Modeling the spatiotemporal distribution of the deep-sea shrimp *Aristeus antennatus* (Crustacea: Decapoda) on the northwestern Mediterranean continental margin crossed by submarine canyons.

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**Highlights**

* Bathymetry shapes deep-sea shrimp spawning areas.

* Canyons hold the highest expected shrimp biomass.

* Variability of shrimp distribution is canyon-dependent

* A 1 °C warmer temperature hardly decreases the shrimp biomass in canyons.

**Keyword:** marine environment; species distribution model; CPUE; fisheries, submarine canyons; Mediterranean Sea

**Abstract**

Submarine canyons aggregate numerous marine species and can affect the structure of benthic communities. However, analyses dedicated to assess the spatial distribution variability among several canyons are rare. In the northwestern Mediterranean Sea, three major submarine canyons consecutively indent the narrow margin. There, the abundance of deep-sea blue and red shrimp *Aristeus antennatus* (Crustacea: Decapoda), one of the most important fishery-targeted species in
the western and central Mediterranean Sea, sustains relatively high incomes for the nearest fishing harbors. To date, the spatial distribution of this shrimp species has only been assessed on known fishing grounds, but it has neither been modeled simultaneously covering several submarine canyons nor according to the environmental conditions. In this study, we aimed to look over the spatiotemporal shrimp distribution in a region of the northwestern Mediterranean Sea with a particular interest in variations in the three submarine canyons. From summer landing data between 2005 and 2014, we implemented a species distribution model with georeferenced catches linked to environmental data of the shrimp habitats. The model showed that the bottom topography was one of the most essential variables to explain the spatial distribution of the catches and that the highest catch rates were between 475 m and 575 m depth. Overall, two canyons (Blanes and Palamós) sheltered high estimates of catches on the shallow and narrow part of their margins (at 510 and 565 m depth). Among them, 60% of estimated summer catches came from the Palamós Canyon, but this estimate shifted to the Blanes Canyon in summer 2008, probably due to variations in fishing fleet behavior. Modeled hypothetical temperature changes scenarios (to 1 °C warmer than the average) suggested the shrimp catches would decrease less in the Blanes Canyon (3% fewer catches than the average) than in the Palamós Canyon (20% fewer catches than the average). The information produced by the species distribution model allowed setting spawning locations and depths, which is useful to better understand the canyon influence on benthic communities and to parameterize larval transport models.

1. Introduction

Good knowledge of species distribution is helpful to assess and forecast the impact of perturbations (e.g., human activities, abiotic and biotic changes) on the biological resources and has implications for management or conservation plans (Brown and Yoder, 2015). In marine systems, the distribution and abundance of populations are altered by fishery activities (Montero et al., 2016), climate change (Jones and Cheung, 2015), water pollutants (Neira et al., 2014), invasive species (Wilkie et al., 2013), and the effectiveness of implementing marine protected areas (Krüger et al., 2015).
Marine species aggregate in highly productive coastal areas, in upwelling systems, and particular topographic areas such as submarine canyons (Leo et al., 2010, Sigman and Hain, 2012). In relatively low productive continental margins, canyons are geomorphological structures gathering multiple favorable ecological conditions (e.g., nutrient and food availability, and habitats; Fernandez-Arcaya et al., 2017) for benthic marine community development (Almeida et al., 2017), including commercially exploited species like hakes, monkfishes, and shrimps (Ramirez-Llodra et al., 2009).

Submarine canyons are environmentally important areas for the megafauna dynamism and the ecology of multiple species. These structures have an effect on the deep-sea species assemblages both within the area itself and on the neighboring open slope (Romano et al., 2017; Tecchio et al., 2013), which populations may be interconnected due to eggs and larval dispersal by water current dynamics, as for the case of Aristeus antennatus (Clavel-Henry et al., 2020). Some benthic communities undertake seasonal and ontogenetic migrations between the canyon area and the open slope, which are detected by observation of the specimen sizes and the distribution of fishing effort throughout the year, as for the case of A. antennatus (Sardà et al., 1997; Sardà et al., 2003a; Tudela et al., 2003) and Merluccius merluccius (Stefanescu et al., 1994). In addition, the submarine canyons support high levels of biodiversity (Almeida et al., 2017; Romano et al., 2013; 2017), which can be structured over the continental slope (Fanelli et al., 2018) and each canyon can be colonized by diverse megafauna assemblages (Ayma et al., 2016; Pierdomenico et al., 2019).

The environmental and morphological features (Fernandez-Arcaya et al., 2017; Romano et al., 2013), including bottom substrates (Fanelli et al., 2018; Pierdomenico et al., 2019) make the submarine canyons to concentrate relatively high species richness, abundance, and biomass suitable for the exploitation of fish stocks of commercial interest (De Leo et al., 2010; Fernandez-Arcaya et al., 2017). In the Catalan Sea, a region of the NW Mediterranean Sea between the latitudes 40.8° N
and 43° N, three major submarine canyons (Cap de Creus, Palamós, and Blanes) cross a continental margin geographically close to fishing harbors. This shortens the access of the fishing fleets to abundant and valuable resources, like the deep-sea blue and red shrimp *Aristeus antennatus*, which is one of the most targeted species of the western Mediterranean Sea.

Most landings of *A. antennatus* take place in the fishing harbors of Palamós and Blanes that are located nearby eponymous submarine canyons (Company et al., 2008). There, the waters conditions are mostly determined by the stable Levantine Intermediate Water (LIW), with water temperatures between 13.0 and 13.8 °C and salinity ranges between 38.48 and 38.60 PSU (Salat and Cruzado, 1981) and match with the physiological preferences of the shrimp (Carbonell et al., 2017). In summer, shrimp landings are particularly high because females aggregate at fishing ground depths between 400 and 900 m (Sardà et al., 2003b). In contrast, winter waters are turbulent and sometimes funneled inside the canyons, which chase the shrimps off the fishing grounds. However, these intense perturbations issued from Dense Shelf Water Cascading (DSWC) events only occur during very cold and dry winters (Company et al., 2008).

Information about the population dynamics of *A. antennatus* originates from different local analyses in canyons (Sardà et al., 2009, Gorelli et al., 2014) and in areas over the open slope (Maynou, 2008, Amores et al., 2014, Carbonell et al., 2017, Cartes et al., 2018). To date, some studies have focused on the spatial distribution of the shrimp by data interpolation (i.e., Maynou et al., 1996, Palmas et al., 2015) or by estimation with environmental variables (i.e., Paradinas, 2017, Masnadi et al., 2018). Nonetheless, the spatial variability of shrimp distribution has not yet been tackled over the whole fishing areas in the NW Mediterranean Sea, including the submarine canyons.

In the present study, we aim to estimate the location of *A. antennatus* spawning sites in the Catalan Sea, their characteristics related to the topography and water masses, and their spatiotemporal
variability in various submarine canyon conditions. Spawning sites were modeled by a species distribution model based on summer georeferenced catches of A. antennatus linked to bottom topography and other near-bottom water characteristics.

2. Methods

Geo-referenced daily catch data of A. antennatus on trawling grounds over the Catalan slope, seafloor characteristics, and environmental variables were processed by a statistical model to estimate the shrimp distribution of their spawning sites. The implementation of the model was based on summer data because it focused on the spawning places of mature females, it neglected the temporal effect from shrimp mobility and seasonal variability of environmental data, and it corresponded to the peak of shrimp catches (Sardà et al., 2003b).

2.1. Catch per unit effort data

Standardized CPUEs were used as the response variable for fitting the species distribution model. Beforehand, a total of 1,645,569 daily geo-referenced catch data of A. antennatus were provided by the General Direction of Fishing and Maritime Affairs (DGPAM) of the Autonomous Catalan Government for the spawning period of the species (June to September) between 2005 and 2014. Each catch data is arranged by shrimp size-category, which differentiates the small shrimps (i.e., < 30 mm at carapace length) from the large ones (i.e., > 30 mm at carapace length). Analyses were conducted on large size-category catches, which have higher rates of ready-to-spawn females (Sardà et al., 1997). Catches per unit of effort (CPUE; in kg day⁻¹ vessel⁻¹) were linked to the fishing location recorded by the Vessel Monitoring System (VMS, see Appendix 1) since 2005 (Martín et al., 2014). The data were provided for the most important shrimp fishing grounds of the Catalan Sea: Llançà, Roses, Palamós, Blanes, Arenys de Mar, Barcelona, Vilanova i la Geltrú, and Tarragona (see Figure 1). However, we omitted some data from the analysis to avoid biasing by
artifactual regional variability because preliminary analyses suggested that CPUEs from Tarragona, Llançà, and Barcelona fishing harbors were unreliable.

Figure 1. Location of fishing harbors, VMS data (small black dots), and shelf-indenting submarine canyons (blue polygons) along the Catalan slope of the northwestern Mediterranean Sea. The location with the highest standardized CPUE is indicated by the orange dot. The 200 and 1000 m depth isobaths represent the bathymetric limits of *A. antennatus* catches. Fishing harbors with data used in the analyses are indicated by stars, while data from fishing harbors located by a full circle were omitted.

Adapting the method by Mamouridis *et al.* (2014), CPUE data were standardized by fitting a multiple linear regression:

\[
\log(\text{CPUE}) = \text{year} + \text{month} + \text{harbor} + \text{year|harbor} + \text{GRT} + \varepsilon, \tag{1}
\]

where \(\log(\text{CPUE})\) represents log-transformed CPUE, \(\text{GRT}\) is the vessel Gross Registered Tonnage, \(\text{year|harbor}\) represents the effect of yearly landings by the harbor, and \(\varepsilon\) the unknown error. This
model explained 33.2% of the data variability and was appropriate according to the residuals analysis (Figure S1).

2.2. Environmental variables and seafloor characteristics.

For fitting the species model distribution, we selected environmental variables and seafloor characteristics relevant to the preferences of *A. antennatus* such as bottom salinity, bottom temperature (Guijarro et al., 2008), bathymetry (Sardà et al., 2004), dissolved oxygen (Cartes et al., 2018).

Monthly gridded environmental data from 2005 to 2014 were provided by outputs from the open-source biogeochemistry and physics reanalysis of the model NEMO-OPA ([http://marine.copernicus.eu](http://marine.copernicus.eu)) with a spatial resolution of 0.06°. The gridded bathymetry was provided by outputs from EmodNET ([http://www.emodnet-bathymetry.eu](http://www.emodnet-bathymetry.eu)) with a spatial resolution of 0.021°. Additionally, other environmental and seafloor variables were derived from the previous outputs, as they may contribute to shape the shrimp CPUEs distribution (Maynou, 2008, Sardà et al., 2009, Amores et al., 2014). The kinetic energy (*KE*) was computed from the meridional (*u*) and zonal (*v*) velocities, such as:

\[ KE = \frac{1}{2}(u^2+v^2). \]  

The rugosity of the floor and the slope were estimated from the gridded bathymetry following the methods of Wilson et al. (2007) and Horn (1981), respectively, on a window of nine grid cells. Rugosity and slope were supplementary topographic data that characterized the three-dimensional relief around the fishing depth. For instance, rugosity values around zero represented an even topography, while rugosity values above zero denoted topography steepness increasing on a relatively short distance (Figure 2).
Figure 2. Rugosity of the Catalan Sea seafloor. The 200 and the 1000 m depth isobaths are represented by continuous black lines. Fishing harbor’s symbols are indicated in Figure 1.

Before fitting the model, we summed up monthly standardized CPUE values to grid cells of 0.015 ° spatial resolution covering a domain between 40.6 – 43 °N and 1 – 5 °E. With this resolution and domain borders, four CPUE grid cells fitted in one grid cell of environmental data. Then, the near-bottom environmental variables (e.g., salinity and water temperature) and seafloor characteristics (e.g., bathymetry, rugosity, and slope) were interpolated to monthly CPUEs location.

2.3. Modeling the link between CPUEs and environmental data

The random regression forest (RF) method R-package RandomForest (Liaw and Wiener 2001) was used to adjust the species distribution model. This method was selected for being able to deal with the expected non-linear relationships between the response variable (log-transformed CPUE of A. antennatus) and predictors (Sardà et al., 2009).
Random forest is a stable algorithm with a good predictive capacity (Šiaulys and Bucas, 2012, Luan et al., 2018) though it is rarely used for marine species distribution models. Described in Breiman (2001), the algorithm starts by randomly sampling several subdatabases (called a bootstrap sample) with replacement from the main dataset (i.e., bagging’s method). The size of each subdatabase is approximately two-thirds of the dataset. Then, a regression tree is fitted on each subdatabase. One tree grows with nodes that are the best split of the subdatabase from randomly-selected predictors. Last, all the regression trees are averaged to obtain the final estimates. The number of decision trees (i.e., the size of the forest and the number of subdatabases) and the number of randomly-selected predictors splitting the tree were fixed to 500 and 4, respectively. Those values were both selected for stabilizing the error rate between the predictions and the observations. After building the random forest, the out-of-bag data (the remaining one-third of the dataset) were used to evaluate the performance of the model (i.e., the proportion of variance explained by the model) and helped for the model validation.

The random forest model was fitted with datasets of non-collinear predictors (i.e., the environmental and topographic variables). In the case of high collinearity ($r$-value > 0.60), we selected the predictors that explained great variability in the model. Thus, dissolved oxygen or salinity was disregarded because of their relatively high collinearity ($r$-value = 0.62). We proceeded similarly for slope and rugosity, as they had very high collinearity ($r$-value = 0.99). The combination of predictors to yield the best model was kept after a stepwise criteria methodology, based on i) the proportion of variance explained by the model, ii) their importance in the model based on mean squared error (MSE) method (Breiman, 2001), and iii) the verification of model residuals (Figure S2). Spatial projection of the residuals and semi-variorams were built on the residuals to detect and correct eventual spatial bias created by the data distribution (Dormann et al.,
Besides, we verified the model performance by ten-fold cross-validation for which ten Root Mean Square Errors (RMSE) were calculated by:

$$\text{RMSE} = \sqrt{\frac{\sum (\text{CPUE}_{\text{estimated}} - \text{CPUE}_{\text{observed}})^2}{N}},$$

where N is the number of CPUE data.

### 2.4. Spawning sites distribution

#### Estimation in the Catalan Sea

Using estimates from the best-fitted random forest model, the spawning sites were characterized according to predictor values and located in the Catalan Sea. For better featuring the variations of standardized and model-estimated CPUEs, we scaled them to the percentage of their respective maximum CPUE values. Thus, the scale ranged from 0% (the minimum CPUE) to 100% (the highest CPUE).

With these scales, we compared the fluctuation of standardized and model-estimated CPUEs and estimated the optimized predictor ranges on which the CPUEs were relatively high (e.g., > 75% of CPUE maximum). The locations of spawning sites were hindcast by the best-fitted random forest on a gridded domain with a grid resolution of 0.015º and the borders between 40.6 – 43 ºN and 1 – 5 ºE from 5 m to 2380 m depth. In total, 40 spatial estimations of CPUEs were predicted based on the monthly values of gridded environmental and topographic variables rescaled on grid resolution of 0.015º (i.e., June, July, August, and September between 2005 and 2014). Then, the spatial shrimp distribution in a specific summer was the summing up of the four-month estimates of CPUEs per grid cell.

#### Estimation in the submarine canyons
To compare the species distribution between the three submarine canyons, we extracted the model-estimated CPUEs per canyon area (see Figure 1). The three canyon areas were shaped by a polygon overlapping head and walls of the canyons as indicated by the isobaths 200 and 1000 m depth. On one hand, we approached the variability of the maximum CPUE percentages across the continental slope (i.e., around 200 to 1400 m) per summer between 2006 and 2014. On the other hand, we estimated the summer contribution of the canyons to the total model-estimated CPUEs, in other words, we evaluated which canyons yielded the highest catches by summer. A ratio of the canyon surface to the biggest canyon surface (i.e., the Blanes Canyon with 436 km²) corrected the total model-estimated CPUEs per canyon in order to account for the canyon size differences.

Additionally, we hindcast CPUEs while increasing and decreasing water temperature by 0.1° up to 1 °C above (warmer water scenario) and below (cooler water scenario) the canyon-averaged temperature. Simulations of CPUE values with water temperature below 13 °C were closer to potential scenarios related to persistent-in-time events of dense shelf water cascading (DSWC), even though the events may not last to summer. For example, in winters 2005 and 2006, a very strong DSWC event lowered the near-bottom water temperature in winter and spring from 13 °C to 10.5 °C (Canals et al., 2006). On the contrary, warmer water scenarios above 13 °C are in line with the reported warming trend of the Western Mediterranean Sea (Schroeder et al., 2016) and with global warming trends (Penuelas et al., 2017).

3. Results

The most suitable environmental conditions and seafloor characteristics for spawning females of *A. antennatus* in the whole Catalan Sea were identified with the Random Forest model and explained 60.1% of the variability. Overall, the performance of RF was stable, as indicated by RMSE from the 10-fold cross-validation (1.669 ± 0.009 kg km⁻² day⁻¹). Residuals analyses indicated that there was no significant spatial correlation and residual normality was followed (Figure S2). Because the
model had good performance ability, we analyzed the predictor ranges associated with high catches and the spatial model-estimated CPUEs in the Catalan Sea with details per canyon.

3.1. Predictor ranges and optimized CPUEs estimates

In order of importance, the predictors included in the model were the combination of summers (i.e., year), bathymetry, CPUE longitudes, seafloor rugosity, CPUE latitudes, month, water temperature, kinetic energy, and salinity (Figures S3 and S4).

The fitted random forest model proved its predictive capacity for capturing the temporal variations of cumulated standardized CPUEs for summer periods during the decade 2005 – 2014 (Figure 3). The landings had two local maxima in summers 2008 and 2012. Particularly, in summer 2012, the CPUE standardized and model-estimated landings reached maxima of 70.7 T and 43.4 T, respectively (Table 1).

Figure 3. Interannual variation of the summer CPUE (percentage of the maximum) from standardized (continuous line) and model-estimated (dashed line) CPUEs.
Table 1. Value of the predictors with CPUE maximums from both the standardized dataset and the model prediction. The column Figure indicates the figure index and panel on which the value of maximum CPUE rescaled the datasets.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Predictors value at the maximum CPUE</th>
<th>Value of the maximum CPUE</th>
<th>CPUE from:</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer year</td>
<td>2012</td>
<td>70 742 kg 43 466 kg</td>
<td>Dataset 3</td>
<td>3</td>
</tr>
<tr>
<td>Bathymetry</td>
<td>-506 m</td>
<td>20.2 kg day⁻¹ km⁻² 13.3 kg day⁻¹ km⁻²</td>
<td>Dataset 4.A)</td>
<td>4.A)</td>
</tr>
<tr>
<td>Temperature</td>
<td>12.97 ºC</td>
<td>21.1 kg day⁻¹ km⁻² 13.7 kg day⁻¹ km⁻²</td>
<td>Dataset 4.B)</td>
<td>4.B)</td>
</tr>
<tr>
<td>Salinity</td>
<td>38.52 PSU</td>
<td>31.0 kg day⁻¹ km⁻² 19.6 kg day⁻¹ km⁻²</td>
<td>Dataset 4.C)</td>
<td>4.C)</td>
</tr>
<tr>
<td>Rugosity</td>
<td>29.24</td>
<td>22.7 kg day⁻¹ km⁻² 14.6 kg day⁻¹ km⁻²</td>
<td>Dataset 4.D)</td>
<td>4.D)</td>
</tr>
<tr>
<td>Coordinates</td>
<td>2.80º E; 41.30º N 3.36º E; 41.88º N</td>
<td>333.6 kg km⁻² summer⁻¹ 142.6 kg km⁻² summer⁻¹</td>
<td>Dataset 1</td>
<td>1</td>
</tr>
</tbody>
</table>

Except for the kinetic energy predictor, *A. antennatus* CPUEs (i.e., standardized and model-estimated) had a comparable Gaussian-like relationship, which, therefore, described the optimal environmental variation for the shrimp distribution (Figure 4). CPUEs were maximum at 506 m depth with 12.97 ºC water temperature, 38.5 PSU salinity, and seafloor rugosity of 29.2 (Table 1), thus providing environmental boundaries for spawning areas. CPUEs near the maximum (i.e., above 75% CPUE) were related to temperature variations of \( \Delta T = 0.30 \) ºC, while the range for salinity was much narrower (\( \Delta S = 0.026 \) PSU).
Figure 4. Distribution of the CPUE (percentage of the maximum) from the standardized (continuous line) and the model-estimated (dashed line) CPUEs, according to A) bathymetry, B) water temperature, C) salinity, and D) rugosity. The shadowed areas represent the range of the predictor values for which the percentage of CPUE is higher than 25% (light grey) and 75% (dark grey). See Table 1 for the maximum CPUE values.

3.2. Spawning sites in the Catalan sea and the submarine canyons.

Over the Catalan Sea, percentages of maximum CPUE were high over a limited bathymetric gradient and in the submarine canyons.

High predicted CPUEs occurred on a narrow band of the bathymetry in the rugged canyons. Over years 2005 – 2015, the bathymetry between 475 and 575 m depth sheltered more than 75% of the maximum predicted CPUE (maximum at 13.3 kg day$^{-1}$ m$^{-2}$, Figure 4). This range narrowed from 480 to 530 m depth in the canyons (see Figure 5). Except for the years 2007, 2012, and 2014, high
estimations of CPUEs were also distributed over bottoms depths between 575 and 625 m in the Palamós Canyon. Over the open slope, high CPUEs were estimated at bottom depths between 480 and 860 m, which was a range four times wider than in the canyons. Additionally, estimations of CPUE were still moderate over open slopes at bottom depths above 480 m (25 to 50% of the maximum CPUE) and below 860 m (i.e., 50 to 75% of the maximum CPUE).

Figure 5. Summer distribution of the model-estimated CPUE (percentage of maximum) over the continental margin (200 m to 1400 m) in the submarine canyons of Cap de Creus, Palamós, and Blanes (see Figure 1) and on the open slope. Percentages of maximum were computed based on the maximum CPUE of each summer between 2005 and 2014.

The width of the bathymetric bands was related to the variation of the rugosity (i.e., the fourth more important predictor) in each canyon and along the open slope. Indeed, over the bottom floor with high estimations of CPUE (i.e., > 75% of the maximum CPUE), no comparable variations of the
rugosity were estimated among the three canyons and the open slope (i.e., *p*-value < 0.05 with a Levene’s Test). Due to the geomorphology of the canyons, the bathymetry changed quickly across and along the continental slope (i.e., rugosity values higher than 100 in Figure 2). Meanwhile, over the open slope, high rugosity values (i.e., 25 – 100 in Figure 2) are localized on the lower part of the continental slope (i.e., below the bottom depth of 500 m in Figure 2). Consequently, across the continental slope, the variability of the rugosity could partially explain the differences in the bottom depths where high CPUE were estimated (Table 2). For example, high estimations of CPUE are around a bottom depth of 535 m in the Cap de Creus Canyon and 594 m over the open slope, where the rugosity values ranged within 60 – 70 (see Table 2).

Table 2. Average values and ranges (minimum/maximum) of the predictors associated with the high model-estimated CPUE (percentage of maximum CPUE < 75%) on the open slope and within the areas of Cap de Creus, Palamós and Blanes canyons.

<table>
<thead>
<tr>
<th>Variable (unit)</th>
<th>Open slope</th>
<th>Cap de Creus</th>
<th>Palamós</th>
<th>Blanes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathymetry (m)</td>
<td>594 (472/921)</td>
<td>535 (471/686)</td>
<td>528 (398/737)</td>
<td>498 (471/581)</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>13.0 (12.8/13.3)</td>
<td>13.2 (13.0/13.6)</td>
<td>13.0 (12.7/13.3)</td>
<td>13.0 (12.7/13.8)</td>
</tr>
<tr>
<td>Salinity (PSU)</td>
<td>38.5 (38.4/38.6)</td>
<td>38.4 (38.3/38.5)</td>
<td>38.5 (38.4/38.6)</td>
<td>38.5 (38.3/38.6)</td>
</tr>
<tr>
<td>Rugosity</td>
<td>67.8 (24.5/152.2)</td>
<td>61.4 (14.1/117.7)</td>
<td>138.3 (51.3/252.5)</td>
<td>121.1 (44.8/ 171.8)</td>
</tr>
<tr>
<td>KE (cm² s⁻¹)</td>
<td>1.47 (0/18)</td>
<td>1.33 (0/22.8)</td>
<td>1.15 (0/23.2)</td>
<td>0.93 (0/8.4)</td>
</tr>
</tbody>
</table>

The model estimated relatively high catches (> 40% of maximum CPUE) in the canyon zones of the Catalan Sea (Figure 6). On average, high CPUEs (> 60% of maximum including the maximum estimate of CPUE of 142 kg km⁻² summer⁻¹; Table 1) were located in the Palamós canyon head and middle upstream wall. Low values of CPUEs (i.e., 20 – 60% of maximum CPUE) were situated on the downstream wall of the Blanes Canyon where the highest standardized catches (i.e., 333 kg km⁻² summer⁻¹; Table 1) were located before the model fitting. In the two canyons, estimated CPUE showed important temporal variability (Figure S5), as expected from the interannual variations shown in Figure 3 and Figure 5. The CPUEs estimated in the Cap de Creus Canyon were barely
higher than estimates on the open slope (< 20%, Figure 6). The estimated CPUEs were low (< 5% of maximum CPUE) on bottom depth below 500 m.

![Map of the Catalan Sea showing CPUE estimates](image)

Figure 6. Average model-estimated CPUE (percentage of the maximum) in the Catalan Sea over the decade 2005 – 2014. Isobaths at 200 and 1000 m depth are represented by continuous black lines. Fishing harbors indicated by a star provided model input data. Fishing harbor’s symbols are indicated in Figure 1.

### 3.3. Evolution of the spawning sites in the submarine canyons

The contribution of the Blanes Canyon to the catches within the three main canyons (Blanes, Palamós, and Cap de Creus) increases with time (see Figure 7). Between 2005 and 2007, high model-estimated catches from Palamós Canyon prevailed in the total catches from all canyons (> 60% of the catches), but in 2008 and from 2011, the relative contribution of catches from the Blanes Canyon (50 to 60% of the CPUE) was dominant. This shift was also identified in the gridded CPUEs estimates (Figures S6.A to S6.J) with contributions lower than 50% of the maximum CPUE.
in the Blanes Canyon up to the year 2007 and starting 2008, with contributions higher than 50%.

The contribution to the total catches by the Cap de Creus Canyon remained relatively stable over time, with an average CPUE of 20%, ranging from 11% in 2007 to 25% in 2008.

![Graph showing CPUE contributions by canyon over years](image)

Figure 7. Variation of annual CPUE contributions (in percentage) from the three submarine canyons. Model-estimated CPUEs in each canyon were divided by the sum of CPUEs in all canyons (200 to 1000 m depth). The variability in canyons sizes (Cap de Creus 350 km²; Palamós 372 km²; Blanes 436 km²) was accounted by rescaling the CPUEs to the size of Blanes Canyon (i.e., multiplying the CPUE by 1.25, 1.17, and 1, respectively).

Except for the seafloor characteristics (i.e., rugosity and bathymetry) and the KE, the remaining environmental conditions in each canyon were barely different (see Table 2). In particular, the near-bottom temperature linked to maximum catches ranged from about 12.9 °C to 13.1 °C. Nonetheless, the hindcast CPUE after changing water temperature differed among canyons (see Figure 8). In the Blanes Canyon, the estimated CPUE was maximum at 13 °C and a decrease or a rise of temperature would barely change the CPUE. In the Palamós Canyon, the rise of temperature would decrease the catches by 20% below the maximum CPUE at 13°C, whereas colder temperature would decrease...
the catches by 7%. In the Cap de Creus Canyon, cold temperatures (<12.8 °C) would generate maximum CPUE values, but from 12.8°C to 13.5°C, the CPUE would decrease by 15%.

![Graph showing model-estimated CPUE](image)

Figure 8. Model-estimated CPUE (percentage of the maximum) in the canyons of Cap de Creus (grey lines), Palamós (black line), and Blanes (black line with diamond tick marks) by artificially decreasing and rising the average water temperature by 1 °C. The dashed line indicates the average near-bottom sea temperature (13 °C) for which the CPUEs are maximum in the canyons of Palamós and Blanes. The dotted line is the sea temperature (12.8 °C) at which the CPUEs in the canyon of Cap de Creus begin to decrease.

4. Discussion

For the first time, the summer spatial distribution of the blue and red deep-sea shrimp over the entire continental slope in the Catalan Sea has been modeled. Boundaries of spawning areas in the Catalan Sea and inside submarine canyons were set by analyses of optimal environmental and seafloor conditions. Then, potential effects of water warming, following the current trend of water temperature (Schroeder et al., 2016) and water cooling due to eventual strong and long-lasting deep-water formation events on spawners catches were tested.
Overall, ranges of optimal environmental and seafloor conditions found by species distribution modeling overlapped with the ranges estimated in several previous studies. Estimation of the depth bottom ranges on which the shrimp distributed (i.e., depths of 400 – 900 m) were in agreement with Demestre and Martín (1993), Cau et al., (2002) and Rinelli et al. (2013), except that relatively high CPUEs of shrimps were particularly concentrated on a narrow and shallow bathymetric band in the canyons. Although the shrimp distribution across the continental slope was described by previous studies (Demestre and Martín, 1993, Sardà et al., 1994, 1997), it was not previously related to the seafloor rugosity. Fanelli et al. (2018) found that the slope of the western Mediterranean Sea canyons influenced the taxonomic composition of the deep-sea megafauna. This led us to assume that the present study, using rugosity instead of slope, would illustrate the results from Fanelli et al. (2018) applied to one deep-sea species (i.e., A. antennatus). We remained aware that some environmental factors with influence on the shrimp distribution at spawning time were not considered in our study. For example, prey distribution, availability of food, suspended organic particles, and chlorophyll may explain high catch rates inside the canyons (Cartes et al., 1994; Company et al., 2008). In fact, data about these factors are hardly available on the spatial gridded-domain tackled in our study. Besides, shrimp-related biological factors like its physiology (e.g., average size, reproduction stages, and sex rates) across the continental margin (Orsi Relini et al., 2013) may also help to precisely define the predicted spawners distribution. For improvement of the species distribution model, this information should be associated with the georeferenced catches in future studies.

In the Catalan Sea, summer estimated landings of large shrimp from Palamós and Blanes fishing grounds were greater than any other fishing grounds of the Spanish continental slope, which is in line with observations in Demestre and Martín (1993), Gorelli et al. (2016) and Sardà et al. (1997). Between these two canyons, a shift in the location of high CPUEs set off from summer 2008 was estimated for the first time and showed that fishery over the Blanes Canyon supported more
landings than fishery over the Palamós Canyon. This shift likely came from georeferenced CPUE that were discontinuously provided over summers (e.g., CPUEs from Arenys harbor were available starting 2008 and CPUEs from Blanes harbor starting 2005). In that context, comparing the canyon capacity by using georeferenced CPUE from the closest fishing harbor (e.g., Palamós and Blanes) would neglect the information recorded at other harbors, which share the same fishing ground. Thus, with our estimations, we inferred that Blanes Canyon could sustain the fisheries from several harbors (e.g., Palamós, Blanes, and Arenys) and would be a potent resource of the deep-sea shrimp.

Within and among the canyons, the shrimp distribution had relatively small but significant spatial variations. First, spatial estimation of shrimp distribution completed and corrected existent maps built by VMS data from ships affiliated to Blanes and Palamós in (Gorelli et al., 2014). For instance, the distribution of the catches over the canyon walls in the present study differed from those provided by Gorelli et al. (2014). This is likely because we included VMS data from Roses and Arenys fishing fleets that were localized over the fishing ground in Palamós and Blanes canyons, respectively. Second, comparing the shrimp distribution in various canyons during the same summer period improved our understanding of the shrimp dynamics and showed that the canyon features and their locations shape the distribution of the shrimp, as similarly seen for benthic communities in the canyons of the NW Mediterranean Sea and of the rest of the Mediterranean Sea (Almeida et al., 2017; Fanelli et al, 2018, Pierdomenico et al., 2019; Romano et al., 2013). In fact, the method for estimating spawning areas in the Catalan submarine canyons can be exported to other Mediterranean canyons where A. antennatus is present e.g., Italy (Orsi Relini and Relini, 1998) and Sardaign (Sabatini et al., 2007). This can help identify other ranges of environmental values supporting the shrimp distribution within the canyons.

Estimation of spawning sites can be of great use for modeling studies implied with egg dispersal and population connectivity and for supporting integrated management plans for the species. Spatial modeling analyses must focus on the shrimp fishery region unit, taking into account all the
important triggers of abundance (i.e., the three canyons in our study), and avoiding the limitations of a local approach. Indeed, our study showed relatively high spawner aggregation on the slopes of Catalan canyons and suggested that aggregations do not only take place on the open slope (Sardà et al., 1994). This illustrated that results from previous studies dealing with single and small areas (e.g., Sardà et al. 1994) can be nuanced when they are related to a wider area. On the other hand, with a spatial scale including the western and central Mediterranean Sea, the studies of Cau et al. (2002) and Fanelli et al. (2018) detected variability in the spatial distribution of the shrimp, including a high biomass in the Italian fishing grounds (i.e., Sardinian and Ionian seas). Nonetheless, the spatial resolution of these studies was too broad to detect the seasonal variability of the shrimp distribution in the NW Mediterranean Sea.

The aspect of our study covering eventual temperature change effect on spawner distribution showed that catches would not drop with hindcast bottom temperatures getting up to 1 °C warmer than the average. Indeed, the deep water of the Mediterranean Sea is expected to warm by 0.2 °C per decade (Borghini et al., 2014), which would imply at least 30 years before dropping the spawner biomass by 20%. Nevertheless, a biomass decrease of 20% in the Palamós fishing grounds, may seriously affect the economy of the harbors, where 40% of the income depends on the sales of A. antennatus. The biomass is not only directly affected by global warming but could also be indirectly influenced by the changes in the trophic chain due to expected biodiversity loss (Yasuohara and Danovaro, 2016; Sweetman et al., 2017). With this in mind, future scenarios hindcasting the shrimp distribution should consider the interaction with its prey and the prey’s sensitivity to environmental changes.

5. Conclusions

The summer distribution of the red shrimp biomass on the continental slope indented by three major canyons in the Catalan sea was estimated from random forest regression tree models in the summers between 2005 and 2014. Based on optimal environmental conditions, the present modeling study
achieved an adequate spatial representation of the distributed CPUE and allowed to identify expected spawning areas with significantly high CPUEs. The species distribution modeling indicated that seafloor characteristics explain most of the shrimp distribution variability and suggested that shrimps aggregate on shallow and narrow parts of the canyon margin rather than on the open slope. In these three canyons, the bathymetric distribution of the shrimp is comparable over the summers of 2005 – 2014. Nevertheless, small changes in temperatures induced a different response in catches per canyon. In addition to spatially estimate high catches in the canyons, these results conveyed the suggestion that spatial shrimp dynamics is specific in each canyon. In short, this study provides valuable information to be used in the simulation of the larval drift with particle-tracking models. These models aim to support the fishery stakeholders by understanding the connectivity of *A. antennatus* populations through the larvae dispersion. The use of the shrimp spatial distribution model would be to adjust places where the larval tracking starts. Finally, yet importantly, the spatial distribution of the shrimp CPUE can support strategies for developing fishery management plans for the species.

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**References**


### General point about artworks

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Appendix 1

Georeferencing the catches
Courtesy of J. A. Garcia et al. (2016)

In this appendix, the method to georeference the catch to coordinates is schemed and illustrated.

General methods
Over the period from 2005 to 2014, two sets of data - the Vessel Monitoring Systems (VMS) data and landings data - were daily recorded by regional administration and public institutions. The VMS data record the fishing boat position per time unit. Then, fishing boat speed is calculated by the distance between two records and we can filter the records for which the fishing boat is trawling according to the boat velocity (i.e., < 4 knots). Landings data are recorded by the fish auction and the fishermen logbooks. They informed about the weight of shrimp catches and their size-category (i.e., commercial size with small and large carapace length) per trawlers and date.

Then, SQL queries assign catch weight from the landing dataset to the trawlers position at rising activity by fishing boat’s ID and date.

Main results
Catches are georeferenced and can be projected on maps like Figure S1.
Figure S1. Catch Per Unit of Effort (CPUE) maps in total kg h\(^{-1}\) km\(^{-2}\) of *Aristeus antennatus* per trimester for the trawling fleets from Blanes and Palamós (Credits to Gorelli *et al.*, 2014)

**References:**
