



**Universidad de Concepción
Dirección de Postgrado
Facultad de Ciencias Naturales y Oceanográficas
Programa de Magíster en Ciencias con Mención en Pesquerías**

**DEPENDENCIA ESPACIAL EN LA PRODUCCIÓN DIARIA DE
HUEVOS DE DOS PECES PELÁGICOS PEQUEÑOS DE LA
ZONA CENTRO-SUR DE CHILE**

Tesis presentada a la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción, para optar al grado de Magíster en Ciencias con Mención en Pesquerías

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**Enero, 2023
Concepción-Chile**

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AGRADECIMIENTOS

Agradezco a mi familia por el apoyo moral y emocional que me dieron durante este proceso, en especial a mis padres y hermanos que estuvieron en todo momento.

Agradezco a mi profesor guía, el Dr. Luis Cubillos Santander, por su motivación, consejos y dedicación para la realización de este trabajo y también por su aliento en el mejoramiento de mi formación profesional y personal.

Al laboratorio EPOMAR por el apoyo económico y por tener un gran equipo, alentándome a seguir en el camino de la ciencia.

Al centro COPAS-COASTAL y a la Universidad de Concepción por el apoyo económico brindado en mis estudios de maestría.

A todos mis amigos, que estuvieron conmigo apoyándome y alentándome continuamente.

A todos y todas muchas gracias.

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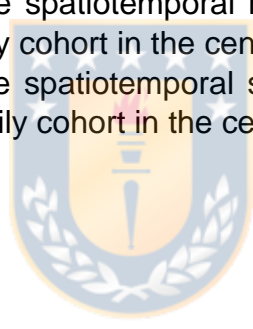
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RESUMEN

La biomasa del stock desovante de los peces pelágicos pequeños se evalúa habitualmente a través del Método de Producción Diaria de Huevos (MPDH), como en el caso de la anchoveta (*Engraulis ringens*) y la sardina (*Strangomera bentincki*) de la zona centro-sur de Chile. La tasa de producción diaria de huevos (P_0), es uno de los parámetros estimados en el MPDH a través de un modelo de supervivencia exponencial negativo sin considerar efectos espaciales de la distribución de las cohortes diarias de huevos. Los efectos espaciales en la distribución del desove pueden ser endógenos (autocorrelación) como exógenos (influencia de variables físico-químicas), determinando una dependencia espacial. Se analizó la dependencia espacial de las cohortes diarias de huevos de anchoveta y sardina en la zona centro-sur de Chile (33°S-41°30'S). Se utilizaron datos del MPDH de un estudio realizado en 2018. Los recuentos de huevos fueron clasificados en estadios de desarrollo y se les determinó la edad en horas con un modelo de desarrollo estadio-temperatura dependiente, para posteriormente agrupar en cohortes diarias. Se ajustó modelos jerárquicos Bayesianos con distribución binomial negativa a la abundancia de de huevos en función de la edad, efectos aleatorios espacio-temporales y la profundidad del fondo, con diferentes campos espaciales gaussianos. Se contrastó un modelo no espacial (Modelo 0) con los siguientes modelos espaciales: a) campo espacial constante o distribución diaria de huevos recurrente (Modelo 1), b) campo espacial cambiante diariamente u oportunista

(Modelo 2), y c) campo espacial correlacionado diariamente (Modelo 3). Se encontró efectos espaciales significativos, cuando el campo espacial cambia diariamente siguiendo una distribución espacial oportunista (Modelo 2). La dependencia espacial se debió a los efectos de la profundidad del fondo, que se interpretaron como una representación de frentes y mezcla del agua. La distribución oportunista reveló que los pequeños cambios diarios en la distribución espacial de los huevos podrían estar asociados a efectos de dispersión y mortalidad, que son difíciles de separar. La dependencia espacial de la profundidad del fondo sugiere una retención costera de huevos, probablemente debida a un hábitat espacial heterogéneo en el que los frentes y los procesos de retención están asociados a la batimetría.



ABSTRACT

The spawning biomass of small pelagic fish is usually assessed through the daily egg production method (DEPM), such as for anchovy (*Engraulis ringens*) and sardine (*Strangomera bentincki*) in the central-southern area of Chile. The daily egg production rate (P_0) is one of the main parameters estimated in DEPM through a negative exponential survival model that do not consider the spatial effects of the daily egg cohort. We analyze the spatial dependence of the daily egg cohorts for anchovy and sardine in central-southern Chile (33°S-41°30'S). We utilized DEPM data from a survey carried out in 2018. Egg counts were staged and aged with Lo's model, and ages were grouped into daily cohorts. We fitted negative binomial Bayesian hierarchical models to the daily egg cohorts as a function of age, spatiotemporal random effects, and bottom depth, considering different gaussian spatial fields. We contrasted a non-spatial model (Model 0) with the following models: a) constant spatial field or recurrent daily egg distribution (Model 1), b) spatial field changing daily (Model 2), and c) daily correlated spatial field (Model 3). We found significative spatial effects, when the spatial field changed daily following an opportunistic distribution (Model 2). The spatial dependence was due to the bottom depth effects, which were interpreted as a proxy of water mixing and fronts. The opportunistic distribution revealed that small daily changes in the spatial egg distribution could be associated with effects of dispersion and mortality, which are difficult to separate. The spatial dependence of bottom depth suggests coastal egg retention, probably due to

heterogeneous spatial habitat where fronts and retention processes are associated with bathymetry.



INTRODUCCIÓN

El Método de Producción Diaria de Huevos (MPDH) permite estimar la biomasa del stock desovante de peces pelágicos pequeños con fecundidad indeterminada como la anchoveta, la sardina común y otras especies pelágicas y demersales (McGarvey et al., 2018; Somarakis et al., 2006; Ward et al., 2021). La tasa de producción diaria de huevos (P_0) es uno de los parámetros principales y menos precisos en el MPDH (Ward et al., 2021), el cual es usualmente estimado mediante la aplicación de un modelo de supervivencia exponencial negativo (McGarvey et al., 2021; Neira y Lyle, 2011; Pájaro et al., 2009; Ward et al., 2011). Normalmente, los datos que intervienen en el MPDH son la posición espacial de cada estación de plancton muestreada, la hora de muestreo y la temperatura, y los recuentos de huevos por estadio embrionario, basados en once etapas morfológicas que ocurren durante la embriogénesis. Posteriormente, se estiman las edades de los huevos con un modelo de desarrollo dependiente de la temperatura basado en experimentos de incubación de huevos (Lasker, 1985; Lo, 1985). La estimación convencional de P_0 implica una estratificación posterior en dos estratos, dependiendo de la presencia o ausencia de huevos en el área muestreada, lo que permite estimar el área de desove dentro del área de estudio (Picquelle y Stauffer, 1985). A continuación, se estiman las edades de los huevos con el procedimiento automatizado de Lo (1985), y luego se agrupa la abundancia de huevos en cohortes diarias. Por último, se ajusta a los datos un modelo de

supervivencia exponencial negativo para estimar la producción diaria de huevos y la mortalidad total (Z) (Lo et al., 2001; Stratoudakis et al., 2006). En el último paso, se utiliza una curva de supervivencia no espacial, y las estimaciones de P_0 y Z se infieren asumiendo estacionalidad, y por tanto independencia en las "observaciones" (densidad de huevos en cada estación).

En un contexto espacial, el modelo de un proceso es estacionario cuando sus propiedades son independientes de la ubicación y dirección absolutas en el espacio. La estacionariedad de segundo grado supone que la media es constante y que la varianza depende solo de la distancia y la dirección que separan dos ubicaciones; es decir, una variable regionalizada. Así, la estacionariedad es un supuesto para hacer inferencias válidas de un modelo que caracteriza un proceso en datos estructurados espacialmente (Dale y Fortin, 2014). Por ejemplo, la naturaleza espacial de las cohortes diarias de huevos se han analizado aplicando técnicas de Modelo Aditivo Generalizado (GAM) (Bernal et al., 2011a; Borchers et al., 1997; Wood, 2017; Wood y Augustin, 2002). El modelado GAM tiene dos ventajas importantes: a) la estratificación previa del área de estudio es innecesaria, y b) la dependencia espacial explícita se analiza relacionando la densidad de huevos de la cohorte con una o más covariables espaciales, como la temperatura superficial del mar, la profundidad del fondo y la posición de latitud y longitud (Bernal et al., 2011a, 2007; Borchers et al., 1997; Wood y Augustin, 2002). El GAM es mejor para capturar las tendencias de la densidad de huevos

en áreas de estudio a gran escala, pero los residuos aún pueden tener una correlación espacial después de eliminar la tendencia espacial.

Un enfoque alternativo son las técnicas geoestadísticas, que pueden describir la estructura espacial cuando hay un proceso subyacente (endógeno) (Dale y Fortin, 2014). Por ejemplo, la agregación de huevos planctónicos está determinada inicialmente por el comportamiento de desove de los adultos desovantes, como las agregaciones efímeras de desove (Ganias, 2008), y las fuerzas físicas que impulsan la difusión oceánica (Hewitt, 1981). Por lo tanto, la distancia media entre los parches o grupos de huevos jóvenes podría ser significativa en la producción diaria de huevos y las biomásas de desove. La geoestadística es una técnica poderosa para evaluar los datos de la cohorte de huevos diarios porque considera las correlaciones espaciales (Bez, 1997; Cressie, 1993; Fletcher y Sumner, 1999; Petitgas, 1993). Las técnicas geoestadísticas basadas en la verosimilitud de Gauss (Diggle et al., 1998; Ribeiro et al., 2003) son una herramienta útil para estimar la biomasa basada en cruceros (Roa-Ureta y Niklitschek, 2007), pero son limitadas cuando intervienen simultáneamente efectos espaciales y temporales. Una alternativa para modelar la dependencia espacial de las cohortes diarias de huevos en la zona de desove es un modelo Bayesiano jerárquico que utiliza el campo gaussiano (GF) como aproximación a un Campo Aleatorio de Markov Gaussiano (GMRF), como el método de aproximación anidada integrada de Laplace (INLA, de sus siglas en inglés) (Rue et al., 2009). Esta aproximación permite aproximar el campo espacial

continuo y, al mismo tiempo, la eficiencia en el coste computacional durante la función de covarianza implicada en los procesos aleatorios espaciales o espaciotemporales. Se propone un modelo jerárquico Bayesiano para la modelización de cohortes diarias de huevos, incorporando efectos espaciales. Los modelos jerárquicos Bayesianos son adecuados porque introducen las incertidumbres secuencialmente en las covariables y los efectos aleatorios espaciales (es decir, el campo aleatorio gaussiano). En lugar de las técnicas de Monte Carlo basados en cadena de Markov para modelar la dependencia espacial de la producción diaria de huevos, se utilizó el enfoque de las ecuaciones diferenciales parciales estocásticas (SPDE, de sus siglas en inglés) (Lindgren y Rue, 2011), combinado con el método INLA (Rue et al., 2009). En la ciencia pesquera, el modelamiento espacial y espacio-temporal Bayesiana a través de los enfoques SPDE e INLA se ha aplicado para modelar las capturas incidentales y los descartes en las pesquerías demersales (Cosandey-Godin et al., 2015; Grazia Pennino et al., 2014), la presencia/abundancia de la anchoveta (Quiroz et al., 2015), la biomasa de la anchoveta (Quiroz y Prates, 2018), las zonas de crianza (Paradinas et al., 2015), las capturas de langostinos por unidad de esfuerzo como abundancia relativa (Cavieres y Nicolis, 2018) y la distribución espacial de la anchoveta (Morón et al., 2019).

En la zona centro-sur de Chile, el MPDH convencional se utiliza para evaluar la biomasa del stock desovante de dos pequeños peces pelágicos, la anchoveta (*Engraulis ringens*) y la sardina común (*Strangomera bentincki*) (Bustos et al.,

2020; Cubillos et al., 2007). Estas especies sustentan flotas artesanales e industriales y las capturas son utilizadas para la producción de harina y aceite de pescado, siendo Talcahuano (37°S) el principal puerto de desembarque (Canales et al., 2020). La captura anual de anchoveta fluctuó entre 115310 y 175208 toneladas, mientras que la de sardina osciló entre 285128 y 344115 toneladas entre los años 1990 y 2021 (SERNAPESCA, 2021).

La anchoveta y la sardina común comparten rasgos demográficos, alimentación, crecimiento, mortalidad y dinámica reproductiva similares, como la madurez al final del primer año y las zonas de desove. Sin embargo, la distribución del desove está influenciada por la topografía costera y la batimetría que interactúan con variables ambientales como las descargas de los ríos, las precipitaciones, los gradientes de salinidad de la superficie y los vientos (alternancia de vientos del norte a vientos del sur durante la transición entre el invierno y la primavera durante la temporada reproductiva) (Castillo-Jordán et al., 2007; Castro y Hernández, 2004; Castro et al., 2000; Cubillos et al., 2001; Soto-Mendoza et al., 2010). La influencia ambiental, incluyendo la topografía y la batimetría, podría determinar las áreas de desove persistentes o recurrentes (Bellier et al., 2007). Por lo tanto, la hipótesis planteada, es que la supervivencia diaria de los huevos entre cohortes podría tener un campo espacial constante. Sin embargo, según Paradinas et al. (2017), la dependencia espacial de las cohortes diarias podría estar asociada a campos espaciales cambiantes en el tiempo (oportunistas) o con autocorrelación temporal (progresivos). Este trabajo tiene como objetivo

evaluar la dependencia espacial en la producción diaria de huevos de anchoveta y sardina común en la zona centro-sur, considerando efectos de la estructura espacial y la influencia de variables ambientales.



HIPÓTESIS

Considerando que la dependencia espacial podría ser una combinación de factores endógenos y exógenos, se plantean las siguientes hipótesis:

Hipótesis de trabajo generales:

Hipótesis 1: La dependencia espacial de la producción diaria de huevos está influenciada sólo por factores endógenos (adultos desovantes, preferencias por el hábitat de desove) que se expresan en la correlación espacial a pequeña escala.

Hipótesis 2: La dependencia espacial de la producción diaria de huevos está influenciada por factores exógenos que se expresan a través de la relación con variables proxy de los procesos que modulan la concentración y retención de huevos.

Hipótesis de trabajo específica

1. La abundancia de las cohortes diarias de huevos presenta una estructura espacial dada por la correlación espacial a pequeña escala.
2. La distribución espacial de la producción diaria de huevos es influenciada por la profundidad de fondo.

3. La distribución espacial de la producción diaria de huevos es influenciada por la salinidad promedio del estrato superficial (10 m).



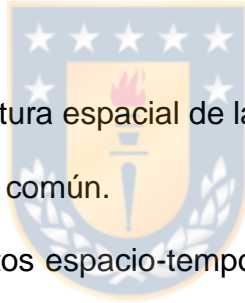
OBJETIVOS

Objetivo General

Evaluar la dependencia espacial en la producción diaria de huevos de anchoveta y sardina común en la zona centro-sur, considerando efectos de la estructura espacial y la influencia de variables ambientales.

Objetivos Específicos:

- a) Determinar la estructura espacial de las cohortes diarias de huevos de anchoveta y sardina común.
- b) Determinar los efectos espacio-temporales en la producción diaria de huevos.
- c) Evaluar la influencia de la profundidad de fondo y salinidad superficial en la producción diaria de huevos.



CHAPTER 1

Spatial dependence of daily egg production in two small pelagic fishes of central-south Chile

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ABSTRACT

The spawning biomass of small pelagic fish is usually evaluated through the daily egg production method (DEPM), such as for anchovy (*Engraulis ringens*) and sardine (*Strangomera bentincki*) in the central-southern area of Chile. The daily egg production rate (P_0) is one of the main parameters estimated in DEPM through a negative exponential survival model that do not consider the spatial effects of the daily egg cohort. We analyze the spatial dependence of the daily egg cohorts for anchovy and sardine in central-southern Chile (33°S-41°30'S). We utilized DEPM data from a survey carried out in 2018. Egg counts were staged and aged with Lo's model, and ages were grouped into daily cohorts. We fitted negative binomial Bayesian hierarchical models to the daily egg cohorts as a function of age, spatiotemporal random effects, and bottom depth, considering different gaussian spatial fields. We contrasted a non-spatial model (Model 0) with the following models: a) constant spatial field or recurrent daily egg distribution (Model 1), b) spatial field changing daily (Model 2), and c) daily correlated spatial field (Model 3). We found significative spatial effects, when the spatial field changed daily following an opportunistic distribution (Model 2). The spatial dependence was due to the bottom depth effects, which were interpreted as a proxy of water mixing and fronts. The opportunistic distribution revealed that small daily changes in the spatial egg distribution could be associated with effects of dispersion and mortality, which are difficult to separate. The spatial dependence of bottom depth

suggests coastal egg retention, probably due to heterogeneous spatial habitat where fronts and retention processes are associated with bathymetry.

Key words: spawning, spatial models, small pelagic fish, DEPM, spde, INLA.



1. Introduction

The Daily Egg Production Method (DEPM) estimates the spawning biomass of small pelagic fish such as anchovy, sardine, and other pelagic and demersal species (McGarvey et al., 2018; Somarakis et al., 2006; Ward et al., 2021). The daily egg production rate (P_0) is one of the main and less precise parameters in DEPM (Ward et al., 2021), estimated by applying a negative exponential survival model (McGarvey et al., 2021; Neira and Lyle, 2011; Pájaro et al., 2009; Ward et al., 2011). Typically, the data involved in a DEPM procedure are the spatial position of each sampled plankton station, the time (hour) of sampling and temperature, and egg counts per embryonic egg stage, based on eleven morphological stages occurring during embryogenesis. Then, egg ages are estimated with a temperature-dependent development model based on egg incubation experiments (Lasker, 1985). The conventional estimation of P_0 involves a post-stratification into two strata, depending on the presence or absence of eggs in the sampled area, enabling estimates of the study area and the spawning area (Picquelle and Stauffer, 1985). Next, egg ages are estimated with the automated procedure of Lo (1985), and then the egg abundance is grouped into daily cohorts. Finally, a negative exponential survival model is fitted to the data to estimate the daily egg production and total mortality (Z) (Lo et al., 2001; Stratoudakis et al., 2006). In the last step, a non-spatial survival curve is utilized, and population

estimates (P_0 and Z) are inferred by assuming stationarity, and therefore independence, in the collected “observations” (egg density at each station).

In a spatial context, the model of a process is stationary when its properties are independent of the absolute location and direction in space. Stationarity assumes that the process parameters, such as the mean and variance, are the same in all parts of the study area; i.e., a regionalized variable. Thus, stationarity is an assumption for making valid inferences from a model characterizing a process in spatially structured data (Dale and Fortin, 2014). For instance, the spatial nature of daily egg cohorts has been incorporated by first applying Generalized Additive Model (GAM) techniques (Bernal et al., 2011a; Borchers et al., 1997; Wood, 2017; Wood and Augustin, 2002). GAM modeling has two significant advantages: a) prior stratification of the study area is unnecessary, and b) explicit spatial dependence is analyzed by relating cohort egg density to one or more spatial covariates, like sea surface temperature, bottom depth, and latitude and longitude position (Bernal et al., 2011a, 2007; Borchers et al., 1997; Wood and Augustin, 2002). GAM is best for capturing egg density trends over large-scale study areas, but residuals still can have a spatial correlation after removing the trend along the smooth surface.

An alternative approach is geostatistical techniques, which might describe the spatial structure when an underlying (endogenous) process is involved (Dale and Fortin, 2014). For example, the aggregation of planktonic eggs is initially

determined by parental spawning behavior like ephemeral spawning aggregations (Ganias, 2008), and physical forces driving oceanic diffusion (Hewitt, 1981). Therefore, the average distance between young egg patches or clusters could be significant in daily egg production and spawning biomasses. Geostatistics is a powerful technique for assessing daily egg cohort data because it considers spatial correlations (Bez, 1997; Cressie, 1993; Fletcher and Sumner, 1999; Petitgas, 1993). The Gaussian likelihood-based geostatistical techniques (Diggle et al., 1998; Ribeiro et al., 2003) is a helpful tool to estimate biomass based on surveys (Roa-Ureta and Niklitschek, 2007) but limited when spatial and temporal effects are involved simultaneously. An alternative to model spatial dependence of daily egg cohorts in the spawning area is a Hierarchical Bayesian model utilizing Gaussian Field (GF) as an approximation to a Gaussian Markov random field (GMRF), such as the integrated nested Laplace approximation (INLA) method (Rue et al., 2009). This approach allows for approximate continuous spatial field and, at the same time, efficiency in the computational cost during the covariance function involved in the spatial or spatiotemporal random processes. We propose a hierarchical Bayesian model for modeling daily egg cohorts, incorporating spatial effects. Hierarchical Bayesian models are suitable since they introduce the uncertainties sequentially in covariates and spatial random effects (i.e., Gaussian random field). Instead of Markov Chain Monte Carlo techniques to model the spatial dependency of the daily egg production, we utilized the stochastic partial differential equations (SPDE) approach (Lindgren and Rue,

2011), combined with the INLA method (Rue et al., 2009). In fishery science, Bayesian spatial and spatiotemporal modeling through SPDE and INLA approaches have been applied to model bycatch and discards in demersal fisheries (Cosandey-Godin et al., 2015; Grazia Pennino et al., 2014), anchovy presence/abundance (Quiroz et al., 2015), the biomass of anchovy (Quiroz and Prates, 2018), nursery areas (Paradinas et al., 2015), squat-lobster catch per unit effort as relative abundance (Cavieres and Nicolis, 2018), and spatial distribution of anchovy (Moron et al., 2019).

In the central-south area of Chile, the conventional DEPM is utilized to assess the spawning stock biomass of two small pelagic fish, i.e., the anchovy (*Engraulis ringens*) and the sardine (*Strangomera bentincki*) (Bustos et al., 2020; Cubillos et al., 2007), locally known as “anchoveta” and “sardina común”. These species support small-scale and industrial fleets and catches are utilized for fishmeal and oil production, with Talcahuano (37°S) as principal port for landings (Canales et al., 2020). The annual catch of anchovy fluctuated between 115310 and 175208, while the sardine catch ranged between 285128 and 344115 from 1990 to 2021 (SERNAPESCA, 2021).

The anchovy and sardine shared similar demographic traits, feeding, growth, mortality, and reproductive dynamics, such as maturity at the end of the first year and spawning areas. However, the distribution of spawning is influenced by topography and bottom depth configurations that interact with environment

variables such as river discharges, precipitations, surface salinity gradients, and winds (alternation from northerly to southerly winds during the transition between winter to spring during the reproductive season) (Castillo-Jordán et al., 2007; Castro and Hernandez, 2004; Castro et al., 2000; Cubillos et al., 2001; Soto-Mendoza et al., 2010). The environmental influence, including topography and bathymetry, could determine persistent or recurrent spawning areas. Therefore, we hypothesized that daily egg survival across cohorts could have a constant spatial field. Nevertheless, according to Paradinas et al. (2017), the spatial dependence of daily cohorts could be associated with either opportunistic or progressive spatial fields. This paper aims to evaluate the spatial dependency of daily cohorts on the daily egg production rate P_0 and mortality Z of anchovy and sardine off the central-southern area of Chile.

2. Materials and methods

2.1. DEPM survey

We conducted a DEPM survey in the central and south zones of Chile from September 9 to October 11, 2018 (Table 1) (Bonicelli et al., 2019). Plankton stations ($n=371$) were spaced four nautical miles apart along E-W transects on the continental shelf (200 m depth) and transect lines separated by five nautical miles (Figure 1). Planktonic samples were collected in vertical hauls with Paironet

nets (25 cm diameter, 0.150 mm mesh size and depressor of 36 kg) (Smith et al., 1985), starting from either a depth of 70 m or near the seabed in depths less than 70 m. Once the plankton sample was on board, the plankton collected were preserved in a 4% formaldehyde solution (10% formalin) in seawater buffered with borax (tetraborate of sodium).

In the laboratory, sardine and anchovy eggs were sorted from the plankton, identified, counted under a stereoscopic microscope, and classified into one of 11 developmental stages based on the sequential morphological stages that occur during embryogenesis, as described by Moser and Ahlstrom (1985), Santander et al. (1984), Sepúlveda et al. (2004), and applied by Cubillos et al. (2007).



2.2. The daily egg production rate

The spawning area was estimated by analyzing the spatial distributions of stations with at least one egg per 0.05 m^{-2} . The area of a given station was computed utilizing a radius equivalent to half of the distance between stations. The radius allowed connecting neighboring stations according to the 'geofun' package of the 'egg' library (<http://sourceforge.net/projects/ichthyoanalysis/>), available for the language and software R (Stratoudakis et al., 2006).

The spawning time is midnight (00:00 h) for anchovy and 23:00 h for sardine (Claramunt et al., 2007). The stage-temperature-dependent model of Lo (1985) based on egg incubation experiments (Claramunt et al., 2007) was used for egg aging. Assuming that the egg abundance declined exponentially, the daily egg production and mortality rates were estimated from the following expression:

$$P_t = P_0 \exp(-Zt) \quad (1)$$

where P_t is the egg density per day at age t (egg per 0.05 m^{-2} per day), P_0 is the daily egg production rate (egg $0.05 \text{ m}^{-2} \text{ d}^{-1}$), and Z is the daily egg total mortality rate of eggs. We discarded ages less than four hours after spawning were discarded and older than 95% of hatching ages. The egg number can be utilized to obtain a linear predictor, i.e.,

$$\log(E(N_{t_i})) = \log(a_i) + \log(P_0) + Zt_i \quad (2)$$

where $\log(a_i)$ is the logarithm of the effective area of the net in the set i , and P_0 and Z were previously defined.

2.3. Spatial Bayesian approach

The non-spatial or conventional model was fitted with INLA, with the intercept added as a covariate term in the list of effects. The egg counts follow a negative

binomial distribution. The non-spatial model is the traditional approach to estimating the daily egg production rate and mortality.

For the spatial models, we utilized INLA (Rue et al., 2009) and the Stochastic Partial Differential Equations (SPDE) approach of Lindgren and Rue (2011) to model a Gaussian spatial process with Matérn covariance. The data (egg counts) observed at locations s_i with $i = 1, \dots, n$, was assumed to be a realization of the Gaussian Field (GF) at locations s_i and measured error. Furthermore, the spatial process was assumed to be stationary and isotropic, meaning that the covariance between any two points only depends on their distance. The Matérn covariance function has a scale parameter $\kappa > 0$ and a smoothness parameter $\nu > 0$. For two locations, s_i and s_j , the stationary isotropic Matérn spatial correlation is:

$$\rho_s(X_s) = \frac{2^{1-\nu}}{\Gamma(\nu)} (\kappa \|s_i - s_j\|)^\nu K_\nu(\kappa \|s_i - s_j\|) \quad (3)$$

where $\|s_i - s_j\|$ denotes the Euclidean distance, and K_ν is the modified Bessel function. The Matérn covariance function is $\sigma^2 \rho_s(X_s)$, where σ^2 is the marginal variance process.

The SPDE approach is a GF solution with Matérn correlation when $\nu > 0$. A two-dimensional space triangulated domain represents the spatial process defined using nodes of a mesh. A projector matrix links the spatial GF to the locations of the observed data. The SPDE model is a function of the mesh and the α parameter. The latter is related to the smoothness parameters of the process ν .

The priors for the marginal standard deviation of the field σ and the practical range, $\sqrt{8\nu\kappa}$, can be set through p such that $P(\sigma > \sigma_0) = p$. Besides, the smoothness parameter ν is fixed as $\alpha = \nu + D/2$, where D is a two-dimensional field.

As previously stated, the egg counts follow a negative binomial distribution, i.e., $Y_{s,t} \sim \text{BN}(\mu_{s,t}, \theta)$. We estimated non-spatial and spatial effects models (Table 2). The models were fitted with INLA with the intercept added as a covariate term in the list of effects, i.e.,

$$\log(\mu_{s,t}) = \log(a_{s,t}) + \beta_0 + Zt_s + V_{s,t} \quad (4)$$

where $\log(a_{s,t})$ is the logarithm of the effective area in the set represented in s and age t , β_0 is the intercept, but not equivalent to $\log(P_0)$ in the non-spatial model. The daily egg mortality Z is equivalent to the non-spatial model, and $V_{s,t}$ is the random spatial effect represented by $V_{s,t} = w_{s,t}$, where $\mathbf{W} \sim \text{N}(0, \mathbf{Q})$. The \mathbf{W} is a stationary geostatistical field with a covariance function defined by the range (r) y standard deviation (σ). The range and standard deviation depend of the hyperparameters κ and τ , i.e., $w_s = (\kappa - \Delta)^{\alpha/2} \tau y(s)$, where $\kappa > 0$ is the scale parameter, τ control the variance of the GF, y_s is a Gaussian random field and w_s is a stationary noise. The matrix \mathbf{Q} is the precision matrix, a sparse matrix defined by SPDE.

To model the spatial effects, we considered the nomenclature of Paradinas et al. (2017) for defining three spatial models (Table 2). Model 1 considered a constant spatial effect across the daily cohorts and indicative of a recurrent spatial distribution (Model M1). Model M2 consisted of a spatial effect changing every daily cohort and representing an opportunistic daily distribution. The third model (Model M3) considered a correlated spatial effect across the daily cohort, indicative of a progressive egg distribution. The Deviance Information Criterion (DIC) (Spiegelhalter et al., 2014) was used to compare between models. Once we selected the best model, we added covariates to the linear predictor, i.e., salinity and the bottom depth (Table 2). To detect non-linear effects of salinity and bottom depth, we utilized a smooth function with a random walk (“rw1”) for depth. In the case of salinity, we applied the random walk to ten salinity groups. We did not attempt to incorporate temperature at 10 m due to the narrow values and non-contrasting effects (Table 1). Salinity and bottom depth indicate recirculation and mixed coastal waters and have been utilized to explain the egg distribution (Castillo-Jordán et al., 2007). The smaller the DIC, the better the compromise between fit and parsimony.

3. Results

3.1. The conventional estimates of the daily egg production

The Daily Egg Production Method in 2018 shows a study area of 11716 km² in the central zone and 13657 km² in the south zone (Table 1). The bottom depth range was similar between the central and south zones, with the sea surface temperature between 10.5 and 14 °C, but a narrow temperature range at 10 m depth (Table 1). Besides, in the south zone, the salinity at 10 m was lower than in the central zone (Table 1).

While the mean count of anchovy eggs was lower in the central sector, the sardine egg count was the lowest and most variable in the south sector (Table 1). Similarly, the standard deviation of egg counts was higher than the mean, suggesting the clumped distribution of the spawning. Thus, anchovy has a larger spawning area in the central zone and lower egg density compared with the south zone. On the other hand, the spawning area of sardine was smaller and fragmented in the south zone compared with north zone (Table 1).

The egg count as a function of age shows a scatter distribution for anchovy and sardine (Figure 2), with sardine showing lower egg abundance. Part of the scatter data points in the survival plot is due to clumped egg distributions and daily changes in egg distributions (Figures 3 and 4). The distribution of daily anchovy egg cohorts shows small dispersion in central and south zones. Instead, sardine

shows the lowest spawning intensity with fragmented and daily changes in egg patches in the south zone.

The conventional estimates of P_0 and Z utilizing model M0 (non-spatial, Table 2) revealed a higher P_0 for sardine than anchovy in the central sector and the opposite in the south sector (Table 1). The anchovy daily egg mortality was lower than sardine in the central sector and higher in the south for both anchovy and sardine (Table 1).

3.2. Spatial models



According to the Deviance Information Criterion (DIC), the statistical performance of the spatial models was better than the non-spatial model (Table 3). The spatial effects of Model M2 (without salinity or bottom depth) adjusted better for anchovy in the central and south zones and sardine in the south zone. Instead, the spatial structure of Model M3 (without salinity or bottom depth) adjusted better for modeling the sardine in the central zone (Table 3). Nevertheless, incorporating salinity and bottom depth improves the performance of model M2 in all of the cases, except the case of sardine in the south sector (see DIC for model M4a, Table 3).

Although model M4a attained the lowest DIC values, the salinity effects were not precise for anchovy in the central and south zones and sardine in the central zone

(Figure 5). Therefore, we selected Model M4b for modeling the spatial effects on the daily egg production rate, except for sardine, in which adding covariates did not improve Model M2 (Table 3).

The parameters of the selected spatial models for anchovy and sardine show a significant negative daily mortality rate, high precision for the dispersion parameter of the negative binomial distribution and bottom depth effects, and a nominal range (km) exhibiting a spatial correlation fluctuating between 13.19 and 43.57 km (Table 4). In addition, the bottom depth effects showed a peak in egg density at a depth lower than 100 m for anchovy and sardine but a secondary peak in anchovy eggs close to 275 m depth in the south zone (Figure 5).

The fitted mean and standard deviation of egg density of anchovy show discrete egg aggregations in the central zone than in the south sector (Figures 6 and 7). Although the egg aggregations tend to remain in similar locations, there are small changes among daily cohorts in some aggregations. Besides, the spatial distribution of the standard deviation, with values > 2 , shows reductions in the spawning area between cohort 1 and cohort 3 (Figures 6 and 7).

In the case of sardine, an important egg aggregation remains in the southern part of the central zone. In contrast, a small egg aggregation in the northern part of the area tends to virtually disappear from cohort 1 to 2, reappearing one egg aggregation in cohort 3 (Figure 6). The spawning of the sardine in the south zone was poor and discrete, showing smaller egg aggregations close to Corral (Figure

6). The standard deviation in the central and south zones was higher than 2.5 to 3, evidencing daily changes in the egg distribution (Figure 7).

4. Discussion

The aim of this study was to evaluate the spatial dependence of daily cohorts of small pelagic fish by considering the spatial correlation. As a result, the spatial models adjusted better than the non-spatial or conventional model frequently utilized to estimate P_0 . Why this difference between the spatial models and the conventional approach to estimate P_0 ? The conventional model has restrictive assumptions, notably that the daily egg production rate is constant and the same in each location of the spawning area and that eggs decline in number only by a constant mortality rate. Other factors that reduce egg density, e.g., aggregation/diffusion of eggs after spawning, are confounded with mortality and not considered explicitly in these models. Therefore, it is essential to consider how spatial variation affects the estimates. Our approach to dealing with spatial correlation has several advantages over the conventional approach.

First, and from a statistical point of view, egg density residuals are rarely analyzed in the conventional estimates of P_0 . Considering the clumped egg distribution, which could be due to the ephemeral spawning behavior of adults (Basilone et al., 2015; Gantias et al., 2014; Gantias, 2008), and a mix of concentration/dispersal

processes in the spawning habitat (Bakun, 1996; Bakun and Csirke, 1998; Sabatés et al., 2007), the assumption of independent and identically distributed residuals could not be effective for proper inference. Therefore, one of the advantages of considering spatial random effects on daily egg production is that spatial structure comes from a mixture of processes driven by the spatial pattern in the spawning of small pelagic fish, which is critical in heterogenous spawning habitats.

Second, although our approach was similar to spatial GAM modeling of P_0 (Bernal et al., 2011b; Borchers et al., 1997), our approach has the advantage of comparing different spatial structures affecting egg distribution to make appropriate inferences (Dale and Fortin, 2014). Thus, our approach considering the spatial structure is an additional advantage.

A third advantage, similar to spatial GAM modeling, is to avoid the poststratification required in the conventional estimates of P_0 into the spawning area (known as positive area) and non-spawning area. For example, all the plankton stations sampled in the egg survey contribute to the estimation of P_0 , but an excess of zeroes would be a problem. Nevertheless, one of the disadvantages is the assumption of absence or no detection in the stations where eggs were not observed. In cases where the number of stations with no detected or no-observed eggs is large, a zero-inflated binomial negative could be more effective. Thus, the fourth advantage of INLA is the higher number of probability functions available.

The spatial dependence of daily egg cohorts revealed that daily egg distribution is not recurrent (constant), but instead, the egg cohorts had an opportunistic distribution changing daily. Different daily realizations in the spatial field can be explained by a decline in egg number (mortality) and daily changes in egg redistribution associated with spatial aggregation/dispersion processes acting simultaneously. The idea of persistent or recurrent egg distribution is valid when aggregation/dispersion processes remain constant daily or without significant influence. Instead, the idea of a progressive or daily correlated egg distribution is valid when the mortality process dominates over the aggregation/dispersion processes. However, egg distribution is a state-dependent process related to the spawning intensity and size of the spawning biomass. A higher spawning intensity could determine higher egg abundance and be insensitive to daily changes in the aggregation/dispersion processes. Hence a progressive distribution could be evident.

According to selected models, the egg mortality rates of anchovy and sardine were similar in the central zone. Therefore, death causes could be identical for pelagic fish eggs in the central zone. However, the sardine had the highest egg mortality in the south zone compared to the anchovy, probably associated with lower spawning intensity during the spring season in 2018. According to McGurk (1986), patchiness explains the mortality of eggs and early-stage larvae. Therefore, in lower spawning intensity, the fragmented egg aggregations of

sardines could be more vulnerable to predation than anchovy egg aggregations in the south zone.

In this study, the spatial correlation range fluctuated between 20.45 and 43.57 km for anchovy and sardine in the central zone, but sardine had a lower range in the south zone (13.19 km). The range is an index of the average size of the spawning aggregations, and the sardine case in the south showed the average size of egg hot-spot distribution. Regarding spatial dependence, the bottom depth was a significant variable in explaining the daily egg distribution of anchovy and sardine. Although pelagic eggs distribute in the water column, the bottom depth effect and topography are a proxy for water mix and fronts, and coastal egg concentration is probably related to northerly winds promoting coastal convergence (Castro and Hernandez, 2004; Castro et al., 2000). Therefore, changes in wind directions, from northern to southern winds, could affect egg redistribution over the continental shelf. In central-southern Chile, the ranges of sea surface temperatures during the spawning of small pelagic are relatively constant, fluctuating between 10 to 13 °C (Bustos et al., 2020; Cubillos et al., 2007). However, subsurface temperatures are relatively homogenous (Sobarzo et al., 2007). The development rate is slower than that observed for anchovy off northern Chile, Peru, or the *E. mordax* off California (Cotero-Altamirano and Green-Ruiz, 1997; Lo, 1985; Santander et al., 1984). Besides, salinity fluctuated between 32.5 and 34.6 PSU, and although salinity influenced the spatial models, it was not precise for the spatial dependence of the daily egg cohorts. Salinity seems

essential for egg buoyancy and the presence of fronts and similar structures, probably close to river discharge and related to redistribution through the topography and bathymetry. Therefore, the bottom depth is a crucial component of the spatial dependence for the spawning of small pelagic in central-southern Chile.

Spatial correlation is essential for estimating daily egg production because eggs are spawned in a given area, configured as potential reproductive habitat. Once spawn occurs, the potential reproductive habitat transforms into a realized spawning habitat where recurrent and occasional spawning sites can be recognized (Bellier et al., 2007; Planque et al., 2007). However, we do not know whether spatial correlation or transitive geostatistics have been used previously to estimate spawning area in the DEPM literature (but see Bellier et al., 2007). Thus, the conventional estimates of daily egg production rate and spawning area should be replaced by a spatial model considering spatially correlated random effects like those proposed here.

For further development of the techniques applied here, the intercept in the spatiotemporal model should be not considered as an estimate for the daily egg production rate. However, like abundance indices obtained from spatiotemporal models (Maunder et al., 2020), the daily egg production rate can be estimated by applying area weighting averaging procedures. However, it requires a prediction from spatiotemporal models and is outside of our objective. Our study

emphasized the spatial dependence of daily cohorts and the structure of the spatial field.

Finally, we conclude that daily egg production must consider spatial effects due to multiple spatial processes affecting egg distribution daily. Therefore, we suggest applying Bayesian linear models like those utilized here.



TABLES

Table 1. Description of the DEPM survey for anchovy and common sardine in the central and south zones off Chile.

Survey	Species	Central	South
Date		Sep. 9 - Oct 11	Oct 1 - Oct 24
Latitude (°S) and Longitude (°W)		34°30'S - 37°10'W	38°00'S-41°20'W
Number of stations (n)		170	201
Positive stations (n)	Anchovy	75	54
	Sardine	31	21
Study area (km ²)		11716	13657
Range bottom depth (m)		7 - 735	12 - 701
Sea surface temperature (°C) (range)		10.5 - 13.0	10.0 – 14.0
Temperature at 10 m (range)		11.0 - 11.6	11.6 - 12.6
Salinity at 10 m (range)		33.6 - 34.6	32.5 - 33.3
Mean egg count (egg per 0.05 m ²)	Anchovy	3.8	18.9
	Sardine	3.3	0.65
Standard deviation (egg per 0.05 m ²)	Anchovy	137.3	15875.4
	Sardine	600.9	17.7
Spawning area (km ²)	Anchovy	5198	3553
	Sardine	2081	1396
Daily egg production P ₀ (egg m ⁻² d ⁻¹)	Anchovy	7.0 (31.2)	81.3 (41.2)
	Sardine	26.2 (58.7)	15.2 (77.3)
Daily mortality rate Z (d ⁻¹)	Anchovy	0.84 (16.3)	1.10 (20.1)
	Sardine	1.15 (28.1)	1.42 (30.4)

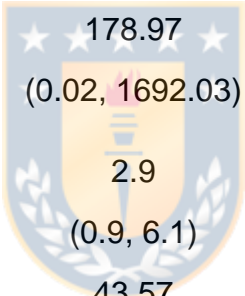
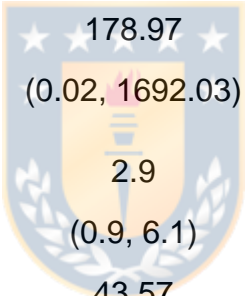
Table 2. Models utilized to incorporate spatial effects in the estimation of the daily egg production rates of anchovy and sardine in the central-southern Chile.

Model	Spatial field	Description
M0	Non spatial	Without spatial field: $V_{s,c} = 0$
M1	Constant	Matérn correlation is the same among daily egg cohort: $V_{s,c} = w_s$
M2	Opportunistic egg distribution per daily cohort	Matérn correlation, but with a different realization every daily egg cohort: $V_{s,c} = w_{s,c}$
M3	Progressive egg distribution per daily cohort.	Matérn correlation, and correlated across daily egg cohort: $V_{s,c} = w_{s,c} + \sum_{k=1}^K \rho_k V_{s(t-k)}$
M4	Based on the best model selected plus covariables	Either M1, M2 or M3 plus salinity or bottom depth.

Table 3. DIC values for all models tested.

Model	Covariable	Central		South	
		anchovy	sardine	anchovy	sardine
M0	-	913.2	511.2	1207.8	276.6
M1	-	789.2	353.6	893.6	203.4
M2	-	687.8	300.7	771.1	138.5**
M3	-	703.7	293.8	791.7	143.8
M4a	M2 +S10 + d	657.0*	282.4*	714.6*	139.2
M4b	M2 + d	668.1**	282.1**	732.9**	141.9

Table 4. Posterior estimates (mean and 95% credibility interval) of model parameters with negative binomial and spatiotemporal structure.

Parameters	Central		South	
	anchovy	Sardine	anchovy	Sardine
Model	M4b	M4b	M4b	M2
Intercept	0.44 (-0.97, 1.77)	-6.35 (-9.435, -3.510)	-1.99 (-3.76, -0.25)	-4.74 (-8.25, -1.59)
Z (h ⁻¹)	-0.034 (-0.061, -0.008)	-0.030 (-0.085, 0.024)	-0.014 (-0.052, 0.023)	-0.021 (-0.075, 0.032)
Precision for NB (1/overdispersion)	15.92 (0.80, 44.54)	 178.97 (0.02, 1692.03)	23.96 (17.35, 30.84)	1864.09 (0.003, 71443.26)
Precision for bottom depth <i>d</i>	36.9 (3.9, 94.4)	 2.9 (0.9, 6.1)	5.9 (1.2, 13.0)	n.a
θ_1	20.45 (11.85, 30.23)	43.57 (25.88, 63.71)	32.470 (25.04, 42.93)	13.19 (6.34, 21.17)
θ_2	2.46 (1.98, 2.97)	3.79 (2.59, 5.12)	2.77 (2.43, 3.03)	4.02 (2.88, 5.25)
Nominal range (km)	20.4 (11.9, 30.2)	43.5 (25.9, 63.6)	32.5 (25.1, 42.9)	13.1 (6.3, 21.1)

FIGURES

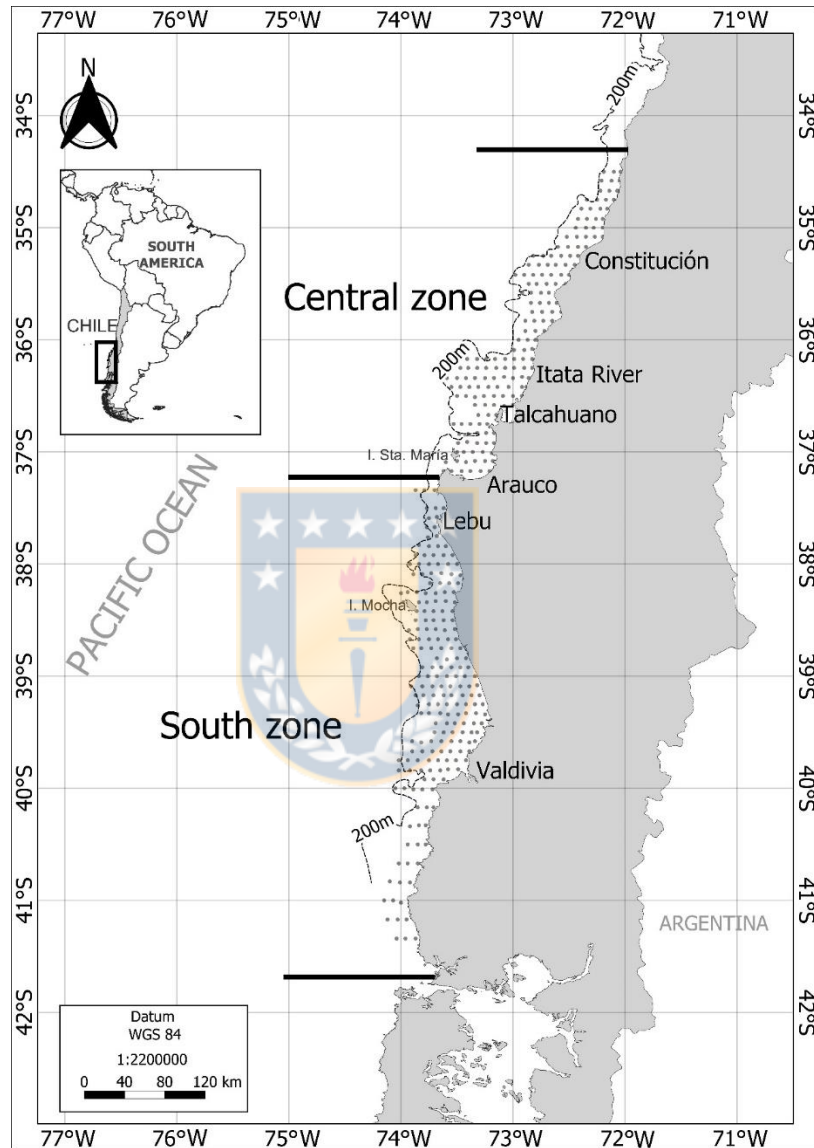


Figure 1. The study area shows two strata sampling design: the central and south zones. The western boundary distribution of the stations is the 200 m bottom depth isobath.

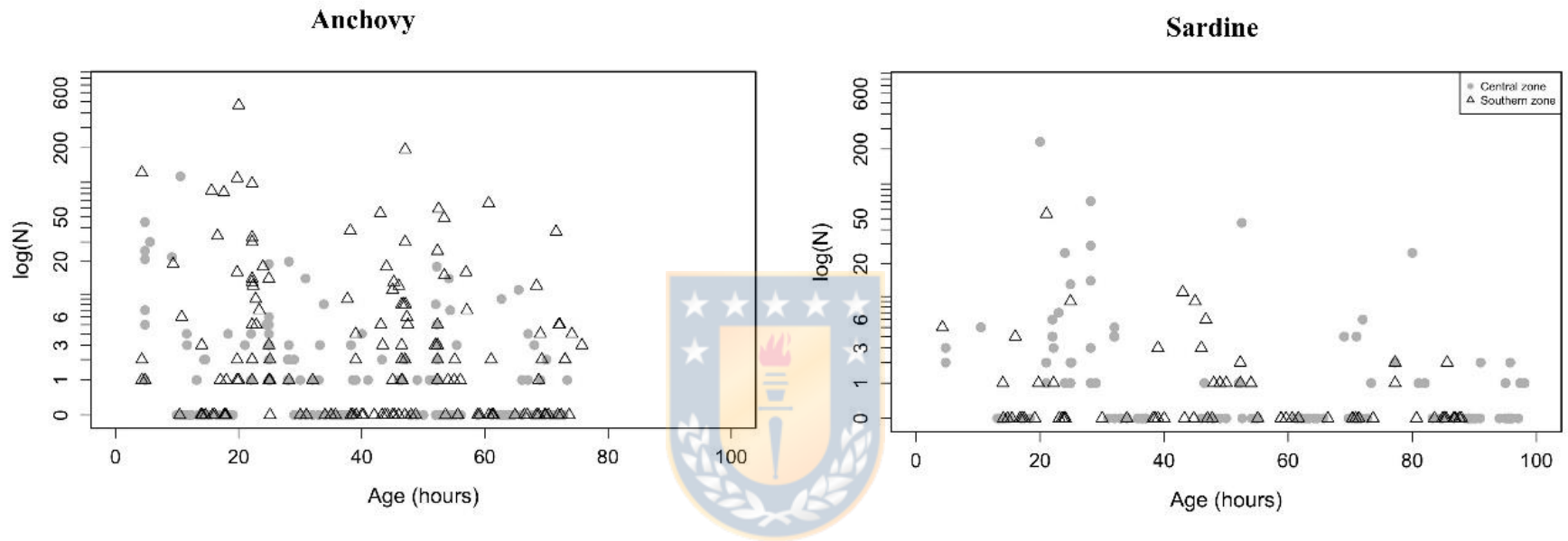
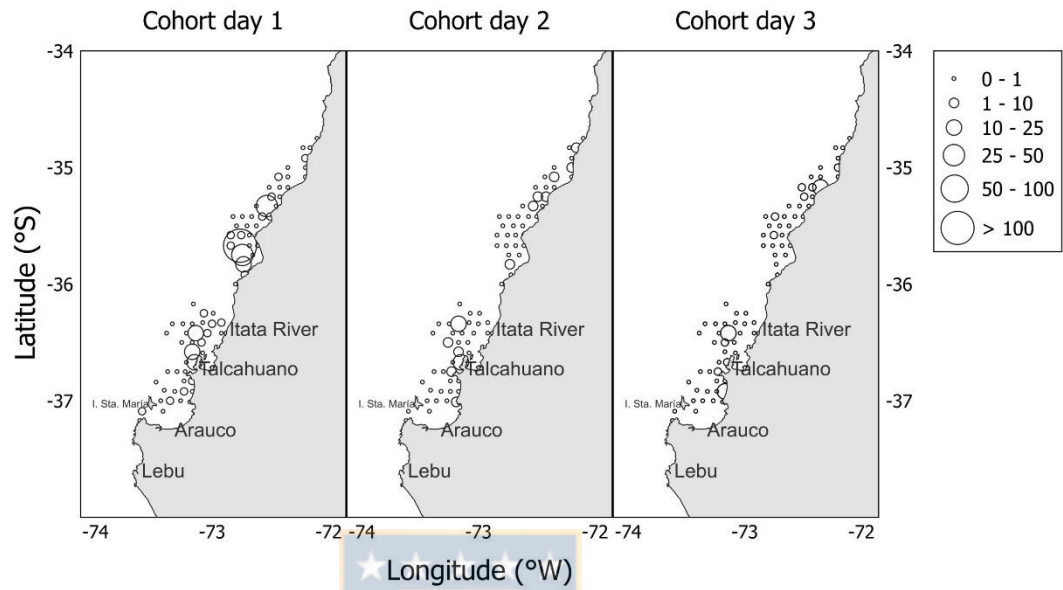


Figure 2. Egg abundance (egg counts per 0.05 m²) against age (hours) for anchovy and sardine in each geographic stratum in 2018.

A) Central



B) South

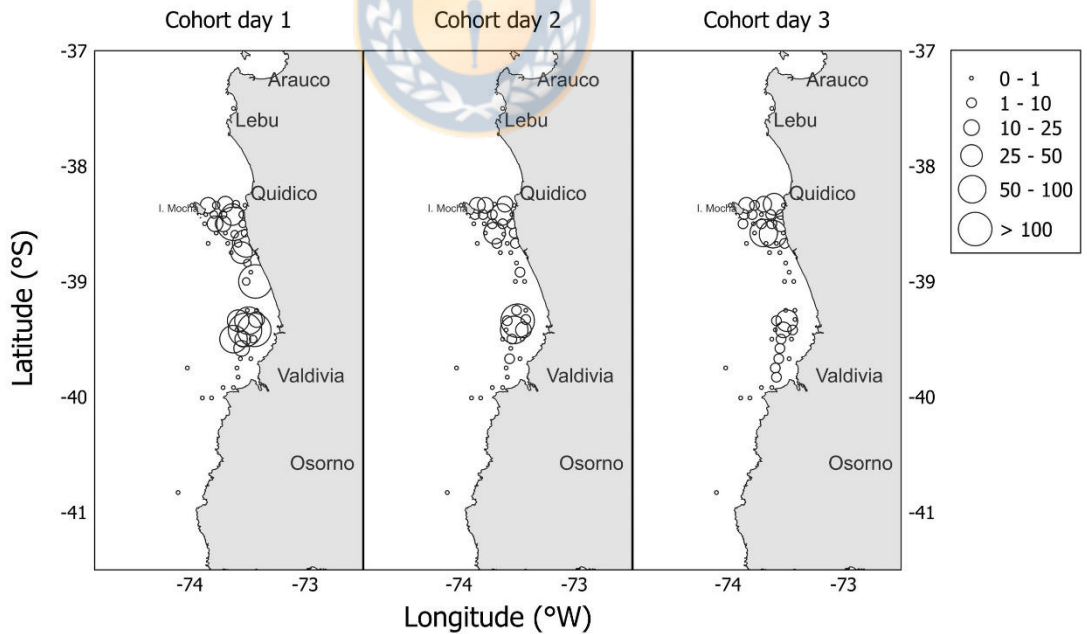
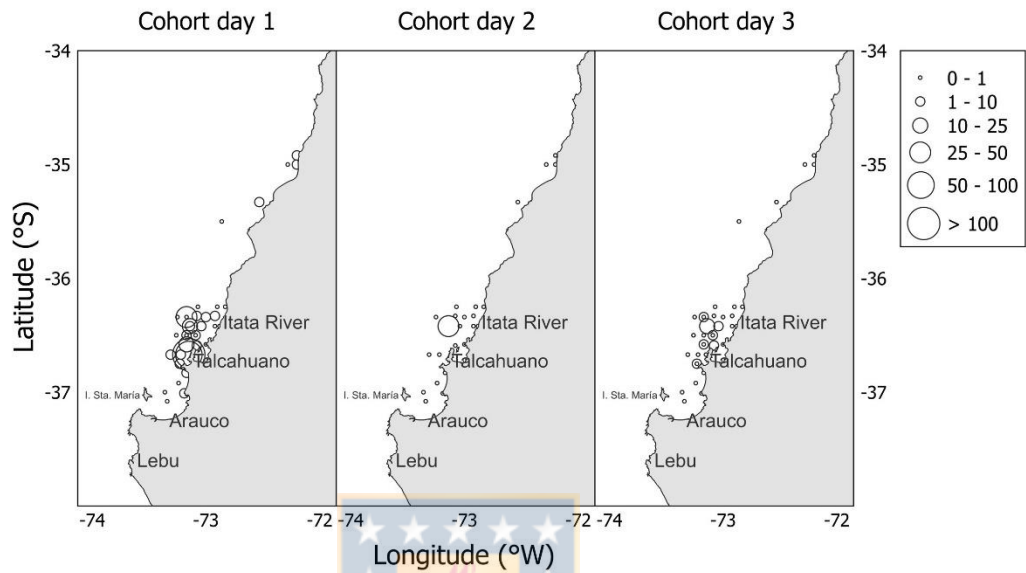


Figure 3. Spatial distribution of daily anchovy egg cohorts in the central and south zones in 2018.

A) Central



B) South

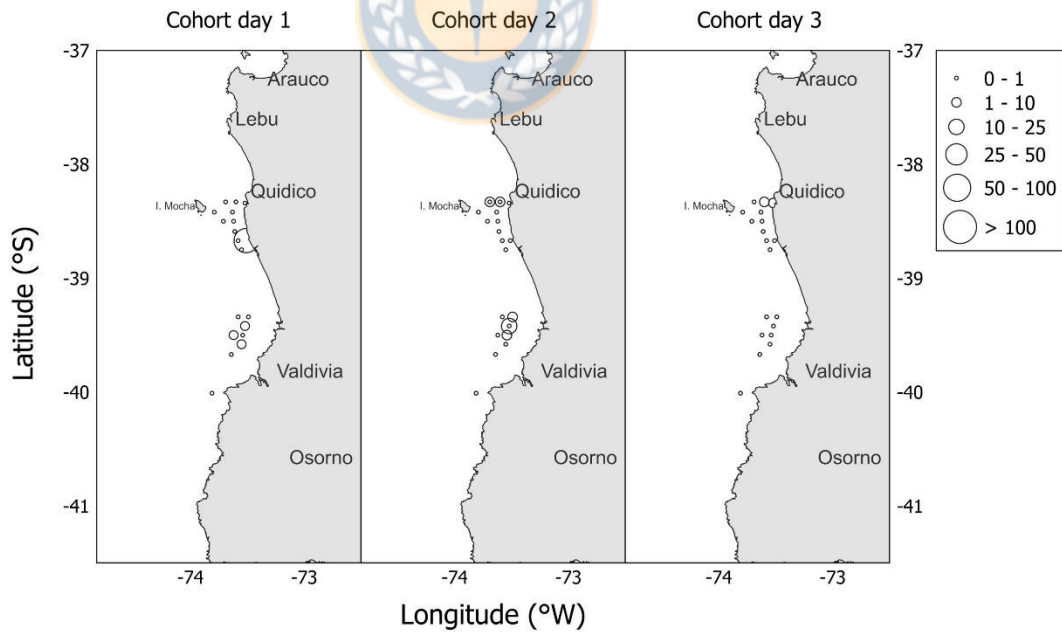


Figure 4. Spatial distribution of daily sardine egg cohorts in the central and south zones in 2018.

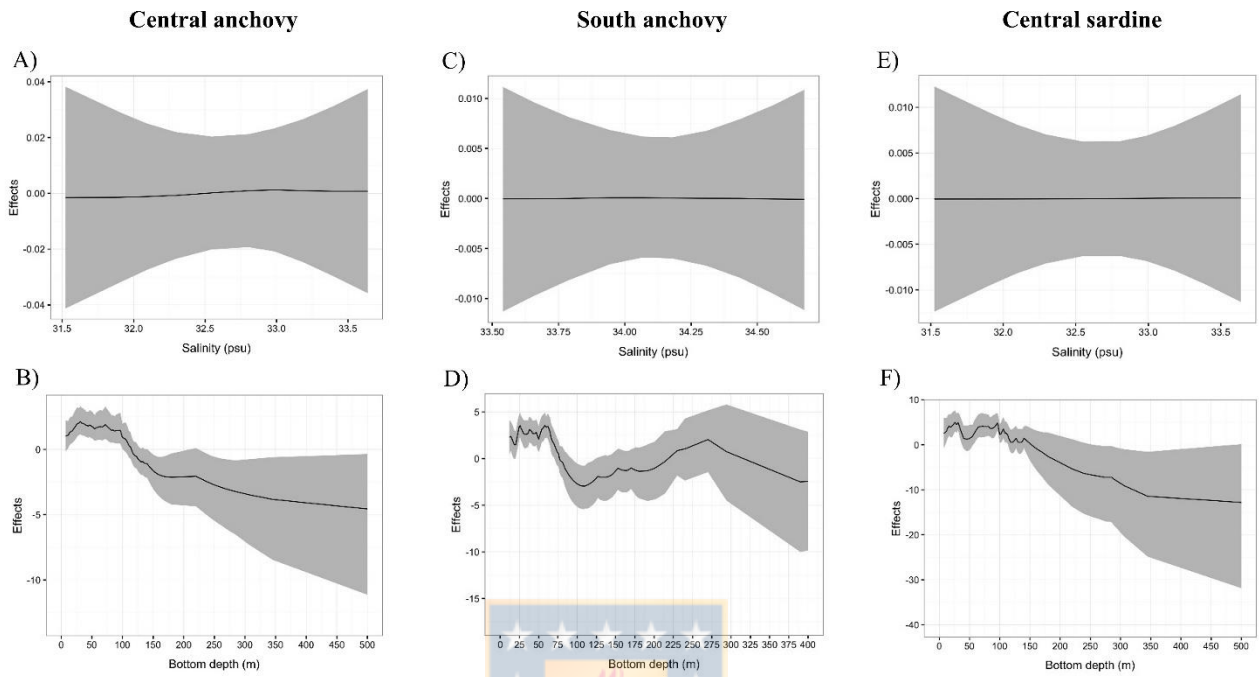
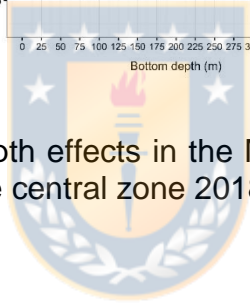


Figure 5. Salinity and bottom depth effects in the Model M4a for anchovy in the central and south zone and sardine in the central zone 2018.



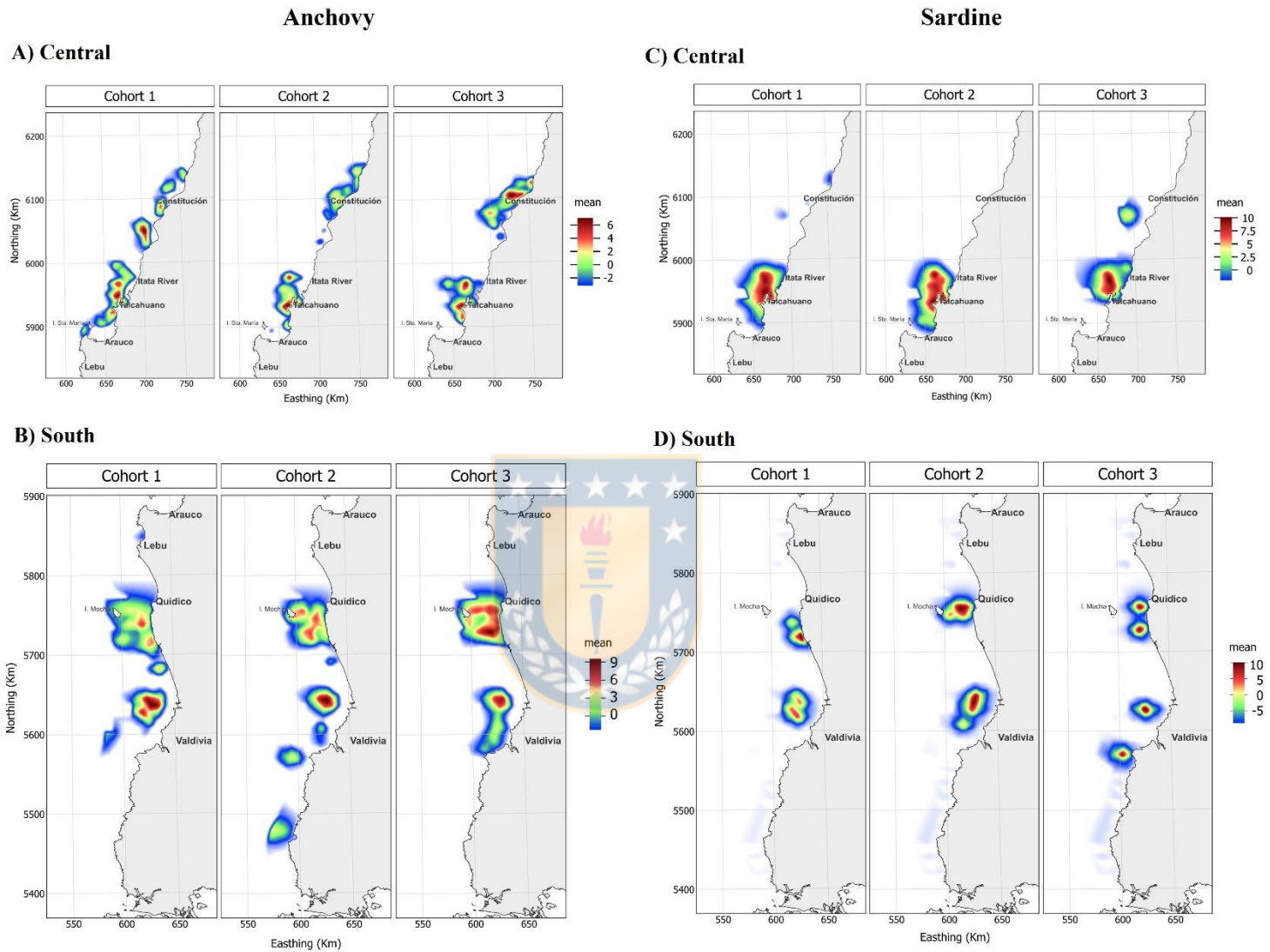


Figure 6. Estimates of the spatiotemporal mean of anchovy and sardine egg density (log-scale) per daily cohort in the central and south zones, 2018.

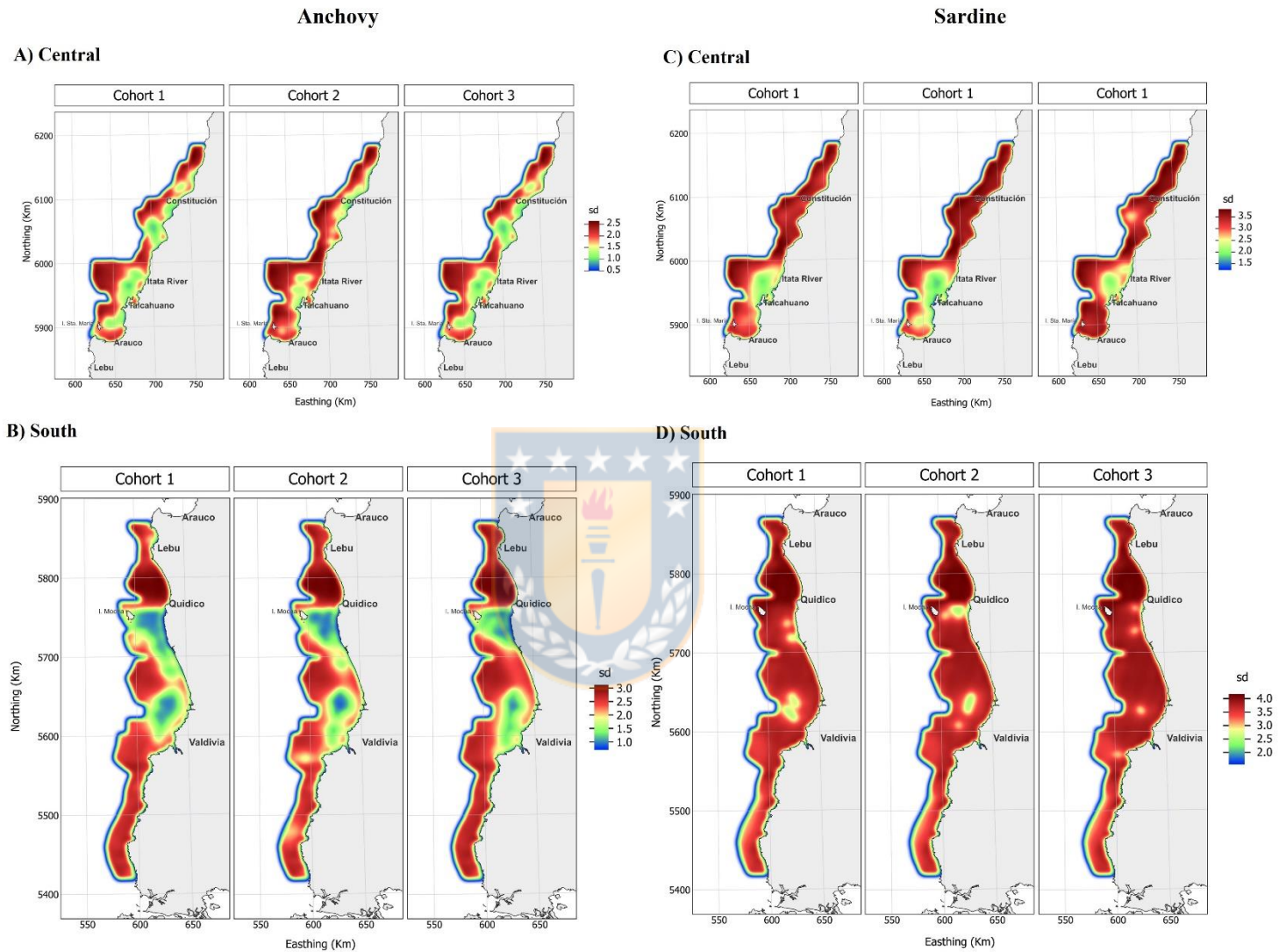


Figure 7. Estimates of the spatiotemporal standard deviation (sd) of anchovy sardine egg density per daily cohort in the central and south zones, 2018

ACKNOWLEDGEMENTS

JA was funded by a COPAS COASTAL scholarship (Masters of Fisheries Science Program), and LAC and LRC by COPAS COASTAL ANID FB210021, Universidad de Concepción, Chile. This paper contributes to Research Line 4 (Sustainability of Fisheries and Conservation) of the COPAS-COASTAL Center and the Stock Assessment and Fisheries Oceanography research lines of the Fisheries Science Master Program of the University of Concepcion. Finally, thanks also go to the support of Lab. EPOMAR and CEPMAR SpA.



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DISCUSIÓN GENERAL

El objetivo de este estudio fue evaluar la dependencia espacial de las cohortes diarias de pequeños pelágicos considerando la correlación espacial. Como resultado, los modelos espaciales se ajustaron mejor que el modelo no espacial o convencional utilizado frecuentemente para estimar P_0 . ¿Por qué esta diferencia entre los modelos espaciales y el enfoque convencional para estimar P_0 ? El modelo convencional tiene suposiciones restrictivas, en particular que la tasa de producción diaria de huevos es constante e igual en cada lugar de la zona de desove y que los huevos disminuyen en número sólo por una tasa de mortalidad constante. Otros factores que reducen la densidad de huevos, por ejemplo, la agregación/dispersión de los huevos después del desove, se confunden con la mortalidad y no se consideran explícitamente en estos modelos. Por lo tanto, es esencial considerar cómo la variación espacial afecta a las estimaciones. Nuestro enfoque para tratar la correlación espacial tiene varias ventajas sobre el enfoque convencional.

En primer lugar, y desde un punto de vista estadístico, los residuos de la densidad de huevos rara vez se analizan en las estimaciones convencionales de P_0 . Teniendo en cuenta la distribución agrupada de los huevos, que podría deberse al comportamiento efímero de desove de los adultos (Basilone et al., 2015; Ganas et al., 2014; Ganas, 2008), y una mezcla de procesos de concentración/dispersión en el hábitat de desove (Bakun, 1996; Bakun y Csirke,

1998; Sabatés et al., 2007), el supuesto de residuos independientes e idénticamente distribuidos podría no ser eficaz para una inferencia adecuada. Por lo tanto, una de las ventajas de considerar los efectos aleatorios espaciales en la producción diaria de huevos es que la estructura espacial proviene de una mezcla de procesos impulsados por el patrón espacial en el desove de pequeños peces pelágicos, lo cual es crítico en hábitats de desove heterogéneos.

En segundo lugar, aunque el enfoque es similar a la modelización GAM espacial de P_0 (Bernal et al., 2011b; Borchers et al., 1997), el enfoque tiene la ventaja de comparar diferentes estructuras espaciales que afectan a la distribución de los huevos para hacer inferencias adecuadas (Dale y Fortin, 2014). Por lo tanto, el enfoque de análisis considera la estructura del campo espacial, lo que representa una ventaja adicional.

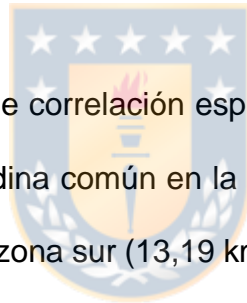
Una tercera ventaja, similar a la modelización GAM espacial, es evitar la post-estratificación requerida en las estimaciones convencionales de P_0 en el área de desove (conocida como área positiva) y el área de no desove. Por ejemplo, todas las estaciones de plancton muestreadas en el estudio de huevos contribuyen a la estimación de P_0 , pero un exceso de ceros podría ser un problema. Sin embargo, una de las desventajas es la suposición de ausencia o no detección en las estaciones donde no se observaron huevos. En los casos en los que el número de estaciones en las que no se detectan o no se observan huevos es grande, una binomial negativa cero-inflado podría ser más eficaz. Así, la cuarta

ventaja del enfoque de modelamiento con INLA es el mayor número de funciones de probabilidad disponibles.

La dependencia espacial de las cohortes diarias de huevos reveló que la distribución diaria de los huevos no es recurrente (constante), sino que las cohortes de huevos tienen una distribución oportunista que cambia diariamente. Las diferentes realizaciones diarias en el campo espacial pueden explicarse por una disminución del número de huevos (mortalidad) y por cambios diarios en la redistribución de los huevos asociados a procesos de agregación/dispersión espacial que actúan simultáneamente. La idea de una distribución de huevos persistente o recurrente es válida cuando los procesos de agregación/dispersión permanecen constantes diariamente o sin influencia significativa. En cambio, la idea de una distribución de huevos progresiva o correlacionada diariamente es válida cuando el proceso de mortalidad domina sobre los procesos de agregación/dispersión. Sin embargo, la distribución de los huevos es un proceso que depende del estado poblacional y está relacionado con la intensidad de desove y el tamaño de la biomasa del stock desovante. Una mayor intensidad de desove podría determinar una mayor abundancia de huevos y ser insensible a los cambios diarios en los procesos de agregación/dispersión. Por lo tanto, podría ser evidente una distribución progresiva.

Según los modelos seleccionados, las tasas de mortalidad de los huevos de anchoveta y sardina común fueron similares en la zona centro. Por lo tanto, las

causas de mortalidad podrían ser idénticas para los huevos de peces pelágicos en la zona centro. Sin embargo, la sardina común tuvo la mayor mortalidad de huevos en la zona sur en comparación con la anchoveta, probablemente asociada a una menor intensidad de desove durante la temporada de primavera en 2018. Según McGurk (1986), la fragmentación explica la mortalidad de los huevos y de las larvas en fase inicial. Por lo tanto, en una menor intensidad de desove, las agregaciones fragmentadas de huevos de sardina común podrían ser más vulnerables a la depredación que las agregaciones de huevos de anchoveta en la zona sur.



En este estudio, el rango de correlación espacial fluctuó entre 20,45 y 43,57 km para la anchoveta y la sardina común en la zona centro, pero la sardina común tuvo un rango menor en la zona sur (13,19 km). El rango es un índice del tamaño medio de las agregaciones de desove, y el caso de la sardina común en el sur mostró el tamaño medio de la distribución de los hot-spot de huevos. En cuanto a la dependencia espacial, la profundidad del fondo fue una variable significativa para explicar la distribución diaria de los huevos de anchoveta y sardina común. Aunque los huevos pelágicos se distribuyen en la columna de agua, el efecto de la profundidad del fondo y la topografía son una aproximación a la mezcla de aguas y frentes, y la concentración costera de huevos está probablemente relacionada con los vientos del norte que promueven la convergencia costera (Castro y Hernández, 2004; Castro et al., 2000). Por lo tanto, los cambios en la dirección de los vientos, de norte a sur, podrían afectar la redistribución de los

huevos sobre la plataforma continental. En el centro-sur de Chile, los rangos de las temperaturas superficiales del mar durante el desove de los pelágicos pequeños son relativamente constantes, fluctuando entre 10 y 13 °C (Bustos et al., 2020; Cubillos et al., 2007). Sin embargo, las temperaturas subsuperficiales son relativamente homogéneas (Sobarzo et al., 2007). La tasa de desarrollo es más lenta que la observada para la anchoveta frente al norte de Chile, Perú o la *E. mordax* frente a California (Cotero-Altamirano y Green-Ruiz, 1997; Lo, 1985; Santander et al., 1984). Además, la salinidad fluctuó entre 32,5 y 34,6 PSU, y aunque la salinidad influyó positivamente en los modelos espaciales, no fue precisa para la dependencia espacial de las cohortes diarias de huevos. La salinidad parece esencial para la flotabilidad de los huevos y la presencia de frentes y estructuras similares, probablemente cerca de la descarga de ríos y relacionada con la redistribución a través de la topografía y la batimetría. Por lo tanto, la profundidad del fondo es un componente crucial de la dependencia espacial para el desove de pequeños pelágicos en el centro-sur de Chile.

La correlación espacial es esencial para estimar la producción diaria de huevos, ya que éstos se desovan en una zona determinada, configurada como hábitat reproductivo potencial. Una vez que se produce el desove, el hábitat reproductivo potencial se transforma en un hábitat de desove realizado en el que se pueden reconocer lugares de desove recurrentes y ocasionales (Bellier et al., 2007; Planque et al., 2007). Sin embargo, no sabemos si la correlación espacial o la geoestadística transitiva se han utilizado previamente para estimar el área de

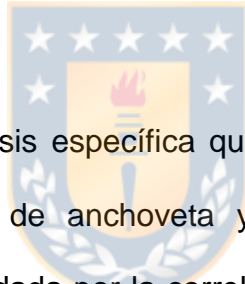
desove en la literatura del MPDH (pero véase Bellier et al., 2007). Por lo tanto, las estimaciones convencionales de la tasa de producción diaria de huevos y del área de desove deberían ser sustituidas por un modelo espacial que considere efectos aleatorios correlacionados espacialmente como los propuestos aquí.

Para un mayor desarrollo de las técnicas que se aplicaron en este trabajo, el intercepto en el modelo espacio-temporal no debería considerarse como una estimación de la tasa de producción diaria de huevos. Sin embargo, al igual que los índices de abundancia obtenidos a partir de modelos espacio-temporales (Maunder et al., 2020), la tasa de producción diaria de huevos puede estimarse aplicando procedimientos de promedios ponderados por área. Sin embargo, requiere una predicción a partir de modelos espaciotemporales y está fuera de nuestro objetivo. Esta tesis puso énfasis en la dependencia espacial de las cohortes diarias y en la estructura del campo espacial.

Finalmente, se concluye que en la estimación de la producción diaria de huevos se deben considerar los efectos espaciales debido a los múltiples procesos espaciales que afectan a la distribución diaria de los huevos. Por lo tanto, sugerimos aplicar modelos lineales bayesianos como los utilizados aquí.

CONCLUSIONES

1. Los efectos espacio-temporales en la producción diaria de huevos muestran que de los modelos implementados, la distribución espacial diaria de huevos es oportunista y modulada por la batimetría en la anchoveta de la zona centro y sur, y sardina común en la zona centro. Para las cohortes diarias de huevos de la sardina común no se detectó efectos de la batimetría en la zona sur debido a la baja intensidad del desove en el 2018.
2. Se acepta la hipótesis específica que la abundancia de las cohortes diarias de huevos de anchoveta y sardina común presenta una estructura espacial dada por la correlación espacial a pequeña escala (H1). En el caso de la anchoveta, para el año 2018, el recuento de huevos en función a la edad muestra que la estructura espacial de las cohortes diarias de huevos está compuesta por parches, mostrando un rango de correlación de 20,4 – 35,5 km, para las tres cohortes de anchoveta en las zonas centro y sur. Para el caso de la sardina común se muestra que la estructura espacial de las cohortes diarias de huevos en la zona sur está fragmenta con cambios en los parches de huevos con un rango de correlación de 13,1 km.



3. Se acepta la hipótesis específica que la distribución espacial de la producción diaria de huevos es influenciada por la profundidad de fondo. Para el 2018, los modelos espaciales muestran influencia significativa de la profundidad de fondo en la distribución espacial de la producción diaria de huevos para la anchoveta de las zonas centro y sur y para la sardina de la zona centro.
4. Se rechaza la hipótesis específica que la distribución espacial de la producción diaria de huevos es influenciada por la salinidad promedio del estrato superficial (10 m). La variable salinidad, por sí sola, no mostró influencia significativa para la anchoveta de las zonas centro y sur y para la sardina de la zona centro.
5. Se acepta la hipótesis general que la dependencia espacial de la producción diaria de huevos está influenciada por factores exógenos que se expresan a través de la relación con variables proxy de los procesos que modulan la concentración y retención de huevos. La dependencia espacial de la producción diaria de huevos estuvo influenciada significativamente por factores exógenos, específicamente con profundidad de fondo.

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