of three possible spawning areas. In the same sense, Balbontín and Fischer (1981) reported latitudinal differences in the size at maturity of hake, also corroborated by Payá et al. (1994), who in addition determined morphological differences and proposed the current four representative zones of the fishery. In addition, George-Nascimento (1996) analyzes the parasitic fauna, suggesting at least two ecological stocks. These researches indirectly account for the ecological heterogeneity of the common hake habitat and suggest differences in the spatial structure of its population.

Notwithstanding this, the management of this fishery assumes the existence of a single population (Aguayo-Hernández, 1995) and



estimates of biological productivity, expressed as annual catch quotas, are estimated based on the assumption of a homogeneous population with invariant life history parameters in time (Tascheri, 2022). In this sense, the main biological processes of common hake, such as reproduction and growth, are considered homogeneous in its extensive geographical distribution covering over 780 nautical miles (Figure 1). This population is currently overexploited (Tascheri, 2022) and it is unknown if this condition is homogeneous throughout its spatial distribution, a very relevant aspect to know in order to implement recovery actions for the hake population. Understanding the spatial structures of fish populations is essential for the development of sustainable and productive fisheries (Cadriñ, 2020). This work evaluates the spatial heterogeneity of the biological traits of common hake from biological samples collected over 26 years of fishery monitoring and acoustic surveys. Exploratorily, the four reference zones of the fishery are analyzed as closed subpopulations. The spawning potential ratio (SPR), fishing mortality ( $F_{cr}$ ), and biological reference points (BRP) are estimated by area of analysis. The impact of considering the spatial heterogeneity of biological attributes in population diagnosis and the prospects for the management and recovery of one of the most important fishing resources in the region is determined.

## 2 Materials and methods

### 2.1 Data source and study zone

Biological samples collected by the Instituto de Fomento Pesquero ([www.IFOP.cl](http://www.IFOP.cl)) from 1996 to 2021, both during fishery monitoring and by acoustic surveys carried out in the distribution range of common hake off Chile (29°10'S to 42°00'S) were analyzed. Fishery monitoring is carried out by a team of scientific observers both on board the vessels and in the main ports and landing coves for hake. On the other hand, the acoustic surveys are carried out between August and September of each year. The survey covers the continental platform between the 50- and 500-meter isobaths. Identification fishing hauls are carried out with bottom trawls on the continental shelf, following a systematic sampling on transects perpendicular to the coast with a spacing of ten nautical miles between them. The individual samples from fisheries corresponded to daily observations taken by landing port and consider, among other attributes: total length (TL), weight (total, gutted, and gonads), sex, and maturity status. Additionally, the haul depth data is included in the acoustic surveys sampling. The information was analyzed based on the four zones defined by Payá et al. (1994) used both in acoustic surveying and in fishery monitoring; zone 1:

29°10'S – 31°25'S, zone 2: 31°25'S – 35°30'S, zone 3: 35°30'S-38°39'S, and zone 4: 38°39'S – 42°00'S (Figure 1).

## 2.2 Statistical modeling

Generalized Linear Mixed Models (GLMM) (Breslow and Clayton, 1993; Tan et al., 2007; Stroup, 2012) were used to analyze the effect of various linear predictors on five biological variables of interest: total weight (TW), gonad weight (GW), gutted weight (GtW), total length (TL), and sexual maturity (Mat) by size. The models were specified and fitted using the language and environment for statistical computing and R graphics (R Core Team, 2020). The *lme4* package library (version 1.1-31) was used to fit linear (*lmer*) and logistic (*glmer*) models to the data. In all the models considered, the linear predictor was made up of the year as a random variable, while sex, quarter, and zone were considered as fixed effects.

Total length (TL) was considered as a continuous predictor variable in the models related to weight and sexual maturity. Similarly, depth was considered a fixed effect in the TL model fitted to acoustic survey data (Table 1). Weight measurements were transformed into a logarithmic scale and assumed to have a normal distribution, while the proportion of mature females was treated based on a binomial distribution and a logistic model considering a “logit” link function. The maturity data collected during fishery monitoring were considered only for the third quarter of each year (July-September), the described period of maximum reproductive activity of this species (Alarcón et al., 2008), coinciding with the moment in which acoustic survey are carried out (Molina et al., 2022). The maturity state was converted to a binary variable (*p*) according to the microscopy scale used by IFOP (Balbontín and Fischer, 1981). Females were considered fully mature for stage values equal to or greater than 3 (*p*=1), and in the other cases zero was set as the value (*p*=0). The size at which 50% of females are mature was calculated by zone using estimator.

$$TL_{50m,z} = -\beta^{-1}(\mu + Z) \tag{1}$$

TABLE 1 Generalized linear mixed models (GLMM) used to describe variability of biological traits (response variables) of common hake off Chile.

Response variable	Predictor variables		
	Fixed effects	Random effects	Continuous variable
Total weight	Zone+Quarter+Sex	Year	log(Length)
Gonad weight			
Gutted weight			
Total length	Zone+Quarter+Sex+Depth (*)	Year	
Maturity (**)	Zone+Quarter	Year	Length

(\*) Considered only in acoustic surveys data modeling.

(\*\*) Only females at 3th quarter were considered.

where  $\mu$  is the intercept of the model,  $\beta$  the TL coefficient, and *Z* the fitted model coefficient in each zone. The hypothesis of spatial homogeneity of biological attributes was evaluated based on the significance of the model coefficients (*p*-value), the *Z* statistic, and the 95% overlapping of confidence intervals.

## 2.3 Spawning potential ratio

We used the LBPA model (Length-based pseudo-cohort analysis) (Canales et al., 2021) to analyze the size compositions of the fishery (by combining data both gillnets and trawls) and generate estimates of the Spawning Potential Ratio (SPR) and fishing mortality by zone. The analyses assumed, exploratorily, that each zone could constitute independent population sub-units. Thus, and recognizing the biological relationship between growth and sexual maturity (e.g. Stamps et al., 1998; Froese and Binohlan, 2000; Araya and Pepe-Victoriano, 2010), the proxy of asymptotic length ( $L_{\infty}$ ) was calculated by zone (*Z*) considering the empirical relationship between the average size at first sexual maturity ( $\overline{TL}_{50m}$ ) and  $L_{\infty}$  average of both sexes estimated by Cerna et al. (2013) ( $L_{\infty}$ =63.6 cm, *k*=0.175) for the entire hake distribution area. The estimator used was:

$$L_{\infty,z} = \overline{L}_{\infty} \frac{TL_{50m,z}}{\overline{TL}_{50m}} \tag{2}$$

On the other hand, both the weight-size relationship parameters (*a* and *b*) and the sexual maturity ogive parameters, sizes at 50% and 95% maturity ( $TL_{50m,z}$  and  $TL_{95m,z}$ ), were calculated from the coefficients obtained in the GLMM model (see 2.2). For comparative purposes, the biological homogeneity scenario considered the growth parameters obtained by Cerna et al. (2013), while those of maturity and weight-length relationship corresponded to the average of the estimates obtained in this work. The instantaneous rate of natural mortality (*M*=0.33) corresponded to the value reported by Tascheri (2022). In order to represent the population status of the most recent period, the LBPA model was adjusted to the size compositions of the fishery over the last five years. The SPR value by zone represents the ratio of current spawning biomass to unfished or virgin biomass. This was calculated based on the spawning biomass per recruit (SSBPR) assumed at the beginning of the reproductive period.

$$SPR_z = \frac{SSBPR_{z,F=F_{cr}}}{SSBPR_{z,F=0}} \tag{3}$$

where  $F_{cr}$  is the full recruitment fishing mortality of the fishery. The SSBPR for the level of fishing mortality was calculated from a recruit analysis from the results of the LBPA model. For diagnostic purposes, the management objective established by the Undersecretariat of Fisheries and Aquaculture of Chile was considered, which corresponds to 40% of the virgin biomass. Thus, the reference fishing mortality corresponded to the equivalent  $F_{40\%} \sim F_{msy}$  (“proxy” of  $F_{msy}$ ) (SUBPESCA, 2023).

The LBPA model assumes equilibrium conditions in fishing mortality and recruitment. It also considers that selectivity is logistical and that the fishing effort is the main responsible factor for the depletion of the largest reproductive individuals. The model

details are given in [Appendix](#) and *a priori* parameters distributions are provided in [Table 2](#).

### 3 Results

Biometric measurements were analyzed from over 610,000 *M. gayi* specimens collected in fishery monitoring, and independently, over 76,000 specimens measured over 25 years of acoustic survey data. The highest frequency of the measured specimens showed sizes between 34 cm and 42 cm, with an average of 38 cm and 422 g of total weight. 60% of the samples consisted of females with average sizes around 40 cm TL, larger than the males (36 cm TL). The prevalence of mature females (reproductive stage greater than three) is higher during the third quarter, when their sizes reach an average of 41.4 cm ([Figure 2A](#)). A boxplot diagram of the average size shows that, regardless of sex, the average size of individuals increases from north (zone 1) to south (zone 4), as does their variability range ([Figure 2C](#)). In zone 1, the fishery is mainly artisanal with gillnets. In zones 2 and 3, artisanal fleets and industrial trawlers operate simultaneously, the latter outside the first 5 nm. Also, this information shows there are no substantial differences neither patterns in mean length between fleets (e.g. zones 2 and 3, trawl vs gillnet) ([Figures 2B, D](#)), being the most differences explained by the spatial particularities analyzed in this paper.

#### 3.1 Biological traits modeling

The GLMM models were fitted to the data according to different specifications. The good performance of the models to the assumptions was corroborated with the qq-plot diagram of the studentized residuals, in which most of the selected points (for a subsample of 10,000 values) are located around the expected straight line of predicted values ([Figure 3](#)). Likewise, the goodness of fit stands out in the variables related to weight (total, gonad, and gutted weight), whose variability was notably reproduced (only a sample of the first 100 values is presented). The individual size (TL)

TABLE 2 Initial LBPA model parameters applied to common hake catch at-length by zone.

Parameters	Symbol	Priors
Asymptotic length (cm)	$L_{\infty}$	47.9; 60.9; 72.1; 73.3 (fixed by zone)
Growth coefficient (year <sup>-1</sup> )	$k$	0.17 (fixed for all zones)
Natural mortality rate (year <sup>-1</sup> )	$M$	0.33 (fixed for all zones)
Fishing mortality rate (year <sup>-1</sup> )	$F_{cr}$	$\sim N(\log(M); 0.5^2)$
Length at 50% selectivity (cm)	$L_{50}$	$\sim N(\log(ML); 0.1^2)$
Selectivity slope (cm)	$d$	$\sim N(\log(0.1L_{50}); 0.1^2)$
Size of recruitment (cm)	$L_r$	$\sim N(\log(0.75L_{50}); 0.1^2)$
c.v. length at-age	$cv$	$\sim N(-2.3; 0.5^2)$

(ML, mean length of size compositions sample).

model stands out with a lower quality of fit, in which case the predictions were mainly determined by spatiotemporal patterns, and to a lesser extent by their variability. In all the cases analyzed, the studentized residuals did not show significant trends regarding the predicted values. Additionally and without prejudice to the models and the significance of the effects on the linear predictor considered, the conditional coefficient of determination was the highest ( $r^2 > 0.95$ ) for the total weight (TW) and gutted weight (GtW) variables, and the lowest value was recorded in the total length (TL) model ( $r^2 < 0.5$ ) ratified in both data sources ([Tables 3, 4](#)).

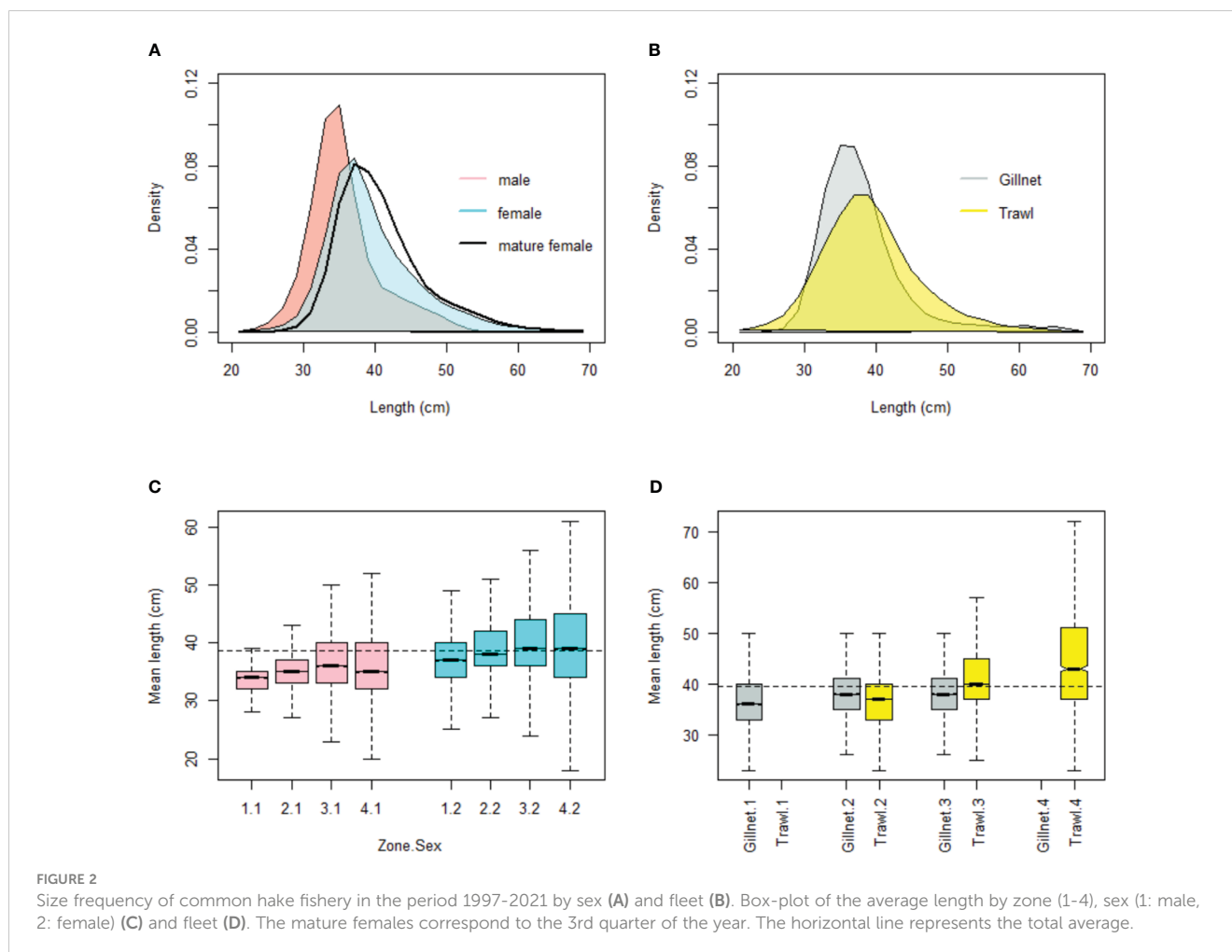
#### 3.2 Body and gonads weight

For most of the fixed effects analyzed, the linear predictor coefficients on the weight-for-size metrics (TW, GW, and GtW) were significant for both the data from fishery monitoring and from acoustic surveys. This was verified with the value  $p < 0.001$  and the t-student statistic of the coefficients related to the zone, sex, and quarter fixed effects ( $|t \text{ value}| > 1.96$ ). The total weight (TW) and gutted weight (GtW) model coefficients indicate that regardless of the size, this variable increases linearly from north (zone 1) to south (zone 4) ([Tables 3, 4](#)), with all coefficients being significantly different from zero and greater than the reference value (zone 1) ( $p < 0.001$ , [Tables 3, 4](#); [Figures 4A, E](#)). The allometric exponent of total weight (TW) at size indicates that *M. gayi* has a slight negative allometry (TL coefficient ( $\log$ )  $< 3$ ) ([Tables 3, 4](#)) and that females weigh significantly more than males (Coeff = 0.015,  $p$ -value  $< 0.001$ ).

The spatial pattern recorded in TW and GtW was not observed in the gonad weight-for-size (GW) model. Indeed, in both data sources (fishery monitoring and acoustic surveys) the effect of zone 2 was not significant ( $p$ -value  $> 0.05$ , [Tables 3, 4](#)) and, therefore, it is considered similar to zone 1 (reference effect). The maximum GW is recorded in zone 3 and decreases slightly in zone 4 ([Tables 3, 4](#); [Figures 4B, F](#)). Like TW, GW presents its highest value during the 3rd quarter of each year ([Table 3](#)), which is expected during the reproductive period of *M. gayi*. In the same sense, GtW shows the lowest value during the fourth quarter of each year (coeff = -0.022, [Table 3](#)) in relation to the post-reproductive period. Notwithstanding the spatial and temporal heterogeneity of these biological traits, the homogeneity exhibited by GW between zones 1 and 2 is noteworthy ( $Z = -1.23$ , [Table 5](#)).

#### 3.3 Total length and maturity at-length

The total length (TL) model for the fishery data shows that females are significantly larger than males (coeff = 0.11,  $p$ -value  $< 0.001$ ) ([Tables 3, 4](#)), and in general the size of *M. gayi* increases from north (zone 1) to south (zones 3-4) ([Table 3](#), [Figure 4C](#)). This situation is partially corroborated in the data from acoustic surveys, as the average size in zone 4 is slightly lower (coeff = 0.059,  $p$ -value  $< 0.001$ ) ([Table 3](#) and [Figure 4G](#)). Likewise, this data source reveals that size increases significantly at greater depths (coeff depth  $> 400 = 0.259$ ,  $p$ -value  $< 0.001$ , [Table 3](#)), while the

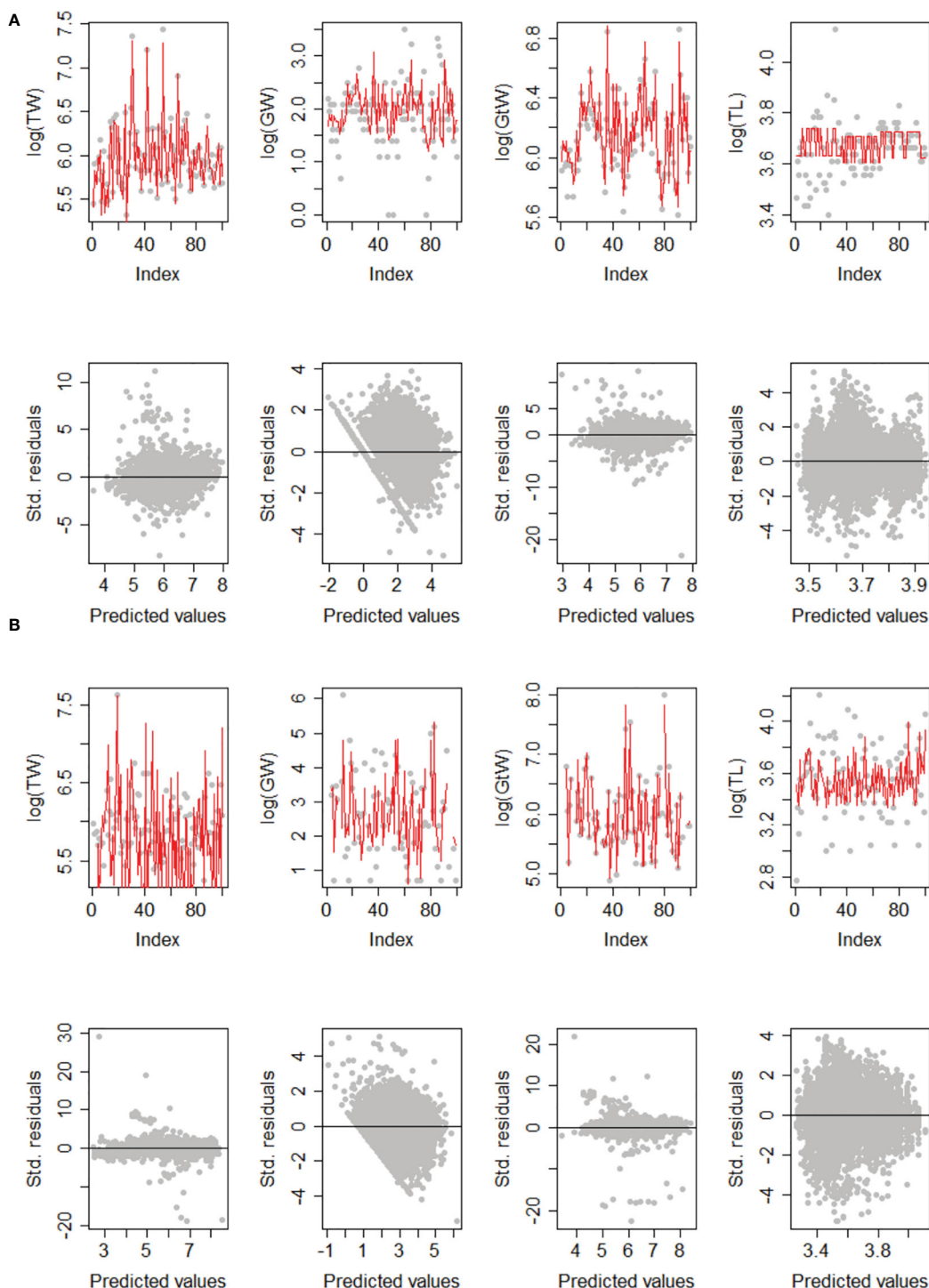


seasonal effect shows that the maximum record is observed in the 3rd quarter of each year (coeff 3rd quarter=0.02  $p$ -value<0.001, Table 3). Despite the spatial heterogeneity exhibited by *M. gayi* TL throughout its distribution, the  $Z$  statistic indicates a significant homogeneity between zones 3 and 4 ( $Z=0.00$ , Table 4).

On the other hand, the maturity to size model shows that all coefficients were significant ( $p$ -value<0.001), as well as being different between zones with a general decrease pattern from north to south between zones 1 and zones 3–4 (coeff=-3.50) (Tables 3, 4; Figures 4D, H). Overall, the  $Z$  test shows high spatial heterogeneity in biological traits ( $Z>1.96$ ) for both the GLMM coefficients of the fishery and the acoustic surveys. As a particular case, the significant homogeneity in sexual maturity stands out between zones 3 and 4 ( $Z=0.40$ , Table 5) according to the data collected in the fishery monitoring, as well as between zones 1 and 2 reflected in acoustic survey data. This is also represented in the sexual maturity to size model in females and in the calculation of size at first sexual maturity (Figure 5). There is a notable difference in maturity ogives and in length at first sexual maturity throughout the distribution of *M. gayi*. The  $TL_{50m}$  increases from north to south by more than 40%, being lower in zone 1 ( $TL_{50m}=23.6$  cm, Figure 5) and greater in zones 3 and 4 ( $TL_{50m}=35$ –36 cm, Figure 5). The  $TL_{50m}$  in zone 2 exhibits an estimated intermediate value of 30.0 cm TL.

### 3.4 Spawning potential ratio and biological reference points

The size compositions of the fishery, growth parameters, natural mortality, and biological traits were integrated around the LBPA estimation model. The model was fitted to the variability of the length frequency data by area for the last five years of the fishery (2017–2021) (Figure 6). The model underestimates the fish proportion around the length, but adequately adjusts both the segment of incompletely recruited specimens to the fishery and the segment representing the largest specimens in the population (Figure 6A). The goodness of fit is confirmed with the distribution of the standardized residuals represented by a normal distribution (Figure 6B). The selectivity curves show that in zones 1 and 2 mainly mature individuals ( $L_{50}>TL_{50m}$ ) are affected (Figure 6C), while in zones 3 and 4 individuals over  $TL_{50m}$  but which have not yet reached full maturity are affected (Figure 6C). Other model parameters indicate that the size at recruitment ( $L_r$ ) to the fishery is smaller in zones 1 (27.2 cm TL) and 4 (27.9 cm TL) and higher in zones 2–3 ( $L_r \sim 31$  cm TL) (Table 6). The highest estimates of SPR are recorded in zones 1 (SPR =0.64) and 4 (SPR=0.38), while the lowest are found in zones 3 and 4 (SPR<0.18), well below a reference value (SPR<sub>msy</sub>=0.4) (Figure 6D; Table 6). As highlighted from the acoustic information and the landings by zone (Figure 1), zones 1



**FIGURE 3** Example of model fit diagnostic for Total weight (TW), Gonad weight (GW), Guttled weight (GtW), and Total length (TL). (A) Models for fisheries monitoring data. (B) Models for data from acoustic surveys.

and 4 present lower density and therefore low interest for the fishing fleet, thus explaining their better population condition. The estimates of fishing mortality ( $F_{cr}$ ) in zones 2 ( $F_{cr}=1.24$ ) and 3 ( $F_{cr}=1.12$ ) are the highest and significantly exceed the reference values ( $F_{msy}$ ) (Table 6), incidentally explaining the SPR values found. The negative correlation between spawning potential (SPR) and fishing mortality ( $F_{cr}$ ) is also highlighted (Figure 6E).

In the same sense and according to the differences in the maturity curves at size, selectivity, mean weight, and asymptotic length, the reference fishing mortality values  $F_{msy}$  between zones turned out to be different with a latitudinal pattern of decrease from north ( $F_{msy}=0.87$ ) to south ( $F_{msy}=0.26$ ) (Table 6).

A Kobe diagram shows the relative position of  $F_{cr}$  and SPR regarding four quadrants of interest. In zones 2 and 3, fishing

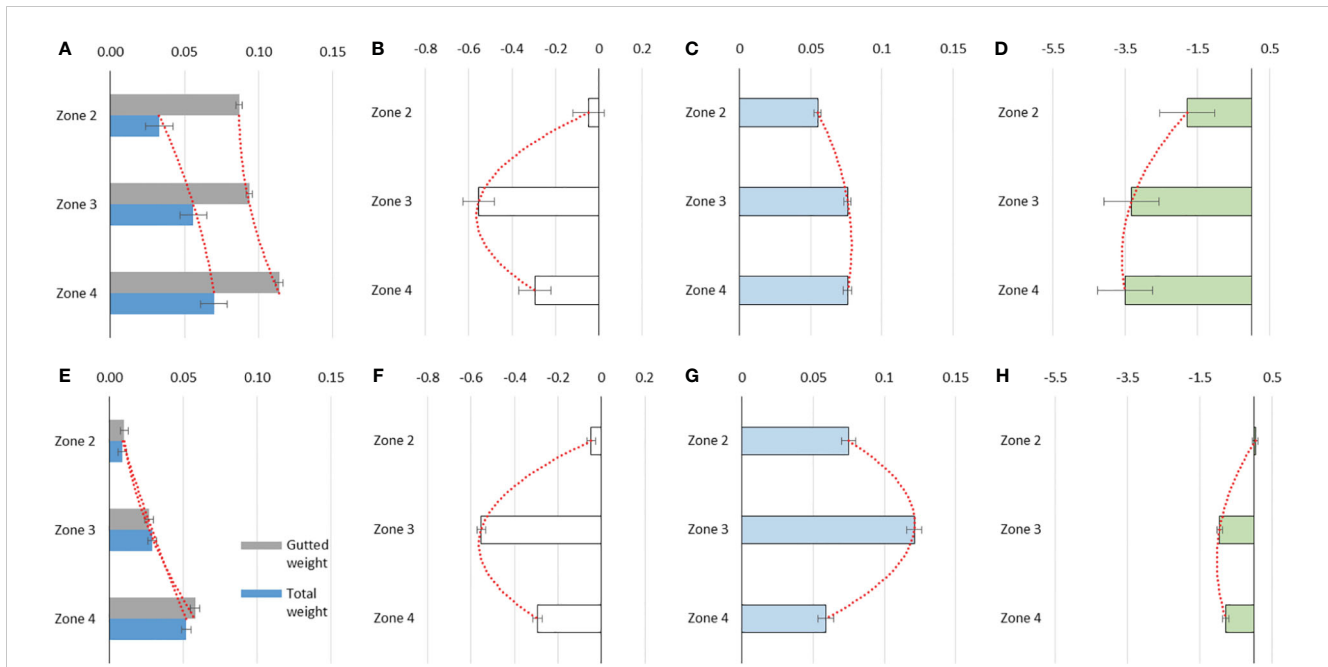
TABLE 3 Main statistics of GLMMs applied to biological variables collected in monitoring of common hake fishery: total weight, gonad weight, gutted weight, total length and maturity proportion.

Predictors	Biological response variable														
	Total weight (TW)			Gonad weight (WG)			Gutted weight (GtW)			Total length (log TL)			Maturity (Mat)		
	Estimates	t value	<i>p</i>	Estimates	t value	<i>p</i>	Estimates	t value	<i>p</i>	Estimates	t value	<i>P</i>	Estimates	z value	<i>P</i>
(Intercept)	-4.495	-566.838	<0.001	-14.331	-220.463	<0.001	-4.557	-589.55	<0.001	3.543	167.464	<0.001	-6.540	-13.69	<0.001
Female	0.015	47.652	<0.001	-0.086	-22.077	<0.001	0.006	12.612	<0.001	0.105	291.876	<0.001			
Zone 2	0.087	76.746	<0.001	-0.047	-1.233	0.218	0.033	6.933	<0.001	0.055	41.985	<0.001	-1.792	-4.48	<0.001
Zone 3	0.094	81.615	<0.001	-0.554	-14.558	<0.001	0.056	11.965	<0.001	0.076	57.428	<0.001	-3.323	-8.30	<0.001
Zone 4	0.114	82.634	<0.001	-0.295	-7.688	<0.001	0.070	14.645	<0.001	0.076	47.488	<0.001	-3.500	-8.66	<0.001
2th Quarter	0.014	33.563	<0.001	0.235	45.361	<0.001	0.006	9.461	<0.001	-0.002	-3.753	<0.001			
3th Quarter	0.018	42.459	<0.001	0.997	189.742	<0.001	-0.013	-19.43	<0.001	0.020	38.454	<0.001			
4th Quarter	-0.015	-35.852	<0.001	0.548	105.581	<0.001	-0.022	-35.03	<0.001	0.010	19.988	<0.001			
TL (log)	2.833	2628.811	<0.001	4.427	397.883	<0.001	2.837	2090.067	<0.001						
TL													0.278	64.57	<0.001
Observations	610,023			203,341			207,448			549,472			38,891		
Conditional <i>r</i> <sup>2</sup>	0.946			0.582			0.968			0.463			0.615		



TABLE 4 Main statistics of GLMMs applied to biological variables collected in acoustic surveys of common hake: total weight, gonad weight, gutted weight, total length and maturity proportion.

Predictors							Biological response variable								
	Total weight (TW)			Gonad weight (WG)			Gutted weight (GtW)			Total length (log TL)			Maturity (Mat)		
	Estimates	t value	P	Estimates	t value	p	Estimates	t value	p	Estimates	t value	p	Estimates	z value	p
(Intercept)	-4.957	-546.458	<0.001	-14.430	-234.529	<0.001	-4.805	-498.137	<0.001	3.355	139.253	<0.001	-7.226	-34.114	<0.001
Female	-0.005	-4.610	<0.001	-0.322	-44.543	<0.001	-0.003	-2.405	0.016	0.115	67.068	<0.001			
Zone 2	0.010	7.128	<0.001	0.020	1.945	0.052	0.009	5.836	<0.001	0.075	29.242	<0.001	0.029	0.716	0.474
Zone 3	0.027	18.697	<0.001	-0.342	-32.710	<0.001	0.029	18.936	<0.001	0.121	45.287	<0.001	-0.959	-23.938	<0.001
Zone 4	0.058	37.546	<0.001	-0.147	-13.210	<0.001	0.052	31.866	<0.001	0.059	20.440	<0.001	-0.792	-18.333	<0.001
TL (log)	2.986	1523.405	<0.001	4.652	312.847	<0.001	2.916	1332.011	<0.001						
Depth 100-200										0.006	2.046	0.041			
Depth 200-300										0.096	33.274	<0.001			
Depth 300-400										0.218	66.697	<0.001			
Depth >400										0.259	55.687	<0.001			
TL													0.22	98.84	<0.001
Observations	76,914			74,612			74,603			76,914			50,303		
Conditional r <sup>2</sup>	0.977			0.644			0.972			0.366			0.662		



**FIGURE 4** Coefficients of the spatial effect in the General Linear Mixed Models (GLMM) fitted to the biological variables of common hake: (A, E) total weight and gutted weight, (B, F) gonad weight, (C, G) total length, (D, H) sexual maturity. Upper panels: Fishery monitoring data. Bottom panels: Acoustic survey data. The segmented red line represents the trend. The error bar represents the 95% confidence interval.

**TABLE 5** Z-test statistics for homogeneity of common hake biological traits between zones and data source; total weight (TW), gonad weight (GW), gutted weight (GtW), total length (TL) and Maturity at size (Mat).

Source		Zone 1		Zone 2		Zone 3	
		Fishery	Surveys	Fishery	Surveys	Fishery	Surveys
	TW	76.80	7.10				
	GW	<b>-1.20</b>	5.10				
Zone 2	GtW	6.90	6.70				
	TL	42.00	29.20				
	Mat	-4.50	<b>0.70</b>				
	TW	81.60	18.70	-6.20	-11.90		
	GW	-14.60	-17.80	13.30	23.70		
Zone 3	GtW	12.00	21.50	-4.80	-15.70		
	TL	57.40	45.30	-16.00	-17.90		
	Mat	-8.30	-23.90	3.80	24.30		
	TW	82.60	37.50	-23.80	-33.60	-17.40	-21.20
	GW	-7.70	15.20	6.50	-12.50	-6.80	-34.70
Zone 4	GtW	14.70	33.30	-7.80	-31.80	-3.00	-15.50
	TL	47.50	20.40	-16.00	6.30	<b>0.00</b>	23.20
	Mat	-8.70	-18.30	4.30	20.20	<b>0.40</b>	-4.20

Bold values reflect non-significant differences.

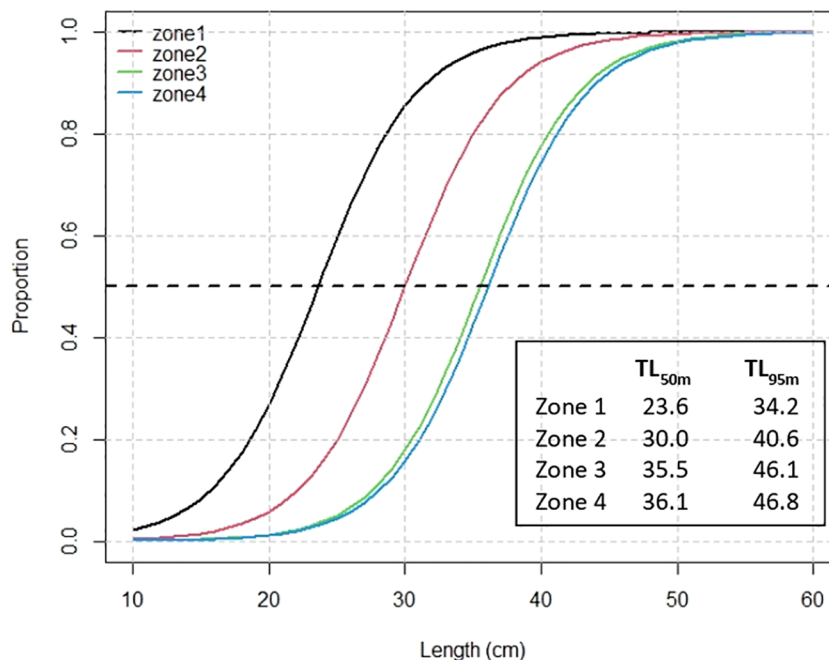


FIGURE 5

Proportion of maturity at-length in females of common hake by zones. TL<sub>50m</sub> and TL<sub>95m</sub> represent the length (in cm) at 50% and 95% maturity by zone, respectively.

mortality is 3.5 and 4.2 times higher than the respective reference values ( $F_{cr}/F_{msy} > 1$ ) (overfishing) (Figure 7). At the same time, the lowest SPR values are recorded in these zones, below the reference value and, therefore, in a state of overexploitation ( $SPR/SPR_{msy} < 1$ ). A better condition is recorded in zone 1, where  $F_{cr}/F_{msy}$  and  $SPR/SPR_{msy}$  levels are far from undesired levels. The exploitation condition in zone 4 is located around the management objective, however the 95% confidence intervals ( $CI_{95\%}$ ) prevent ruling out the risks of overfishing and overexploitation (Figure 7). In all analyzed cases, a positive correlation stands out between the  $CI_{95\%}$  amplitude and the value of their respective variables. This same figure shows that, if the differences in biological traits were disregarded, zones 1, 2, and 3 would represent overfished and overexploited populations (Figure 7), while zone 4 would be far from any risk of conservation ( $SPR/SPR_{msy} > 1$  and  $F_{cr}/F_{msy} < 1$ ). The coincidence of results in zone 2 is also highlighted, which would be due to the similarity of the life history parameters used in this zone versus those reported by Cerna et al. (2013).

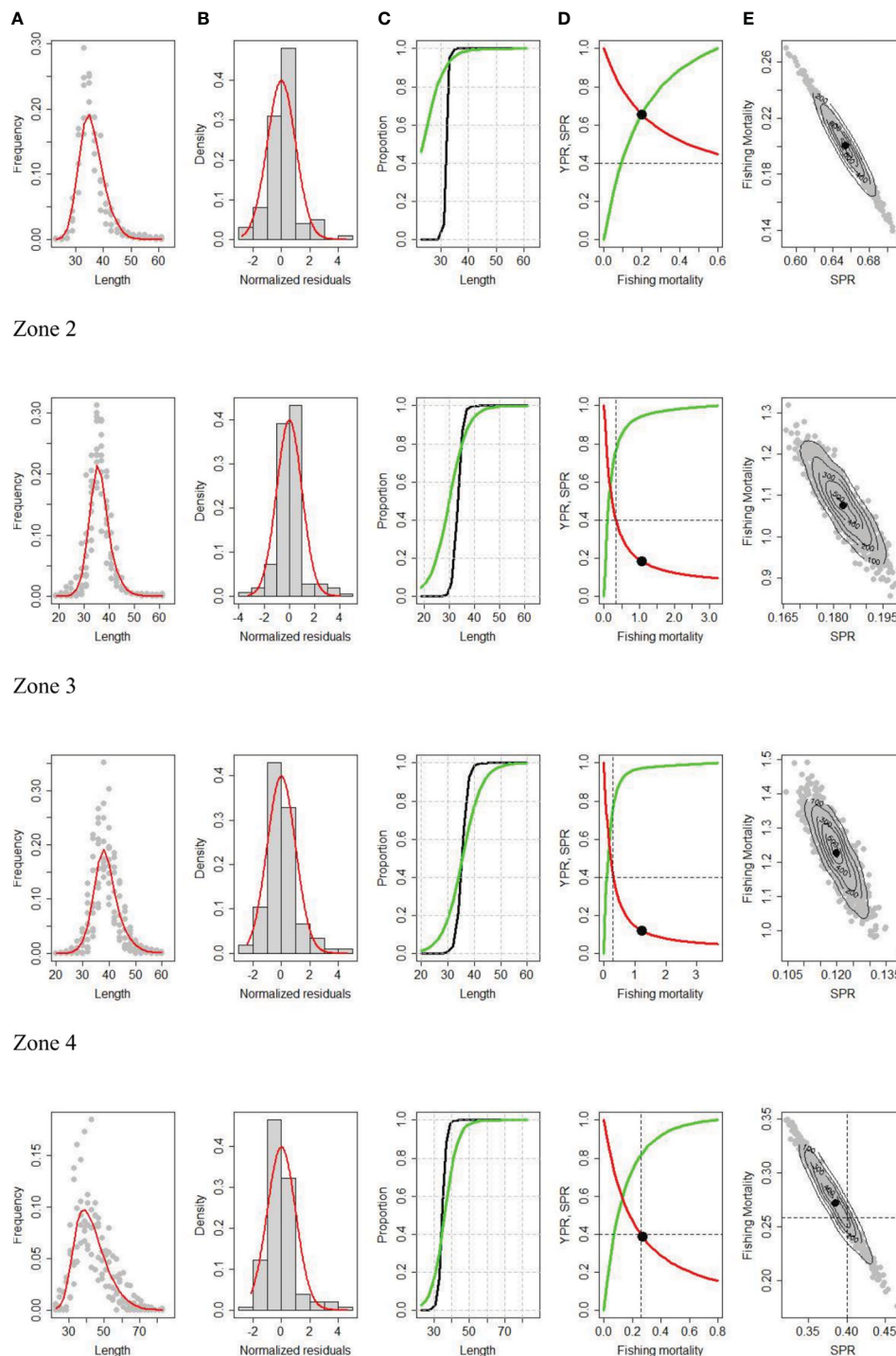
In comparative terms, the current relative biomass level based on a single stock and biological homogeneity  $SPR/SPR_{msy} \sim 0.5$  (Tascheri, 2022), is double that estimated in the most important hake fishing area (zone 3), and simultaneously less when assuming homogeneity of biological traits with spatial population differentiation (blue dots) (Figure 7). The discrepancy in the fishing mortality axis with respect to that reported by Tascheri (2022), is due to the fact that LBPA accounts for average fishing mortality values (equilibrium) responsible for the current conditions of the hake population.

## 4 Discussion

### 4.1 Spatial heterogeneity

This study provides evidence of significant heterogeneity in the spatial and temporal patterns of the main biological traits of common hake. The large amount of information analyzed, both from fishery monitoring and from acoustic surveys, allowed determining that independently of the size of the fish and the fleets selectivity, in the four main distribution areas of this species, the individual weight of the gonads, gutted weight, and total weight, as well as the proportion of mature females, differ geographically. The general pattern of these variables showed that the northern distributions of *M. gayi* presents individuals with lower weights and females maturing at smaller sizes. It is known that these types of phenotypic trait patterns can vary within populations of the same species or between species, in response to natural adaptive plasticity (Santoul et al., 2005) and genetic variability (e.g. Cadrin et al., 2010; Crozier and Hutchings, 2014; Denechaud et al., 2020). Similarly, and in the same area of analysis, Canales et al. (2016) found similar patterns in the condition and size at sexual maturity factor of *Heterocarpus reedi* (Crustacea Decapoda), explained by the greater supply of food around coastal upwelling areas and the mouths of major rivers located south of 32°S.

The particular spatial heterogeneity where inhabits this species, would explain why *M. gayi* specimens are larger in this area and have a better condition factor. The greater availability of food is determined mainly by the current system, the greater presence of upwelling areas (Arcos and Navarro, 1986; Landaeta and Castro,



**FIGURE 6**  
 LBPA model fit to length composition data (A), histograms of residuals (B), selectivity (black) and maturity (green) curves (C), yield (green) and spawning biomass (red) per recruit curves (D), and correlation between SPR and fishing mortality (E) for common hake by zone.

2006; Gatica et al., 2015), and the contribution of nutrients from river discharge (Sobarzo et al., 2007; Canales et al., 2016). Additionally, these conditions are favorable as spawning and nursery areas for epipelagic and mesopelagic species (Castillo et al., 1991; Castro et al., 1993; Landaeta and Castro, 2002).

The evidence found in this study regarding the heterogeneity of biological traits in *M. gayi* suggest that this population is spatially

structured. This statement is reinforced by parasitological studies carried out by George-Nascimento (1996) and Oliva and Ballón (2002), who suggested the existence of two stock units. Additionally, mitochondrial DNA analyses indicated the existence of at least three different genetic units (Vidal et al., 2012). The results suggest that biologically zones 1 and 2 exhibit greater differences than zones 3 and 4, so these latter could be considered as a common

TABLE 6 LBPA model's parameters and variables estimated by zone.

Parameters/variable	Zone 1	Zone 2	Zone 3	Zone 4
$F_{cr}$	0.219 (0.023)	1.241 (0.091)	1.121 (0.072)	0.272 (0.029)
$L_{50}$ (cm)	32.166 (0.198)	34.004 (0.217)	35.054 (0.348)	34.760 (0.382)
$d$ (cm)	1.082 (0.089)	2.840 (0.177)	2.959 (0.222)	3.269 (0.349)
$L_r$ (cm)	27.273 (0.203)	30.765 (0.180)	31.023 (0.177)	27.943 (0.851)
$cv$	0.103 (0.002)	0.094 (0.003)	0.088 (0.003)	0.120 (0.007)
SPR	0.642 (0.019)	0.178 (0.006)	0.115 (0.005)	0.386 (0.024)
$F_{msy}$	0.873 (0.023)	0.352 (0.091)	0.262 (0.072)	0.258 (0.029)

The values in parentheses indicate the standard deviation.

homogeneous zone. This emphasizes the need to delve further into the findings reported by different researchers in view of the implications for the fishery management of this resource.

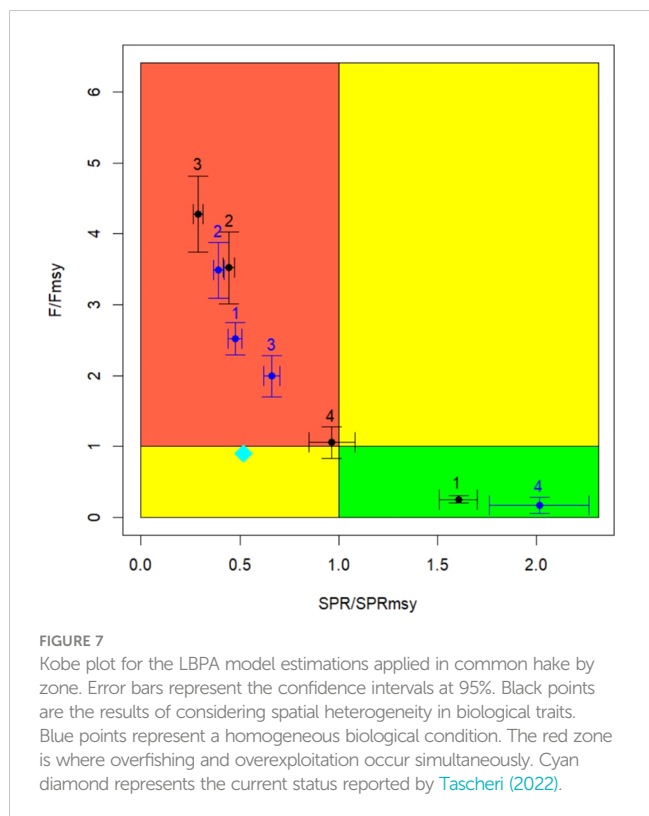
### 4.2 Biological traits and management implications

One of the most distinctive features found in *M. gayi* is the geographic heterogeneity in sexual maturity at size (and most likely

also in individual growth), a key variable for determining the reference fishing mortality  $F_{msy}$ . Often these evidences are not considered for purposes of managing fishery resources (e.g. Jansen et al., 2016). This study showed that if the information is analyzed by fishing zone, the subpopulation located towards the south of the distribution (zone 4) could radically change its status when using the appropriate sexual maturity ogive and selectivity pattern. Similarly, this consideration would reduce the high level of overfishing reported in zone 3, one of the main fishing areas for this resource. According to this, the overexploitation of common hake ( $SPR/SPR_{msy} \sim 0.5$ ; Tascheri, 2022) does not represent the current condition of the population throughout its entire distribution, and overestimates its status in the two most important areas of the fishery (zones 2 and 3). If the assumption of exploitation pattern (logistic) were a dome-shape model, the condition of the hake stock could even improve because this model type tends to underestimate the fishing mortality of the oldest (spawners) fish.

Although the assumption of independent stock units could be strengthened with additional analyses, we believe that a spatially explicit stock assessment analysis would have less bias compared to assuming a common pool as currently used to manage this resource. This analysis allows identifying the notable implications that the incorrect specification of biological variables can have for population diagnosis, an aspect that has already been demonstrated in other works (e.g. Truesdell et al., 2016; Barrett et al., 2022).

The sustainability of the fishery and the conservation of the resource depend on the application of adequate levels of exploitation in accordance with the biological aspects of the species in an area of interest, and in particular, its effects on the estimation of the biological reference points (Hintzen et al., 2015; Barrett et al., 2022). In the case analyzed, the highest levels of fishing mortality reference  $F_{msy}$  were estimated to the north of the *M. gayi* distribution, which translates into areas that are more tolerant to the potential increase in fishing effort. The latter is explained by the smaller size at first sexual maturity in regards to the catch size or



current selectivity, which allows the natural protection of spawners in the population. This type of evidence should be considered in a recovery plan for this resource, for example, directing part of the fishing effort from more overexploited areas to lower latitudes. In order to implement this, the Fisheries and Aquaculture Law in force in Chile allows the definition of spatial units of fisheries management based on the best available scientific evidence and the biological characteristics of the resources, and in this sense, the results found in this work emerge as the most robust by considering the appreciable volume of information analyzed.

### 4.3 Population structure for assessment

The temporal reproducibility of geographic patterns in the phenotypic characteristics of a species (e.g. size and maturity) are typical characteristics of discrete populations with low levels of admixture (Cadrin, 2020), and are considered determining aspects for stock assessment purposes (Begg et al., 2005). The spatial differences in the biological traits of hake could be considered sufficient reason to carry out spatially explicit stock assessments (e.g. Punt, 2019). The results obtained in this research are evidence against the assumption of a single homogeneous stock unit in the distribution area of common hake off Chile. The common hake population is likely to have a high affinity with its areas of origin (spawning) and to be spatially structured into subpopulations with various levels of connectivity. In this regard, Cope and Punt (2011) indicate that all populations and fisheries of a species exhibit mixing patterns, or different levels of connectivity (Ciannelli et al., 2013), or the same population may contribute to different management units and vice versa (e.g. Smedbol and Stephenson, 2001; Reiss et al., 2009). The results found in this work thus suggest that the stock assessment approach currently in use should leave aside the common-pool concept and incorporate some spatial structuring (e.g. Goethel et al., 2011; Punt, 2019), for example, in the form of a metapopulation (e.g. Canales et al., 2016; Jardim et al., 2018). Finally, and in addition to the results obtained, an analysis of the biological traits at a higher spatial resolution would allow accurately identifying the geographic limits of proposed population sub-units.

## 5 Conclusions

In this study, 26 years of information from biological samplings of *M. gayi*, carried out both in fishery management and in acoustic survey throughout its entire spatial distribution, were integrated. The modeling of the main biological traits revealed important spatio-temporal patterns that contradict the bases that support the evaluation and fisheries management of this resource in Chile. Considering the implications of these aspects for the purposes of sustainable fishery management, we suggest complementing this work with studies that would provide greater precision and justification to the spatial structuring of hake stock. An example of this is the estimation of parameters of growth and natural

mortality by area. Similarly, the performance of integrated stock assessment models with a spatially explicit structure (metapopulations or in discrete population units) should be explored. While this happens, we recommend considering the results and the approach used in this research in order to provide guidelines at the moment of allocating effort or catches, an aspect that is mainly useful for a recovery plan for this important fishing resource in the Southeastern region of the Pacific Ocean.

## Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: <https://drive.google.com/drive/folders/1WiX55Eimzj7bhf1-mkrQ8ZLr7-05lf9X?usp=sharing>.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

CC developed the original idea and conducted statistical analyses. NS conducted LBPA analysis. Both authors contributed to figures and tables productions, and the manuscript writing. NA performed redaction and revision of the Discussion segment, particularly on the matters of understanding spatial heterogeneity implications, and management implications and contributed to the revision of the whole article. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

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

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## Appendix

### Length-based pseudocohort analysis (LBPA)

The LBPA model (Canales et al., 2021) (<https://github.com/criscan/LBPA>) corresponds to an equilibrium age-based analysis formulated to obtain information on fishing mortality (F) and Spawning Potential Ratio (SPR) from catch length-frequency data. The model is fitted to multiple years of CLF data simultaneously.

The per-recruit survival is represented as a function of age ( $N_a$ ), natural mortality (M) and age-specific fishing mortality:

$$N_a = \begin{cases} 1 & a = a_r \\ N_{a-1}S_{a-1} & a_r < A < A_+ \\ N_a/(1 - S_a) & a = A_+ \end{cases} \quad (1)$$

$$S_a = e^{-F_a - M} \quad (2)$$

where  $a$  is age,  $A_+$  is the plus group,  $F_a$  is age-specific fishing mortality as a function of selectivity at-age ( $\varphi_a$ ) and a logistic length-specific selectivity  $\varphi_l$ :

$$F_a = \varphi_a F \quad (3)$$

$$\varphi_l = \left(1 + e^{-\log(19)\left[\frac{l-L_{50}}{\Delta}\right]}\right)^{-1} \quad (4)$$

$$\varphi_a = \pi_a \varphi_l \quad (5)$$

where  $L_{50}$  corresponds to the length where 50% of individuals are retained by fishing gear and  $\Delta$  is a slope parameter. The expected catch at length (Eq. 7) is calculated from the conversion of catch at-age (Eq. 6) by a length at-age probability matrix  $\pi_{a,l}$  (Eq. 8).

$$C_a = \left(\frac{F_a}{F_a + M}\right) N_a (1 - S_a) \quad (6)$$

$$\hat{C}_l = C_a \pi_{a,l} \quad (7)$$

$$\pi_a = \int_{l_i}^{l_{i+1}} e^{-0.5\left(\frac{l-l_a}{\delta_a}\right)^2} dl \quad (8)$$

Matrix  $\pi_a$  is determined using a growth equation (Eq. 10) parameterized in terms of  $L_{\infty}$ ,  $k$ , and the coefficient of variation of the length at age ( $cv$ ) (Eqs. 9, 10).

$$L_a = L_{a-1}e^{-k} + L_{\infty}(1 - e^{-k}) \quad (9)$$

$$\delta_a = cv L_a \quad (10)$$

The initial length at-age corresponds to the size at the age of fishery recruitment  $L_a = L_{a_r}$ . The spawning biomass-per-recruit (SSBPR) is calculated as:

$$SSBPR = \sum_l \left( (N_a e^{-\gamma Z_a}) \pi_a \right) O_l w_l \quad (11)$$

Where  $Z_a = F_a + M$  is the total mortality by age,  $\gamma = 0.583$  is the fraction of the year when common hake spawns,  $O_l$  is the maturity proportion at-length, and  $w_l$  is the average weight-at-length. Virgin spawning biomass-per-recruit  $SSBPR_0$  is calculated using Eq. 11 when  $Z = M$  and the Spawning Potential Ratio (SPR) is the ratio  $SSBPR/SSBPR_0$ . LBPA parameters ( $\theta = [L_{a_r}, L_{50}, \Delta, F, cv]$ ) are estimated using penalized maximum likelihood. The length-composition data are assumed to be multinomial and the model parameters ( $\theta$ ) are estimated by minimizing a penalized log-likelihood as:

$$ll = -\dot{N} \sum_l p_{l,y} \log(\hat{p}_l) + \sum_j \left( \frac{\log(\theta_j) - \log(\hat{\theta}_j)}{\sigma_{\theta_j}} \right)^2 \quad (12)$$

where  $\dot{N}$  is the effective sample size (e.g.,  $\dot{N} = 100$ ),  $p_{l,y}$  is the catch proportion at length-class  $l$  by year, and  $\hat{p}_l$  is the model-predicted proportion of the catch by length class  $l$ . The second term in Eqn 12 are the model penalties, where  $\theta_j$  represents the *a priori* value of the  $j$ -th parameter and  $\sigma_{\theta_j}$  its standard deviation in log-space.