Spawning habitat selection by the common cuttlefish *Sepia officinalis* in the Cíes Islands (Northwest Spain)

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Handled by George A. Rose

Abstract

We evaluated specific habitat features (bottom substrate type, depth, temperature, season and latitude-longitude) at random locations in the Cíes Islands (Galician Atlantic Islands National Park, Northwest Spain) to determine their impact on *Sepia officinalis* spawning habitat use. We performed underwater visual transects via scuba diving. In total, 94 transects were conducted between April 30, 2012 and July 17, 2015. Habitat features were evaluated as predictors of the presence/absence of egg clusters using Generalised Additive Models. Statistical analyses revealed the following: (a) the probability of finding eggs was significantly higher on hard bottom substrate type containing sea fans and sea tube worms; (b) the sectors where the egg presence was highest were the most shelters zones of Bajo de Viños and Piedra del Borrón, two hard bottom shoals covered by sea fans and sea worms and located in the central Cíes Islands or Faro Island; (c) The preferential depth ranged from 8 to 13 m; (d) as temperatures rose, the probability of finding eggs decreased, which was a sign of the seasonality of the spawning event of the species; and (e) eggs were most common in the winter. A total of 18 additional non-random underwater visual transects were then performed in the Viños and Borrón shoals between December 10, 2014 and August 20, 2015. We calculated the number of egg clusters found in two fenced areas (0.04 ha) located in Viños and Borrón, which showed that Viños was a most suitable spawning habitat than Borrón. The number of eggs per cluster varied from 4 to 82. The spawning period for this species lasted from the beginning of December until the end of June, when bottom temperature ranged from 12.5 °C to 14.75 °C. These microhabitat data reveal indicators of common cuttlefish spawning habitat utilisation and should help identify targets for habitat improvement projects and ecosystem management approaches within this national park and elsewhere.

Keywords: Habitat selection; Spawning habitat; *Sepia officinalis*; NE Atlantic

1 Introduction

Small-scale fisheries (SSFs) are of great importance to the European Union (EU) in terms of job opportunities, and they contribute to the economies of many coastal communities (Natale et al., 2015). It has been estimated that SSFs generate approximately 53% of direct employment in the EU catching sector, representing approximately 83% of the fishing vessels and one-quarter of the catch value (Guyader et al., 2013).

In 2014, the SSFs of Galicia comprised 4000 vessels less than 16 m in length and less than 50 gross register tonnage (GRT), providing employment to 12,650 people (CZFFV, 2014). Galician SSFs involve a variety of fishing gear and species, and the management of these fisheries can be difficult (Freire and García-Allut, 2000), with those for the common cuttlefish (*Sepia officinalis* L. 1758) being no exception (Rocha et al., 2006).

The geographic distribution of *S. officinalis* in the northeast Atlantic extends from the Shetland Islands and southern Norway to approximately 16°N northwest of Africa (Reid et al., 2005), and it includes the Ría de Vigo and the Cies Islands, which are located within the Galician Atlantic Islands National Park (GAINAP). The common cuttlefish is abundant in these two areas (Guerra and Castro, 1988), and this species is harvested by SSFs using several different types of fishing gear, the most important being trammel nets (Arnaiz et al., 2002).

Total official landings of *S. officinalis* in the Ría de Vigo and the Cíes Islands were 132.5 tons on average between 2011 and 2015, which represented 24.8% of the Galician total landings of this species for that period (RAGG, 2016). SSF targeting *S. officinalis* must obey the following restrictions: (i) a minimum size of 80 mm mantle length; (ii) a variable period of closure (generally from May 1st to July 1st); (iii) a maximum length for the trammel nets; and (iv) fishing must be performed at less than 5 m depth for boats less than 2.5 GRT (RAGG, 2015).

At present, there are no studies addressing the exploitation of this natural resource in the National Park. However, eelgrass meadows, one of the preferred habitats of this species, have been continuously disappearing from the Ría de Vigo and Cíes Islands over the past three decades, primarily due to the poorly planned anthropogenic impacts in the Ría de Vigo, like the effect of some shellfish fishing gears, urban and industrial pollution and invasive species (Guerra et al., 2008). Landing Galician official statistics for this species showed a significant (38%) drop over the last two years (2014–2015), whereas the exploitation rate of this and other species have not decreased in the Ría and the GAINAP (RAGG, 2016), impeding the ability of protected areas to adequately fulfil their function as sanctuaries for marine plants and animals.

We believe a comprehensive approach involving planning and regulation of human activity can be developed that minimises social conflict while ensuring the long-term sustainability of *S. officinalis* SSFs. Such integrated management (IM) strategies rely on the collaboration and participation of the main stakeholders in a flexible, responsible and transparent planning process that is respectful of existing rights and duties. Effective IM strategies recognise the need for protecting the ecosystem while at the same time allowing for multiple uses and sustainable development (García et al., 2003). One of the difficulties involved in adopting this type of governance is to define and characterise the habitats and ecosystems to be managed (Forcada, 2007). Nevertheless, such an approach should be feasible in those areas where *S. officinalis* females brood, considering that this species commonly spawns in well-defined areas (Bloor et al., 2013).

S. officinalis is an intermittent terminal spawner sensu Rocha et al. (2001). The spawning season for this species varies with geographic distribution area, and the spawning grounds of this species tend to occur in shallow areas between 5 and 60 m deep. Bloor et al. (2013) recorded twenty-four distinct types of natural structures, including plants, sessile and mobile animals and artificial structures that are used by *S. officinalis* for egg laying in the northeast Atlantic.

The density of eggs laid at a given spawning site can vary spatially and/or temporally, depending on environmental conditions. For *S. officinalis* and other benthic spawners, it is likely that substrate type (e.g. *Loligo reynaudii*; Sauer et al., 1992), biogenic structure (e.g. *Sepia apama*; Hall and Hanlon, 2002; *S. pharaonis*; Lee, 2015) and the physical characteristics of the water mass (e.g. *Loligo reynaudii*; Roberts and Sauer, 1994) are all instrumental factors in determining the intensity and location of spawning in any given year (Moltschaniwskyj and Pecl, 2003).

The aim of this study was to identify and characterise the preferential spawning habitats of *S. officinalis*. Specifically, we focused on the effects of the following variables on spawning: bottom substrate type, zone, depth, temperature and season. The hypothesis underlying this work was that common brooding cuttlefish females carefully select the habitat in which they deposit their eggs. We consider this report to be a first step towards developing contingency plans to protect and preserve the spawning areas of the species within the GAINAP and elsewhere, assuming that habitat choice is consistent across areas.

2 Materials and methods

2.1 Study area

Observations were made within the GAINAP, which has a total maritime surface of 7285 ha and comprises the islands of Cíes, Ons, Sálvora and Cortegada. Within GAINAP, our work was carried out around the Cíes Islands, whose maritime area covers 2,637.77 ha and is located at the mouth of the Ría de Vigo (Fig. 1).

Fig. 1 Mapa de las Islas Cíes mostrando los underwater visual transects (UVT) realizados y la presencia o ausencia de *Sepia officinalis* egg clusters.

alt-text: Fig. 1

2.2 Underwater visual transects (UVTs)

Scuba sampling of the UVTs was performed in two phases: First, UVTs were conducted following the methodology of Guerra et al. (2015b) in which UVTs were randomly performed. In particular, bottom substrate types were classified into four categories: (1) soft; (2) hard with sea fans and fan worms, which is an animal structure independent of the season; (3) hard with algae, a bottom substrate type dependent of the season; and (4) hard without vegetation in any season. Behind these four types there were a review on the composition and distribution of the bottom substrates types in the Ría de Vigo (Vilas et al., 2008). Second, a non-random set of UVTs was carried out in the preferred cuttlefish spawning areas, which were identified through random sampling during the previous phase, after the statistical models described below were applied. The objective of the first phase was to identify the preferred

habitats for spawning cuttlefish and the to estimate the probability of finding eggs in these preferred areas, whereas the objective of the second phase was to determine egg mass abundance and characteristics, as well as to identify the seasons in which they appeared.

The surface area of each identified zone was calculated using the satellite imagery mapping software Google Earth (version 6.2). Two areas measuring 20 × 20 m (0.04 ha) were selected within the identified areas, and all egg masses within those areas were identified with a numbered buoy.

2.3 Data recording

Results were stored in three databases: (1) images, (2) bottom substrate type, oceanographic and other variables, and (3) observations and incidents. The first two databases were processed into files suitable for use in a geographical information system (GIS). The ArcGIS software program (version 9.3) was chosen to represent the maps of environmental preferences, defining the essential *S. officinalis* habitat, according to the methodology of [Valavanis et al. \(2002, 2004\)](#) in the way of the aggregation of abiotic and biotic parameters that are suitable for supporting and sustaining fish population during of stages of the life cycle.

Image analysis was used to determine the number of egg masses in each structure type. The number of eggs in each mass was also estimated from these images.

2.4 Statistical analysis

Habitat features (bottom substrate type, depth, temperature, season and latitude-longitude) were evaluated as predictors of the presence/absence of cuttlefish egg clusters using Generalised Additive Models (GAMs; [Hastie and Tibshirani, 1990](#); [Wood, 2006a](#)) on the 94 UVTs performed between April 30, 2012 and July 17, 2014.

A GAM can be expressed as:

$$E(Y_i) = g^{-1}(X_i^* \theta^* + f_1(x_{i1}) + f_2(x_{i2}) + \dots + f_p(x_{ip}))$$

where g is a monotonic known function (the link function), Y_i a univariate response that follows an exponential family distribution, X_i^* is the i -th row of X^* , which is the model matrix for any strictly parametric model components (such as factors, linear effects, etc.) with corresponding parameter vector θ^* , and $f_1, f_2, \dots, f_p$ are smooth and unknown functions of the covariates x_j ($j = 1, \dots, p$).

Accordingly, the number of egg clusters found during each sampling was converted to a binary variable (i.e., presence [1] or absence [0]) and then, it was used as the response variable in the model. The selected link was the logit function and thin plate regression splines were used as smoothing basis. The optimal degrees of freedom were chosen by means of (Generalised) Cross-Validation ([Wood, 2004](#)).

Firstly, the effect of each variable was investigated through independent GAMs performing a univariate logistic regression analysis. Each of the explanatory variables in [Table 1](#) was regressed with presence/absence of egg clusters. This univariate analysis can show the strength of the relationship and the association of each independent variable with the response variable. When the estimated degrees of freedom of the explanatory variable were equal to 1 (i.e. linear relationship), the regression model was refitted considering a linear effect for this covariate on the response, resulting in a Generalised Linear Model (GLM; [McCullagh and Nelder, 1989](#)). Note that because it is more appropriate to consider the dependence of nests on spatial location as a bivariate surface, latitude and longitude were smoothed as interaction terms using a full tensor product smooth ([Wood, 2006b](#)).

Table 1 Estimated effects (with 95% confidence intervals) for each variable by fitting independent GAMs or GLMs between each variable and the occurrence of *Sepia officinalis* egg clusters: edf: effective degrees of freedom; te (): tensor product; CI: confidence interval; *p*-value: (**) <0.05.

alt-text: Table 1			
Effects	edf	Coefficient (95% CI)	p-value
Bottom substrate type 1	1.000	−3.400 (−6.861, −1.686)	0.001 **
Bottom substrate type 3	1.000	−3.099 (−5.430, −1.584)	0.001 **
Bottom substrate type 4	1.000	−4.780 (−Inf, −2.522)	0.002 **
Depth	1.000	−0.156 (−0.311, −0.034)	0.024 **
Temperature	1.000	−1.056 (−1.837, −0.450)	0.003 **
Season: Fall	1.000	−2.241 (−4.475, −0.737)	0.008 **

Season: Spring	1.000	−1.653 (−3.292, −0.310)	0.022 **
Season: Summer	1.000	−3.970 (−Inf, 1.728)	0.010 **
te (Latitude, Longitude)	3.76	–	0.034 **

Secondly, once the individual effects of the covariates were evaluated, the final model was constructed in order to perform inference procedures. To select this model, the model that explained the most information using the fewest number of variables, a selection algorithm was used (Sestelo et al., 2016). This algorithm is a new forward stepwise-based selection procedure that includes two topics: (i) using a step-by-step procedure to select the best combinations of q variables and (ii) using bootstrap resampling methods to determine the number of covariates to be included in the model.

All statistical analyses was performed with the free R software (R Core Team, 2016) using the mgcv package (Wood, 2006a) for fitting the model and the FWDselect package (Sestelo et al., 2015) for selecting the model to be used.

3 Results

Data gathered from 94 UVTs, which were randomly performed between April 30, 2012 and July 17, 2015, are shown in the Appendix A. The total swept area in these transects was 126.04 ha.

The results of the univariate models are shown in Table 1 and Fig. 2. These results showed that type of substrate, depth, temperature, season and spatial localisation had significant effects on the presence/absence of *Sepia* egg masses. We concluded the following:

- 1) The probability of finding cuttlefish eggs was greatest in bottom substrate type 2. The most abundant species of sea fans, tube worms and algae are shown in Table 2.

able 2(Table within text margins.) Sea fans, tube worms and algae species where *Sepia officinalis* egg clusters were attached in the Bajo de Viños Borrón and Piedra del Borrón in the Cíes Islands.

alt-text: Table 2

Sea fans (Gorgoniidae)	Species
	<i>Leptogorgia sarmentosa</i> (Esper, 1789)
	<i>Corynactis viridis</i> (Allman, 1846)
	<i>Gymnangium montagui</i> (Billard, 1912)
	<i>Eunicella verrucosa</i> (Pallas, 1766)
	<i>Nemertesia antennina</i> (Linnaeus, 1758)
	<i>Aglaophenia tubulifera</i> (Hincks, 1861)
	<i>A. pluma</i> (Linnaeus, 1758)
	<i>Calliactis parasítica</i> (Couch, 1842)
	<i>Eunicella verrucosa</i> (Pallas, 1766)
	<i>Kirchenpaueria pinnata</i> (Linnaeus, 1758)
	<i>Alcyonum digitatum</i> (Linnaeus, 1758)
Tube worms (Polychaeta, Sabellida)	<i>Sabella spalanzanii</i> (Gmelin, 1791)
	<i>Bispira volutacornis</i> (Montagu, 1804)
	<i>Serpula vermicularis</i> (Linnaeus, 1758)
Algae	<i>Cystoseira</i> spp (mainly <i>baccata</i> , <i>tamariscifolia</i>

	and <i>usneoides</i>)
	<i>Laminaria ochroleuca</i>
	<i>Saccorhiza polyschides</i>
	<i>Distyota dichotoma</i> ,
	<i>Dictyopteris polypodioides</i>
	<i>Halydris siliquosa</i>
	<i>Codium tomentosum</i>
	<i>Halimena cf. latifolia</i>
	<i>Sciniaia furcellata</i>

- ii) The preferred depth for cuttlefish and egg deposits was between 8 and 13 m. Occasionally, eggs were deposited as deep as 25 m.
- iii) Increased temperature resulted in a decrease in the response variable. The optimal temperature ranged between 12.5 °C and 14.75 °C.
- iv) The probability of finding cuttlefish eggs was highest in the winter. According to the data from the first sampling phase, the spawning season of *S. officinalis* ranges from December to April.
- v) There was a clear effect for spatial localisation (tensor product of the latitude and longitude) on the presence of eggs (Table 1). There were two easily identifiable preferred spawning zones for this species. Both zones are located in the central island of Cíes (Faro Island), or more precisely, in the Bajo de Viños and Piedra del Borrón (Fig. 1).

Fig. 2 Estimates of the probability of occurrence of egg clusters of *Sepia officinalis* obtained with univariate models for bottom substrate type (upper left), depth (upper right), temperature (middle left), season (middle right) and spatial location as tensor product of latitude and longitude (bottom). The shaded areas and bars indicate the 95% confidence interval.

alt-text: Fig. 2

Table 2 Sea fans, tube worms and algae species where *Sepia officinalis* (Italics, please.) egg clusters were attached in the Bajo de Viños Borrón and Piedra del Borrón in the Cíes Islands.

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	<i>A. pluma</i> (Linnaeus, 1758)
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	<i>Eunicella verrucosa</i> (Pallas, 1766)
	<i>Kirchenpaueria pinnata</i> (Linnaeus, 1758)
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	<i>Saccorhiza polyschides</i>
	<i>Distyota dichotoma</i> ,
	<i>Dictyopteris polypodioides</i>
	<i>Halydris siliquosa</i>
	<i>Codium tomentosum</i>
	<i>Halimenia cf. latifolia</i>
	<i>Sciniaia furcellata</i>

The final statistical model incorporating the combined effect of several predictors, which was obtained by selecting the optimal subset of the above variables, indicated that spawning habitats for *S. officinalis* could best be predicted using the categorical variables bottom substrate type and season as well as the continuous variable temperature (as a linear effect). The effects estimated for each variable included in this model (together with their 95% confidence intervals) are shown in [Table 3](#). [Fig. 3](#) shows the partial effects of each of these variables.

Table 3 Estimated effects (with 95% confidence intervals) for each variable for each variable included in the GLM final model. CI: confidence interval; p-value: (**) <0.05, (*) <0.1.

alt-text: Table 3

Effects	edf	Coefficient (95% CI)	p-value
Bottom substrate type 1	1.000	−3.200 (−9.001, −0.839)	0.016 **
Bottom substrate type 3	1.000	−2.524 (−6.923, −0.546)	0.020 **
Bottom substrate type 4	1.000	−5.356 (−Inf, −2.769)	0.001 **
Temperature	1.000	−0.786 (−2.743, −0.097)	0.042 **

Season: Fall	1.000	−1.345 (−5.979, 2.048)	0.325
Season: Spring	1.000	0.221 (−2.297, 4.114)	0.854
Season: Summer	1.000	−3.273 (−Inf, 0.387)	0.067

Fig. 3 Partial effects of the covariates on the occurrence of egg clusters of *Sepia officinalis* obtained with the final model. The shaded area and the bars indicate the 95% confidence interval for the partial effects.

alt-text: Fig. 3

As seen in the univariate analysis, there was a marked effect of substrate type on the presence/absence of eggs deposited by *S. officinalis*, with a clear preference for type 2 substrates. The effect of temperature was also clear, as egg presence decreased as water temperature rose. The time of year also had a significant effect on the response variable. In particular, we found that summer yields were significantly different (negative) from yields during colder seasons.

Finally, Fig. 4 shows the estimations, at the response scale, obtained from the final model. The left panel (A) shows the estimates as a function of temperature and season, with bottom substrate type fixed at 2.

The right panel (B) displays these estimates as a function of temperature and bottom substrate type, with the season fixed as winter.

Fig. 4 Estimates of the probability of occurrence of egg clusters of *Sepia officinalis* obtained with the final model with bottom substrate type, temperature and season as predictors. (A) Estimates as function of temperature and season with bottom substrate type fixed a 2; (B) estimates as a function of the temperature and bottom substrate type with the season fixed as winter.

alt-text: Fig. 4

In panel A we see that for the highest temperatures (e.g. 17.5 °C), there is low probability of finding eggs irrespectively of season, but at temperatures below 15 °C the probability of finding eggs at each given temperature is related to season (i.e. the species spawning season: higher probability in winter and spring and lower in summer). On the other hand, the probability of finding eggs is always higher in bottom substrate type 2 than in bottom substrate types 1, 3 and 4, and always low in bottom substrate type 4, irrespectively of temperature. In summary, these results indicate that *S. officinalis* has a strong preference for spawning in zones with bottom substrate type 2 in spring and winter, and within these seasons in zones where bottom temperature is below 15 °C.

Moreover, relatively small increased temperatures (2.25 °C (12.5 in December to 14.75 °C in June)) in the identified preferred zones for spawning - Bajo de Vinos and Piedra del Borrón - lead to a decreased probability of egg presence for all seasons, with the probability being highest during winter and spring, so seasonal temperature variations seem to have a significant effect. However, due to lack of data, it was not possible to determine which season had the highest probability (p value = 0.854).

[Table 4](#) shows the data for 18 non-random UVTs conducted between December 10, 2014 and August 20, 2015 in the two identified zones, Bajo de Viños and Piedra del Borrón, which had total surface area of 5.37 ha and 2.05 ha, respectively. Considering the data obtained in both zones, the spawning time for this species in the Cies Islands mainly extended from the beginning of December to the end of June ([Table 5](#)). Bottom temperature ranged between 12.5 °C and 14.75 °C. Courtship, copulation, spawning and hatching were observed in both zones (Viños and Borrón).

Table 4 *Sepia officinalis*. Data of the non-randomly 18 underwater visual transect carried out from December 10, 2014 to August, 20, 2015 in Viños and Borrón. UVT: Underwater Visual transect number; D: depth (m); BT: bottom substrate type, 1: soft; 2: hard with sea fans and fan worms; 3: hard with algae; 4: hard without vegetation; SP: specimens, 1: presence; 0: absence; EC: egg clusters, 1: presence; 2: absence; T: bottom temperature (° Celsius); Ila: initial latitude (N); Ilo: initial longitude (W).

alt-text: Table 4

UVT	D	BT	SP	EC	T	Date (d/m/y)	Ila	Ilo
95	13	2	1	0	14.75	10/12/2014	42.12.778	08.53.875
96	8	3	1	1	12.50	21/12/2014	42.13.466	08.53.976
97	14	2	1	0	12.50	21/12/2014	42.12.816	08.53.970
98	12	2	1	1	12.50	26/01/2015	42.13.466	08.53.976
99	8	2	1	1	12.50	26/01/2015	42.13.619	08.53.694

100	12	2	1	1	12.65	10/02/2015	42.13.812	08.53.877
101	8	2	1	1	12.50	10/02/2015	42.13.472	08.53.977
102	7	2	1	1	12.65	12/03/2015	42.13.489	08.54.000
103	8	2	1	1	12.65	12/03/2015	42.13.472	08.53.977
104	8	2	1	1	13.65	08/04/2015	42.13.477	08.54.016
105	12	2	1	1	13.60	08/04/2015	42.12.709	08.53.954
106	24	1	0	0	13.35	16/04/2015	42.14.487	08.54.000
107	11	2	0	0	13.60	16/04/2015	42.13.768	08.53.686
108	8	2	1	1	13.45	25/04/2015	42.13.477	08.54.016
109	19	4	0	0	14.50	25/05/2015	42.13.347	08.54.750
110	8	3	1	1	13.65	25/05/2015	42.13.477	08.54.016
110	12	3	1	1	14.35	11/06/2015	42.13.466	08.53.976
111	8	3	1	0	14.75	11/06/2015	42.13.477	08.54.016
112	8	1	1	0	14.75	28/07/2015	42.13.477	08.54.016
113	9	3	1	1	14.75	20/08/2015	42.13.477	08.54.016

Table 5 Natural structures that have been recorded as used by *S. officinalis* for egg laying in the Cíes Islands. NEC; number of egg clusters; ENC: egg number per cluster (see [Fig. 1](#) for sites location).

alt-text: Table 5

VCN	Date (d/m/y)	Site	Structure	NEC (ENC)
1	30/03/2012	Bajo de Viños	Inside an old creel	1
38	17/01/2013	Bajo de Viños	<i>Leptogorgia sarmentosa</i> + <i>Sabella spallanzani</i>	2
41	04/02/2013	Cantareira, North of Muxieiro	<i>Leptogorgia sarmentosa</i> + <i>Sabella spallanzani</i>	2
43	28/02/2013	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	4
44	27/03/2013	Muxieiro	<i>Leptogorgia sarmentosa</i>	2
78	05/12/2013	Los Ciegos-West of the Borrón	<i>Leptogorgia sarmentosa</i>	2
79	05/12/2013	Freu da Porta- West of Viños	<i>Leptogorgia sarmentosa</i>	1
82	19/02/2014	Muxieiro	<i>Leptogorgia sarmentosa</i>	1
83	19/02/2014	Piedra del Borrón	<i>Sabella spallanzani</i>	2
84	07/03/2014	Carrumeiro	<i>Leptogorgia sarmentosa</i>	1
86	12/03/2014	Xesteira, South of Carrumeiro	<i>Leptogorgia sarmentosa</i>	1
88	20/03/2014	Freu da Porta- West of Viños	<i>Leptogorgia sarmentosa</i>	1
90	10/04/2014	Cantareira North of Muxieiro	<i>Leptogorgia sarmentosa</i>	1

96	21/12/2014	Piedra del Borrón	<i>Cystoseira</i> spp.	1
98	26/01/2015	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1
99	26/01/2015	Piedra del Borrón	<i>Leptogorgia sarmentosa</i>	1
100	10/02/2015	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (12)
101	10/02/2015	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (11)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (60)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	4 (18,20,9,55)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (45)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (40)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	2 (20,20)
102/103	12/03/2015	Bajo de Viños	<i>Halydris silicuada</i>	1 (8)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (82)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (60)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (20)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (40)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (6)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (15)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (20)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (4)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (10)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	1 (12)
	12/03/2015	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	5 (20,40,60,60,20)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	2 (25,15)
		Bajo de Viños	<i>Cystoseira</i> spp.	2 (25,12)
		Bajo de Viños	<i>Cystoseira</i> spp.	3 (7,46,20)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (30)
		Bajo de Viños	<i>Cystoseira</i> spp.	2 (60,10)
		Bajo de Viños	<i>Cystoseira</i> spp.	2 (30,14)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (13)
		Bajo de Viños	<i>Cystoseira</i> spp.	1 (45)
		Bajo de Viños	<i>Sabella spallanzani</i>	1 (74)
104	08/04/2015	Piedra del Borrón	<i>Cystoseira</i> spp.	1 (25)

		Piedra del Borrón	<i>Cystoseira</i> spp.	3 (2,30,15)
		Piedra del Borrón	<i>Cystoseira</i> spp.	1 (40)
		Piedra del Borrón	<i>Cystoseira</i> spp.	2 (20,15)
		Piedra del Borrón	<i>Cystoseira</i> spp.	2 (30,15)
		Piedra del Borrón	<i>Cystoseira</i> spp.	2 (60,20)
		Piedra del Borrón	<i>Cystoseira</i> spp.	1(40)
		Piedra del Borrón	<i>Halimena</i> cf. <i>latifolia</i>	3 (40,45,26)
105	08/04/2015	Piedra del Borrón	<i>Leptogorgia sarmentosa</i>	1 (30)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	2 (14)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	4 (12,15,20,20)
		Bajo de Viños	<i>Leptogorgia sarmentosa</i>	4 (10,8,15,20)
108	25/04/2015	Piedra del Borrón	<i>Leptogorgia sarmentosa</i>	1 (6)
110	25/05/2015	Piedra del Borrón	Cabo del boyarín	1
111	11/06/2015	Bajo de Viños	<i>Leptogorgia sarmentosa</i>	2
112	11/06/2015	Piedra del Borrón	<i>Leptogorgia sarmentosa</i>	2
113	28/07/2015	Piedra del Borrón	<i>Leptogorgia sarmentosa</i>	2

Fig. 5 shows the number of cuttlefish egg masses according to substrate type that were found in each of the two 0.04 ha quadrants sampled in Viños and Borrón. The total number of egg masses estimated from the recorded images was 93 (72% and 28% in Viños and in Borrón, respectively). In the first of these zones, the number of eggs per egg cluster ranged from four to 82, whereas in the second zone it ranged from six to 74 (Table 5).

Fig. 5 Number of *Sepia officinalis* egg clusters per type of structure where were fixed. LS: *Leptogorgia sarmentosa*; SS: *Sabella spallanzani*; Csp: *Cystoseira* spp.; Hs/Hl: *Halydris silicuosa*/ *Halimena* cf. *latifolia*. Others: inside a creel and in the wire of a bo. The minimum and maximum number of eggs per type of structure indicated on the top of each histogram, in “others” this data is unknown.

alt-text: Fig. 5

4 Discussion

Sexually mature specimens of *S. officinalis* from the Cíes islands had a particular preference for reproduction and egg deposition on hard bottom substrates containing structural fauna such as sea fans and tube worms. The average estimation of probability demonstrates that the second most important bottom substrate type was type 3 (Fig. 4B). There was, however, no statistical evidence to conclude that bottom substrate type 3 is actually preferable to type 1. The natural structures to which the eggs were fastened are summarised in a review conducted by Bloor et al. (2013). In some cases, sandy substrates (with or without pebbles and/or rocks) and associated flora (e.g., seagrass or seaweeds), as well as artificial substrata, were also utilised.

Guerra and Castro (1988) reported that *S. officinalis* in the Ría de Vigo deposited eggs in the San Simon inlet at depths ranging from two to 22 m, particularly on muddy bottoms covered with algae, *Zostera* and sponges, with significant salinity and temperature fluctuations. There are hardly any of bottoms of this type in the Cíes Islands, largely due to the disappearance of *Zostera* bottoms for a variety of reasons (Guerra et al., 2008). It was also reported that *S. officinalis* deposited eggs in the central and outlying area of the Ría de Vigo at depths ranging from two to 24 m, on muddy, sandy and rocky bottoms covered with algae. Guerra and Castro (1988) did not find egg masses on bottoms with structured fauna (mainly tube worms of the families Serpulidae and Sabellidae), which was likely due to the type of sampling gear used, small towed nets, that were not employed on this bottom substrate type to avoid habitat destruction.

The length of the spawning season for this species was variable over the geographical distribution range (Le Goff and Daguzan, 1991), with temperature acting as the regulating factor (Richard, 1971). In warmer waters (>10 °C during winter), the breeding season can extend year round. Based on the maturation and spawning data, the main spawning season for this species in the Ría de Vigo covers spring and summer, although winter spawning was also observed (Guerra and Castro, 1988). The present study shows that, indeed, the spawning period of this species extends from early December through the end of June. Furthermore, the spawning period in northwest Spain is more extensive than that observed for colder water. Thus, in the English Channel, the spawning season occurs from early spring to midsummer (Boletzky, 1983; Le Goff and Daguzan, 1991; Dunn, 1999).

Spawning grounds of *S. officinalis* tend to occur in shallow waters (between five and 60 m deep) (Bloor et al., 2013). In the two preferred zones found in the Cíes Islands, the most suitable depth ranged from eight to 13 m. However, one egg cluster was found at a depth of 25 m.

Temperatures between 9.5 °C and 20 °C and a salinity of at least 28 are considered optimal for the reproduction of this species (Mangold-Wirz, 1963; Paulij et al., 1990; Guerra, 2006). Spawning occurred at temperatures between 11 °C and 22 °C in the Ría de Vigo (Guerra and Castro, 1988). On the Cíes Islands, spawning events were mainly present when the bottom temperature ranged from 12.5 °C to 14.75 °C. The salinity ranged from 33.69 to 35.30 during the observation period (data not shown). Seasonal pattern of temperature in south mouth of the Ría de Vigo (close to Cíes Islands) ranges from a minimum of 12.5 °C in mid-February to 16.0 °C in mid-October at 10 m depth; while the salinity pattern varies between 34.7 in February and 35.60 in August also at 10 m depth (INTECMAR, <http://www.intecmar.org/Ctd/Default.aspx>).

In Viños, the number of eggs per egg mass ranged from four to 82, whereas in Borrón, eggs per egg mass ranged from six to 74. These quantities are less than the 150-1,500 eggs per egg mass that the common cuttlefish females can sometimes release in the wild, depending on their size (Guerra et al., 2015). However, as the origin of each egg mass observed in both zones was unknown, it cannot be concluded that females of the Cíes Islands deposit fewer eggs per egg mass than do those in other zones. It is possible that different egg masses originated from the same female that moved from one sea fan stalk to another, or from one worm tube to another, depositing her eggs in smaller batches. What the reproductive traits do indicate is that egg laying occurred in separate batches and that the spawning period covered seven months. Therefore, *S. officinalis* should be categorised as an “intermittent terminal spawner”, which agrees with Rocha et al. (2001). This does not mean that an individual female laid eggs over 7 months, but, as it was observed, that females do not lay all her eggs simultaneously, but in several batches and during a relatively extensive period.

Although fishing pressure has not declined in the last five years, *S. officinalis* landings in the Ría de Vigo and the Cíes Islands decreased a 38% between the period 2011-2013 and 2014-2015 (RAGG, 2016). This suggests that there has been a significant drop in their preferred habitats, particularly those covered by *Zostera*, but also bottom substrate types 2 and 3 (Guerra et al., 2008). For this reason, as well as to decrease the high rate of exploitation that is still carried out within the GAINAP, we propose that the Bajo de Viños and the Piedra del Borrón zones be protected and conserved. Such measures would require an ecosystem approach to the management of this species, and they would not only protect two preferred spawning habitats for this species but also protect and conserve two biodiversity hot spots (Guerra, 2014). Furthermore, if these two zones were protected, other commercially important species would also benefit, as has been observed in the Ría de Vigo and Arousa for juvenile pods of spider crab (*Maja brachydactyla*) (González-Gurriarán and Freire, 1994; Sampedro and González-Gurriarán, 2004), juveniles and adults of the velvet swimming crab (*Necora puber*) (Freire and González-Gurriarán, 1995) and the ballan wrasse (*Labrus bergylta*) (Villegas-Ríos et al., 2013).

Thus, ensuring two fully protected zones within the GAINAP would conserve and improve a preferential habitat for *S. officinalis*. In addition to the presence of *S. officinalis* egg masses, these two zones have three additional interesting features: (1) their total surface area is very small (7.42 ha, equivalent to 0.28% of the total marine area of the Cíes Islands); (2) they are clearly defined; and (3) both could be well signposted and would not be excessively costly to monitor. Furthermore, to minimise social conflicts between users, we suggest that the implementation of management measures should be gradual, perhaps through

an adaptation plan. The management measures we propose would fulfil one of the most important conclusions of the GESCIES (Ourens et al., 2010) project, which was “the urgent need for new regulation of the fisheries within the GAINAP.” These authors emphasised the need for regulatory practices to create a harmonious balance between marine conservation and sustainable resource exploitation by the fishing industry.

Acknowledgements

We wish to acknowledge Alex Chamorro, Francisco de la Granda (IIM, CSIC, Vigo), Enrique Poza (ECITMAT) and José Castro (Merak Nautica). We are also very grateful to the National Park authorities: José Antonio Fernández-Bouzas, Montserrat Martínez and Mercedes Olmedo, and the keepers of the GAINAP for their invaluable assistance in the development of various aspects of this project. M. Sestelo's research was supported by research grant SFRH/BPD/93928/2013 of "Fundação para a Ciência e a Tecnologia" (FCT) and by [FEDER Funds through "Programa Operacional Factores de Competitividade—COMPETE"](#) and by [Portuguese Funds through FCT](#), in the form of grant PEst-OE/MAT/UI0013/2014. Project financial support was provided by the [Organismo Autónomo de Parques Naturales de España of the Ministerio de Agricultura, Alimentación y Medio Ambiente \(CEFAPARQUES, Project number: 458/2011\)](#).

Appendix A

Sepia officinalis. Data of the 94 randomly underwater visual transects carried out from April 30, 2012 to July 17, 2015. UVT: Underwater Visual Transect number; D: depth (m); SA: swept area (ha); BT: bottom substrate type, 1: soft; 2: hard with sea fans and fan worms; 3: hard with algae; 4: hard without vegetation; SP: specimens, 1: presence; 0: absence; EC: egg clusters, 1: presence; 2: absence; BT: bottom temperature (° Celsius); Ila: latitude initial (N); Ilo: longitude initial (W).

[illegible]

20	10	0.096	1	1	0	13	27/07/2012	42 12.459	08 54.265
21	27	0.036	3	0	0	13	08/08/2012	42 12.401	08 54.385
22	10	1.092	3	0	0	14	08/08/2012	42 12.458	08 54.488
23	30	2.240	4	0	0	14	27/08/2012	42 15.015	08 54.485
24	18	2.220	3	0	0	14	27/08/2012	42 14.983	08 54.556
25	29	0.096	3	0	0	14	05/09/2012	42 10.253	08 54.793
26	15	1.040	3	0	0	14	05/09/2012	42 10.428	08 53.953
27	18	0.015	1	0	0	14	21/09/2012	42 11.767	08 53.255
28	10	0.648	3	0	0	14	21/09/2012	42 11.942	08 53.607
29	10	0.516	3	0	0	14	21/09/2012	42 11.848	08 53.607
30	19	1.280	1	1	0	15	10/10/2012	42 14.243	08 53.636
31	24	0.600	3	1	0	15	10/10/2012	42 14.881	08 54.354
32	17	0.768	5	0	0	17	29/10/2012	42 14.708	08 54.118
33	15	1.560	3	1	0	17	29/10/2012	42 13.775	08 53.732
34	20	1.080	3	0	0	16	09/11/2012	42 11.290	08 54.186
35	18	1.520	5	0	0	16	09/11/2012	42 11.152	08 53.343
36	18	1.024	5	0	0	12	11/12/2012	42 14.346	08 53.801
37	15	1.568	1	0	0	13	11/12/2012	42 12.747	08 54.104
38	13	1.600	2	0	1	13	17/01/2013	42 12.782	08 53.960
39	12	1.536	3	1	0	13	17/01/2013	42 14.095	08 53.801
40	21	1.032	5	0	0	13	04/02/2013	42 14.857	08 54.368
41	12	1.752	2	1	1	13	04/02/2013	42 12.852	08 53.996
42	24	0.420	5	0	0	13	28/02/2013	42 11.197	08 53.754
43	12	1.856	2	1	1	12	28/02/2013	42 12.610	08 53.617
44	13	0.402	2	0	1	13	27/03/2013	42 13.656	08 53.635
45	17	1.710	5	0	0	14	19/04/2013	42 12.635	08 54.597
46	12	1.248	1	0	0	14	19/04/2013	42 12.752	08 53.957
47	25	0.180	5	0	0	13	30/04/2013	42 12.174	08 55.010
48	9	0.756	1	1	0	13	30/04/2013	42 12.024	08 53.984
49	22	0.758	5	0	0	12	24/05/2013	42 11.159	08 54.189
50	10	1.480	1	1	0	12	24/05/2013	42 12.780	08 54.013
51	24	0.732	5	0	0	12	28/05/2013	42 14.848	08 54.367

52	10	1.575	5	0	0	12	04/06/2013	42 13.618	08 53.632
53	12	9.360	2	0	0	14	04/06/2013	42 13.612	08 53.682
54	13	7.740	5	0	0	13	16/06/2013	42 12.681	08 54.428
55	14	2.200	2	0	0	14	25/06/2013	42 12.681	08 54.428
56	13	1.100	1	0	0	14	25/06/2013	42.13.162	08.53.457
57	14	0.492	1	0	0	14	25/06/2013	42.13.059	08.53.454
58	10	0.636	1	0	0	15	26/06/2013	42.13.176	08.53.529
59	24	0.480	5	0	0	12	26/06/2013	42.13.145	08.53.740
60	8	1.120	1	0	0	14	01/07/2013	42 13.079	08 53.493
61	10	1.664	5	0	0	13	31/07/2013	42 12.686	08 54.871
62	22	0.780	5	0	0	15	07/08/2013	42 15.140	08 54.547
63	15	1.200	5	0	0	19	29/08/2013	42 15.030	08 55.140
64	10	1.560	2	0	0	14	18/09/2013	42 11.784	08 53.506
65	21	0.774	2	0	0	13	18/09/2013	42 11.799	08 53.271
66	11	0.738	3	0	0	13	25/09/2013	42 12.726	08 53.970
67	21	0.990	3	1	0	13	25/09/2013	42 14.478	08 53.807
68	15	0.990	1	1	0	13	07/10/2013	42 14.738	08 54.214
69	20	0.660	1	0	0	17	07/10/2013	42 13.291	08 53.744
70	11	1.400	5	0	0	18	30/10/2013	42 13.300	08 53.830
71	18	0.900	1	0	0	16	30/10/2013	42 11.550	08 53.187
72	10	0.510	1	0	0	16	14/11/2013	42 12.700	08 54.364
73	20	1.180	1	0	0	15	14/11/2013	42 12.492	08 54.815
74	12	1.925	3	1	0	15	26/11/2013	42 12.773	08 53.972
75	21	1.760	5	0	0	12	26/11/2013	42 11.268	08 54.505
76	14	2.400	1	0	0	12	03/12/2013	42 11.525	08 53.789
77	29	2.400	5	0	0	12	03/12/2013	42 14.901	08 54.296
78	17	3.420	2	1	1	12	05/12/2013	42 12.649	08 54.669
79	18	0.459	2	1	1	11	05/12/2013	42 12.902	08 53.396
80	12	1.760	5	0	0	12	21/01/2014	42 12.649	08 54.482
81	28	0.704	5	0	0	14	21/01/2014	42.14,842	08.54.074
82	12	1.360	2	0	1	14	19/02/2014	42.13.688	08.53.650
83	25	0.160	2	0	1	12	19/02/2014	42.13.677	08.53.418

84	8	0.152	2	1	1	12	07/03/2014	42.13.548	08.53.846
85	18	0.420	3	1	0	12	07/03/2014	42.11.579	08.56.093
86	10	0.492	2	1	1	12	12/03/2014	42.11.587	08.53.306
87	18	0.432	5	0	0	13	12/03/2014	42.11.371	08.53.343
88	11	0.360	2	0	1	13	20/03/2014	42.11.657	08.53.375
89	20	0.480	5	0	0	13	20/03/2014	42.14.396	08.53.597
90	11	0.936	3	1	1	13	10/04/2014	42.12.732	08.54.275
91	22	1.575	5	0	0	14	10/04/2014	42.14.477	08.53.637
92	14	3.675	5	0	0	13	16/04/2014	42.14.487	08.54.000
93	22	3.540	5	0	0	14	16/04/2014	42.14.959	08.54.428
94	31	2.347	5	0	0	14	17/07/2014	42.14.901	08.54.296

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Answer: Richard, A., Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de *Sepia officinalis* L. (Mollusque, Céphalopode). Thèse de Doctorat d'État, Université de Lille (N° 243), 1971, 264 pp.

Query: Please check the Figure 5 caption for correctness.

Answer: Fig 5. Number of *Sepia officinalis* egg masses per type of structure.

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Change boy for buoy.

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Remove (*)<0.1.

May be data inside the table could be improved by centring them.