Original Article

Influence of habitat and population density on recruitment and spatial dynamics of the sea urchin Paracentrotus lividus: implications for harvest refugia

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We studied the spatial variation in recruitment and the population dynamics of the sea urchin Paracentrotus lividus, analysing the effect of depth and presence of sea urchin aggregations on population structure. Over 90% of the observed recruits (individuals under 1 year of age) were concentrated in aggregations found in shallow waters. In these areas, a positive linear relationship was found between adult and recruit density, possibly due to higher survival rates of juveniles taking refuge among the spines of adults. The scarcity of recruits and the presence of adult sea urchins at depths of 8 and 12 m suggest the migration of part of the population towards deep areas when individuals reach a size of ≈40 mm. In light of these results, the implementation of harvest refugia for sea urchins in shallow areas could constitute an effective fishery management tool for this species. High population densities could enhance recruitment, given the inverse density dependence of this process, while their migratory pattern would guarantee biomass exportation towards deeper fishing grounds.

Keywords: density dependence, echinoid, Northeast Atlantic, Paracentrotus lividus, population dynamics, recruitment.

Introduction

Recruitment, understood as the incorporation of juveniles of a specific age or size range into a population, can be considered as a population bottleneck for many benthic invertebrates with larval developmental stages (Hunt and Scheibling, 1997). Accordingly, many studies carried out during recent decades have focused on researching the causes of spatial and temporal variability in this process (see Ebert, 1983).

Distribution and abundance patterns of recruitment in these organisms depend on reproductive success, larval supply, settlement, and mortality and migration of post-metamorphic individuals (Hunt and Scheibling, 1997; Balch and Scheibling, 2000). Factors influencing these processes operate and interact at different levels; therefore, variability in recruitment takes place at different spatial and temporal scales as well (Pineda, 2000; Botsford, 2001; Pineda et al., 2009). As such, coastal oceanographic and geomorphological characteristics mainly affect the larval pool and its transport towards settlement areas, thus acting on a spatial scale of tens to thousands of kilometres, depending on the species (Wing et al., 1995, 1998; Morgan et al., 2000; Lagos et al., 2008; Ebert, 2010). Similarly, recruitment also shows small-scale (tens—hundreds of metres) variations, as it is influenced by factors with a local impact on processes such as settlement or early mortality of post-metamorphic individuals. Such is the case of substrate availability for settlement, as well as the presence of local currents or microhabitats (Pineda, 1994; Hunt and Scheibling, 1997).

Local variability in recruitment largely determines the spatial structure of populations of benthic organisms. In this sense, the study of recruitment is of great relevance in fishery research, because ignoring the spatial structure of populations (and therefore
of fishing operations) may result in misleading interpretations of productivity and, consequently, inadequate management strategies (Orenzanz and Jamieson, 1998; Booth, 2000).

The purpose of this paper is to identify the factors that cause local variability in recruitment of the sea urchin *Paracentrotus lividus*. This echinoid has been subject to exploitation by many European countries in recent decades, and several cases of overexploitation and collapse have been reported (Le Gall, 1987; Moylan, 1997; Andrew et al., 2002; Fernández-Boán et al., 2012). With this information, we will try to understand the population dynamics and structure of *P. lividus*, aspects of which must be taken into account in sea urchin fishery management.

In order to fulfill this objective, the influence of habitat and population density on size structure and, particularly, on the fraction corresponding to newly recruited individuals, has been analysed. The dense aggregations formed by sea urchins are associated with food-rich habitats (Vadas et al., 1986; Unger and Lott, 1994; Alvarado, 2008) and also constitute a defense mechanism against the effects of waves and predators (Pearse and Arch, 1969; Freeman, 2003; Vega-Suárez and Romero-Kutzner, 2011). These circumstances generate a specific microhabitat within said aggregations, which could enhance recruit survival. Additionally, we have analysed the possible density dependence of recruitment within aggregations, a mechanism already identified for some echinoderm species, and which can be key for management success. On the other hand, depth creates a gradient in many environmental variables that may act on the structure and dynamics of benthic communities (Garrabou et al., 2002). Both depth and the formation of aggregations have already been identified as responsible for the variations in growth and reproduction of *P. lividus* (Ourens et al., 2013a, 2013b).

**Material and methods**

**Study area and sampling strategy**

The study was carried out in Galicia (Northwest Spain), specifically in the coastal areas of Lira (42°47.8’ N 9°8.94’ W) and Porto do Son (42°39.6’ N 9°4.2’ W). Monthly samples were collected between June 2006 and May 2008 at two fishing grounds in each site: Ardeleiro and Os Forcados in Lira, and Son and Queiruga in Porto do Son (a map of the area is presented in Ourens et al., 2013a). Because all areas are similar both in wave exposure and habitats, they were considered replicates. The substrate consists of large flat rocks alternating with vertical walls oriented in different directions. Algal cover is abundant, mainly in the shallow areas and during spring and summer months, and the species *Saccorhiza polyschides*, *Cystoseira baccata*, and *Laminaria spp.* can form large forests. *Halidrys siliquosa*, *Codium spp.*, *Desmarestia spp.*, and the invasive species *Sargassum muticum* are also abundant (Veiga-Villar, 1999; Otero-Schmitt and Pérez-Cirera, 2002; Casal et al., 2011).

Each ground was sampled by diving at depths of 4, 8 and 12 m. Due to the aggregate behaviour of sea urchins (Freeman, 2003), the spatial distribution of *P. lividus* is not homogeneous (Morgan and Shepherd, 2006), and it is possible to visually identify high-density areas, where large numbers of individuals aggregate forming patches (10s m²), and low-density areas, where sea urchins are scattered and do not form patches. Both distribution types (aggregated vs. dispersed) were qualitatively identified at each sampling depth by means of visual density estimates; subsequently, the correspondence of the resulting classification with high- and low-density areas was tested. Thus, Lira grounds were sampled in six different habitats, resulting from the combination of the variables depth and distribution type. At the fishing ground of Queiruga, specimens were only present in low-density areas (only three habitats sampled), perhaps as a consequence of the fishing activity, while at the fishing ground of Son, sea urchins were found only at the 4-m depth, but showing both distribution types (two habitats sampled).

Using a 50 × 50 cm metal square, sea urchins were collected in the central zone of three different aggregations for each depth. In low-density areas, a 3-m long rope with a weight on one end was used to describe a circle with 3-m radius, and all sea urchins included in it were collected. As for the aggregation areas, three replicates were obtained for each depth using this method.

**Spatial distribution of populations**

The hypothesis that high-density areas correspond to an aggregated distribution, while sea urchins in low-density areas are less abundant and do not constitute aggregations, was tested using Lloyd’s index (Lloyd, 1967). The selected index presents the advantage of being relatively independent from sample size and mean population density (Hurlbert, 1990), and it has already been successfully used for quantifying the dispersion pattern of other echinoderm species (Freeman et al., 2001; Freeman, 2003).

Lloyd’s index is estimated as:

\[ L = \frac{m}{\bar{x}} \]  \hspace{1cm} (1)

where \( \bar{x} \) is the mean density of *P. lividus* in each habitat and \( m \) is the mean aggregation index, which represents the number of individuals cohabiting with a given individual. This is calculated as:

\[ m = \bar{x} + \frac{s^2}{\bar{x}} - 1 \]  \hspace{1cm} (2)

where \( s^2 \) is sample variance. When \( L \geq 1 \), species distribution is considered to be aggregated, otherwise it is considered to be random.

We then measured diameter (maximum equatorial dimension without spines) of all individuals with a Vernier caliper (precision ± 0.1 mm). Size and population density distributions were compared between habitats and sampling grounds for the whole sampling period. Pairwise comparisons were carried out using the function `sm.density.compare()` in the R package sm, which performs equality tests considering kernel density estimators and a bootstrap procedure (Bowman and Azzalini, 2010). All \( p \)-values were adjusted for multiple comparisons using the procedure proposed by Benjamini and Hochberg (1995) (see Supplementary Data 1 for details of the statistical procedure applied).

**Factors causing local variability in recruitment**

We define recruitment as the occurrence of individuals with sizes between 5 and 16 mm, corresponding to an average age of 3 months (González-Irusta, 2009) and 1 year (Ourens et al., 2013b), respectively. Although we occasionally collected individuals around 2 mm diameter, these are not easily detected with the naked eye, so their frequency may be underestimated. Contrarily, sea urchins greater than 5 mm in size were highly represented during samples; therefore, we considered these sizes to be within the divers’ visible range.
Spatial and temporal variability in recruit numbers was studied through generalized additive models for location, scale, and shape (GAMLSS, Rigby and Stasinopoulos, 2001, 2005) employing the gamlss [http://www.gamlss.org/ (last accessed October 2013)] package of the software R (v. 2.15.0, R Development Core Team, 2012). These models show great flexibility for selecting the parametric data distribution, allowing for distributions with high skewness and kurtosis. In addition to position (associated with the mean), GAMLSS allow modelling the scale and shape parameters of the distribution, which are related to the dispersion, skewness and kurtosis of the variable of interest (Rigby and Stasinopoulos, 2001).

In this study, we tested the fitting of nine distributions that are frequently used to model discrete variables: Poisson distribution, negative binomial types I and II, zero-inflated models I and II, Delaporte, Poisson-inverse Gaussian, and Sichel distributions I and II (see distribution functions in Stasinopoulos et al., 2008). Following the Akaike (AIC; Akaike, 1974) and Bayesian (BIC; Schwarz, 1978) criteria, we selected the distribution that best fitted our data, and subsequently assessed the effect of the categorical variables depth and distribution type (disperse or aggregated) on the number of recruits. Temporal variability in recruitment was assessed by introducing smoothing of the numerical variable Month employing cubic splines. According to Rigby and Stasinopoulos (2005), the level of smoothing was restricted to the range between the values minimizing AIC and BIC, and the final smoothed value was visually selected. In our case, we assumed six effective degrees of freedom that we obtained a good balance between smoothing and data fitting.

Variability caused by sampling grounds and years was incorporated into the random structure of the model. In order to do so, we created a new variable called Ground-Year (eight levels), as the result of combining the variables Ground (four levels: Ardeleiro, Os Forcados, Son, Queiruga) and Year (two levels: 2006/2007, 2007/2008). Since the sampled area was different for high- and low-density zones, it was necessary to introduce the logarithm of the sampled area as an offset variable in the equation. All independent variables were introduced to model the different parameters of the distribution; we subsequently eliminated those that did not significantly improve model fitting through a backward elimination procedure.

We assessed the performance of the selected model by checking the independence of residuals on the response variable as well as the residuals’ normality (see Supplementary Data 2), properties that guarantee that the model describes all the systematic information, leaving out only independent and identically distributed random noise.

Given the protection that adults offer to juveniles in other echinoid species (Tegner and Dayton, 1977; Nishizaki and Ackerman, 2007), the existence of a direct relationship between densities of recruits and adults (sea urchins with diameters larger than 24.7 mm, Ourêns et al., 2013a) was studied. This analysis was performed using quantile regression models [see Cade and Noon (2003) for an interesting introduction to this method], fitted using the function nlrq() in the R package quantreg (Koenker, 2013).

Two complementary hypotheses about the nature of density dependence were tested. One first option would be that this relationship was linear, assuming that the protected area is proportional to the area occupied by adults. However, a second option would be the existence of a power-law relationship if recruits use aggregations as three-dimensional structures, so that their density would depend on volume rather than area of the aggregations.

**Results**

**Population structure**

The average Lloyd’s index estimated for high-density areas was >1 for all sampled fishing grounds and depths, thus corresponding to an aggregate distribution (Figure 1). Conversely, this index was considerably <1 in all the analysed low-density areas, which indicates a uniform distribution. According to these results, the sampling methods employed in high- and low-density areas were suitable for discerning the two distribution types that sea urchins show in the study area.

As expected, density distribution was very different for areas with and without sea urchin aggregation (Figure 2), with an average density of 95.88 ± 4.07 (mean ± s.e.) no. m⁻² for aggregations, and 0.47 ± 0.01 no. m⁻² in areas without aggregations. Density was significantly higher at a depth of 4 m than it was at depths of 8 and 12 m, both in high- and low-density areas and for all fishing grounds (Table 1). The aggregations with higher densities were observed in Son, where they reached maximum values of 684 no. m⁻². This area also showed the smallest average size (37.3 ± 0.3 mm), because of the presence of a large number of juveniles.

In general, individuals under 40 mm were infrequent at depths of 8 and 12 m (Figure 3); consequently, mean diameter was significantly higher in deep areas (47.6 ± 0.2 mm at 4 m, 64.1 ± 0.2 mm at 8 m, and 67.3 ± 0.1 mm at 12 m). Similarly, maximum sea urchin size increased with depth, and while sea urchins up to 96 mm in diameter were observed at 12 m, maximum size at 4 m was 87 mm. According to the statistic test performed, distribution
type also affected size structure (Table 1). Individuals located in low-density areas were, on average, larger than those in aggregations (61.2 ± 0.1 and 49.5 ± 0.2 mm, respectively), because of a low representation of juvenile sea urchins in these areas. These differences were minimized as depth increased.

Spatial and temporal variability in recruitment

As was the case for adults, recruits showed a spatial distribution with a high aggregation level, being absent in 87% of the samples. Nevertheless, their density was high in those areas where they were present, reaching average values of 36.9 ± 6.4 recruits m$^{-2}$ at a depth of 4 m, and decreasing to values of 2.03 ± 0.66 and 1.81 ± 0.69 recruits m$^{-2}$ at 8 and 12 m, respectively. Their presence was particularly important in sea urchin aggregations, where 92.3% of the observed recruits were found (Table 2).

Abundance of recruits also varied between sampling sites, and their highest density was found in Son, with an average value of 61.7 ± 12.5 recruits m$^{-2}$. These spatial differences, which take place at a scale of tens of kilometres, are possibly related to currents and larval advection. In any case, this study does not allow identifying the causes leading to these variations, and thus the variability associated with sampling sites was included in the random structure of statistical models.

The Poisson-inverse Gaussian (PIG) distribution, which allows for a higher skewness than negative binomial and Poisson

Table 1. Mean ± standard error of the population density (no. m$^{-2}$) and diameter (mm) of P. lividus for each sampled habitat.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Population density</th>
<th>Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Son</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 m, LD</td>
<td>0.61 ± 0.08 a</td>
<td>49.7 ± 0.3 a</td>
</tr>
<tr>
<td>4 m, HD</td>
<td>227.88 ± 15.55 b</td>
<td>37.3 ± 0.3 b</td>
</tr>
<tr>
<td>Queiruga</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 m, LD</td>
<td>0.36 ± 0.04 a</td>
<td>66.1 ± 0.3 a</td>
</tr>
<tr>
<td>8 m, LD</td>
<td>0.45 ± 0.05 a</td>
<td>66.1 ± 0.3 b</td>
</tr>
<tr>
<td>4 m, LD</td>
<td>0.69 ± 0.06 b</td>
<td>63.1 ± 0.3 c</td>
</tr>
<tr>
<td>Ardeleiro</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 m, LD</td>
<td>0.42 ± 0.03 a</td>
<td>67.8 ± 0.3 a</td>
</tr>
<tr>
<td>8 m, LD</td>
<td>0.46 ± 0.02 a</td>
<td>63.2 ± 0.3 b</td>
</tr>
<tr>
<td>4 m, LD</td>
<td>0.56 ± 0.03 b</td>
<td>56.3 ± 0.4 c</td>
</tr>
<tr>
<td>12 m, HD</td>
<td>57.40 ± 3.33 c</td>
<td>67.2 ± 0.3 a</td>
</tr>
<tr>
<td>8 m, HD</td>
<td>61.90 ± 3.74 c,d</td>
<td>60.6 ± 0.4 d</td>
</tr>
<tr>
<td>4 m, HD</td>
<td>76.44 ± 4.86 d</td>
<td>53.0 ± 0.4 e</td>
</tr>
<tr>
<td>Os Forcados</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 m, LD</td>
<td>0.49 ± 0.04 a</td>
<td>67.0 ± 0.2 a</td>
</tr>
<tr>
<td>8 m, LD</td>
<td>0.42 ± 0.02 a</td>
<td>65.7 ± 0.3 b</td>
</tr>
<tr>
<td>4 m, LD</td>
<td>0.78 ± 0.04 b</td>
<td>51.9 ± 0.3 c</td>
</tr>
<tr>
<td>12 m, HD</td>
<td>0.78 ± 0.05 c</td>
<td>67.2 ± 0.3 a</td>
</tr>
<tr>
<td>8 m, HD</td>
<td>0.78 ± 0.06 c</td>
<td>64.7 ± 0.4 b</td>
</tr>
<tr>
<td>4 m, HD</td>
<td>0.78 ± 0.07 d</td>
<td>44.8 ± 0.3 c</td>
</tr>
</tbody>
</table>

Same letters within each column and sampling ground indicate homogeneous groups (significant differences at 1%). HD = high population density areas (aggregations), LD = low population density areas.

Figure 2. Distribution of population densities of P. lividus for each sampling ground and depth. Dashed lines correspond to low-density areas, and solid lines correspond to sea urchin aggregations. Note that the densities are in logarithmic scale.
distributions, was the one with the best fit (AIC and BIC for this distribution were 2 and 7 units lower, respectively, than for the second best-fitting model).

Mean ($\mu$) and standard deviation ($\sigma$) of the distribution were related to covariables through a logarithmic function. Following the AIC criterion, the final model was simplified from the initial one in the logarithmic function for standard deviation, while the function for mean was left invariable. The final adjusted model was as follows:

$$\ln(\mu) = \beta_0 + \beta_1 \cdot \text{Depth}_8 + \beta_2 \cdot \text{Depth}_{12} + \beta_3 \cdot \text{Distribution} + g(\text{Month}) + \ln(\text{Area}) + \gamma \cdot \text{Ground} - \text{Year}$$

and

$$\ln(\sigma) = \delta_0 + \delta_1 \cdot \text{Depth}_8 + \delta_2 \cdot \text{Depth}_{12} + \ln(\text{Area})$$

where $\beta_0$, $\beta_1$, $\beta_2$, and $\beta_3$ are the fixed effects determining the linear part of the model for $\ln(\mu)$, $g(\cdot)$ represents a non-linear function of the fixed variable $\text{Month}$, and $\gamma$ is the random effect, which in our model follows an $N(0, 1.74)$ distribution. On the other hand, $\delta_0$, $\delta_1$, $\delta_2$ are the fixed effects associated with the linear model for $\ln(\sigma)$. $\text{Depth}_8$ and $\text{Depth}_{12}$ are dummy variables taking the value 1 when the depth is 8 or 12 m, and 0 in any other case. Analogously, $\text{Distribution}$ is the dummy variable taking the value 1 when dispersed and 0 when aggregated.

Figure 3. Size distributions of $P.\ lividus$ for each sampling ground and depth. Dashed lines correspond to low-density areas, and solid lines correspond to sea urchin aggregations.

Table 2. Number of samples obtained for each habitat and total number of sea urchins collected.

<table>
<thead>
<tr>
<th>Sites</th>
<th>No. samples</th>
<th>No. urchins</th>
<th>No. recruits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>4 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>HD</td>
</tr>
<tr>
<td>Ardeleiro</td>
<td>352</td>
<td>5340</td>
<td>38</td>
</tr>
<tr>
<td>Os Forcados</td>
<td>363</td>
<td>6617</td>
<td>199</td>
</tr>
<tr>
<td>Queiruga</td>
<td>152</td>
<td>2137</td>
<td>-</td>
</tr>
<tr>
<td>Son</td>
<td>113</td>
<td>4288</td>
<td>787</td>
</tr>
</tbody>
</table>

The number of $P.\ lividus$ recruits observed in each studied habitat during the two sampling years is shown. HD = high density, LD = low density.
Recruit density decreased with depth, being 45- and 66-fold higher at 4 m than at 8 (p < 0.01) and 12 m (p < 0.01), respectively (Table 3). The standard deviation of the distribution followed the same pattern: while it showed a value of 22.97 at 4 m, it decreased to 0.75 and 0.20 at 8 and 12 m, respectively. However, none of the two parameters showed significant differences between 8 and 12 m (p = 0.52 for mean and p = 0.62 for standard deviation).

Aggregation areas were the preferential habitats for recruitment, since recruit density in these areas was, on average, 76-fold higher than in areas with low population density, according to the statistical model (Table 3). This process showed seasonal variations as well; although recruits were found throughout the year (which is partly because of our definition of recruits), these were more frequent during summer and autumn (Figure 4).

Finally, because the deviances of the linear and power regression (1670 and 1673, respectively for the 0.50 quantile) between recruit and adult densities were similar, we selected the linear model because it is the simplest. The intercept was fixed at 0 for all quantiles, as the presence of recruits in the absence of adults was not observed in the field. The positive relationship between recruit and adult densities that we observed (Figure 5) confirms that recruitment is subject to depensatory mechanisms. However, recruits appeared on many occasions at low densities, even though the abundance of adult sea urchins was high, showing that the distribution of recruit densities for a given adult density is asymmetrical, and the probability of recruit occurrence is concentrated at low densities. For this reason, median (y = 0.15 · x) is lower than mean regression (y = 0.33 · x), and the 0.90 quantile is distanced from the rest in order to fit higher and scarce values of recruit density.

**Discussion**

**Spatial variability in recruitment**

A total of 92.1% of the recruitment observed in this study was concentrated in aggregations of sea urchins in shallow areas, which demonstrates that depth and population density play a very important role in the recruitment of *P. lividus*. Dense aggregations of sea urchins offer protection to recruits from predators and waves. This situation leads to an inverse density dependence of recruitment, which has already been documented in numerous studies on several echinoid species (Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987; Rogers-Bennett et al., 1995; Palleiro-Nayar et al., 2011). According to our study, this positive relationship between adult and recruit densities is linear, as the protected surface is proportional to the area occupied by adults.

Regarding the bathymetric pattern of recruitment, Rogers-Bennett et al. (1995) suggest for *Strongylocentrotus franciscanus* that urchins in shallow habitats are more suitable as canopy providers for juveniles, since they are more sedentary than urchins in deeper habitats. High food availability for echinoids in the shallowest subtidal zone (Kempf, 1962; Keats et al., 1984; Zabala and Ballesteros, Table 3. Effect of the explanatory variables on mean recruit density of *P. lividus* (μ) and on standard deviation of the distribution (σ), according to the fixed structure of the GAMLSS model.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>s.e.</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ln (μ)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.307</td>
<td>0.324</td>
<td>4.037</td>
</tr>
<tr>
<td>8 m</td>
<td>-3.815</td>
<td>0.401</td>
<td>-9.516</td>
</tr>
<tr>
<td>12 m</td>
<td>-4.185</td>
<td>0.405</td>
<td>-10.340</td>
</tr>
<tr>
<td>Low density</td>
<td>-4.335</td>
<td>0.314</td>
<td>-13.787</td>
</tr>
<tr>
<td>Month</td>
<td>0.108</td>
<td>0.041</td>
<td>2.650</td>
</tr>
<tr>
<td><strong>ln (σ)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>3.134</td>
<td>0.199</td>
<td>15.759</td>
</tr>
<tr>
<td>8 m</td>
<td>-3.416</td>
<td>1.407</td>
<td>-2.428</td>
</tr>
<tr>
<td>12 m</td>
<td>-4.752</td>
<td>2.049</td>
<td>-2.319</td>
</tr>
</tbody>
</table>

High population density areas at a depth of 4 m were taken as a reference.
of the maximum exploitation limit that aggregations of *P. lividus* can support.

Second, establishing harvest refugia for sea urchins in shallow areas (~5 m) would protect an important portion of the reproductive stock (Oureñas *et al.*, 2013a) and would increase recruitment, given the high population densities to be reached in the protected area. Once the individuals reached a suitable size, the formerly described migration would take place towards deeper habitats, subject to exploitation. In addition, according to fishermen’s communications, frequent storms in Galicia during the fishing season (October–April) and the increase in mean size of sea urchins with depth contribute to the fleet operating in deep areas (~10 m), where wave impact is lower and 93% of sea urchins in our study area were above minimum commercial size (55 mm). Because of this fishing behaviour, the implementation of harvest refugia in shallow habitats should not be unpopular with fishermen in Galicia, while preventing fishing activity from extending to recruitment habitats in case of a decrease in abundance in deeper areas. This paper is thus in concordance with other studies on echinoids, which suggest the implementation of harvest refugia as a fishery management tool (Quinn *et al.*, 1993; Botsford *et al.*, 1999; Bertelsen and Cox, 2001; Carter and VanBlaricom, 2002; Lipcius *et al.*, 2003) and, specifically, with Rogers-Bennett *et al.* (1995), who previously suggested shallow beds of sea urchins as harvest refugia for *S. franciscanus*.

**Supplementary data**

Supplementary material is available at ICES Journal of Marine Science online. Section 1 contains the statistical procedure applied to compare size and population density distributions between habitats. Section 2 contains the graphic assessment of the adequacy of the final fitted model.

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