Accounting for spatial dependence improves relative abundance estimates in a sessile marine species structured as a metapopulation

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Abstract

Sea urchin (*Loxechinus albus*) is one of the most important benthic resource in Chile. Due to their large-scale spatial metapopulation structure, sea urchin subpopulations are interconnected by larval dispersion, so the recovery of local abundance depends on distance and hydrodynamic characteristics of their spatial domain. Currently, this resource is evaluated with classical stock assessment models, using standardized catch per unit effort (an index of relative abundance) as a key piece of information to determine catch quotas and achieve sustainability. However, these estimates assume hyperstability for the total population, ignoring spatial dependence among fishing sites, which is a fundamental concept for populations structured as metapopulation. We propose a Bayesian model with explicit spatial dependence approximating a GRF by a GRMF under the SPDE method for the observations in the spatial domain under study. The proposed model performs statistically better compared to a model without spatial dependence, based on leave-one-out cross-validation (`loo`). Subsequent predictive distributions also show that parameter estimation is consistent with the data. We show that the incorporation of the spatial random effect improves the estimated relative abundance index in a population structured as a metapopulation. Our improved index of abundance will lead to better assessments and management advice, thus improving the sustainability of the stock.

Keywords: Metapopulation, catch per unit effort (CPUE), spatial model, Bayesian inference, Sea urchin (*Loxechinus albus*)

1. Introduction

Catch per unit effort (CPUE) is a crucial variable in fishery science and considered proportional to the abundance of a particular fishery resource. But many factors are ignored. For example, the assumption of proportionality does not hold when factors affect catchability but not abundance ([13][14]). Hence, it is necessary to incorporate influences that are not related to population abundance (e.g., spatial variation in effort and temporal gear efficiency changes) and should be accounted for in CPUE standardization ([15]). CPUE is a key source of information used in such models as a "relative abundance index" so we can assume that the variable is robust enough for detecting trends and informing stock assessments, provided that catchability (q) and selectivity are constant through time and space (i.e., $CPUE = qN$) ([14]). This concept is also assumed when we want to estimate a

relative abundance index for an invertebrate marine species', specifically assuming CPUE is proportional in the species' entire spatial domain. Thus, the concept ignores the spatial population structure or larval dispersion among the fishing sites.

One example of a such an invertebrate is the sea urchin (*Loxechinus albus*), which figures among Chile's most important benthic resources economically, socially, and ecologically ([1][2][3][4]), with an extensive spatial distribution from Peru (starting at 6°) to Chile's far south (55°). Chile has the most important sea urchin fishery in the world ([43]), and catches account for around 50 percent of global landings [43]. The resource's population is structured as a metapopulation across a large spatial scale ([8][9]), namely a number of relatively sedentary adult local populations linked by dispersal of a planktonic larval stage where the recruitment to local populations is likely dependent on immigration of larvae from other local populations subject to the environmental influences and coastal circulation in a given year ([56]). Studies of metapopulations' biology have focused on the effects of local population dynamics regarding the populations' spatial structure and describe how populations within their domain are connected via limited migration ([10]). The sea urchin population has been evaluated recently under classical stock assessment models ([55]) to generate management strategies and achieve sustainability. The CPUE in these models is an important source of information because it represents the relative abundance of a marine resource. CPUE standardization has been estimated for sea urchin with generalized linear models (GLM; [16]) and generalized linear mixed models (GLMM; [17]). But these methodologies ignore catches' spatial patterns ([19][20]), or in the case of sea urchin, spatial dependence among fishing sites.

Many authors have implemented models that incorporated spatial and temporal variations into the statistical model for other marine populations. One was proposed by [21], who showed the importance of spatial models for estimating the strength of density dependence, and [22] built a delta generalized model to improve the estimations in a relative abundance index with statistical software Template Model Builder (`TMB`; [23]). Other works were developed for this purpose. For example, [15] evaluated the effect of longline hook spacing on the standardization of CPUE and [24] used a Bayesian spatiotemporal model to standardize CPUE for yellow squat lobster (*Cervimunida johni*) in Chile with `R-INLA` ([25][26][27]). Recently, [28] evaluated the impact of different spatiotemporal variations in CPUE standardization and [29] studied the impact of including depth in CPUE standardization.

Obtaining a reliable relative abundance index is crucial for fisheries structured around metapopulations. An emphasis on the spatial population structure requires identifying the scale of observation, type of analysis, and proper and continuous management of the resource within a certain spatial domain. Recovering local populations depends on the distance of larval dispersion and the hydrodynamic characteristics within the metapopulation's domain ([11]). Thus, the spatial scales used to analyze the populations of individual specimens and the respective fishery must be considered ([12]). Yet no spatiotemporal model to estimate a relative abundance index has been developed for benthic species whose populations are generally structured on metapopulations with temporal variations.

In this work we develop a Bayesian spatiotemporal model to obtain a relative abundance index to test spatial importance in a population structured as a metapopulation. Dependence was established by incorporating a spatial random effect and we compared the results with a model without spatial random effect. The main goal was to prove that incorporating a spatial random effect improves the

57 estimation of a relative abundance index for use in stock assessment models.

2. Materials and Methods

2.1. Data

60 The sea urchin fishery is located in the south of Chile, specifically north of Chiloé. Respective data
61 came from monitoring undertaken by the Instituto de Fomento Pesquero (Spanish acronym IFOP)
62 from 1996-2016. The fishery is artisanal with vessels of up 12 meters. Catches by site are random,
63 some sites are big with a high abundance while the fishers change sites when abundance falls or sea
64 urchin size is small. Figure 1 shows the observed CPUE (Kg/hour of diving) for each fishing site.
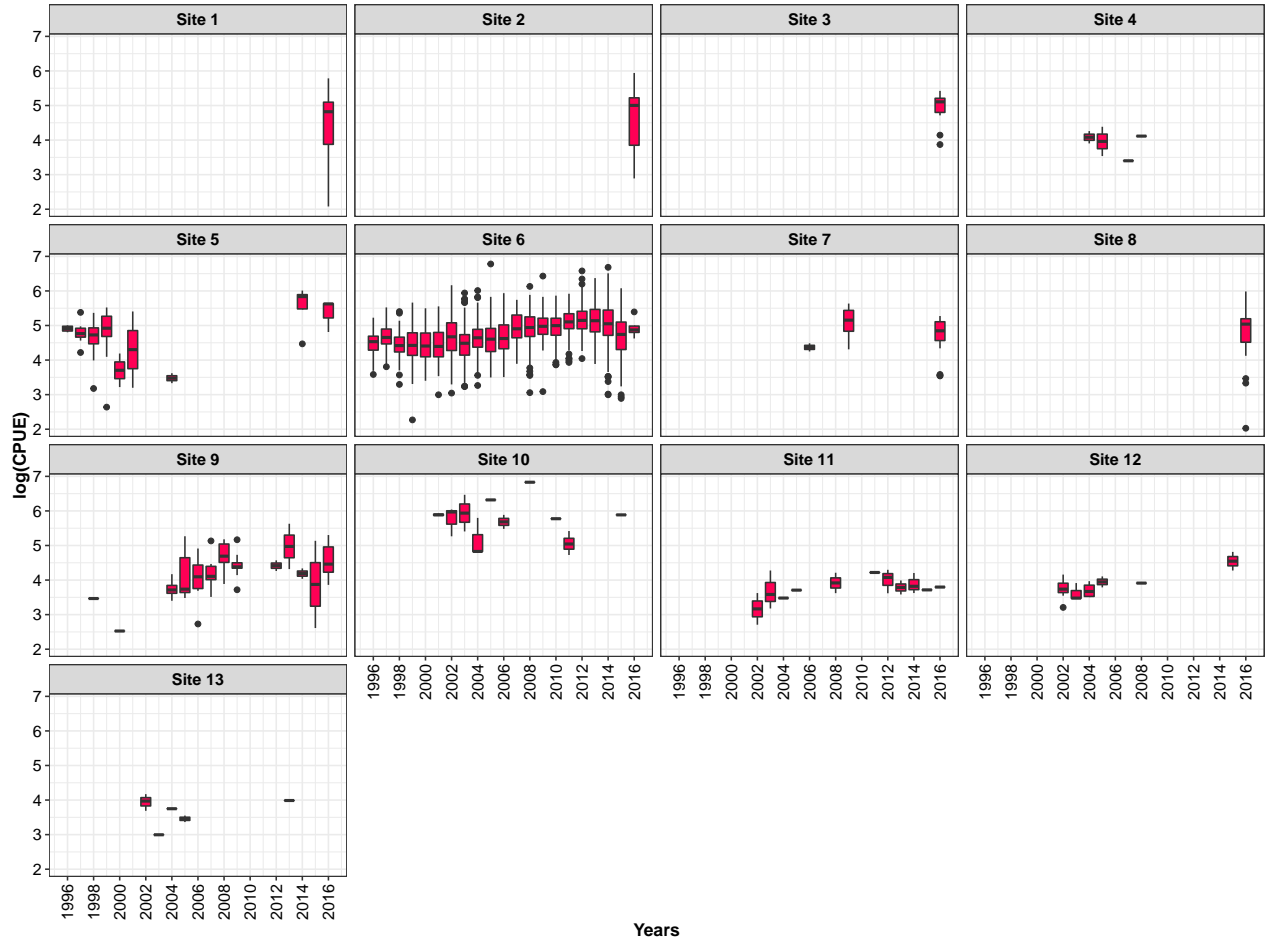

Figure 1: Log catch per unit effort (CPUE; kg/hour of diving) by fishing site for sea urchin (*Loxechinus albus*) from 1996-2016 north of Chiloé, Chile.

65 Covariates information available for modeling include "year" (as a factor), "depth" (average depth
66 of catches), "quarter" (season of the year), and the variable "market." This latter variable has two
67 categories, depending on sea urchin size and sale to the commercial industry or the general public.
68 We do not have complete observations for all fishing sites because data could not be obtained for
69 all years. Reasons include inability to gather data, lack of catch records for certain months, or bad
70 weather conditions.

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2.2. Mathematical formulation

2.2.1. The model

We use a hiearchical Bayesian spatiotemporal model where the first level (1) is the prior distribution for the hyperparameters in the model, and CPUE (3) is conditioned by a spatial random effect in the second level (2).

$$\boldsymbol{\theta} \sim \pi(\boldsymbol{\theta}) \tag{1}$$

$$\boldsymbol{\omega} \mid \boldsymbol{\theta} \sim \mathcal{N}(\mathbf{0}, \boldsymbol{Q}(\boldsymbol{\theta})^{-1}) \tag{2}$$

$$\boldsymbol{y} \mid \boldsymbol{\omega}, \boldsymbol{\theta} \sim \prod_i \pi(\boldsymbol{y} \mid \boldsymbol{\eta}, \boldsymbol{\theta}) \tag{3}$$

Following the approach by [15], $\boldsymbol{\theta}$ is the vector of the hyperparameters with $log(\tau) = \theta_1$, $log(\kappa) = \theta_2$ and $log(\sigma) = \theta_3$, $\boldsymbol{\omega}$ is the spatial random field (GRF) with precision matrix $\boldsymbol{Q}(\boldsymbol{\theta})$, $\boldsymbol{\eta} = \boldsymbol{X}\boldsymbol{\beta} + \boldsymbol{\omega}(\boldsymbol{s})$, where $\boldsymbol{X}\boldsymbol{\beta} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4$, with covariates $x_1 = year$, $x_2 = depth$, $x_3 = quarter$ and $x_4 = market$. $\boldsymbol{y}$ is the observation vector that corresponds to the CPUE and distribution function $f(\cdot \mid \boldsymbol{\omega}, \boldsymbol{\theta})$.

2.2.2. Spatial random field

A spatial process in d dimensions is defined by $\{Y(\boldsymbol{s}) : \boldsymbol{s} \in D \subset \mathcal{R}^d\}$, where $\boldsymbol{s}$ is the location of process $Y(\boldsymbol{s})$ with variation in domain D. We say that the spatial process is a Gaussian random field (GRF) if $\{Y(\boldsymbol{s}_1), ..., Y(\boldsymbol{s}_n)\} \sim \mathcal{N}_n(0, \Sigma)$, where the process is completely specified by mean function $\mu = \mathbb{E}(Y(\boldsymbol{s}))$, and covariance function $C(\boldsymbol{s}_1, \boldsymbol{s}_2) = Cov(Y(\boldsymbol{s}_1), Y(\boldsymbol{s}_2))$. The GRF can be assumed as stationary (strictly or weakly) and isotropic. A stationary isotropic random field has covariance functions that depend only on distance not direction between points, that is $C(\boldsymbol{s}_1, \boldsymbol{s}_2) = Cov(\|\boldsymbol{s}_1 - \boldsymbol{s}_2\|)$. Dependence on the spatial structure is built through the covariance function, generally modeled with a Matérn function.

Incorporating the spatial dependence directly with a large number of observations using a GRF can be computationally expensive. To solve this problem [32] proposed a new parameterization of the GRF but with Markovian properties transforming it into a Gaussian Markov Random Field (GMRF) [32]. This spatial structure uses a dependence conditional through a precision matrix $\boldsymbol{Q}$, where $\boldsymbol{Q}$ is the inverse of covariance matrix $\boldsymbol{\Sigma}$, that is $\boldsymbol{Q}^{-1} = \boldsymbol{\Sigma}$. [30] proposed a new methodology to approximate a GRF with a GMRF through stochastic partial differential equations (SPDE). This methodology approximates GMRF with weighted sum of simple basis functions, allowing to remain within the domain's continuous space, while the computational algorithms only see the discrete structures with Markov properties ([33]). With this stochastically weak solution of the SPDE, the direct implication is to enable building a sparse precision matrix on a continuously-indexed region in a way that approximates a Matérn field with lower computational cost because we passed from $O(n^2)$ in the GRF to $O(n^{3/2})$ of the GMRF ([7]). The spatial random field in this analysis is represented by $\boldsymbol{\omega}$ that is the same as GRF (latent variable).

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2.3. Choosing the prior

The most common SPDE parameterization to approximate GRF is through hyperparameters $\log(\tau) = \theta_1$ and $\log(\kappa) = \theta_2$. These hyperparameters usually have a joint normal prior distribution in a stationary model ([7]). Yet it also showed poor mixing of chains during model development with respect to $\log(\tau) = \theta_1$, so we assumed a reasonable initial value and tested the sensitivity for different values of this hyperparameter. The value of the base case came from the construction of the SPDE object in INLA, and this same value was scaled by 0.25 and 4 as a sensitivity analysis. The prior distribution for the other hyperparameters are: $\theta_2 \sim \mathcal{N}(2,2)$ and for the variance we assume $\log(\sigma) = \theta_3 \sim Cauchy(0,2)$ ([34]). Given the above, the hyperparameters' vector is expressed by $\boldsymbol{\theta} = \{\theta_1, \theta_2, \theta_3\}$. In relation to the prior distribution for the vector of the fixed effects $\boldsymbol{\beta}$, we assumed a prior normal distribution $\mathcal{N}(0,5)$.

2.4. Model selection

We proposed four models to obtain a relative abundance index (Table 1). To select the best model we used leave-one-out cross-validation (loo). loo was computed with Pareto smoothed importance sampling (PSIS) that provides a fast and accurate estimate. From loo we obtained elpd_loo that estimated the difference in expected predictive accuracy and compared the proposed models ([44]). These models were: CPUE distributed as $\log(\boldsymbol{y}) \sim \mathcal{N}(\mu, \sigma^2)$ and CPUE distributed as $\boldsymbol{y} \sim \text{Gamma(a, b)}$. One model included non-random effects and the other included spatial random effects ($\boldsymbol{\omega}$).We consider these distributions because they are the most commonly used in index standardization [14].

Table 1: Proposed models to obtain a relative abundance index.

	Distribution	Random effect
Model$_{1,1}$	$\log\boldsymbol{y} \sim \mathcal{N}(\mu, \sigma^2)$	Non-spatial random effect
Model$_{1,2}$		Spatial random effect ($\boldsymbol{\omega}$)
Model$_{2,1}$	$\boldsymbol{y} \sim Gamma(a,b)$	Non-spatial random effect
Model$_{2,2}$		Spatial random effect ($\boldsymbol{\omega}$)

2.5. Posterior predictive distribution

To evaluate model fit we used the posterior predictive checking ([45]). Its main purpose is to assess the fit between a particular model and the data. We simulate a specific number of observations (CPUE) but using the parameters drawn from the posterior distribution and if the model captures the structure of the data, then simulated data should look similar to the observed CPUE.

2.6. Modeling platform

Template Model Builder (TMB)[23] was used for modeling purposes. TMB is an open source package in R [53], allowing quick implementation of complex nonlinear random (latent variable) effect models.

The analyst defines the joint likelihood for the data and random effects within a $C++$ template, but all other operations like reading data, determing parameters, and running the model are done directly in R. TMB is capable of maximum marginal likelihood estimation by using the Laplace approximation to marginalize out the random effects [54]. It is also capable of efficient Bayesian integration (see below), because gradients can be efficiently calculated using automatic differentiation of the marginal or joint likelihood [23]. In TMB we also evaluated the random effects as GRF or GMRF in the spatial statistics context.

2.7. Bayesian inference

Inference was performed with tmbstan[31] which facilitates linkage between TMB and Stan ([6][5]). Stan is a Bayesian inference framework for models with continuous parameters through Markov chain Monte Carlo methods (i.e., No-U-Turn sampler or Hamiltonian Monte Carlo). With tmbstan, models built in TMB and their gradients are passed to the Bayesian samplers in Stan through an R interface. We integrated the joint posterior with four No-U-Turn sampler chains of 3,500 iterations (700 of which were wamup) and the control parameters max_treedepth = 13, adapt_delta = 0.9.

3. Results

Figure 2 shows the locations of fishing sites north of Chiloé (a) and the triangulation of the spatial domain to approximate GRF through the SPDE method (b).
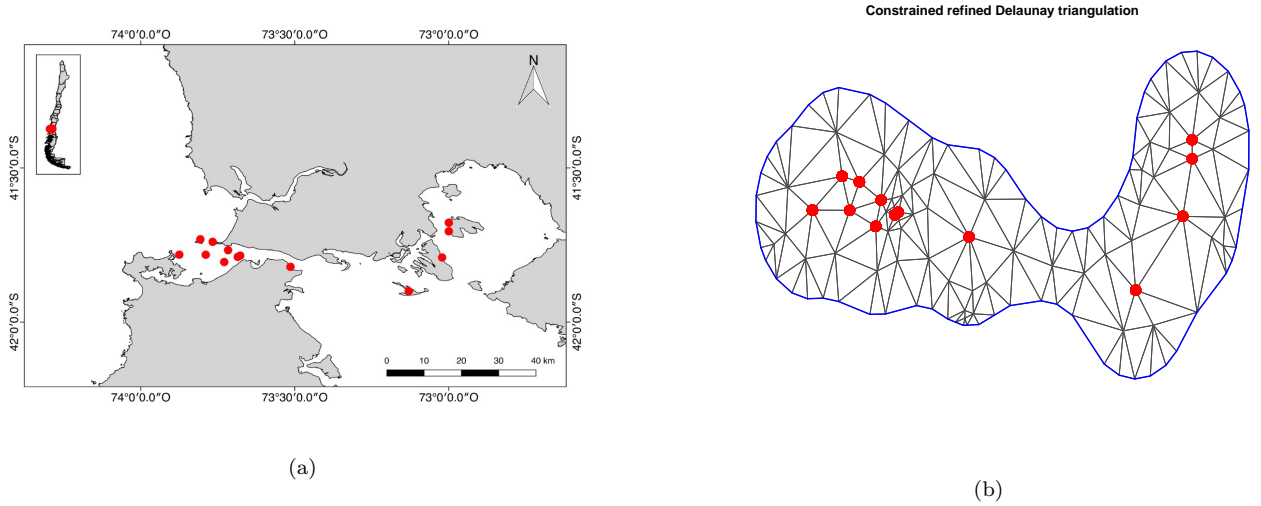

(a)

(b)

Figure 2: Geographical position (latitude - longitude) of fishing sites (a) and triangulation of the spatial domain with SPDE method to approximate GRF (b)

The loo value was used to compare the performance of each proposed model structure (with and without spatial random effects) and different distributions for the data (lognormal and Gamma; Table 1). Table 2 shows that all models with spatial random effects performed statistically better than the models without them. The model with best statistical performance was Model$_{2,2}$ (red color in the table) with the lowest score of elpd_diff value, meaning that Gamma distribution incorporating

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spatial random effects fit the CPUE data better than the other models. Figure 3 shows the simulation of 1,000 posterior predictive data sets for each model compared to the observed data.

Table 2: Comparison with `loo` criterion for each model.

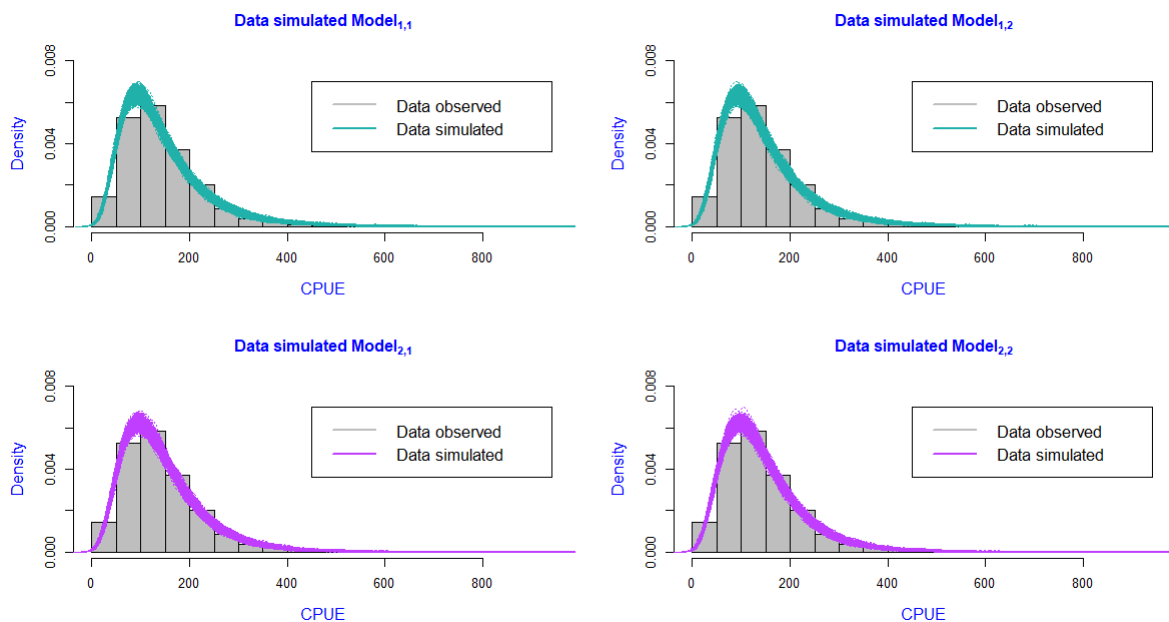|		loo		
Models	Non-random spatial effect	Spatial random effect (ω)	elpd_diff	se_diff
$Model_{2,2}$	-	✓	0.00	0.00
$Model_{1,2}$	-	✓	-42.23	22.89
$Model_{1,1}$	✓	-	-88.33	17.76
$Model_{2,1}$	✓	-	-125.45	27.99

Figure 3: Observed data (histogram) and density estimates (lines) of 1,000 posterior predictive data simulated from $Model_{1,1}$ and $Model_{1,2}$ (top panel) and for $Model_{2,1}$ and $Model_{2,2}$ (bottom panel). The observed and simulated data match suggesting the models fit well.

Figure 4 shows the posterior predictive distribution for different assumed values of $\log(\tau)$. The first histogram (A) shows the Model$_{2,2}$ chosen in accordance with loo criterion and with $\log(\tau)$ value fixed at -3.78 (from INLA). Histogram (B) shows the predictive posterior distribution for a specific model with an initial value of -0.945 for $\log(\tau)$, four times less in comparison with the initial value in Model$_{2,2}$, and histogram (C) shows the posterior predictive distribution for an initial value of -15.12, four times higher than the initial value in Model$_{2,2}$. How we see the different initial values $\log(\tau)$ does not affect the estimations and, as a consequence, the predictive posterior distribution for Model$_{2,2}$.
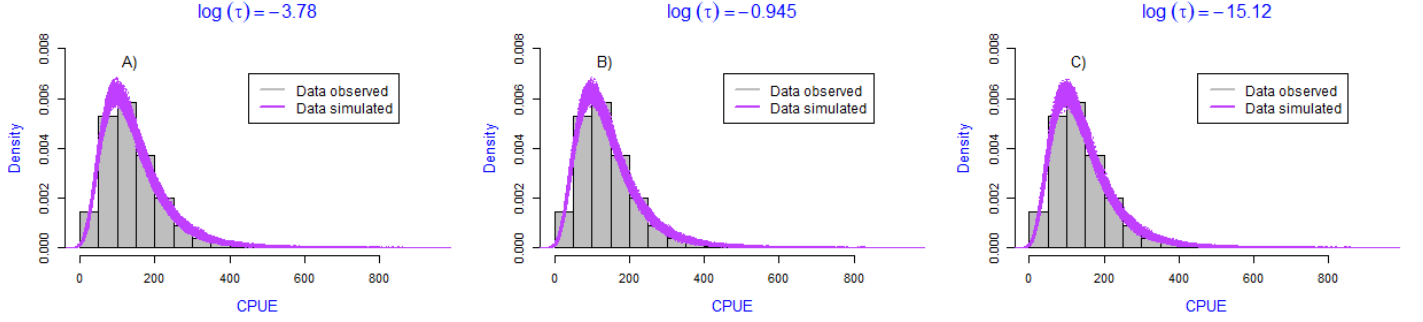

Figure 4: Results of the sensitivity analysis for the assumed values for hyperparameter $\log(\tau)$. Posterior predictive distributions are compared across the three levels tested (see Figure 3 for further interpretation).

Figure 5 shows the difference between the trend in time for a relative abundance index estimated via the Model$_{2,1}$ and the Model$_{2,2}$. The trends behaved similarly; even from 2005 to 2013 both models showed a positive increase, but for the last year, the Model$_{2,1}$ showed positive increase while the Model$_{2,2}$ continued with a negative trend. Model$_{2,2}$ showed better statistical performance. For the above, it is necessary to evaluate this small change in the coefficients because it could represent a biomass variation estimated under the stock assessment model.
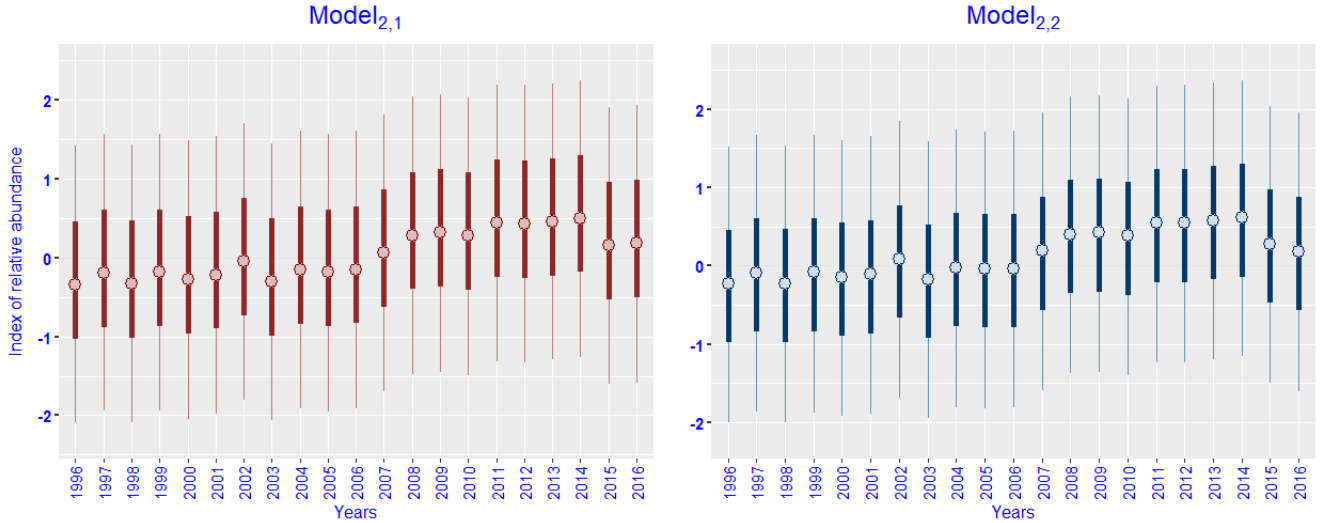

Figure 5: Comparison of the coefficients (relative abundance indices) estimated with Model$_{2,1}$ and Model$_{2,2}$.

Since fishing sites 1, 2, 3 and 8 have data only for 2016, `loo` could be too optimistic for the evaluation and posterior comparison of the models. Thus, the spatial random effect models could be sensitive to variations in the number of observations or influenced by outliers. To evaluate this possible problem, we made two additional model comparisons, `loo₁` and `loo₂`. Here `loo₁` (excludes site 1) and `loo₂` (excludes sites 1, 2, 3 and 8). The results appear in Table 3 along with the respective graphic for the Pareto k diagnostic values (Figure 6 and Figure 7).

Table 3: Additional comparisons with `loo`

`loo₁`: comparison excluding site 1				
Models	Non-random spatial effect	Spatial random effect (ω)	`elpd_diff`	`se_diff`
`Model`$_{2,2}$	-	✓	0.00	0.00
`Model`$_{1,2}$	-	✓	-14.653	22.676
`Model`$_{2,1}$	✓	-	-89.062	17.839
`Model`$_{1,1}$	✓	-	-94.641	27.285

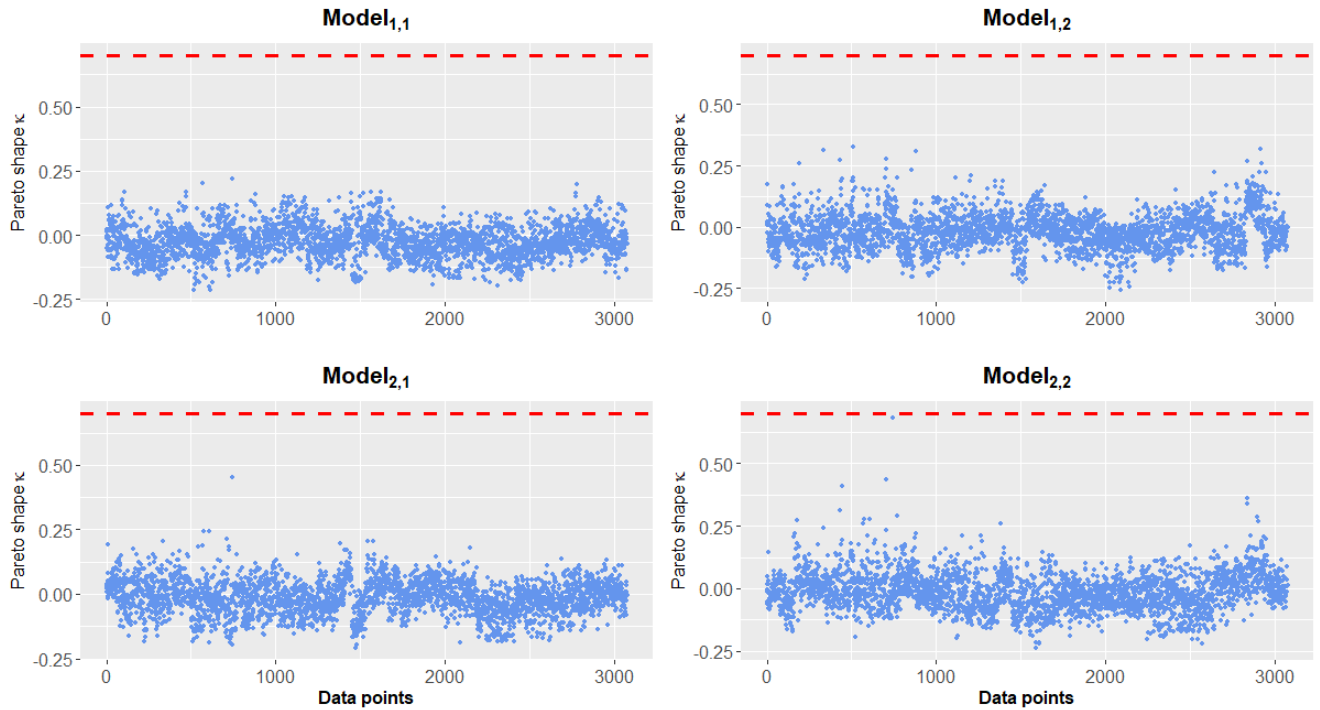| `loo₂`: comparison excluding sites 1, 2, 3 and 8				
Models	Non-random spatial effect	Spatial random effect (ω)	`elpd_diff`	`se_diff`
`Model`$_{1,2}$	-	✓	0.00	0.00
`Model`$_{2,2}$	-	✓	-4.744	21.720
`Model`$_{1,1}$	✓	-	-69.601	16.053
`Model`$_{2,1}$	✓	-	-81.398	27.533

Figure 6: Pareto shape k contribution to `loo₁`. For all the models $\kappa < 0.7$ (segmented red line) which indicates a good `PSIS_LOO` approximation.
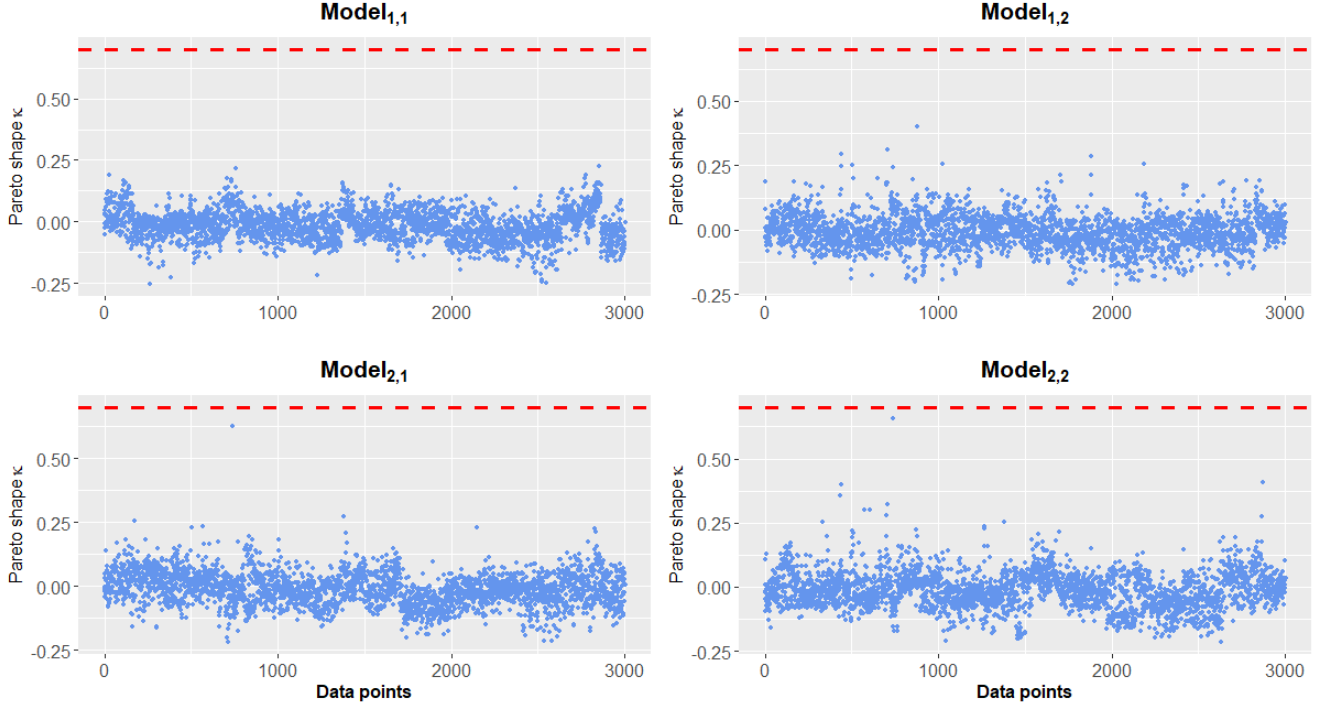
Figure 7: Pareto shape k contribution to $\mathtt{loo_2}$. For all the models $\kappa < 0.7$ (segmented red line) which indicates a good $\mathtt{PSIS\_LOO}$ approximation.

The $\mathtt{loo_1}$ and $\mathtt{loo_2}$ comparisons show that the models are not overly sensitive to dropping out those specific observations. In all additional comparisons, the models with a spatial random effect that incorporated an explicit dependence into the observations performed statistically better than the ones without a spatial dependence structure. In the second case, ($\mathtt{loo_2}$), the best model assumed a lognormal distribution for CPUE, which could stem from the number of observations removed from the total data set, but the model still included a spatial random effect as main component.

Finally, we show the mean and standard deviation estimated for the spatial random effect in $\mathtt{Model_{2,2}}$. The high values were concentrated in the center and on the left side of the spatial domain, but to the right we see how the values decreased and with them the spatial dependence among these fishing sites. The standard deviation was constant across the spatial domain around the fishing sites, which allowed us to assume that the supposed constant variance in the spatial random effect is justified.
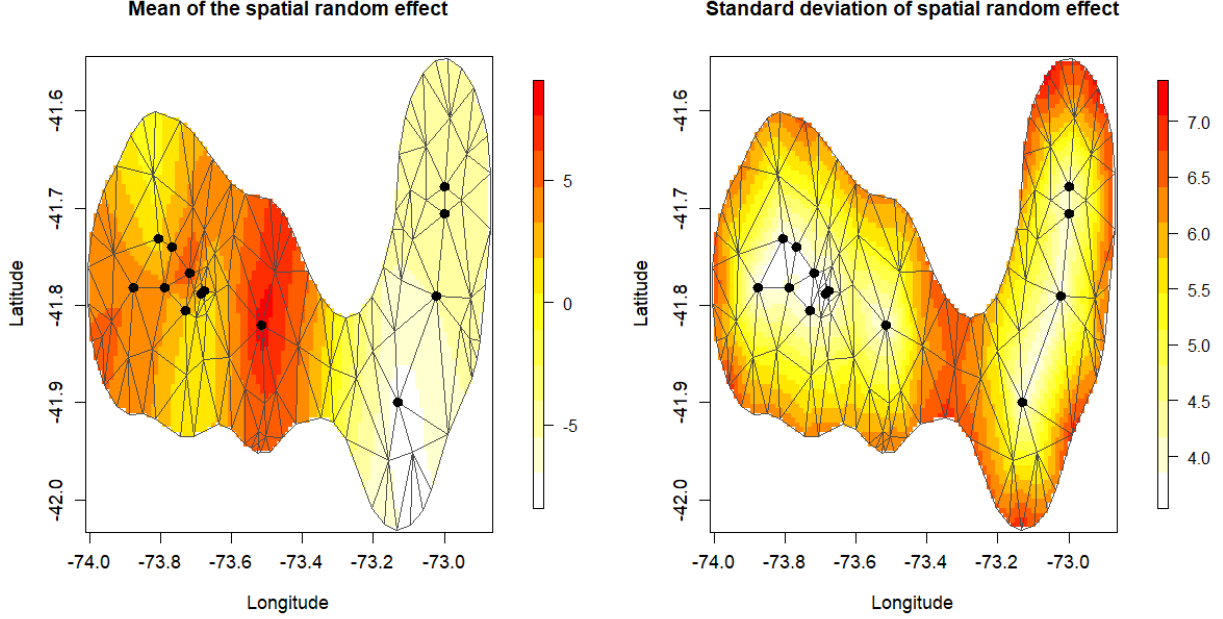
Figure 8: Mean (left) and standard deviation (right) of the spatial random effect estimated by $\texttt{Model}_{2,2}$.

4. Discussion

Obtaining an accurate relative abundance index for benthic resources has been one of the most important challenges for stock assessment modeling to determine fishing quotas for economically important marine resources. The sea urchin resource is structured as metapopulation ([8], [9]), meaning a population of subpopulations, but if one of these populations disappeared, the total population would still be relatively constant due the link between subpopulations, and specifically because of the individuals that occupy the spaces formerly occupied by the individuals of the extinct populations - hence a probable link among fishing sites and certain spatial dependence.

A metapopulation is a population within populations in which each individual population is subject to extinction and recolonization [46], but other empirical studies have used a less restrictive definition [47]. Larval dispersal patterns, influenced by coastal circulation, result in patchy settlement, which influences the abundance and population dynamics at sea urchin recruitment sites. Understanding the spatial pattern of larval dispersal is an important aspect for a complete understanding of the role of recruitment dynamics in determining sustainable catch quotas ([48]), and even more for more realistic models that emphasize spatiotemporal variability in population dynamics and connections through dispersal of sea urchin [49].

We had some issues estimating the parameter τ. In many situations and analyses this hyperparameter, related to the variance of GRF, resulted in poor mixing of the Markov chain Monte Carlo chains used for inference. We used the standard parameterization to approximate GRF by SPDE/ GMRF, using the τ and κ hyperparameters. An alternative parameterization of the spatial random field is available through marginal standard deviation (σ) and the (ρ) range [50] or the proposal by [52] and [51] using priors that penalize the complexity of the GRF (PC prior's). The latter is more convenient because we can apply it directly as a prior to build a Matérn GRF that is independent of the observation process. A PC prior's can be used for any spatial design and any observation process

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but is computationally inexpensive. It also has a much simpler form than the reference priors for GRF's in the literature [51]. However, through sensitivity analysis for different values of τ we showed that our results were insensitive to this value, and that estimation for every other parameter of the proposed model is unproblematic.

The analysis used a Hamiltonian Monte Carlo algorithm to integrate all model parameters to obtain the convergence with a specific number of chains and a large number of the iterations. Yet the main problem with the method remains computational efficiency. `TMB` allows integrating the best from the frequentist and Bayesian paradigms, taking advantage in two ways. First, `TMB` allows the use of the Laplace approximation to obtain the marginal likelihood by integrating out the spatial random effects for fast frequentist inference. Also, building the model in `TMB` allowed us to gain greater flexibility in comparison with `INLA`. Second, and probably the most important feature of `tmbstan` in the Bayesian framework, is the use of sparse matrices that are still not implemented in `Stan`. This facilitates lower computational cost in the estimation. However, the option to approximate the GRF by a GRMF ([30]) together with the proposal by [37][27][7] [38][39] using `R − INLA` (www.r-inla.org) package seems to be more efficient for solving a spatial or spatiotemporal model within the Bayesian framework. Recently, [40] proposed using a Tucker tensor analysis for Matérn functions, where the low-rank tensor approximation reduces estimation and storage cost. [41] proposed a spatiotemporal model where estimation is performed with pairwise likelihood using sparse matrices and parallelization of computing, while [42] proposed a likelihood approximation with hierarchical matrices to approximate inhomogeneous covariance functions to reduce computing time drastically. Each of these methodologies have the potential to improve computational efficiency, and we suggest future exploration of their performance within the Bayesian framework.

5. Conclusions

Incorporating a spatial random effect to obtain a relative abundance index for sea urchin (*Loxechinus albus*) enabled better statistical performance than models without spatial random effect. With such models, we could consider explicitly the spatial dependence among observations, the main property of this sessile marine population with metapopulation structure. Although the trends of the estimated indices with and without spatial effects are similar, statistical diagnostics clearly indicate that the spatial model outperformed the non-spatial version and fit the data better. Additionally, the estimated trend in the last year differs between these models, either suggesting an increase or decrease depending on the model version used. This difference could have important impacts on the estimated status and trend of the stock, and ultimately the catch quota, so assessing the stock with both indices would be valuable. It is beyond the scope of this analysis to explore this effect, but we recommend it as an important next step given our conclusions here.

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