Bayesian spatial predictive models for data-poor fisheries

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ABSTRACT

Understanding the spatial distribution and identifying environmental variables that drive endangered fish species abundance are key factors to implement sustainable fishery management strategies. In the present study we proposed hierarchical Bayesian spatial models to quantify and map sensitive habitats for juveniles, adults and overall abundance of the vulnerable lane snapper (*Lutjanus synagris*) present in the northeastern Brazil. Data were collected by fishery-unbiased gillnet surveys, and fitted through the Integrated Nested Laplace Approximations (INLA) and the Stochastic Partial Differential Equations (SPDE) tools, both implemented in the R environment by the R-INLA library (http://www.r-inla.org). Our results confirmed that the abundance of juveniles and adults of *L. synagris* are spatially correlated, have patchy distributions along the Rio Grande do Norte coast, and are mainly affected by environmental predictors such as distance to coast, chlorophyll-*a* concentration, bathymetry and sea surface temperature. By means of our results we intended to consolidate a recently introduced Bayesian geostatistical model into fisheries science, highlighting its potential for establishing more reliable measures for the conservation and management of vulnerable fish species even when data are sparse.

1. Introduction

Fisheries action as well as environmental fluctuations may induce many changes in fish stocks, which are commonly related to their abundance, size and spatial distribution (Haddon, 2001; King, 2007). In this sense, detecting the main environmental factors driving natural abundance fluctuation and understanding how these associations vary over space and time are key concepts in ecology and in fisheries sciences (Ross et al., 2012).

The links between fish stock dynamics and its surrounding environment are therefore of fundamental importance in order to improve sustainable fisheries' management and conservation strategies (Babcok et al., 2005; Valavanis et al., 2008). The way in which we may access the species-environment relationships are commonly treated in the specialized literature as Species Distri-

bution Models (SDMs), and are frequently analyzed in the context of statistical tools to evaluate a species distribution with respect to environmental variables (Franklin, 2010). The main goal of SDMs relies on the prediction, identification and understanding of a species spatial distribution, and may be considered as those habitats where it fulfills some of its biological process, such as reproduction, spawning and feeding. When dealing with marine species, and particularly with fishes, the output provided by the SDMs designate the term *Essential Fish Habitat* (EFH), which constitute areas that promote the fishes most favorable habitats for spawning, feeding, or growth to maturity.

Over the past three decades a huge effort has been spent in the development of powerful statistical models to explore more realistic scenarios regarding the species-environmental relationships. Artificial Neural Networks (ANN, e.g., SPECIES), Maximum Entropy (ME, e.g., MAXENT), Climatic Envelops (CE, e.g., BIOCLIM), Classification and Regression Trees (CART, e.g., BIOMOD) and regression models such as Generalized Linear and Additive (Mixed) Models (GLM/GLMM/GAM/GAMM) are among the many methodological tools that have been proposed for modelling the species distribution (Franklin, 2010; Guisan and Thuiller, 2005).

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Although these applications are considered robust, they usually address only explanatory models that simply aim to verify the relationship between the response variable (e.g. presence or abundance of the species) and some environmental predictors (e.g. bathymetry and chlorophyll-*a* concentration in marine context), without considering explicitly the spatial component (Ciannelli et al., 2008). This may result in a poor characterization of the species response to environmental factors by underestimating the degree of uncertainty in its predictors (Latimer et al., 2006).

Considering that the marine environment is an extremely heterogeneous domain, and that a given marine species has biological and ecological constraints, it is commonly noted that biological resources like most fish species present a gregarious distribution. Hence, ignoring spatial autocorrelation violates the main assumption of classical inference, which assumes that the data are independent and identically distributed, and thus can lead to biased estimates. Spatial correlation should therefore be considered since species are generally subject to similar environmental factors (Muñoz et al., 2013). Such spatial models allow constructing powerful predictive models that not only provide the estimation of processes that influence species distribution, but also promote the possibility of predicting their occurrence in unsampled areas (Chakraborty et al., 2010).

Additionally, it is advantageous to incorporate Bayesian inference in predictive models, given that it is possible to integrate all types of uncertainties using exclusively the probability as its metric. Combining the uncertainty in the data (expressed by the likelihood) with extra-data information (expressed by prior distributions), posterior probability distributions are built for all unknown quantities of interest using Bayes' theorem (Kinas and Andrade, 2010).

Hierarchical Bayesian Models (HBMs) are very suitable for such situations, as they allow to introduce sequentially the uncertainties associated with the entire fishery phenomenon, as well as a spatial random effect in the form of a Gaussian random field (GRF) (Cosandey-Godin et al., 2015). Traditionally HBMs relied on simulation techniques such as Markov Chain Monte Carlo (MCMC). However, with increased model complexity the computational time required to approximate the posterior distributions became unfeasible. To sidestep this limitation, Rue et al. (2009) proposed an alternative numerical computation to obtain posterior distributions, called Integrated Nested Laplace Approximations (INLA), and which is currently implemented in the R environment by the *R-INLA* package (http://www.r-inla.org). Rather than using stochastic simulation techniques, INLA uses numerical approximations by means of the Laplace operator, which revealed to be much faster, flexible and accurate than MCMC whenever applicable.

Thanks to Illian et al. (2013) and Muñoz et al. (2013), spatiotemporal models were introduced to the ecological community in order to fit point process and point-referenced data through the INLA approach. In regard to marine ecology and fisheries research, more studies have slowly emerged since then using exclusively INLA for spatial and temporal purposes (Cosandey-Godin et al., 2015; Muñoz et al., 2013; Paradinas et al., 2015; Pennino et al., 2013, 2014; Quiroz et al., 2015; Roos et al., 2015; Ward et al., 2015; Bakka et al., 2016; Damasio et al., 2016; Paradinas et al., 2016; Pennino et al., 2016).

However, most of these studies relied on "data-rich" fisheries, where certainly any quantitative method would have had good performance. On the other hand, in developing countries such as Brazil, fisheries tend to be poorly documented and inadequately managed due to lack of research funding for monitoring and analysis (Honey et al., 2010). Conventional analytical fisheries stock assessment tools that demand big data sets may not be applicable in "data-poor" situations like these. Therefore, flexible and reliable statistical tools with good performance albeit limited information are paramount (Bentley, 2014).

In order to expand the use of such tools in data limited fisheries, we will demonstrate the flexibility and usefulness of the Bayesian modelling approach for some important fisheries issues, such as delimiting fish stocks into age groupings and evaluating the spatial distribution of these age groupings. Specifically, our main objectives are: (i) predict abundance and age groupings of the target lane snapper (*Lutjanus synagris*) along a fraction of the northeastern coast of Brazil; and (ii) identify environmental drivers that affect lane snapper's abundance and so, provide important insights of its spatial distribution.

This paper is organized as follows: firstly we describe the importance of our study subject, how the main dataset was obtained and how we achieve age groupings using Bayesian logistic regression. Thereafter, we apply hierarchical Bayesian spatial models into EFH's, and discuss the entire modelling procedures used in this study. Finally, we describe and discuss our results, outlining opportunities for future spatial fisheries management.

2. Material & methods

2.1. Case study

As a case study, we modelled the spatial occurrence of *Lutjanus synagris* (Linnaeus, 1758), popularly known as lane snapper and which is considered one of the most important fishing resource caught within the Lutjanidae family (Luckhurst et al., 2000). Lane snappers inhabit a variety of habitats from coastal waters to depths up to 400 m, often occurring in coral reefs and vegetation on sandy bottoms (Carpenter, 2002), and are widely distributed throughout the tropical region of the western Atlantic, from North Carolina to southeastern Brazil, including the Gulf of Mexico and the Caribbean Sea (McEachran and Fechhelm, 2005).

Given its high commercial and recreational value, this species is one of the mainstays of artisanal fisheries not only in Venezuela and the Caribbean Sea, but also in northeastern Brazil (Gómez et al., 2001; Luckhurst et al., 2000; Rezende et al., 2003). According to Lessa et al. (2009), catches of lane snapper in northeastern Brazil have been recorded since the late 1970's where it is suffering strong fishing pressure which, despite their high abundance, is leading to its decline over the past few decades.

In general, most information about *L. synagris* relies on its biology, whereas its population dynamics and spatial distribution remain poorly understood (Cavalcante et al., 2012; Freitas et al., 2011, 2014). Therefore, knowing their spatial distribution and identifying environmental variables that drive their abundance are key factors to implement sustainable fishery management strategies.

2.2. Study area and data survey

Situated in the northeast of Brazil, the Rio Grande do Norte state (RN) is located in an important coastline transition zone which abruptly changes its direction from south-north to east-west. Between July 2012 and June 2014, about three experimental fisheries were monthly conducted by fishing vessels of the artisanal fleets which operate with bottom gillnets along the RN coast. Throughout this period, 126 fishing events were reported whose depths ranged from 5 to 50 m (Fig. 1). Biological sampling was recorded along with extra information for each fishery including geolocation (latitude and longitude), bathymetry (m), sea surface temperature (°C), distance to coast (km), month (from January to December), gill net length (m) and height (m), as well as its soaking time (h).

It is noteworthy that data collected from artisanal fleets would usually characterize a clear example of preferential sampling, since fleets are commercially driven to catch target species hotspots.
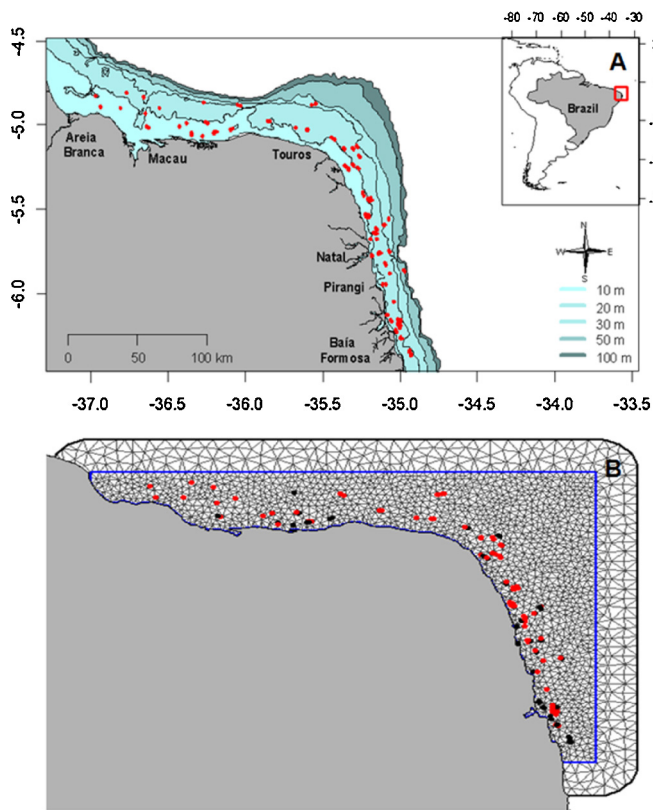
Fig. 1. (A) Study area highlighting the sample stations (dots); (B) Triangulation used to calculate the GMRF for the SPDE approach. The dots are referring if the species was present (red) or absent (black) during the sample stations (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Hence, the preferred sampled fishing locations tend to be repeated producing fishery-biased data (fishery-dependent data). If this is ignored during the statistical modelling process, it may lead to biased estimates (Diggle and Ribeiro, 2007; Pennino et al., 2016). The experimental design of this study avoids this problem by covering the entire study area with regular distances between the fishing bids and without repeating them. Thus, we claim that the fishing effort is stochastically independent from the sampling stations, resulting in spatial fishery-unbiased data (fishery-independent data).

All captured individuals were weighted (g) and measured for its total length (TL, cm). At the end of each fishing event, a representative subsample was randomly selected and taken to the laboratory. Sex and macroscopic maturation states were determined for each specimen according to Vazzoler (1996).

2.3. Bayesian modelling for data-poor fisheries

This section aims to describe the use of Bayesian models in two important fisheries issues, namely the estimation of the size at which a species reaches first maturity (L_{50}) and the prediction of a species spatial distribution. Defining age groupings of a fish stock by means of L_{50} represents a major challenge in most cases, since a large quantity of data is needed. This helps explain why spatial predictions for age groupings are usually scarce in scientific reports. Spatial prediction for abundance is preferred as this kind of information tends to be more accessible. Appendix A of the supplementary material summarizes how the estimation of L_{50} is connected to the spatial modelling procedures.

2.3.1. Bayesian estimation of mean length at first maturity

The knowledge of population parameters is essential for monitoring fisheries dynamics since they are potential exploitation indicators (King, 2007). Among these parameters, the size at first maturation (L_{50}) stands out, which corresponds to the average length at which 50% of the individuals reach sexual maturity (Vazzoler, 1996). One of the main objectives of determining L_{50} is to delimit the young (mean length < L_{50}) and adult stocks (mean length $\geq L_{50}$).

Of the subsamples taken to the laboratory, 89 individuals of lane snapper were analyzed (Table D.1 of supplementary Appendix D). The L_{50} is commonly calculated using a logistic regression, whose parameters (β_0 and β_1) are traditionally estimated by Maximum Likelihood method (Karna and Panda, 2011). However, when the sample is small, this method gives biased estimates and confidence limits cannot be adequately calculated (Peduzzi et al., 1996). Therefore we relied on Bayesian inference to estimate L_{50} (Doll and Lauer, 2013).

Initially, k length classes were established for the set of data, where the total number of individuals in size class i (n_i) and the number of mature individuals (Y_i) were registered for each class (Table D.1 of supplementary Appendix D). We defined as "mature" all individuals that were at least in stage C. The number of mature individuals by size class was modelled according to a logistic regression as described by Kinas and Andrade (2010), whose probability of an individual of length-class i (for i = 1, 2, . . ., k) being mature assumes a binomial distribution:

$$Y_i \sim \text{Binomial}\,(n_i, p_i)$$

$$g\,(p_i) = \log\left(p_i/1 - p_i\right) = \beta_0 + \beta_1\,(x_i - \bar{x})$$

$$\bar{x} = \sum x_i/k = (x_1 + x_2 + \ldots + x_k)\,/k$$

where p_i denotes the probability of an individual of the *i-th* length-class be sexually mature; $g(p_i)$ represents the logit link function; β_0 is the logit probability that an individual with the mean length $\bar{x}$ is sexually mature; β_1 is the average increase in the logit of p_i for each centimeter added to length; x_i denotes the average length of size class i, and k represents the number of length classes that was established for the dataset.

Estimates of L_{50} were provided from the equation $[(-\beta_0/\beta_1)+\bar{x}]$. Whereas the parameters of the logistic regression were estimated by a Bayesian framework, a prior sensitivity analysis for its parameters was previously conducted. Four different prior alternatives were evaluated: a Gaussian $N\,(0, 100)$, a Gaussian $N(0, 10000)$, a heavy-tailed Student (5 degrees of freedom) and a Cauchy distribution (with scale 2.5). Since the resulting posterior distribution for L_{50} had negligible effect between each of the evaluated alternatives (Fig. D.1 of Supplementary Appendix D), we assumed a Normal vague prior distribution for the mean and the variance for the parameters ($\beta_0 \sim N\,(0, 100)$; $\beta_1 \sim (0, 100)$).

The posterior probability distributions were simulated by means of Markov Chain Monte Carlo (MCMC) methods using the *R2jags* package (Su and Yajima, 2014). We simulated three different situations, where the parameters were derived from grouped sexes (females + males − case 1) or separated sexes (males only − case 2; females only − case 3). For each of these cases we ran three MCMC chains simultaneously for a total of 60,000 iterations, where the first 20,000 iterations were discarded as a burn-in period and each 20th step was stored (thinning) in order to reduce autocorrelation.

The chains' convergence was assessed using conventional graphical methods such as iteration and autocorrelation graphs, and by convergence indicator $\hat{R}$ which denotes the ratio of variance between and within chains (Gelman, 1996). Finally, a Bayesian hypothesis test was performed to assess whether there were significant differences between the posterior distributions of female

L_{50} and male L_{50}. For this purpose, the posterior distribution of the difference $d = L_{50male} - L_{50female}$ was obtained and evaluated with respect to the probability ratio $p(d \geq 0)/p(d < 0)$; with ratios away from one (e.g., larger than 5 or lower than 1/5) suggesting relevant differences. The posterior median was taken as point estimate of L_{50}, and used as cutoff to delimit the lane snapper stocks into young and adult groupings.

2.3.2. Bayesian spatial modelling for abundance and age groupings

We used hierarchical Bayesian spatial models in order to estimate and predict overall abundance (case 1), number of adults (case 2) and number of juveniles (case 3) of *L. synagris* with respect to several environmental predictors. As abundance index we used catch-per-unit-effort (CPUE), which was defined as lane snapper's total catch (g) weighted by the fishing effort. Fishing effort was defined as gillnet area (m^2) multiplied by soaking time (h).

Similar to a GLM approach, the response variable Y_i is assumed to have a probability distribution that belongs to the exponential family, with mean $\mu_i = E(Y_i)$ linked to a structured additive predictor η_i through a link function $g(\cdot)$ such that $g(\mu_i) = \eta_i$:Where i is the index for each sampling statio

$$\eta_i = \beta_0 + \sum_{m=1}^{M} \beta_m X_{m_i} + \sum_{l=1}^{L} f_l(v_{l_i}) + \text{offset}(i) ; i = 1, \ldots, n$$

where i is the index for each sampling station, n represents the total number of sampling stations, η_i is the linear predictor either for CPUE or for count data, β_0 is a scalar representing the intercept, M denotes the total number of linear covariates, β_m is the coefficient which quantifies the effect of some covariates X_m on the response, L refers to the total number of non-linear covariates, and $f_l(\cdot)$ are functions defined v_l for a set of covariates.

The $f(\cdot)$ terms can be used either to relax the linearity of the covariates (e.g. smooth effects), or to introduce random effects (e.g. spatial and/or temporal effect) (Rue et al., 2009). In the present study we used the $f(\cdot)$ to test smooth effects for some predictors and to include a Gaussian Markov Random Field (GMRF) (See supplementary Appendix C for details), which concerns the spatially structured random effect (W).

To model CPUE data, we tested both Gamma and log-Normal distributions as they are commonly used to model such kind of fisheries data (Venables and Dichmont, 2004). Because neither of these two distributions can contain zeros, we added a constant equal to 10% of the CPUEs median to all data previous to model fitting. With respect to the count models for adults and juveniles, we expected to observe a high amount of zeros as there could be spatial segregation. Thus, four different distributions were tested: Poisson (P), zero-inflated Poisson (ZIP), Negative Binomial (NB) and zero-inflated negative-binomial (ZINB). Also, an offset was used in the count data models in order to account for the fishing effort.

To evaluate lane snappers habitat suitability with respect its abundance and age groupings, we used month or season and six environmental predictors: sea surface temperature (SST, °C), distance to coast (km), bathymetry (m), rugosity (index), slope of the seabed (°) and chlorophyll-*a* concentration (mg/m^3) (See supplementary Appendix B).

Bayesian parameter estimates and prediction in the form of marginal posterior distributions were obtained throughout the INLA approach. Default priors were assigned for all fixed-effect parameters as recommended by Held et al. (2010), which are approximations of non-informative priors designed to have little influence on the posterior distribution. For the spatial component (W) we used the SPDE approach (See supplementary Appendix C for details). As recommended by Lindgren and Rue (2013), multivari-ate Gaussian distributions with mean zero and spatially structured covariance matrix were assumed for the spatial component.

For all models, variable selection proceeded by a manually forward stepwise entry. In order to compare the goodness-of-fit of these models, we used the Deviance Information Criterion (DIC) which is equivalent to the Akaike Information Criterion (AIC) but better suited for HBMs (Spiegelhalter et al., 2002), and which is also directly computed by R-INLA. Additionally, as used by Muñoz et al. (2013) and Pennino et al. (2014), we evaluated the logarithmic score of Conditional Predictive Ordinate (LCPO) as a measurement of predictive power. Lower values for both DIC and LCPO are indicative of better fit and predictive power, respectively. A best (and parsimonious) model was chosen based on a combination of low values for LCPO and DIC, containing only relevant predictors; i.e., those predictors with 95% credibility intervals not covering zero.

Finally, selected models were also evaluated for goodness-of-fit according to standard graphical checks, such as observed versus predicted scatter plots and residuals Quantile-Quantile plots. Since linearity is expected between the observed and predicted values, Pearson's correlation coefficient (ρ) was calculated and tested. Models with $\rho \geq 0.7$ and p-value ≤ 0.05 were considered acceptable and thus used for final prediction.

3. Results

3.1. Length at first maturity & age grouping

Graphical evaluation of the logistic models revealed good convergence of the chains for all cases. Fig. 2 shows the joint distribution of the logistic regression parameters for grouped and separated sexes. Despite all three cases had a reasonable fit, grouped sexes revealed a slightly better fit as the joint distribution of model's parameters was almost entirely concentrated within the right upper quadrant where $\beta_1 > 0$ (Fig. 2).

Table 1 gives basic statistic summaries of the posterior distribution for the logistic models. A good convergence was also observed by the numerical outputs, whose $\hat{R}$ values were all situated close to 1.0. With respect the L_{50} estimation, both mean and median values either for females and males were very similar (Table 1) (Fig. 3A and B).

The Bayesian hypothesis test pointed out that there was no relevant difference between the L_{50} of males and females $(p(d \geq 0)/p(d < 0) = 1.32)$ (Fig. 3D). Based upon this information, we decided to use the L_{50} estimation derived from the grouped sexes model and used its median (25.17 cm) to split the sampled lane snapper's into juveniles and adults for the models of the next section.

3.2. Data overview

Among the 126 sample stations, lane snapper occurred at 83 (66.14%) whose distance to coast ranged from 2.8 to 41 km (mean = 11.58 km; sd = 7.86) and depths from 5.1 to 52.7 m (mean = 16.8 m; sd = 8.85). The total weight caught during this period was 259.808 kg, whereas CPUE ranged from 0 to 6.12 g/m^2*h (mean = 0.35 g/m^2*h; sd = 0.85). Total length of all specimen varied from 18.5 cm to 46 cm (mean = 30.1 cm; sd = 3.92). According to the adopted L_{50} we counted a total of 101 juveniles and 505 adults individuals, thereby evidencing that catches were mostly composed by adult individuals (83.3%). Whereas adults occurred in almost all sample stations (81), juveniles occurred in 36 sample station only.

3.3. Model selection

Among all environmental predictors, only bathymetry and distance to coast were highly correlated ($\rho > 0.7$), and therefore never
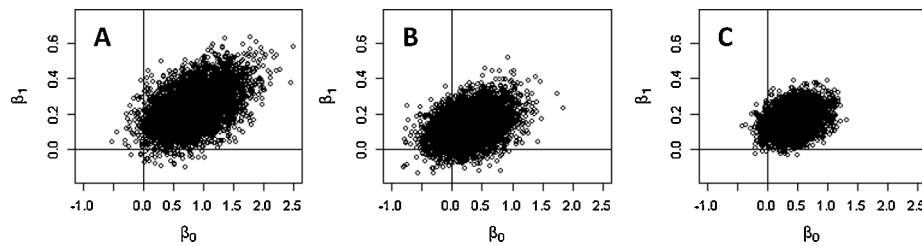
Fig. 2. Posterior joint distribution of logistic regression parameters for females (A), males (B) and grouped sexes (C).

Table 1
Summary of parameters and their associated statistics resulted from the logistic model (Sd = standard deviation; CI$_{95\%}$ = 95% credible interval).

| Sex	Parameters	Mean	Median	Sd	CI$_{95\%}$		$\hat{R}$
					Q$_{0.025}$	Q$_{0.975}$	
Females	β_0	0.835	0.820	0.387	0.112	1.633	1.001
	β_1	0.230	0.227	0.103	0.041	0.450	1.001
	L$_{50}$	25.332	25.870	12.757	16.835	29.002	1.063
	Deviance	16.728	16.163	2.004	14.749	22.280	1.001
Males	β_0	0.306	0.297	0.331	−0.322	0.978	1.001
	β_1	0.128	0.125	0.080	−0.022	0.291	1.001
	L$_{50}$	25.375	25.072	77.786	10.546	37.669	1.068
	Deviance	24.368	23.758	2.111	22.37	29.831	1.001
Females & Males	β_0	0.457	0.456	0.238	−0.010	0.927	1.002
	β_1	0.161	0.159	0.061	0.044	0.285	1.002
	L$_{50}$	24.653	25.174	5.996	18.701	28.094	1.038
	Deviance	35.062	34.443	2.026	33.075	40.667	1.001
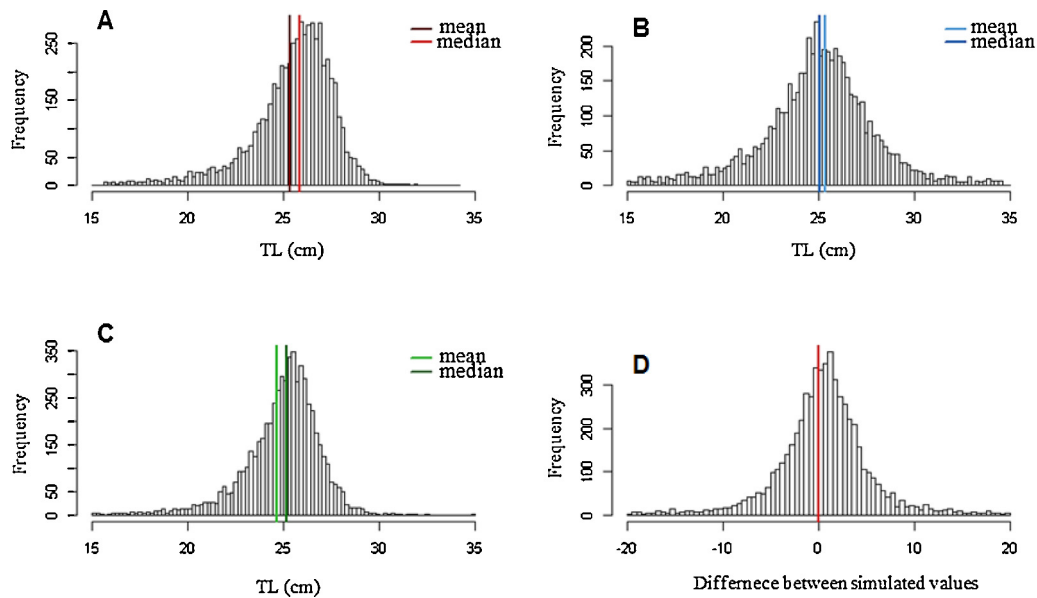
Fig. 3. Posterior distribution histograms of females (A), males (B), females & males (C) and the difference between males and females (D) total length (TL) simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

used together during the modelling procedures. Several models with different probability distributions were tested according to data nature. We also tested models that included quadratic terms and/or smoothing effects which, however, did not show any relevant fit improvement.

Table D2 (see supplementary Appendix D) summarizes the most relevant models regarding different combinations of environmental predictors for lane snappers CPUE. LCPO and DIC did not differ greatly among models of each distribution. However, DIC differed significantly between models with different distributions, with Gamma models always having a better fit. The best model included only distance to coast and the spatial effect (model 1, Table D.2 of supplementary Appendix D).

With respect to models for adult and for juvenile individuals, both agree on the NB distribution when LCPO and DIC were analyzed sequentially (See Table D.3 and D.4, respectively, in supplementary Appendix D). The best selected NB model for adults count data included as relevant predictors distance to coast, chlorophyll-*a* concentration and the spatial effect (model 8, Table D.3 of Appendix D), whereas for juveniles count data the selected model contained sea surface temperature, bathymetry and the spatial effect as relevant predictors (model 7, Table D.4 of supplementary Appendix D). Posterior summary statistics for all parameter of each selected model are shown in Table 2.

Fig. 4 denotes 2 types of models fit evaluation. Predicted versus observed CPUE, number of adults and number of juveniles are dis-
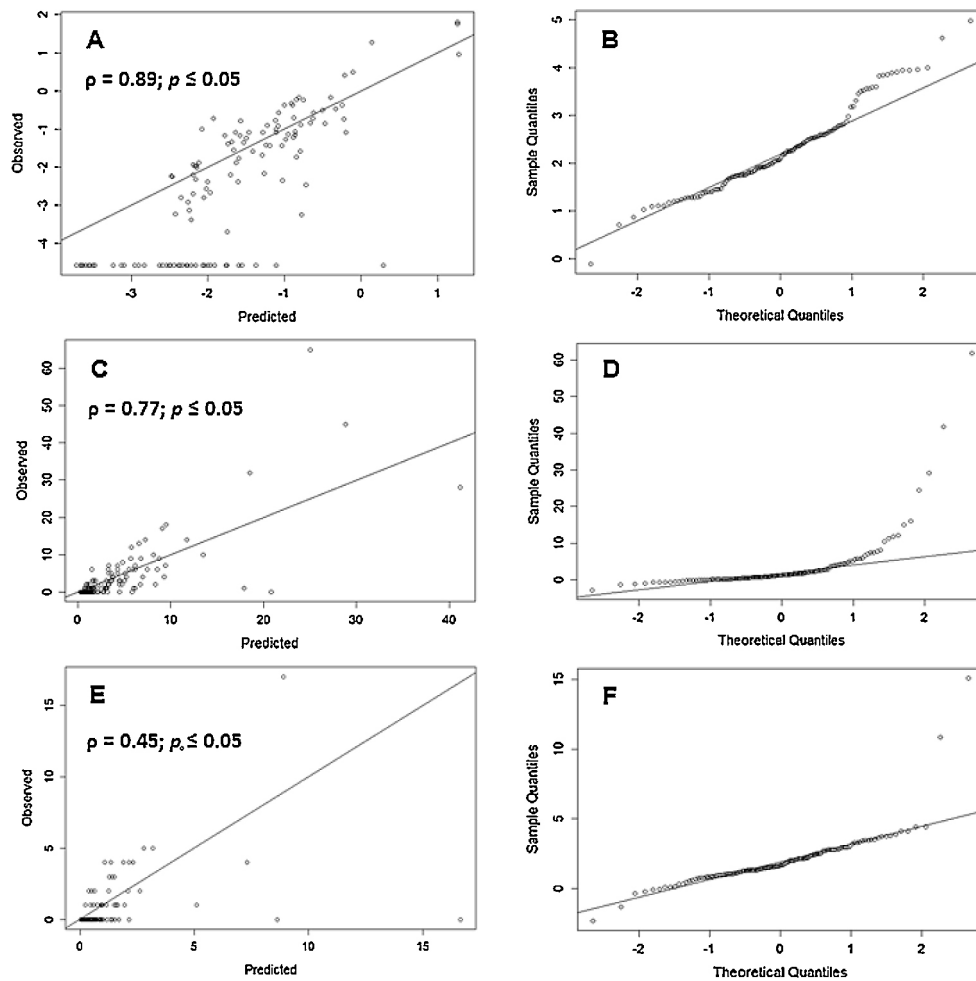
Fig. 4. Observed versus predicted values for log(CPUE) (A), number of adults (C) and number of juveniles (E). The right panels show quantile-quantile plots for each evaluated case.

Table 2
Summary of the marginal posterior distribution for model parameters provided by the selected model for each considered case. The hyperparameters φ_G and φ_{NB} are the precision parameters of the gamma and negative binomial observations, respectively, and τ and κ represents the variance and scaling parameter of the spatial effect, respectively.

Response variable	Parameters	Mean	Sd	CI$_{95\%}$	
				Q$_{0.025}$	Q$_{0.975}$
CPUE (model 1)	(Intercept)	−1.957	0.224	−2.410	−1.525
	DC	0.572	0.204	0.170	0.976
	τ	−5.576	0.593	−6.796	−4.472
	κ	3.996	0.458	3.140	4.937
	ρ (km)	0.053	0.020	0.015	0.109
	Φ_G	0.961	1.441	0.709	1.274
Adults (model 8)	(Intercept)	−8.222	0.255	−8.762	−7.756
	DC	0.951	0.264	0.441	1.487
	CHLa	0.650	0.308	−0.059	1.279
	τ	−6.002	0.757	−7.549	−4.582
	κ	4.281	0.529	3.284	5.359
	ρ (km)	0.040	0.018	0.009	0.091
	Φ_{NB}	1.322	0.455	0.658	2.421
Juveniles (model 7)	(Intercept)	−10.330	0.834	−12.135	−8.617
	SST	−0.702	0.318	−1.368	−0.113
	B	0.615	0.296	0.077	1.250
	τ	−4.066	1.160	−6.114	−1.596
	κ	2.438	0.992	0.332	4.743
	ρ (km)	0.233	0.242	0.018	1.371
	Φ_{NB}	0.748	0.435	0.218	1.858

played in the left panels of Fig. 4. As it can be noticed, for all three cases the predicted versus observed values were positively and significantly correlated ($0.45 < \rho < 0.89$, $p < 0.05$) (Fig. 4A, C and E). Q-Q plots showed reasonable normal distribution for the residuals of the selected CPUE model. Some outliers were presented for juveniles and adults, suggesting that some observed counts are much higher than the model would predict (right panels of Fig. 4 B, D and F). The CPUE model was able to predict fairly non-zero values while values around zero were highly overestimated (Fig. 4A). Thus, together with the respective Q-Q plot both figures clearly suggests that our data is splitted into two data-sets, one regarding the zeros and another regarding non-zero values. For adults and juveniles, both models were able to predict with more accuracy small to medium values (Fig. 4C and E).

3.4. Prediction of essential fish habitat for the lane snapper

When combining both the fixed effects and the model output from the random field, we can easily display the mean and standard deviation of the posterior mean of the linear predictor as well for the random field itself. Fig. 5 displays mean prediction and standard deviation maps. According to the linear predictor maps (Fig. 5A, C and E), CPUE, adults and juveniles had similar patchy distributions along the entire coast, differing solely on their spatial extent. Specifically, it was possible to identify four major hotspots, two of them located on the east coast and two on the north coast. The standard deviation maps for all linear predictors (Fig. 5 B, D and
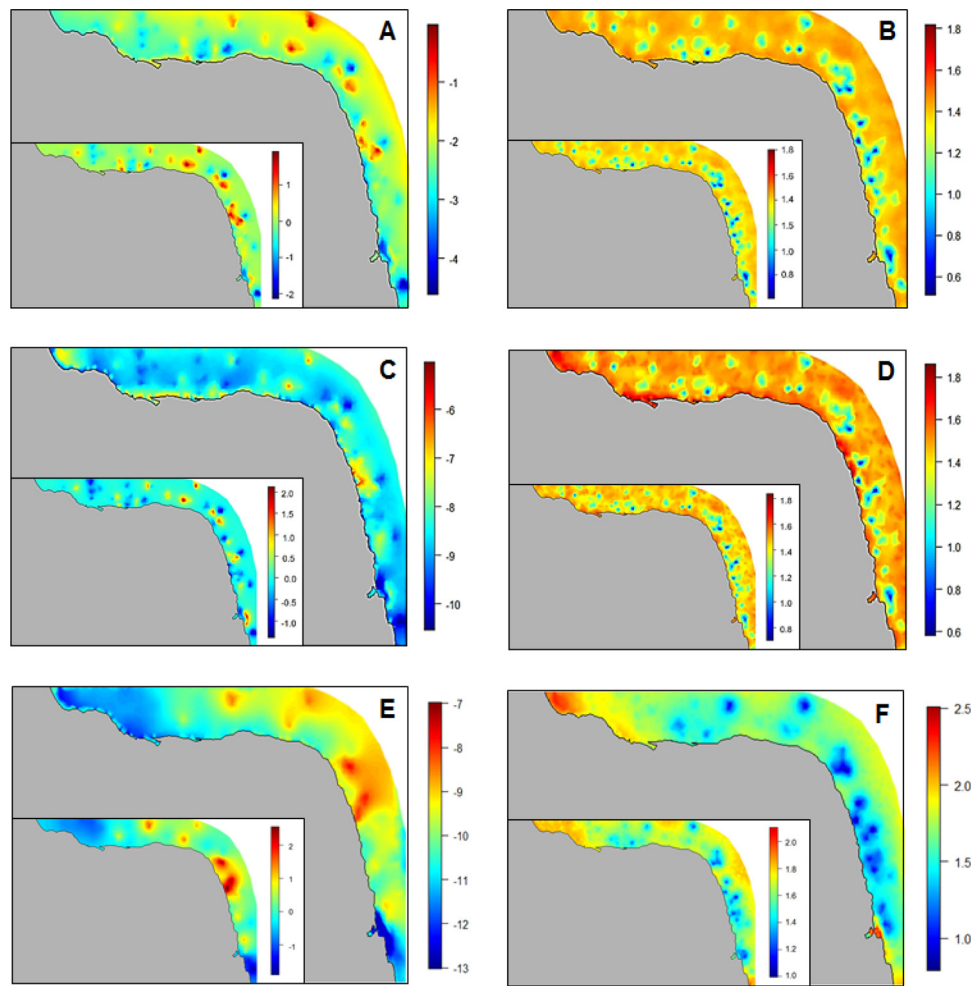
Fig. 5. Posterior mean (left panels) and standard deviation (right panels) of the predictive distribution of lane snappers CPUE (A, B), number of adults (C, D) and number of juveniles (E, F). Small panels represent the mean and standard deviation of the spatial random effect for their respective response variable. It is worth mentioning that all maps are log-scaled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

F), as expected, showed several smaller patches of lower standard deviation values, which correspond to areas where data were sampled. Comparatively, higher standard deviations were more or less constant along the entire domain in non-sampled areas.

The smaller panels in each figure reflect the spatial random effect and indicates the intrinsic variability of the lane snappers distribution when removing all covariables. It may reflect other hidden factors that were not accounted for in the models, such as biotic processes (e.g., competition and predation) and abiotic characteristics (e.g., sea surface salinity and currents). Again, for all three considered cases the patterns of mean spatial random effect behaved in a similar way, with a higher number of aggregation spots along the coast and which differed only in their spatial extent (smaller panels of Fig. 5A, C and E). Regarding the standard deviation of the spatial component, all three cases had similar distribution patterns as observed for the standard deviation of their respective linear predictors, with smaller and higher values corresponding to sampled and non-sampled areas, respectively (smaller panels of Fig. 5 B, D and F).

4. Discussion

4.1. Biological discussion: size at first maturity

The first part of our result aimed to estimate the size of first maturity for *L. synagris*. Although differences in this parameter among sexes are commonly reported for lane snappers from different regions (Aiken, 2001; Figuerola et al., 1998; Freitas et al., 2014; Luckhurst et al., 2000; Manickchand-Dass, 1980), our results indicated otherwise. Thus an overall size for both sexes was estimated at lengths of 25.17 cm. Our estimation agreed with those from Cavalcante et al. (2012) also conducted in the RN state, which reported median sizes of 25.7 cm for grouped sexes, well within the posterior 95% credibility bounds.

4.2. Model discussion

The Bayesian spatial modelling analysis yielded some clear results with respect to the environmental preferences of adults, juveniles and their overall abundance (CPUE). Despite most models fitted well to the data, some of them suggested that they were inappropriate (producing by *NA* and −*Inf*. in Table D.2–D.4 of supplementary Appendix D). Moreover, when attempted to the count models (Table D.3 and D.4 of supplementary Appendix D), it seemed that the number of adults and juveniles always fitted better (lower DICs) according to Poisson or its Zero-inflated version when compared to the alternative models belonging to other probability distributions. Nevertheless, these models also displayed the worst predictive measures (higher LCPOs). This could be explained since extreme low values of CPO are indicative of outliers and influential observations. Thus, the lower CPO values the higher LCPO values

which, in turn, reveal that these model parameters were biased and consequently inappropriate for prediction purposes.

Regarding the models for CPUE, we concluded that besides the spatial effect, only distance to coast was statistically relevant to explain the variability in CPUE (Table D.2 of supplementary Appendix D). Table II revealed a positive relationship between the response and the fixed effect, indicating that the CPUE of *L. synagris* increases toward offshore areas. The remaining parameters are the hyperparameters that specify the relevance of the spatial effect in the model.

R-INLA usually provides the simplest internal representation of these parameters, namely $\log(\tau) = \theta_1$ and $\log(\kappa) = \theta_2$. However, it is more natural to construct these parameters as a function of the spatial correlation range (ρ), since τ and κ have joint influence on the marginal variances of the resulting spatial field. For practical purposes, we exposed all hyperparameters, but mainly focused on ρ as it has a more intuitive interpretation. In this way, the mean value of (ρ) was 0.053 which represents the distance at which correlation is reduced to approximately 0.13. The posterior mean of the precision for the gamma observations (Φ) was 0.961. It is worth noting that the selected CPUE model suggested that our data would have probably been better fitted, if we had conditioned the zero values. Thus, if we had modelled our CPUE according a Gamma hurdle model as done by Quiroz et al. (2015) with Peruvian anchovies biomass, then we maybe could have had more precise estimations and predictions.

With respect to the count models applied to number of adults and juveniles, we were able to affirm that they respond differently to distinct environmental predictors. Distance to coast and chlorophyll-*a* concentration were statistically relevant to explain the variation in the number of adults (Table D.3 of supplementary Appendix D). Furthermore, Table 2 revealed that all fixed effects had also positive coefficients, indicating that the number of adults increases toward offshore areas and higher chlorophyll-*a* concentration. Number of juveniles, instead, showed a different response pattern, where sea surface temperature and bathymetry were statistically relevant (Table D.4 of supplementary Appendix D). According to Table 2, it was found that number of juveniles increases toward areas with lower sea surface temperature as well as toward offshore areas (higher bathymetry).

Concerning the hyperparameters from both count models, it was noted that juveniles showed slightly higher values for the mean variance and smaller values for the scaling parameter when compared to adults (Table 2). The mean spatial correlation range (ρ) for adults and juveniles were 0.04 and 0.233, respectively (Table 2). Contrasting these numbers with that from CPUE (0.053), it seems that despite an overall weak spatial correlation in all cases, it is apparently stronger for juveniles.

It is worth mentioning that each selected model discussed in this section was also tested without spatial effect (see penultimate models in Table D.2 to D.4 of supplementary Appendix D) as they had small spatial correlation ranges. These models used to have higher DICs and LCPOs when compared to the remaining models, which reveals that the spatial effect, despite small, was indeed relevant in all three cases.

4.3. Ecological discussion

Through the HBMs we were able to investigate the relationship between the life stages of *L. synagris* and environmental predictors, and therefore quantify and define suitable habitats according to relevant predictors. Although all three considered cases had slightly different environmental preferences, they showed similar spatial distributions. Specifically, distance to coast and bathymetry were the main predictors that drove the spatial distribution of *L. synagris*, indicating preference towards offshore areas. By means of our pre-

diction maps, we identified four main hotspots located in offshore areas, which also curiously correspond to the major reef, beach rock and sand complexes present in the RN coast (Vital et al., 2010).

Moreover, regarding particularly the differences between adults and juveniles of *L. synagris*, they showed specific preferences for chlorophyll-*a* concentration and sea surface temperature, respectively. Both predictors are commonly related to marine productivity, and may be used as potential indicators of thermal and productivity-enhancing fronts (Valavanis et al., 2008). Due to higher nutrient availability and sunlight incidence, higher chlorophyll-*a* concentration occur mainly in coastal areas and in upwelling fronts, the latter being characterized by cold water temperatures. Reefs, in particular, are areas of high primary productivity, and thus support higher trophic food webs from which adults and juveniles of *L. synagris* also benefit (Crossland et al., 1991).

Although juveniles appeared to be more widely distributed than the adults, their spatial distribution mostly overlapped with that of adults. In this sense, our results were somewhat surprising since a spatial segregation between adult and juveniles is commonly reported for *L. synagris* (Rodríguez and Páramo, 2012) and, to a wider extent, for marine fauna (Gillanders et al., 2003). The literature usually reports the occurrence of juvenile lane snappers over muddy bottoms near to marine estuaries and seagrass beds, whereas adults tend to prefer consolidated bottoms towards offshore areas (Doncel and Paramo, 2010; Rodríguez and Páramo, 2012).

However, we believe that our results probably reflect more a limited definition of juveniles in this work. Since the catches were predominately composed by adults, this study revealed that the fishing gear used in this work had a clear size selectivity for the *L. synagris* populations. Among the few catches of juveniles, it was observed that they already had relatively large sizes measuring at least 18.5 cm. Whereas the terminology *juveniles* is usually applied to individuals with sizes shorter than 10 cm (Franks and VanderKooy, 2000; Lindeman et al., 1998; Mikulas and Rooker, 2008; Pimentel and Joyeux, 2010), we concluded that individuals denoted as *juveniles* in this study should be better regarded as subadults. Thus, what we might be observing is, in fact, the spatial segregation among adult and sub-adults of *L. synagris*.

5. Concluding remarks

A set of statistical approaches was used in order to extend the scope of a data-poor fishery. By means of Bayesian models and Geographic Information Systems (GIS) schemes we provided some novel insights of the potential spatial distribution for abundance and different life stages of the vulnerable lane snapper. However, our case study attempted to present an emerging SDM tool, rather than focusing solely on traditional biological and ecological discussions.

Marine ecosystems constitute dynamic areas, where fisheries experiments are almost impossible and vulnerable to several error sources associated with observations, sampling procedures, model structure and parameters. In this sense, it is convenient to apply Bayesian inference into fisheries modelling procedures, since the posterior distribution itself is a dynamic process initially shaped according to our prior beliefs, which turns out a relevant model stabilizing factor in data-poor situations and adapts itself automatically as we acquire more and more data.

The hierarchical Bayesian spatial models proposed in this study are extremely powerful and suit perfectly in fisheries science, by quantifying both the spatial magnitude and the different sources of uncertainty. Spatial predictions, therefore, became much more accurate and consistent with reality. Furthermore, as we are dealing within a Bayesian framework, posterior predictive distribution

maps such as those defining the probability of the most favorable areas for conservation, would be antagonistic within traditional frequentist concepts of probability but are of enormous value for fisheries management.

However, it is noteworthy that the models presented in this study are limited not only in space but also in time. Thus, the fitted and predicted models revealed only a snapshot of the ecological process. Since fisheries are dynamic in space and time, we encourage the use of both effects as they may improve even more the wanted realism. Bayesian spatio-temporal models were already applied in some important fisheries issues, such as discard and by-catch problems (Cosandey-Godin et al., 2015; Pennino et al., 2014). Moreover, when dealing with fishery-dependent data, it is important to account for distinct sources of biases as those are related to fisher's behavior, and which has also been introduced recently by Roos et al. (2015) and Pennino et al. (2016).

Our study, demonstrated once more how easy it is nowadays to account for random effects in HBMs when performed through the INLA methodology. R-INLA revolutionized the way we may perform easily in otherwise sophisticated Bayesian inference, since its interface is similar to the conventional *glm* function in R and thus we do not have to write minutely the models as needed in BUGS and JAGS, although MCMC is still a slightly more flexible approach. Besides this, R-INLA is continuously evolving and greatly extending the scope of Bayesian models for applied scientists. Using R-INLA enables us to fit complex models at considerable lesser time and with more accuracy when compared to standard MCMC methods.

Finally, it is worth mentioning that R-INLA can also be used to fit models that do not have necessarily spatial and/or temporal components in its structure. Rue et al. (2009) provide some other examples, which include generalized linear and additive (mixed) models, dynamic linear models, survival models, spline smoothing and semiparametric regressions, among many others. In this way, we also encourage the use of R-INLA when performing ecological Bayesian modelling with conventional GLMs or GAMs, since the package's interface displays similarity with already existing *glm* and *gam* tools in R. At least, we have shown that, even for "data-poor" fisheries, this modelling approach has good performance.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.01.022.

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