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# Quantifying abundance trends and environmental effects on a population of queen scallop *Aequipecten opercularis* targeted by artisanal fishers in a

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coastal upwelling area (Ría de Arousa, NW Spain) using a Bayesian

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# ABSTRACT

Queen scallop *Aequipecten opercularis*, is exploited by small-scale trawlers in separated aggregations along the east Atlantic coast and the Mediterranean Sea. However, population performance is poorly known. Here, we combine official information and on-board observers' data over two decades to study the fishery ecology of an aggregation occurring in a coastal upwelling system (Ría de Arousa, NW Spain). Annual landings fluctuated around a mean of 170 tons while beam trawlers declined at a rate of 11 vessels per decade. A hurdle Bayesian spatial model fitted to observers' catch and effort data showed that the probability of occurrence and abundance of the species increased with fishing effort and decreased in sandy bottoms. Moreover, abundance increased with upwelling intensity and decreased with continental runoff and along the fishing season. Furthermore, occurrence was higher in the inner part of the embayment while abundance increased in the central channel. The predicted index of standardized abundance correlated with the trend in landings, and year-to-year fluctuations in abundance were negatively and positively related to upwelling intensity and net primary production, respectively, during the spawning and settlement period.

# 1. Introduction

Small-scale fisheries (SSFs) play a major role in worldwide fish catches while contributing to food security. Globally, SSFs provide employment to the largest number of fishers, as compared to industrial fisheries, and contribute to the development, growth and wellbeing of local economies, societies and cultures (Chuenpagdee and Pauly, 2008; Teh and Sumaila, 2013; Weeratunge et al., 2014). However, despite its importance, artisanal fisheries are often marginalized and poorly studied resulting in underreporting of statistics to governmental agencies and to international bodies such as the Food and Agriculture Organization of the United Nations (FAO) precluding accurate assessments of the status of these fisheries elsewhere (Costello et al., 2012; Lloret et al.,

# 2018).

Galicia (NW Spain, Fig. 1A) is a region with strong ties to the sea and fishing activity in particular with deep roots in history (Fernández, 1998). This long-standing tradition has made the region extraordinarily dependent on the fishing industry which is widely diverse, from aquaculture, especially on floating rafts for mussels, to shellfish harvesting on foot for intertidal bivalves and fishing in distant waters and coastal fishing (Surís-Regueiro and Santiago, 2014). The latter sector counts a large fleet of small-sized vessels (89.1 % of the total fishing fleet was composed of small-scale vessels in 2019; Xunta de Galicia, 2020) and, together with the shellfish harvesting, constitutes the core of Galician fisheries (Eiroa del Río, 1986) and is of outstanding socio-economic importance (Garza-Gil and Amigo-Dobaño, 2008). This region is

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located in the north-western corner of the Iberian Peninsula, at the northern boundary of the Iberian-Canary current upwelling ecosystem. The Galician coast is characterized by the presence of the "rías" that are tectonic estuaries penetrating the coast almost perpendicular to the coastline (Méndez and Vilas, 2005). These "rías" receive the freshwater mainly at their heads, and the inner positive circulation and water exchange with the shelf are both affected by the continental runoff and coastal wind-driven upwelling. The combination of the topographic features and coastal orientation with the oceanographic conditions makes Galician waters be very productive (Arístegui et al., 2009) and able to support extensive costal fisheries and shellfish harvesting (Surís-Regueiro and Santiago, 2014). The largest and most productive embayment in Galician waters is the Ría de Arousa (Pérez et al., 2000) (Fig. 1B) which concentrates, among other species, the most important fishery of queen scallop *Aequipecten opercularis* (Linnaeus, 1758).

Queen scallop is a pectinid species widely distributed along the Atlantic European continental shelf and the Mediterranean and Adriatic Seas (Brand, 2016). It has a patchy distribution occurring in a wide variety of substrates such as shelly bottoms, hard gravel or maërl beds from just below the low water mark to a depth of more than 150 m (Brand, 2016). Queen scallop is a short-lived and fast grower species with maximum growth rates in Galician waters between late autumn and early winter (Román et al., 1999). It attains sexual maturity between 1 and 2 years of age at roughly 40 mm of shell length. The main spawning time spans from winter to the middle of summer characterized by the release of different cohorts of mature oocytes over that period (Román et al., 2002). Subsequent settlement occurs from May to October with a peak in late May and early June (Iglesias et al., 2010). While some research suggests clean silt-free surfaces of multiple sources are prone to larvae settlement (Cragg, 2016), other studies have shown the preference of the larvae to recruit in maërl beds (Kamenos et al., 2004a). However, recruitment zones might vary from year to year (Brand, 2016) and be dependent on spawner abundance (Vause et al., 2007). Finally, 2-year-olds queen scallops attain commercial size at the end of summer and beginning of autumn thus becoming vulnerable to fishing during that period and the following months.

Queen scallop dynamics are highly dependent on the environment. Several experiments in semi-natural conditions have identified temperature and food availability as the main factors affecting growth rate, gonad development or reserve storage (Broom and Mason, 1978; Román et al., 1999; Iglesias et al., 2012). Biogenic substrates can also facilitate high growth rates for this species (Kamenos et al., 2004b), and several other factors such as salinity, current speed, competitors, predators or population density may affect larval distribution, recruitment dynamics or cohort strength (Vause et al., 2007; Brand, 2016). This influence of the environmental variability, combined with the life strategy of the species, results in a highly dynamic pattern of occurrence in time and space with typically high-density patches of limited continuance (Heilmayer et al., 2004).

Pectinids have been commercially exploited in Europe for more than 100 years. Directed fishing in most countries commenced in the 1930s and modern dredge fisheries started to fully develop in the 1950s and 1960s mainly based on stocks of king scallop, Pecten maximus, and queen scallop around the coasts of the British Isles and France (Duncan et al., 2016). Total annual European landings of queen scallop have fluctuated around 10,000 tons from mid 1970s, presumably due to the variability in the recruitment strength, and reaching record catches of 60,000 tons in 2012 with the Irish sea traditionally concentrating up to 80 % of total landings and a great part of the fishery operating around the Isle of Man (Duncan et al., 2016). Regarding Galician waters, over the last two decades landings of queen scallop averaged ~173 tons per fishing season reaching a maximum of around 400 tons in mid 2000s. This species is the target of small-scale beam trawlers (locally known as "bou de vara") which are restricted to in-shore waters of the Ría de Arousa and is not allowed in the other Galician rías. The species can be also accidentally caught by artisanal dredges targeting king scallop. Assessment and management of queen scallop include various measures implemented differently along the range of distribution; however, analytical stock assessment is only applied to the Isle of Man fishery (Orensanz et al., 2016). In Galicia, the fishery is regulated by the regional government based on a fishing season, coupled to the species reproductive resting cycle, which typically extends from November to March with a maximum number of 40 authorized days. Fishers can only keep aboard individuals larger than 40 mm of shell length, and the allowable catch is 50 kg per fisher per day without exceeding 150 kg per vessel per day (DOG., 2016). Despite implemented regulations, there is a lack of basic



**Fig. 1.** (A) Map of Galician region highlighting the specific study area: the Ría de Arousa. The red dot in the inset indicates the cell were the upwelling index was calculated. (B) Distribution of sampled hauls colored by port of origin of the monitored vessels. The location of those ports is indicated with triangles using the same color coding. The black dots indicate the oceanographic stations labelled by their names, and the black squares the location of the two main rivers draining in the Ría de Arousa. The blue polygons show the mussel raft areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

reliable knowledge on the stock status, spatial distribution of the species, and environmental influence on its dynamics threaten the sustainability of this resource in the Ría de Arousa.

Common to SSFs elsewhere, and to the queen scallop fishery in particular, is the lack or sparseness of reliable data to implement a proper stock assessment with the notable exception of the Isle of Man fishery (Bloor et al., 2019). A powerful source of information when scientific surveys are not available or not possible to be undertaken is fishery-dependent data collected by on-board observers. These type of data and the fitting of well-developed standardization methods (Maunder and Punt, 2004) coupled with assessment models have been extensively used to provide advice for large pelagic species and others (e.g. Campbell, 2015), and it is starting to be very valuable for SSFs too (e.g. Alonso-Fernández et al., 2019). However, fishery-dependent data have well recognized issues, which are starting to be taken into account thanks to the development of new modeling techniques. For instance, spatial autocorrelation could be a crucial factor, and not taking it into account might bias population abundance and distribution (Shelton et al., 2014), thus affecting stock assessment performance and management decisions (Maunder et al., 2020). Therefore, it is recommended fitting models that can account for spatial dependency aiming for more accurate and precise estimates of population abundance that would allow improving subsequent stock assessment (e.g. Cao et al., 2017). Overall, stock assessment models that incorporate the spatial dimension are recognized to be more suitable for the management of sea scallop fisheries (Smith et al., 2017).

Hence, the objectives of the present study were to evaluate the current performance of the fishery and to study the population ecology of the queen scallop aggregation in the Ría de Arousa. In doing so, we first describe several aspects of the fishery using official data. Second, we analyze the spatial distribution, infer the temporal pattern in relative abundance, and quantify the influence of the environmental conditions on the catch rates of the species. To accomplish the latter objective we fitted a set of hierarchical Bayesian spatial models using Integrated Nested Laplace Approximation methods to catch and effort data obtained from on-board observer monitoring compiled during the last two decades. Finally, the predicted index of relative abundance was related to lagged environmental conditions to evaluate the abiotic influence on the early life of the species.

# 2. Material and methods

# 2.1. Species data

To date, two main sources of information about stock performance are available for queen scallop in Galician waters: i) official landings and fleet statistics compiled by the regional government, and ii) catch and effort data collected by on-board observers.

i) Official statistics: the regional government of Galicia through its department of maritime affairs (i.e. Consellería do Mar, Xunta de Galicia) is in charge of compiling data on landings directly from the auctions since 1997 (Xunta de Galicia, 2020). This information was used to summarize the time-series of landings of queen scallop per port and year. In addition, the regional government compiles and maintains comprehensive data on fleet statistics from the fishers' guilds since 2004 (Xunta de Galicia, 2020). In particular, the number of vessels authorized to use beam trawls. This information was used to summarize the characteristics of the fleet that targets queen scallop, and to evaluate the trends in potential effort for this particular fishery.

ii) Observers data: the Galician SSF is characterized for being multispecies and multi-gear, and this complex fleet is monitored by the regional government through its Technical Unit of Artisanal Fisheries (Unidade Técnica de Pesca de Baixura, UTPB, in Galician) since 1999 (Alonso-Fernández et al., 2019). More specifically, on-board observers are assigned to fishing vessels randomly selected from the pool of the artisanal fleet and covering the full set of gears used in Galician waters and all along the geographical range. In a single trip/day each vessel usually performs several hauls. At each haul, observers record all basic operational data such as date, geographical position, fishing depth, gear size, haul length, vessel power, and gross registered tonnage (GRT). For this study, we focused on beam trawlers which is the only fishing gear explicitly targeting queen scallop in the Ría de Arousa. Apart from the operational data, observers also record the number and weight of all retained (> 40 mm of shell length) and discarded (< 40 mm) queen scallop individuals. The resultant database analyzed in this study counts 1170 hauls performed in 135 unique fishing trips by 71 different vessels from fishing season 1999/00–2016/17 (Fig. 1B, Table S1, Fig. S1).

# 2.2. Environmental data

The catch rates were linked on the spatial model (see below) to three environmental predictors defining daily upwelling conditions, daily river flow, and sediment characteristics. The upwelling intensity for the study area, which is a rough estimation of the volume of upwelled water per unit of time and unit of coastal length, was used to evaluate the effects of coastal upwelling on the queen scallop dynamics. The daily upwelling index (UI) values in a  $1^{\circ} \times 1^{\circ}$  geostrophic cell centered at 42 °N, 10 °W (Fig. 1A), were taken from the website of the Instituto Español de Oceanografía (http://www.indicedeafloramiento.ieo.es). Negative values of UI indicate transport of the Ekman layer to the south (producing coastal downwelling), whereas positive values of UI indicate transport of the Ekman layer to the north (producing coastal upwelling). All specific estimation details can be seen in González-Nuevo et al. (2014). In this study, values of UI included in the spatial model were averaged over 15 days prior to each haul. These values would represent the accumulated effects of the main meteorological and hydrological factors on primary production dynamics as shown for the study zone (Pérez et al., 2000). Before computing the averages, daily upwelling data were deseasonalized using a Generalized Additive Model (GAM; Wood, 2006) as described below.

With regards to continental waters, two main rivers drain in the Ría de Arousa: the Ulla and Umia (Fig. 1B), and they were used to evaluate the effects of continental flow on the queen scallop dynamics. River data were taken from the network of gauging stations operated by the regional agency Augas de Galicia and downloaded from the Spanish Ministry for an Ecological Transition (https://www.miteco.gob.es/es/). Daily river discharges (Q<sub>R</sub>) were normalized to the total catchment area (C<sub>t</sub>) of each river from the river discharges (R<sub>g</sub>) and catchment area at the gauging station (C<sub>g</sub>) applying the Horton's law (Rosón et al., 1991): Q<sub>R</sub> = R<sub>g</sub> · C<sub>t</sub>/C<sub>g</sub>. In this study, the influence of the rivers was included in the spatial model as the square root of the sum of inverse distances to river mouths weighted with rivers' average Q<sub>R</sub> over 15 days prior to each haul. Before computing the averages, daily river discharge data were deseasonalized using a GAM as described below.

Sediment characteristics were obtained from Vilas et al. (1999). In particular, we assigned a percentage of sand (grain size from 0.068 to 1.41 mm) to each haul by means of ordinary kriging. We fitted an exponential variogram to the proportion of sand recorded in sediments of the Ría de Arousa (Vilas et al., 1999) and used the variogram for spatial prediction.

Sea water conditions in the study region were further characterized using satellite data and local sampling. First, data on sea surface temperature (SST, in °C), chlorophyll *a* concentration (Chla, in mg m<sup>-3</sup>) and net primary production (NPP, in g C m<sup>-2</sup>d<sup>-1</sup>) were obtained for shelf waters over the period 1998–2016 and taken from Beca-Carretero et al. (2019). Second, local oceanographic conditions on water temperature (°C), salinity and fluorescence ( $\mu$ g Chla L<sup>-1</sup>) were obtained from the biweekly CTD sampling carried out by the regional agency INTECMAR (http://www.intecmar.gal) and available for the period 2006–2016 (Fig. 1B).

# 2.3. Statistical analyses

For characterizing the seasonal patterns of the environmental conditions we used GAMs of the following form:

$$Y_i = \alpha + f(\text{DoY}_i) + \varepsilon_i \tag{1}$$

where Y is the environmental variable recorded at a day *i*,  $\alpha$  is the intercept, *f* is a non-parametric smoothing function specifying the effect of the day of the year (DoY), and  $\varepsilon$  is the error term assumed to be normally distributed. The smoothing function was fit by a penalized cyclic cubic regression spline restricting the maximum number of knots to 6.

For modeling the observers' data, we used the species distribution modeling approach (Elith and Leathwick, 2009) and the standardization of catch and effort framework (Maunder and Punt, 2004). Typically, when standardizing catch rates researchers have to deal with count data, that is, the number of fish caught per haul, tow, set, etc. This kind of data often include many zero-valued observations (31 % in our case), being this fact particularly relevant for less abundant or by-catch species. Additionally, there is often a large spatiotemporal variability intrinsic to the dynamics of marine ecosystems. Therefore, these facts (presence of zeroes and variability in space and time) should be taken into account to provide more accurate and precise estimates of relative population abundance. In doing so, we used hierarchical Bayesian spatial models based on Integrated Nested Laplace Approximation (INLA) methods (Rue et al., 2017). INLA provides accurate numerical approximations to the posterior marginal distributions of a large class of hierarchical models that can be expressed as latent Gaussian Markov Random Fields (GMRF) (Rue and Held, 2005), and have been increasingly used in fisheries science (e.g. Cosandey-Godin et al., 2015; Pennino et al., 2019).

We standardized the catch rate and the spatial variation of queen scallop catches per unit of effort (CPUE) by modeling the number of individuals caught (N) in each individual haul at location *i* using a zeroaltered generalized linear mixed model or hurdle model (e.g. Paradinas et al., 2015). More specifically, counts were standardized by means of fitting a zero-altered negative binomial (ZANB) model to the observers' data where we assumed that the absence and presence of queen scallop follows a binomial distribution, and, when present, the non-zero abundances follow a zero-truncated negative binomial distribution. By adopting this delta approach with two sub-models we were able to address the questions of what is driving the absence and presence of queen scallop, and, once present, what drives its abundance (Shelton et al., 2014). The ZANB with spatial correlation was defined as follows:

 $N_i\sim ZANB(\pi_{i_2}\mu_{i_3}k)$  with expected mean  $E(N_i)=\pi_i/1-P_0\times\mu_i$  where  $P_0=(k/\mu_i+k)^k$  and variance

 $var(N_i) = \pi_i/1 - P_0 \times (\mu_i^2 + \mu_i + \mu_i^2/k) - (\pi_i/1 - P_0 \times \mu_i)^2$ . The parameter k would be dispersion parameter representing the amount of over-dispersion relative to the Poisson distribution.

The term  $\pi_i$  is the probability of presence and was modeled using a binomial GLMM with logit link:

 $logit(\pi_i) = \alpha + FS_i + \beta_1 SD_i + \beta_2 SA_i + \beta_3 EP_i + \beta_4 DE_i + \beta_5 SP_i + \beta_6 UI_i + \beta_7 QR_i + u_i$  (2)

where  $u_i \sim \text{GMRF}(0, \Sigma)$ .

The term  $\mu_i$  is the mean abundance and was modeled using a zero-truncated negative binomial GLMM with log link:

$$\log(\mu_i) = \gamma + FS_i + \beta_1 SD_i + \beta_2 SA_i + \beta_3 EP_i + \beta_4 DE_i + \beta_5 SP_i + \beta_6 UI_i + \beta_7 QR_i + v_i \quad (3)$$

where  $v_i \sim \text{GMRF}(0, \Sigma)$ .

For both Eqs. 2 and 3  $\alpha$  and  $\gamma$  are intercepts, and  $\beta_n$  are regression parameters that differ between models (note that parameter for the categorical covariate FS was omitted to simplify notation). These parameters represent the fixed effects of the covariates and were defined as follows: FS is the fishing season starting when the fishery opens on November 1st each year and ending on March 30th of the following year. In some years, the fishery was allowed in October and April too. SD specifies the fishing season day, that is, the day when a haul was performed from 1 (on 1st October) to 213 (on 30th April). SA is the fishing effort defined as the swept area and calculated as the length of the haul times the wide of the beam, EP is the engine power assumed to account for specific characteristics that define each vessel, DE is the average depth of the haul, SP is the proportion of sand in the sediments, and UI and QR are the upwelling index and river runoff, respectively, as explained above. Prior to model fitting SA, EP and QR were logtransformed, and all continuous covariates were normalized to mean 0 and standard deviation 1. A brief description of all explanatory variables is provided in Table S2.

The terms  $u_i$  and  $v_i$  in Eqs. 2 and 3 are spatially structured random effects at location *i* in the binary and count part of the model, respectively, which are GMRFs with mean 0 and covariance matrix  $\Sigma$  (Bakka et al., 2018). The Matérn correlation function was used to parameterize the covariance matrix, and parameters were approximated by the stochastic partial differential equation (SPDE) method (Krainski et al., 2019) over an irregular mesh of 2345 vertices (see Fig. S2 for further details on building the mesh). For simplicity, we used two different spatial random fields for each part of the ZANB model but sharing the same set of Matérn covariance parameters (Zuur and Ieno, 2018).

For both models depicted in Eqs. 2 and 3, we have assigned default vague priors for all the fixed parameters due to a lack of prior information which is typically the case in these type of studies (e.g. Paradinas et al., 2015). Vague priors were also used for the dispersion parameter of the NB model. However, for the hyperparameters defining the geostatistical term, that is, the range (r) and the standard deviation ( $\sigma$ ) of the spatial random field, we used penalized complexity priors as described in Fuglstad et al. (2019). More specifically, we set that the probability of r (the distance at which spatial autocorrelation is small) is < 1.5 km = 0.001, and that the probability of  $\sigma$  is > 4 = 0.001. These values were selected based on the spatial distribution of the data and the range of the response variable. The picked values ensured that the range was not too small and the standard deviation was not too large in order to avoid overfiting the model. A sensitivity analysis was also performed by experimenting with other values. The final choice was visually validated by verifying that the posterior distributions were consistent and concentrated around the chosen prior values.

The hurdle model was compared with other models assuming different distributions (i.e Poisson, Negative Binomial) and structures (i. e. including and non-including a spatial random effect and accounting for physical barriers). Statistical comparison was performed using the deviance information criterion (DIC) and the widely applicable information criterion (WAIC) (Krainski et al., 2019).

Finally, the fishing season-to-fishing season fluctuations in standardized abundance (conditional on presence) predicted by the spatial model were modeled as a function of the upwelling intensity and net primary production (other variables such as SST and Chla did not show significant effects during the exploratory analyses) characterizing the summer (from May to September) when the bulk of the fished cohort was spawned and settled. The purpose of this analysis was to evaluate the influence of lagged environmental effects on the interannual variability in predicted abundance. Therefore, these two environmental variables were assumed to define the hydrographic and feeding conditions during the early life stages of the species over the year preceding the fishing season (e.g. upwelling and primary production in summer 2006 would affect abundance in fishing season 2007/08). A Generalized Linear Model (GLM) was fitted to the data assuming a negative binomial (NB) distribution.

All treatment of data and analyses were performed with R language (R version 4.0.3, R Core Team., 2020), and models were fitted using the package R-INLA 20.03.17 (Rue and Lindgren, 2015).

# 3. Results

# 3.1. Environmental conditions of the study region

Environmental conditions in the location of the study showed welldefined seasonal cycles with upwelling (Fig. 2A) and continental runoff (Fig. 2B) having a maximum and a minimum, respectively in July–August. SST (Fig. 2C) and NPP (Fig. 2E) peaked also in summer months, while Chla (Fig. 2D) showed a bimodal seasonal cycle with maximums in late winter and summer and a minimum in late spring. This oceanographic setting defined by the environmental conditions recorded by the satellite were also reflected inside the Ría de Arousa. More specifically, water column-integrated temperature was correlated with satellite SST (Fig. S3A), and water column-integrated fluorescence was correlated with satellite NPP (Fig. S3B). Furthermore, water column-integrated salinity was correlated with continental runoff from both rivers of influence (Fig. S3C, D).

# 3.2. Queen scallop landings and fleet characteristics

Since 1997, when official catch records started to be publicly available, data on queen scallop landings in Galician ports showed annual fluctuations with an average of 173 ( $\pm$ 118) tons and a peak of maximum catches at around 400 tons for fishing seasons 2006-2010 and a minimum of 8 tons in season 2002/03 when the Prestige oil spill occurred (Fig. 3A). During the two decades of the study period, landings increased at a rate of 6.3 tons per fishing season and the majority of catches were taken in the Ría de Arousa representing 100 % of catches in the last decade (Fig. 3A). There were two main ports in terms of landings and fleet (Fig. 3A, B): Rianxo, in the inner part of the Ría accounting for 18-54% of the catches depending on the season, and Cambados, in the middle part of the Ría accounting for 44-77% of the catches depending also on the season (Fig. 3A). Mean annual landed value in these two ports since 2001 reached 0.4 million euros with a peak of 0.8 million euros in season 2018/19 and a minimum of 0.05 million euros in season 2002/03.

Beam trawl is the unique fishing gear explicitly targeting queen scallop (Fig. 3B). However, the artisanal dredging fleet fishing king scallop can capture queen scallop as bycatch, though numbers are negligible; indeed, in Galician waters, and the Ría de Arousa in particular,  $\sim$ 90 % of queen scallop landings can be attributed to beam trawlers and the rest would be landed by the artisanal dredgers. Since 2004, when official fishing fleet records started to be publicly available, authorized beam trawlers in the Ría de Arousa declined at a rate of 11 vessels per decade, from 107 in 2004 to 87 in 2019 (Fig. 3C). Vessel length averaged 8 m, ranging from 4 to 12 m, with a mean power of around 20 kW. In terms of tonnage, the beam trawling fleet increased slightly from 3.1–3.3 GRT (Fig. 3C).

#### 3.3. Observer's catch and effort model

The most optimal model in terms of DIC and WAIC was the ZANB that included the spatial random effect (Table S3). The model did not show any important remaining pattern in the residuals, however, it had difficulties to reproduce large observations (Fig. S4). The numerical results for the optimal model are shown in Table S4 and the posterior distribution of the fixed effects for each model part is illustrated in Fig. 4. Putting more fishing effort and using vessels with a high engine power resulted in a greater probability of fishing queen scallop (Fig. 4A) and obtaining higher abundances (Figs. 4B, 5 A). Hauls performed in seafloors with a larger proportion of sandy sediment were associated with a lower probability of fishing queen scallop (Fig. 4A) and also getting lower abundances (Figs. 4B, 5 B). Furthermore, abundance was positively and negatively related to the upwelling strength and continental runoff, respectively, and decreased along the fishing season (Figs. 4B, 5 C–E). Finally, haul depth was not an important variable in either the



Fig. 2. Environmental conditions in the study region. Seasonal cycles of (A) upwelling, (B) continental runoff, (C) SST, (D) Chla, and (E) NPP.



**Fig. 3.** (A) Spatial distribution of average queen scallop landings in ports of the Ría de Arousa during the fishing seasons 1997/98 to 2019/20. Shown are also timeseries of total landings in Galicia, the Ría de Arousa and in the four main ports of the Ría de Arousa in terms of landings (Ribeira, Rianxo, Cambados and O Grove). A correlation matrix among landings is provided too. (B) Spatial distribution of the number of authorized beam trawlers averaged per port in the Ría de Arousa during the period 2004–2019. (C) Temporal dynamics of authorized beam trawlers in the Ría de Arousa over the period 2004–2019. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



Fig. 4. Posterior distributions of the fixed effects sizes of the optimal ZANB spatial model. Shown are the median (black line) and 95 % credible intervals (gray shade) of each covariate for the (A) binary (occurrence) and (B) count (abundance) parts of the model. Note that intercepts and coefficients for the fishing season covariate were omitted for simplicity. See Table S4 for the complete numerical results.

binary (Fig. 4A) or the positive count (Fig. 4B) part of the model.

The spatial random field for the binomial part of the ZANB showed that, once accounted for the covariates, the probability of presence was

higher in the inner part of the Ría and in a spot located between Illa de Arousa and O Grove (Fig. 6A). The spatial random field for the count part of the model showed that abundance increased along the central

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**Fig. 5.** Posterior mean fitted values (±95 % credible intervals) from the positive count part of the ZANB model for (A) fishing effort, (B) sand proportion, (C) upwelling intensity, (D) continental runoff, and (E) fishing season. For obtaining the predictions, continuous covariates were kept at their mean and fishing season held at 2008/09.



**Fig. 6.** Posterior distribution of the mean of the spatial random field for the (A) binary and (B) positive count parts of the ZANB model, respectively. The gray dots indicate the location of the sampled hauls. These graphs show partial effects, that is, they take into account the effects of the other covariates. See Fig. S5 for the standard deviation of the spatial random field. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



Fig. 7. Temporal trend (mean ±95 % credible intervals) of standardized abundance (queen scallop numbers) predicted from the positive count part of the ZANB model. Continuous covariates were held at their mean for obtaining the predictions.

axis and outer channel of the Ría (Fig. 6B). The posterior mean for the range determined that the distance at which the correlation was lower that 0.1-ish would be 2623.1 and 1856.3 m (Table S4, Fig. S6) for the binomial and count model, respectively, indicating that the spatial dependency diminished for distances larger than 2.6 and 1.8 km.

The temporal fluctuations in standardized catch rates conditional on presence showed that the relative abundance of queen scallop in the Ría de Arousa was higher from mid to end of 2000s with a peak in fishing seasons 2007/08 and 2008/09 (Fig. 7). The overall annual trend in standardized abundance resembled the pattern in official catches (Fig. 3A), indeed both patterns were correlated (Spearman rank correlation = 0.80), although it was also evident that while catches remained high and stable the standardized abundance declined. Finally, the annual fluctuations in relative abundance were related with the environmental conditions, upwelling and production, resulting in that yearto-year fluctuations in relative abundance decreased with greater upwelling while increased when net primary production was higher during the spawning and settlement of the species (Fig. 8, Table S5 and Fig. S7).

# 4. Discussion

Artisanal fisheries are typically poor in data preventing effective management in most cases (Costello et al., 2012). Here, we provide a comprehensive analysis of an artisanal resource, the queen scallop in Ría de Arousa, Galicia, from fishery and fleet evolution to spatial modeling of catch and effort and evaluation of the impact of the environment, that will foster the improvement of the current management plans. The importance of queen scallop as a marine resource is well recognized in northeastern European Atlantic waters mostly in the Celtic Sea and English Channel (Duncan et al., 2016). However, there are other important fisheries along the range of distribution of the species not as big in terms of absolute landings, though crucial for local small-scale fisheries as the one we described here for the Ría de Arousa (Outeiro et al., 2018a), and surprisingly not considered by the corresponding international bodies (ICES, 2018).

Landings in the study zone were basically dominated by fleets belonging to two different ports, Rianxo and Cambados, operating in the inner and outer part of the embayment, respectively. The volume of catches varied from year to year showing peaks and troughs as commonly recorded for this species (Duncan et al., 2016). However, two distinct periods were evident, one from fishing season 1997/98–2005/06 with average catches around 50 tons, and a second stage from fishing season 2006/07 until present with catches fluctuating around an average of 200 tons despite the number of authorized vessels

decreased substantially over that period. During the low catch years, a minimum was observed in fishing season 2002/03 caused by the closure of the fishing activity due to the Prestige oil spill that happened in Galician offshore waters in November 2002. The accident implied the immediate cease of fisheries, which were also anomalous the next season 2003/04 (Garza-Gil and Amigo-Dobaño, 2008), and had a strong initial impact on the biota during the first year after the spill and a recovery by 2004 (Penela-Arenaz et al., 2009). Thus, low landings during those seasons could be ascribed to the anomalous fleet behavior and deleterious effects caused by the tanker accident. In subsequent years, catches increased reaching maximum values in mid to end 2000s coinciding with the peak of landings in other grounds such as the Isle of Man fishery (Bloor et al., 2019). The causes of these explosive peaks remain unknown though some reasons can be postulated. These might include favorable oceanographic conditions improving growth (Broom and Mason, 1978) and recruitment (Orensanz et al., 2016), and/or fishery-related dynamics such as the relaxation of fishing mortality which, in our case associated to the reduced activity caused by the tanker spill, can contribute to increase the cohort strength, indeed, intracohort relationships have been observed for this species in the Isle of Man fishery (Vause et al., 2007). Notwithstanding, while catches remained relatively stable up until recent years, the relative abundance dropped slightly since the peak reached in the 2007/08 and 2008/09 fishing season. A sustained fishing pressure with presumably a high rate of fishing mortality as shown in landings, combined with the prevailing environmental conditions are probably the main factors driving the fishing season-to-fishing season fluctuations in the queen scallop population occurring in the Ría the Arousa.

The spatially-explicit modeling fitted to the observers' data showed that while the probability of occurrence of queen scallop did not vary along the fishing season, abundance decreased continuously along time. This fact concurs with what was previously found for the Isle of Man king scallop dredge fisheries (Murray et al., 2011), and suggests that the patchy distribution of queen scallops does not affect the likelihood of occurrence, but an increase in patchiness towards the end of the season due to the resource depletion reduces catch rates. Additionally, putting more effort (i.e. sweeping larger areas) and vessels with higher capacity (i.e. greater engine power) increased the catchability and abundance of queen scallops in the study area. This result is also consistent with previous observations in king scallop dredge fisheries for which vessel capacity is an important predictor of catches per unit of effort (Murray et al., 2011). However, in our case, vessel capacity was less important for getting higher catch rates. Furthermore, the model did not detect any clear effect of depth either on the presence or abundance of queen



Fig. 8. Partial relationships between predicted annual standardized abundance conditional on presence (Fig. 7) and (A) upwelling intensity and (B) satellite-derived net primary production as obtained from fitting a generalized linear model assuming a negative binomial distribution. Note that environmental variables were averaged from May to September over the year preceding the fishing season as explained in the text. See Table S5 for the complete numerical results and Fig. S7 for residuals check.

scallop, suggesting that bathymetry itself does not drive the distribution of queen scallop. It is well known that depth affects many aspects of the biology of several scallop species, for instance, intermediate depth would be a factor favoring greater growth rates of queen scallop as observed in suspended culture experiments (Roman et al., 1999). However, the depth-related effect is usually associated to more specific factors such as changes in temperature, food availability or substrate type (Brand, 2016). In line with this, while bathymetry did not show important effects, seafloor characteristics was a key variable influencing both queen scallop occurrence and abundance. When the composition of sediments had a greater proportion of sand, catchability and relative abundance of queen scallop decreased. In the studied embayment, sandy substrates are richer in carbonate content and poorer in organic matter (Vilas et al., 2005), suggesting that queen scallop in the Ría de Arousa has a greater affinity for siliciclastic muddy substrates richer in organic matter and located in the inner part and main channel of the embayment under low wave action (Vilas et al., 1999, 2005). Substrate type is typically a habitat characteristic that influences the distribution and abundance patterns of other sea scallop species aggregations (e.g. Mendo et al., 2014).

Finally, the spatial model detected a subtle positive and negative effect of the upwelling intensity and continental runoff, respectively, that were more important on affecting abundance than presence of queen scallop. These two variables would be indicators of the feeding conditions which would probably influence the burrowing strategy into the substrate. Nutrient fertilization by upwelling would favor catchability, whereas mineral particles of terrestrial origin transported by rivers would diminish the quality of the food reducing the likelihood of catching queen scallops. Upwelling and continental runoff effects are commonly detected in our study region. For instance, year-to-year fluctuation in flesh yield of cultivated mussels in a neighboring ría was also positively and negatively related to upwelling and continental runoff, reflecting the benefit and detrimental effect of oceanic and continental fertilization, respectively (Álvarez-Salgado et al., 2017).

Once accounted for the effects of the covariates discussed above, the random spatial field revealed clear patches of occurrence and abundance that may be related to at least three factors: the inherent spatial complexities of the bottom substrates including the presence of maërl beds in certain zones, the location of mussel rafts areas which have important implications for the benthic environment and fishing strategies, and the currents and circulation pattern in the embayment. Overall, the inner part of the Ría was in general characterized for showing high probability of occurrence but low abundance of the species. Bottom substrates in this part of the Ría are very muddy (Vilas et al., 2005) which seems to favor the presence of queen scallop as discussed above. Moreover, this zone contains the greatest concentration of mussel rafts polygons which are indeed a source of mud that is later mobilized to the central axis of the Ría due to the action of waves and currents (Méndez-Martínez et al., 2011). However, the presence of mussel rafts may influence the composition of the benthic community (Outeiro et al., 2018b) and determine the fishing strategies just because of the presence of the floating structures which implies that trawl tows are shorter thus reducing abundance. Indeed the distance of the hauls to the polygons affects the composition of the catch being more heterogeneous near the rafts (Outeiro et al., 2020). The probability of presence was also high in a spot located to the southeastern side of the Ría between Illa de Arousa and O Grove. This spot coincides with one of the most important maërl beds in the Ría de Arousa (Peña and Bárbara, 2009). Maërl beds and macroalgae have been described as important habitats where queen scallop spat tend to settle (Howarth et al., 2011). Within these complex habitats, queen scallops would found optimal conditions for their early life stages (Kamenos et al., 2004a) such as refugee and high growth potential (Kamenos et al., 2004b). The central channel of the Ría was in general characterized for showing low probability of occurrence but high abundance of queen scallops. Substrates in this central axis are moderately muddy and the presence of mussel rafts is minor thus favoring abundance.

An important factor not accounted for in our model but potentially determinant in driving spatial structure would be the currents and circulation pattern. Queen scallop, as other scallops, has been associated with strong currents which provide favorable conditions for these benthic filter feeders (Brand, 2016). Currents are also important drivers of spatial structure influencing larval retention and recruitment and determining the connectivity among stocks which has implications for management (Nicolle et al., 2017). Hydrodynamic model carried out in the Ría de Arousa showed that currents are mainly due to tides and wind forcing (Pinho et al., 2001). Simulations for a spring tide (representative of the queen scallop spawning period) shows that velocity reaches high values in the inner section of the Ría (i.e. Ulla estuary), in the main channel, and in the zone between Arousa Island and O Grove. These are zones of high occurrence and abundance, suggesting that tide-currents may influence the distribution of early life stages of queen scallop. Additionally, simulations carried out under prevailing summer (winds blowing from the north) and winter (winds blowing from the south) conditions identified the formation of two gyres, one in the internal part of the ría and another one at the central part including the southeast region of Illa de Arousa. The internal gyre would facilitate the concentration of individuals in that part of the Ría, whereas the other eddy would help distribute the species in the central axis of the embayment and transport individuals to the western side where a patch of high abundance was apparent. The patch with the lowest probability of occurrence would fall in the center of the external eddy. Finally, the residual circulation in the Ría in summer, when winds from the north predominate and cause upwelling, was described by a two-layer circulation with a surface current towards the open ocean and an opposite current through the deeper layer (Pinho et al., 2001). This general situation is indeed more complex and characterized by a succession of upwelling episodes that extend from 5 to 15 days separated by periods of wind relaxation or even downwelling episodes (Arístegui et al., 2009). This sequence ensures the fertilization of the coast with oceanic nutrients during the spin-up phase of upwelling and its subsequent utilisation during the spin-down and relaxation phases to efficiently produce the phytoplankton biomass that feed filter feeders such as the queen scallop. This upwelling intermittency would contribute also to retain larvae and favor settlement inside the embayment. Finally, other factors not accounted for in the model can have an effect on distribution, for instance, turbidity and salinity (Brand, 2016). These two factors could help explain the absence of queen scallop close to the Ulla and Umia estuaries, which partially emerge during low tide too, and the low abundance near the mussel rafts.

The time-series model of the standardized abundance showed that catch rate decreased with greater upwelling whereas it increased when net primary production was high during the spawning and settlement of the species in spring and summer (Román et al., 1996). While upwelling exerts a positive effect on the ecosystem through nutrient fertilization, the physical effect of water movement can have detrimental effects for the population. That is, when upwelling is strong, surface currents could transport the larvae away from the retention zones impeding self-recruitment and reducing cohort strength. Moreover, upwelled waters are colder and this could diminish growth rates (Román et al., 1999). On the other hand, high net primary production has a positive effect on later abundance probably associated to the high concentration of chlorophyl favoring good feeding opportunities increasing the cohort strength (Broom and Mason, 1978; Román et al., 1999). The importance of the cohort strength in population dynamics and later fishery has been already shown for queen scallop (Vause et al., 2007) and other scallops such as the king scallop (Beukers-Stewart et al., 2003). In summary, we postulate that upwelling conditions would be necessary for the oceanic fertilization of the Ría, combined with moderate wind conditions that would facilitate larval retention and optimal feeding conditions as suggested for other species in the same region (Otero et al., 2008). These conditions would help explain high abundance peaks such as those

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recorded in 2007/08 and 2008/09 associated with good oceanographic conditions in the preceding years (Beca-Carretero et al., 2019; Doval et al., 2016).

The model presented here is in line with the growing effort for explicitly including the spatial dimension to develop indices of relative abundance when working with fishery-dependent data (Maunder et al., 2020). This approach may produce more precise indices than conventional surveys especially for benthic species which distribution depends on habitat features as would be the case here. More accurate indices can subsequently be the input to stock assessment models and help to take better management decisions (Cao et al., 2017). Assessment of queen scallop in the study region is under a specific management plan that does not include an analytical stock assessment. Our results should be an initial step in order to develop such analytical framework already used to manage other queen scallop stocks (e.g. Isle of Man, Bloor et al., 2019). Our results are also relevant to understand the ecological factors that play a significant role in determining the distribution and interannual fluctuation of an important socio-economic resource exploited by the most notorious Galician artisanal fleet and one of the most relevant in Europe (Outeiro et al., 2018a).

# Data availability statement

The on-board observers' data underlying this article cannot be shared publicly because it is owned by a third party. It was provided by the Xunta de Galicia by permission. Data will be shared on request to the first author with permission of the Xunta de Galicia.

#### CRediT authorship contribution statement

Luis Outeiro: designed the project and collated the data. Jaime Otero: analyzed the data with assists from Luis Outeiro and Alexandre Alonso-Fernández; Luis Outeiro and Jaime Otero: wrote the manuscript with assists from Rafael Bañón and Juliano Palacios-Abrantes. And Luis Outeiro, Jaime Otero, Alexandre Alonso-Fernández, Rafael Bañón and Juliano Palacios-Abrantes: approved the final article.

# **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.S

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# Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2021.105963.

#### References

abundance trends of key species from a highly developed small-scale fishery off NE Atlantic. Fish. Res. 209, 101–116.

- Álvarez-Salgado, X.A., Labarta, U., Vinseiro, V., Fernández-Reiriz, M.J., 2017. Environmental drivers of mussels flesh yield in a coastal upwelling system. Ecol. Ind. Russ. 79, 323–329.
- Arístegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machú, E., Demarcq, H., 2009. Subregional ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33-48.
- Bakka, H., Rue, H., Fuglstad, G.-A., Riebler, A., Bolin, D., Illian, J., Krainski, E., Simpson, D., Lindgren, F., 2018. Spatial modelling with R-INLA: a review. WIREs Comp. Stat. 10, e1443.
- Beca-Carretero, P.P., Otero, J., Land, P.E., Groom, S., Álvarez-Salgado, X.A., 2019. Seasonal and inter-annual variability of net primary production in the NW Iberian margin (1998–2016) in relation to wind stress and sea surface temperature. Prog. Oceanogr. 178, 102135.
- Beukers-Stewart, D.D., Mosley, M.W.J., Brand, A.R., 2003. Population dynamics and predictions in the Isle of Man fishery for the great scallop, (*Pecten maximus*, L.). ICES J. Mar. Sci. 60, 224–242.
- Bloor, I.S.M., Emmerson, J., Jenkins, S.R., 2019. Assessment of Queen Scallop Stock Status for the Isle of Man Territorial Sea 2019/2020. SFAG Report No. 1. Bangor University, pp. 18.
- Brand, A.R., 2016. Scallop ecology: distributions and behaviour. In: Shumway, S.E., Parsons, G.J. (Eds.), Scallops: Biology, Ecology, Aquaculture and Fisheries. Dev. Aqua. Fish. Sci. vol. 40, 469–533.
- Broom, M.J., Mason, J., 1978. Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. Mar. Biol. 47, 277–285.
- Campbell, R.A., 2015. Constructing stock abundance indices from catch and effort data: some nuts and bolts. Fish. Res. 161, 109–130.
- Cao, J., Thorson, J.T., Richards, R.A., Chen, Y., 2017. Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 74, 1781–1793.
- Chuenpagdee, R., Pauly, D., 2008. Small is beautiful? A database approach for global assessment of small-scale fisheries: preliminary results and hypotheses. Am. Fish. Soc. Symp. 49, 575–583.
- Cosandey-Godin, A., Krainski, E.T., Worm, B., Flemming, J.M., 2015. Applying Bayesian spatiotemporal models to fisheries bycatch in the Canadian Arctic. Can. J. Fish. Aquat. Sci. 72, 186–197.
- Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., Lester, S.E., 2012. Status and solutions for the World's unassessed fisheries. Science 338, 517–520.
- Cragg, S.M., 2016. Biology and ecology of scallop larvae. In: Shumway, S.E., Parsons, G. J. (Eds.), Scallops: Biology, Ecology, Aquaculture and Fisheries. Dev. Aqua. Fish. Sci. vol. 40, 31–83.
- DOG, 2016. Orde do 23 de decembro de 2016 pola que se aproba o plan xeral de explotación marisqueira para o ano 2017. Diario Oficial de Galicia. Num 249, 56905.
- Doval, M.D., López, A., Madriñán, M., 2016. Temporal variation and trends of inorganic nutrients in the coastal upwelling of the NW Spain (Atlantic Galician rías). J. Sea Res. 108, 19–29.
- Duncan, P.F., Brand, A.R., Strand, Ø., Foucher, E., 2016. The European scallop fisheries for *Pecten maximus, Aequipecten opercularis, Chlamys islandica*, and *Mimachlamys varia*. In: Shumway, S.E., Parsons, G.J. (Eds.), Scallops: Biology, Ecology, Aquaculture and Fisheries. Dev. Aqua. Fish. Sci. vol. 40, 781–858.
- Eiroa del Río, F., 1986. La pesca artesanal en Galicia. Edicións do Castro, Sada (A Coruña), Spain, 191 pp. (In Spanish).
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.
- Fernández, C., 1998. Historia da pesca en Galicia. Biblioteca de Divulgación, Universidade de Santiago, Santiago de Compostela, Spain (In Galician).
- Fuglstad, G.-A., Simpson, D., Lindgren, F., Rue, H., 2019. Constructing priors that
- penalize the complexity of Gaussian random fields. J. Am. Stat. Assoc. 114, 445–452. Garza-Gil, M.D., Amigo-Dobaño, L., 2008. The profitability of the artisanal Galician fleet. Mar. Pol. 32, 74–78.
- González-Nuevo, G., Gago, J., Cabanas, J.M., 2014. Upwelling index: a powerful tool for marine research in the NW Iberian upwelling index. J. Operat. Oceanogr. 7, 47–57.
- Heilmayer, O., Brey, T., Storch, D., Mackensen, A., Arntz, W.E., 2004. Population dynamics and metabolism of *Aequipecten opercularis* (L.) from the western English Channel (Roscoff, France). J. Sea Res. 52, 33–44.
- Howarth, L.M., Wood, H.L., Turner, A.P., Beukers-Stewart, B.D., 2011. Complex habitat boosts scallop recruitment in a fully protected marine reserve. Mar. Biol. 158, 1767–1780.
- ICES, 2018. Report of the ICES Scallop Assessment Working Group (WGScallop). ICES CM 2018/EPDSG:13.
- Iglesias, P., Louro, Á., Román, G., 2010. Settlement of queen scallop Aequipecten opercularis on artificial substrates in Aldan, Ría de Pontevedra, Galicia, northwest Spain. J. Shell. Res. 29, 827–832.
- Iglesias, P., Louro, Á., Román, G., 2012. The effect of depth on the reproductive and reserve storage cycles of the pectinids *Aequipecten opercularis* (L., 1758) and *Chlamys varia* (L., 1758) in Galicia, Northwest Spain. J. Shell. Res 31, 677–684.
- Kamenos, N.A., Moore, P.G., Hall-Spencer, J.M., 2004a. Nursery-area function of maerl grounds for juvenile queen scallops *Aequipecten opercularis* and other. Mar. Ecol. Prog. Ser. 274, 183–189.
- Kamenos, N.A., Moore, P.G., Hall-Spencer, J.M., 2004b. Maerl grounds provide both refuge and high growth potential for juvenile queen scallops (*Aequipecten opercularis* L.). J. Exp. Mar. Biol. Ecol. 313, 241–254.

Alonso-Fernández, A., Otero, J., Bañón, R., Campelos, J.M., Quintero, F., Ribó, J., Filgueira, F., Juncal, L., Lamas, F., Gancedo, A., Molares, J., 2019. Inferring

#### L. Outeiro et al.

Krainski, E.T., Gómez-Rubio, V., Bakka, H., Lenzi, A., Castro-Camilo, D., Simpson, D., Lindgren, F.K., Rue, H., 2019. Advanced Spatial Modelling With Stochastic Partial Differential Equations Using R and INLA. CRC Press, Boca Raton, FL, USA.

Lloret, J., Cowx, I.G., Cabral, H., Castro, M., Font, T., Gonçalves, J.M., Gordoa, A., Hoefnagel, E., Matic-Skoko, S., Mikkelsen, E., Morales-Nin, B., Moutopoulos, D.K., Muñoz, M., dos Santos, M.N., Pintassilgo, P., Pita, C., Sterigou, K.I., Ünai, V., Veiga, P., Erzini, K., 2018. Small-scale coastal fisheries in European Seas are not what they were: ecological, social and economic changes. Mar. Pol. 98, 176–186.

Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70, 141–159.

Maunder, M.N., Thorson, J.T., Xu, H., Oliveros-Ramos, R., Hoyle, S.D., Tremblay-Boyer, L., Lee, H.H., Kai, M., Chang, S.-K., Kitakado, T., Albertsen, C.M., Minte-Vera, C.V., Lennert-Cody, C.E., da Silva, A.M.A., Piner, K.R., 2020. The need for spatio-temporal modeling to determine catch-per-unit effort based indices of abundance and associated composition data for inclusion in stock assessment models. Fish. Res. 229, 105594.

Méndez, G., Vilas, F., 2005. Geological antecedents of the Rias Baixas (Galicia, Northwest Iberian Peninsula). J. Mar. Syst. 54, 195–207.

Méndez-Martínez, G., Ovejero-Campos, A., Gómez-Vilar, E., Lastra-Mier, R.E., Pérez-Arlucea, M., 2011. Changes induced by mussel raft aquaculture in benthic environment of the Rías Baixas (Galicia, Spain). J. Coast Res. SI 64, 786–789.

Mendo, T., Lyle, J.M., Moltschaniwskyj, N.A., Tracey, S.R., Semmens, J.M., 2014. Habitat characteristics predicting distribution and abundance patterns of scallops in D'Entrecasteaux channel. Tasmania. PLoS One 9, e85895.

Murray, L.G., Hinz, H., Kaiser, M.J., 2011. Functional response of fishers in the Isle of Man scallop fishery. Mar. Ecol. Prog. Ser. 430, 157–169.

Nicolle, A., Moitié, R., Ogor, J., Dumas, F., Foveau, A., Foucher, E., Thiébaut, E., 2017. Modelling larval dispersal of *Pecten maximus* in the English Channel: a tool for the spatial management of the stocks. ICES J. Mar. Sci. 74, 1812–1825.

Orensanz, J.M., Parma, A.M., Smith, S.J., 2016. Dynamics, assessment, and management of exploited natural scallop populations. In: Shumway, S.E., Parsons, G.J. (Eds.), Scallops: Biology, Ecology, Aquaculture and Fisheries. Dev. Aqua. Fish. Sci. vol. 40, 611–695.

Otero, J., Álvarez-Salgado, X.A., González, A.F., Miranda, A., Groom, S.B., Cabanas, J.M., Casas, G., Wheatley, B., Guerra, A., 2008. Bottom-up control of common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean. Mar. Ecol. Prog. Ser. 362, 181–192.

Outeiro, L., Villasante, S., Sumaila, R., 2018a. Estimating fishers' net income in smallscale fisheries: minimum wage or average wage? Ocean Coast. Manag. 165, 307–318.

Outeiro, L., Byron, C., Angelini, R., 2018b. Ecosystem maturity as a proxy of mussel aquaculture carrying capacity in Ría de Arousa (NW Spain): a food web modeling perspective. Aquaculture 496, 270–284.

Outeiro, L., Rodríguez-Mendoza, Ř., Bañón, R., Alonso-Fernández, A., 2020. Influence of aquaculture on fishing strategies: insights from Galician small-scale fisheries. Aquaculture 521, 735043.

Paradinas, I., Conesa, D., Pennino, M.G., Muñoz, F., Fernández, A.M., López-Quílez, A., Bellido, J.M., 2015. Bayesian spatio-temporal approach to identifying fish nurseries by validating persistence areas. Mar. Ecol. Prog. Ser. 528, 245–255.

Peña, V., Bárbara, I., 2009. Distribution of the Galician maerl beds and their shape classes (Atlantic Iberian Peninsula): proposal of areas in future conservation actions. Cahiers Biol. Mar. 50, 353–368.

Penela-Arenaz, M., Bellas, J., Vázquez, E., 2009. Effects of the Prestige Oil Spill on the biota of NW Spain: 5 years of learning. Adv. Mar. Biol. 56, 365–396.

Pennino, M.G., Guijarro-García, E., Vilela, R., del Río, J.L., Bellido, J.M., 2019. Modeling the distribution of thorny skate (*Amblyraja radiata*) in the southern Grand Banks (Newfoundland, Canada). Can. J. Fish. Aquat. Sci. 76, 2121–2130. Pérez, F.F., Álvarez-Salgado, X.A., Rosón, G., 2000. Stoichiometry of the net ecosystem metabolism in a coastal inlet affected by upwelling. The Ría de Arousa (NW Spain). Mar. Chem. 69, 217–236.

Pinho, J.L.S., Vieira, J.M.P., Antunes do Carmo, J.S., 2001. Hydrodynamics and water quality studies in Ria de Arosa applying mathematical modelling. In: Proc. Oceans III Mmillennium, 1st International Congress on Marine Science and Technology. Pontevedra, Spain, pp. 24–27.

R Core Team, 2020. R: a Language and Environment for Statistical Computing. URL:. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Román, G., Campos, M.J., Acosta, C.P., 1996. Relationships among environment, spawning and settlement of Queen scallop in the Ría Arosa (Galicia, NW Spain). Aquac. Int. 4, 225–236.

Román, G., Campos, M.J., Acosta, C.P., Cano, J., 1999. Growth of the queen scallop (Aequipecten opercularis) in suspended culture: influence of density and depth. Aquaculture 178, 43–62.

Román, G., Campos, M.J., Cano, J., Acosta, C.P., Iglesias, P., García, O., 2002. Reproductive and reserve storage in *Aequipecten opercularis* (L., 1758) in Galicia, NW Spain. J. Shell. Res 21, 577–584.

Rosón, G., Pérez, F.F., Álvarez-Salgado, X.A., Ríos, A.F., 1991. Flujos de los aportes de agua continental a la ría de Arosa. Sci. Mar. 55, 583-589.

Rue, H., Held, L., 2005. Gaussian Markov Random Fields: Theory and Applications. CRC press.

Rue, H., Lindgren, F.K., 2015. Bayesian spatial modelling with R-INLA. J. Stat. Soft. 63, 19.

Rue, H., Riebler, A., Sørbye, S.H., Illian, J.B., Simpson, D.P., Lindgren, F.K., 2017. Bayesian computing with INLA: a review. Annu. Rev. Stat. Appl. 4, 395–421.

Shelton, A., Thorson, J.T., Ward, E.J., Feist, B.E., 2014. Spatial semiparametric models improve estimates of species abundance and distribution. Can. J. Fish. Aquat. Sci. 71, 1655–1666.

Smith, S.J., Sameoto, J.A., Brown, C.J., 2017. Setting biological reference points for sea scallops (*Placopecten magellanicus*) allowing for the spatial distribution of productivity and fishing effort. Can. J. Fish. Aquat. Sci. 74, 650–667.

Surfs-Regueiro, J.C., Santiago, J.L., 2014. Characterization of fisheries dependence in Galicia (Spain). Marine Policy 47, 99–109.

Teh, L.C.L., Sumaila, U.R., 2013. Contribution of marine fisheries to worldwide employment. Fish Fish. Oxf. (Oxf) 14, 77–88.

Vause, B.J., Beukers-Stewart, B.D., Brand, A.R., 2007. Fluctuations and forecasts in the fishery for queen scallops (*Aequipecten opercularis*) around the Isle of Man. ICES J. Mar. Sci. 64, 1124–1135.

Vilas, F., García-Gil, E., García-Gil, S., Nombela, M.A., Alejo, I., Francés, G., Méndez, G., 1999. Ría de Arousa. Cartografía de sedimentos submarinos. Escala 1:50000 (Memoria y Mapas). Xunta de Galicia, Santiago de Compostela, Spain, 32 pp.

Vilas, F., Bernabeu, A.M., Méndez, G., 2005. Sediment distribution pattern in the Rias Baixas (NW Spain): main facies and hydrodynamic dependence. J. Mar. Syst. 54, 261–276.

Weeratunge, N., Béné, C., Siriwardane, R., Charles, A., Johnson, D., Allison, E.H., Nayak, P.K., Badjeck, M.-C., 2014. Small-scale fisheries through the wellbeing lens. Fish Fish. Oxf. (Oxf) 15, 255–279.

Wood, S.N., 2006. Generalized Additive Models: an Introduction. R. Chapman & Hall/ CRC Press.

Xunta de Galicia, 2020. Consellería do Mar (last accessed 14/May/2020). www. pescadegalicia.gal.

Zuur, A.F., Ieno, E.N., 2018. Spatial, Temporal and Spatial-temporal Ecological Data Analysis With R-INLA: GAM and Zero-inflated Models. Highland Statistics Ltd., Newburg, UK.