Spawning habitat selection by *Octopus vulgaris*: New insights for a more effective management of this resource

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ABSTRACT

The selection of spawning habitat of a population of *Octopus vulgaris* that is subject to a small-scale exploitation was studied in the Cíes Islands within the National Park of the Atlantic Islands of Galicia (NW Spain). The technique used was visual censuses by scuba diving. We conducted 93 visual censuses from April 2012 to April 2014. The total swept area was 123.69 ha. Habitat features (season, depth, zone, bottom temperature, swept area, bottom substrate type, and creels fishing impact) were evaluated as predictors of the presence/absence of spawning dens using GAM models. *O. vulgaris* has a noteworthy preference for spawning in areas with hard bottom substrate and moderate depth (approximately 20 meters). The higher density of spawning dens (1.08/ha) was found in a surveyed area of 50.14 ha located in the northeastern part of the northern Cíes Island. We propose to protect the area comprised from Punta Escodelo to Punta Ferreiro between 5 and 30 m depth. This area has a surface of 158 ha equivalent to 5.98 % of the total marine area of the Cíes islands. The strengths and weaknesses of a management strategy based on the protection of the species' spawning habitat are discussed.

KEYWORDS: *Octopus vulgaris*, spawning dens, habitat selection, essential areas, marine protected areas.

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1. Introduction

Cephalopod landings in Galicia (NW Spain) accounted for 11,633-7,190 tonnes in the period 2011-2014 (RAGG, 2014). The most important cephalopod species in Galicia is the common octopus (*Octopus vulgaris* Cuvier, 1797), which yielded an average annual catch ranging from 3,405 to 2,586 tonnes between 2011 and 2014, with revenues of over € 12.8-13.7 million in that period (RAGG, 2014).

Galician small-scale creel fishery targeting *O. vulgaris* is seasonal and includes the Rías. The species is caught on sea bottoms ranging from 5-7 m to a maximum depth of 150 m (Otero et al., 2005; RAGG, 2006). Nowadays, 1,289 boats have permission to use common octopus baited creels, and a total of 710 boats with permission landed catches during 2013-2014 fishing season (Molares, 2015). Approximately 320 boats operate in the Ría of Vigo and adjacent areas in 2004 (RAGG, 2006), which include the National Park of the Atlantic Islands of Galicia (NAPAIG).

The current management measures for the *O. vulgaris* fishery in Galicia is complex (RAGG, 2006; Molares, 2015), and they are subject to Annual Management Plans (AMPs). The main management measures to 2014-2015 AMP in the western Atlantic zone of Galicia include: 1) a period of fishing closure from May 31 to July 1; 2) a minimum legal weight of 1 kg per individual; 3) a maximum number of fishing creels that varied from 200 to 600 per crew member depending on boat register tons; 4) a schedule of fishing of 6:00 a.m. up to 17:00 p.m. with mandatory rest the weekends; and 4) a maximum daily catch quota of 350 kg per boat (Xunta de Galicia, 2014). Despite these or very similar management measures in each AMP, *O. vulgaris* landings decreased from 4,205 t in 2010 to 2,586 in 2014, which represents a drop of 61% (RAGG, 2014). However, other Galician official source valued that landings drop in 50.1% (Xunta de Galicia, 2014). Moreover, the poorly planned anthropogenic impact in the Ría of Vigo (Galicia, NW Iberian Peninsula) caused the disappearance of fertile areas of fishing and shell

fishing, the exhaustion (and even the disappearance) of some aquatic living resources, and the loss of biological and cultural diversity (Guerra *et al.*, 2008).

One of the most interesting conclusions of the GESCIES project carried out by Ourens *et al.*, (2010) was the urgent need for new regulation of the fisheries within the NAPIAG. The authors emphasised the regulatory aspect because of the unavoidable need to harmonise the requirement of a marine conservation area with the requirements of sustainable resource exploitation by the fishing industry.

Managing the small-scale fishery of Galicia is difficult due to its great complexity (Freire *et al.*, 2002), and the situation of *O. vulgaris* is not an exception (Otero *et al.* 2005). An approach that involves the comprehensive planning and regulation of human activities in the context of a complex set of interacting objectives with the aim of minimising social conflicts, while ensuring long-term sustainability of the *O. vulgaris* artisanal fishery, would be very appropriate. This Integrated Management (IM) recognises the need for protecting the ecosystem, as well as addressing the implications of multiple uses, and aims at sustainable development (García *et al.*, 2003). One of the difficulties in adopting this type of governance is to define and characterise the habitats and ecosystems to be managed (Forcada, 2007). We consider that this approach could be feasibly applied in those areas for brooding *O. vulgaris* females, considering that the spawn of this species is commonly set in easily protected rocky crevices (Hanlon and Messenger, 1996; Mangold, 1983).

Understanding the relationship between environmental variation and nurseries, spawning grounds and successful recruitment is an emerging issue and has been undertaken for *O. vulgaris* using both fishery-dependant and fishery independent data (Faure *et al.*, 2000; Garofalo *et al.*, 2010; Katsanevakis and Verriopoulos, 2006; Moreno *et al.*, 2014; Otero *et al.*, 2009; Pierce *et al.*, 2008). Den ecology of *O. vulgaris* on soft sediment and the availability and types of shelter were studied by Katsanevakis and Verriopoulos (2004a, b). However, other types of

requirements for bottom substrate have not been closely examined for their influence on common octopus habitat use, and, except for some few and recent studies (e.g. Mereu *et al.*, 2014), the specifics of this species' habitat use remain largely unknown. There is, however, some previous information on other octopus species (e.g., *Enteroctopus dofleini* by Hartwick and Thorarinsson, 1978 and Schell, 2002; *Octopus tehuatl* by Iribarne, 1990; *O. bimaculoides* by Cigliano, 1993; *O. cyanea* by Forsythe and Hanlon, 1997; *O. tetricus* by Anderson, 1997; *O. insularis* by Leite *et al.*, 2009) that indicated protection from predators and dominant conspecifics, including den availability, preference for back reef over reef top, fore reef habitat, hard bottom substrates, depth and some hydrographic parameters influence habitat selection and use. However, information on the spawning habitat selection for any octopus species is very scarce (Moreno *et al.*, 2014).

The main goal of this paper is to identify and characterise preferential spawning habitats for *O. vulgaris* (PSHO) within the NAPAIG. Specifically, we seek to target: 1) the role of bottom substrate characteristics, depth and seasons, and 2) the role of the fishing creels. The hypothesis underlying this work is that common octopus brooding females carefully select the habitat in which to deposit their eggs. We also aim to confer potential insights for management plan achieving sustainable yield of this meaningful marine resource in NW Iberian waters based on PSHO.

2. Material and methods

2.1. Study area

Observations were made in the NAPAIG, which has a total maritime surface of 7,285 ha and comprises the islands of Cíes, Ons, Sálvora and Cortegada. Within NAPAIG, 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 of Vigo (Fig. 1).

2.2. Visual censuses

Four visual censuses were performed monthly, from April 2012 to April 2014, in subtidal areas of the Cíes Islands. The location of each visual census was performed using GPS. Two or three scuba divers carried out each census simultaneously at depths between 5 and 30 m.; any substantive information was recorded with a SONY video camera, HDR-CX700. The scuba divers swam in parallel, keeping visual contact at a variable distance depending on the horizontal visibility. The census duration and the distance between scuba-divers were recorded. Average depth was estimated as the mean depth between the beginning and end of each census. The average speed of the divers was estimated from previous tests carried out by the same divers around the Cíes Islands at depths and in atmospheric conditions similar to those prevailing when the visual censuses were undertaken for this study. Bottom temperature was recorded with a diving computer. Visual censuses were carried out in daylight and with a horizontal visibility of ≥ 3 meters.

Once in the laboratory, the recorded images were examined to verify the type of bottom substrate, the presence of octopus, and the number of egg clusters and/or spawning dens. The type of bottom substrate was defined by the dominant underlying matrix and classified as soft or hard. The bottom substrate recorded as soft included sand, “maërl”, sand with some rock outcrops and gravel. The hard bottom substrate included cobble (>100 mm to 1 m), bedrock, and outcrop. Spawning dens were identified by two signs: i) the presence of egg strings to which eggs were attached, and/or ii) the presence of medium size stones placed in such a way that they were clearly indicating a spawning den, based on our experience and the architectural characteristics of typical spawning dens (Hanlon and Messenger, 1996).

In order to evaluate the relationship between creel octopus fishing with the presence of spawning dens within NAPIAG, the number of boats that were going fishing in the area during

every visual census was registered. These quantitative data were treated as binary variables (presence/absence) in the statistical models.

2.3. Swept area

The marine area around the Cíes Islands at a depth between 5 and 25 meters was divided into 52 cells with an average surface area of 27.7 ha each. The sampling cells were classified into three zones: north, central and south (Fig. 1; Table 1). Initially, the sampling protocol was randomly designed, but prevailing weather conditions occasionally modified the initial pattern.

The swept area in each census (*SAC*) was calculated as follows:

1) The effective sampling time (*EST*) was calculated by the formula:

$$EST = Dt - (At + Rt)$$

where *Dt* is the total time spent in each dive. the time spent in returning to the surface (*At*) (for decompression stops required to meet safety standards in diving) and the recording time (*Rt*) in which divers were inactive were discounted from the total time.

2) The net sampling distance (*NSD*) on every census was calculated using the formula:

$$NSD = EST \times ADS$$

where *ADS* is the average diving speed (estimated at 10 meters/minute).

3) The total swept area sampled in each census (*SAC*) was calculated using the formula:

$$SAC = NSD \times [HV \times (Nd + 1)]$$

where *HV* was the horizontal visibility, and *Nd* was the number of divers who participated in each census. Horizontal visibility (*HV*) was measured as the distance at which a diver kept his/her companion visible, which was calculated with a tape measure held by both divers; this distance calculation has an accuracy of 0.5 m.

As indicated above, during each visual census, divers remained aligned and separated by the maximum distance allowed for horizontal visibility. As a result, the total visual field was obtained by multiplying *HV* by the number of divers plus one (see Fig. 2).

2.4. Data recording

Data were stored in three bases: 1) images, 2) substrate, oceanographic and other variables and 3) observations and incidents. The first two were processed into files suitable for use in a GIS. ArcGIS software was chosen to represent the maps of environmental preferences defining the Essential Octopus Habitat, following the methodology of Valavanis *et al.* (2002, 2004).

2.5. Statistical analysis

Habitat features (such as season, depth, zone, bottom temperature, swept area, bottom substrate type, and fishing impact) were evaluated as predictors of the presence/absence of spawning dens using Generalised Additive Models (GAM), (Hastie and Tibshirani, 1990; Wood, 2006a). In this case, a GAM can be expressed as:

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

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

The number of spawning dens found during each sampling were converted to a binary variable (i.e., presence [1] or absence [0]) and used as the response variable in the model. The logit function was used as a link and thin plate regression splines were used as a 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 2 was regressed with presence/absence of spawning dens. This univariate analysis can show the strength of the relationship and the association of each independent variable with the response variable. The regression model was refitted considering a linear effect of this covariate on the

response. Note that because it is more appropriate to consider the dependence of dens on spatial location as a bivariate surface, latitude and longitude were smoothed as interaction terms, using a tensor product (Wood, 2006b).

Once the individual effects of the covariates were evaluated, the final model was constructed in order to perform inference procedures. To select the final model, the model that explained the most information using the fewest number of variables, a selection algorithm was used (Sestelo *et al.*, 2014). 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, 2013) using the *mgcv* package (Wood, 2006a) for fitting the model and the *FWDselect* package (Sestelo *et al.*, 2013) to select the model to be used.

3. Results

A total of 93 visual censuses were undertaken off the Cíes Islands (NAPAIG) from April 2012 to April 2014 (Table 1; Fig. 1). These censuses comprised 104.2 net diving hours. The distribution of censuses by geographic location, date and depth are shown in Table 1. A total of 41 cells (28 in the inner side and 13 in the outer side of the islands) were sampled. The average swept area in each census was 1.33 ha and the total swept area was 123.69 ha (Table 1), equivalent to 4.69 % of the total marine area of the Cíes Islands.

Octopus vulgaris were distributed widely in the study area. During the censuses, 369 octopuses were found at depths ranging from 8 to 30 m (Table 1); among them, 21 were females taking care of their egg masses (Fig. 3a). The temperature where brooding females were found ranged from 12 to 17°C (Table 1). A pair of mating octopuses was observed on the 20th of June

in census 12, in which the male was situated near the female and extended the hectocotilised third right arm towards her (Fig. 3b). Besides 21 brooding females, 33 spawning dens were observed (Table 1; see an example of the typical architecture of a spawning den in Fig 3c). The probability of occurrence of egg clusters (EC) during the spring-summer season was significantly higher ($\chi^2=13.33$; $p>0.01$) than in the autumn (Table 1).

The swept area in the North Zone was 50.14 ha (Table 1), equivalent to 1.90 % of the total marine area of the Cíes Islands. The density of egg clusters and spawning dens was 1.08/ha in this zone (Fig. 1).

Coefficients and significance of predictors and total deviance explained by the GAM final model are shown in Table 2.

The results of the univariate regression models are shown in Table 3 and Fig. 4. Our statistical results showed that the variable presence/absence of creels targeting *O. vulgaris* was significantly related with the occurrence of egg clusters in the Cíes Islands (data not shown). Nevertheless, a significant effect of presence/absence of creels variable was not seen when the presence of spawning dens was considered as a response variable (Table 3; “Creels Yes” p -value = 0.471). The presence of spawning dens was not significantly related to the season (Table 3; Fig. 4). Taking into account a nominal level of 0.05, the occurrence of spawning dens is significantly influenced by the “Depth” by the “Spatial location” (tensor product of latitude and longitude) and by the variables “Zone” and “Bottom substrate”. Note that, in the case of using a categorical predictor with k levels, only the results of $k-1$ levels are shown. This is due to the parameterisation of the model with respect to a reference group (in this case, “Zone north” and “Soft bottom substrate”) where the mean of the first group is considered as the reference and the deviations of the remaining groups are measured with respect to it. The estimated effects of the predictors can be observed in Fig. 4. The Depth variable seems to produce an increase in the response, more notable in the range of 8 to 20 m. In relation to “Spatial location”, it is clear that

the presence of spawning dens is minimal for the smallest values of longitude (at any latitude). This location agrees with the external side of the islands. Considering a division of the Cíes Islands in north, central and south (given by the categorical variable “Zone”), we obtain differences for the presence of these spawning dens that show a notable preference for the north zone. The last significant effect we found relates to the type of “Bottom substrate”, with a predisposition for *O. vulgaris* to locate its spawning dens on hard substrates (Table 4).

The selection algorithm mentioned above was used to decide which variables to include in the final model. The results indicated that the best model to identify and characterise spawning habitat of preference for *O. vulgaris* includes the categorical variables “Zone” and “Bottom substrate” and the continuous variable “Depth” (as a smooth effect). The estimates — in the scale of the response — obtained with this model are shown in Fig. 5. The upper panel displays these estimates as a function of “Depth” and “Zone”. The highest probability is obtained in the north of the Cíes Islands at depths of approximately 20 meters. The middle panel refers to the cited probability as a function of “Depth” and “Bottom substrate”. In this case, the probability of presence of spawning dens on hard substrates is approximately 45% higher than on soft ones (Fig. 5). The lower panel shows the estimates obtained as a function of the two categorical variables “Zone” and “Bottom substrate”. It can be clearly seen that the probability of occurrence increases with the latitude and is higher for hard substrates than for soft ones (Table 4). In summary, these results lead to the conclusion that *O. vulgaris* has a remarkable preference for spawning in areas with hard bottom substrate and moderate depths (approximately 20 meters), characteristics that are found in the north zone of Cíes Islands (see Fig. 1 and Tables 3 and 4).

4. Discussion

4.1. Methodology

We were unable to find a standardised protocol to measure the area swept in each visual census (SAC) in the scuba-diving literature. Consequently, we had to develop an original methodology. This methodology provides fairly accurate data on the swept area in each visual census.

The characteristic behaviour of brooding *O. vulgaris* females, in which they stop leaving the den to forage for food (Hanlon and Messenger, 1996), is the main reason why females are not amenable to fishing gear or conventional sampling techniques and scuba diving is the most suitable method to locate *O. vulgaris* females at that stage of their life cycle.

Generalised Additive Models (GAMs) were applied to define habitat preferences in other cephalopod species, for example, for the post-recruit life stages of the squid *Loligo forbesii* (Smith *et al.*, 2013) or for *Octopus vulgaris* (Moreno *et al.*, 2014). This kind of model has also been combined with GIS to identify the potential habitats of *Loligo vulgaris* in the North-western Mediterranean (Sánchez *et al.*, 2008). Predictions based on such models are useful for fishers to target the species more effectively and can assist managers wishing to protect spawning and/or fishing grounds (Smith *et al.*, 2013).

The decision to use only the variable “spawning dens” instead of “presence of eggs clusters” in the statistical models, although both variables are obviously related, was taken to avoid a seasonal effect. Using the variable “spawning dens”, which proved to be non-significant depending on the season (Fig. 4; Table 3), averted important bias.

The type of bottom substrate categories defined in this paper reflected a continuum of hardness. However, the classification of soft and hard substrates proved to be useful, and seems to reflect the behaviour of shallow-water benthic octopuses in relation to the bottom substrate at different stages of their life cycle. Soft bottom substrates are mainly suitable for small and immature octopuses of a variety of species (Anderson, 1997; Guerra *et al.*, 2014; Katsanevakis

and Verriopoulos, 2004a, b; Yarnall, 1969), while hard bottom substrates are mainly suitable for brooding females and adult males (Anderson, 1997; Hanlon and Messenger, 1996).

4.2. *Habitat preference*

The highest density of egg masses and spawning dens (1.08/ ha) was found in the northeastern part of the northern Cíes Islands. Although the surveyed area with visual censuses was 50.14 ha, we propose that the area to be protected should run from Punta Escodelo to Punta Ferreiro and between 5 and 30 m depth (Fig. 1). Its bottom surface is 158 ha, equivalent to 5.98 % of the total marine area of the Cíes Island. We studied this zone undertaking of two rapid surveys where we found that the bottom structure fully agree with that of the area in which the visual censuses were carried out.

The higher preference for the north zones of the Cíes Islands, as opposed to the lower preference for the central and south zones, may be explained by the abundance of suitable substrates in the north zone: hard bottoms, which include cobble, bedrock, or outcrop, and a large number of natural crevices and holes, which are the preferable habitats for egg deposition by brooding females and adult males, both in their natural habitats (Leite *et al.* 2009) and in experimental tanks (Boyle, 1980; Boletzky, 2004).

4.3. *Spawning season*

Our data showed a significantly higher probability of the occurrence of egg clusters during the spring-summer than in the autumn-winter season (Table 1). This result agrees with the observed reproductive strategy of *O. vulgaris* in Galicia, which is characterised by an extended spawning period with a strong peak during the spring (Otero *et al.*, 2007). The discrepancies found in the spawning season of *O. vulgaris* in other areas of the North Atlantic (Gonçalves, 1993; Hatanaka, 1979; Hernández-García *et al.*, 2002; Rodríguez-Rúa *et al.*, 2005; Silva *et al.*, 2002) could be explained due to differences in the upwelling regime in those areas. The onset of the upwelling season in Galician waters (41°-49°N) occurs from the beginning of April to the end of May and

its cessation occurs from middle September to middle October (Álvarez-Salgado *et al.*, 2009). The upwelling in the coastal region from Gibraltar (36°N) to Cape Blanc (21°N) is more intense during the summer months. Between Cape Blanc and Cape Vert (15°N), the upwelling has a marked seasonal periodicity, reaching its peak intensity during winter (Arístegui *et al.*, 2006). Our results are confirmed by the peak of early-hatched paralarvae occurring at the end of summer and autumn months, during the early stage of the relaxation phase of coastal upwelling events (Otero *et al.*, 2009; Roura, 2013).

4.4. Management

Taking into account the preferred habitat for *O. vulgaris* for the safe depositing of egg clusters, we consider our results as a first but relevant step that fosters our understanding of the maintenance, development and management of the conditions under which that octopus population thrives. Thus, ensuring a fully protected area within the NAPAIG would conserve and enhance preferential habitat for the species. In addition to the presence of brooding females, this area has several interesting features: 1) its total surface area is relatively small (158 ha, equivalent to 5.98% of the total marine area of the Cíes Islands within the NPAIAG); 2) it is clearly defined, extending from Punta Escodelo to Punta Ferreiro and from 5 to 30 m depth (Fig. 1); 3) it could be well signposted and would not be excessively costly to monitor; and 4) it is an area of high fishing productivity and high marine biodiversity (e.g., Junoy and Herrera-Bachiller, 2009; Ourens *et al.*, 2010; Peña and Bárbara, 2006; Guerra, 2015). Furthermore, in order to minimise social conflicts between all users, the implementation of this management measure should be gradual, through an adaptation plan.

The effect of the management strategy will depend on the life history of the target species, and protecting an area may not necessarily lead to an increase in the parental stock and long-term survival of the local population. Although *O. vulgaris* has a planktonic very dispersive and related with the seasonal upwelling event (Otero *et al.*, 2009; Roura, 2013), settlement of small

octopuses occurred in soft bottoms within the NPAIG (Guerra *et al.*, 2014). On the other hand, recently settled animals (6-15g) were frequently found in adjacent zones on soft and maërl bottoms covered with seaweeds (*Laminaria* spp and *Sacorrhyza polyshides*) from 8 to 27 m depth at the end of summer and the beginning of the autumn (divers J.L González and M.E. Garci per. com.). Consequently, we consider that the protection of SPHO would have a positive effect on the management strategy on the recruitment of *O. vulgaris*. Since this species has a wide area of distribution of in the Atlantic Ocean and the Mediterranean Sea (Jereb *et al.*, 2014), the SPHO protecting strategy could be extended and applied in other zones within the geographical range of the species.

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Figure legends

Figure 1. *Octopus vulgaris*. Map of the Cíes Islands inside the National Park of the Atlantic Islands of Galicia (NW Iberian Peninsula) showing sampled cells, visual censuses, abundance of spawning dens, bottom substrate type and the area in which brooding females were more abundant.

Figure 2. Diagrammatic drawing illustrating the methodology used to calculate the swept area in each census. RTS: real-time sampling, Dt: diving time, At: ascent time, Rt: recording time, NSD: net sampling distance, ADS: average diving speed, SAC: swept area in each census, HV: horizontal visibility, Nd: number of divers.

Figure 3. *Octopus vulgaris*. a: a female protecting its eggs; b: mating; c: typical spawning den.

Figure 4. Estimated effects (solid lines) of the covariates on the occurrence of spawning dens of *O. vulgaris*. The results are reported on the scale of the linear predictor. Independent GAMs for: Swept area (a), Depth (b), Temperature (c), spatial location (tensor product of Latitude and Longitude) (d), Zone (e), Creels (f), Season (g), and Bottom substrate (h). The shaded area in (a) and (b) indicates the 95% Bayesian confidence and the numbers in brackets are the estimated degrees of freedom. The broken lines indicate the 95% confidence interval for the partial effects.

Figure 5. Estimates of the probability of occurrence of spawning dens of *O. vulgaris* obtained with the final model with Zone, Bottom substrate and Depth as predictors.

Table 1. *Octopus vulgaris* sampling data. VCN: visual census number; Z: zone (a: south; b: central; c: north); D: depth (m); SA: swept area (ha); TB: type of bottom substrate, 1: soft; 2: hard; NO: number of specimens; EC: number of egg clusters; SD: spawning dens; HV: horizontal visibility (m); BT: bottom temperature (° Celsius); C: absence (0)/presence (1) of creels; Ila: latitude initial (N); Ilo: longitude initial (W).

VCN	Z	D	SA	TB	NO	EC	SD	HV	BT	C	Date (d/m/y)	Ila	Ilo
1	b	13	1.128	1	1	0	0	8	14	0	30/04/2012	42 12.768	08 53.981
2	c	15	3.720	1	4	0	0	15	13	1	17/04/2012	42 11.767	08 53.357
3	b	13	2.580	2	0	0	0	15	13	1	17/04/2012	42 12.746	08 53.894
4	b	13	1.664	1	1	0	0	8	13	0	07/05/2012	42 13.466	08 53.976
5	b	29	0.140	2	0	0	0	5	14	0	14/05/2012	42 13.521	08 54.824
6	b	15	1.024	1	6	0	0	4	14	0	14/06/2012	42 13.330	08 53.882
7	c	18	0.405	2	1	0	1	3	15	0	23/05/2012	42 11.577	08 53.100
8	b	9	0.441	2	0	0	0	3	16	0	23/05/2012	42 12.769	08 54.258
9	c	21	1.000	1	3	0	0	10	16	0	04/06/2012	42 10.715	08 54.257
10	b	20	1.280	2	2	1	1	10	17	0	04/06/2012	42 12.650	08 54.816
11	a	17	2.160	2	5	0	1	20	16	0	20/06/2012	42 15.115	08 55.061
12	a	20	1.120	2	7	0	1	20	16	0	20/06/2012	42 14.848	08 54.367
13	a	19	1.760	2	0	0	0	10	16	1	09/07/2012	42 14.467	08 54.008
14	a	20	0.630	2	5	1	1	10	16	1	09/07/2012	42 14.842	08 54.369
15	a	20	1.720	2	7	4	4	8	15	1	17/07/2012	42 14.858	08 54.367
16	b	13	1.696	2	0	0	0	8	16	0	17/07/2012	42 12.681	08 54.428
17	c	15	0.425	2	1	0	0	5	15	0	24/07/2012	42 11.820	08 53.261
18	a	17	0.560	2	2	2	2	4	13	0	27/07/2012	42 14.406	08 55.834
19	c	26	0.336	1	2	0	0	4	13	0	27/07/2012	42 12.281	08 53.585
20	b	10	0.096	1	0	0	0	4	13	0	27/07/2012	42 12.459	08 54.265
21	b	27	0.036	2	0	0	0	4	13	0	08/08/2012	42 12.401	08 54.385
22	b	10	1.092	2	3	0	0	7	14	0	08/08/2012	42 12.458	08 54.488
23	a	30	2.240	2	1	1	1	20	14	1	27/08/2012	42 15.015	08 54.485
24	a	18	2.220	2	2	1	1	15	14	0	27/08/2012	42 14.983	08 54.556
25	c	29	0.096	2	0	0	0	8	14	0	05/09/2012	42 10.253	08 54.793
26	c	15	1.040	2	1	1	1	5	14	0	05/09/2012	42 10.428	08 53.353
27	c	18	0.015	1	1	0	0	0.5	14	0	21/09/2012	42 11.767	08 53.255
28	c	10	0.648	2	0	0	0	4	14	1	21/09/2012	42 11.942	08 53.875
29	c	10	0.516	2	1	0	0	4	14	0	21/09/2012	42 11.848	08 53.607
30	a	19	1.280	1	0	0	0	10	15	0	10/10/2012	42 14.243	08 53.636
31	a	24	0.60	2	1	1	3	10	15	1	10/10/2012	42 14.881	08 54.354
32	a	17	0.768	2	3	1	3	8	17	1	29/10/2012	42 14.708	08 54.118
33	a	15	1.560	2	3	0	0	10	17	1	29/10/2012	42 13.775	08 53.732
34	c	20	1.080	2	6	0	0	10	16	1	09/11/2012	42 11.290	08 54.186
35	c	18	1.520	2	3	0	3	10	16	0	09/11/2012	42 11.152	08 53.343
36	a	18	1.024	2	4	0	4	8	12	0	11/12/2012	42 14.346	08 53.801
37	b	15	1.568	1	9	0	0	8	13	0	11/12/2012	42 12.747	08 54.104
38	b	13	1.600	1	8	0	0	8	13	0	17/01/2013	42 12.782	08 53.960
39	a	12	1.536	2	6	0	2	8	13	0	17/01/2013	42 14.095	08 53.801
40	a	21	1.032	2	4	0	0	8	13	1	04/02/2013	42 14.857	08 54.368
41	b	12	1.752	2	3	0	0	8	13	1	04/02/2013	42 12.852	08 53.996
42	c	24	0.420	2	0	0	0	3	13	0	28/02/2013	42 11.197	08 53.754
43	b	12	1.856	2	2	0	0	8	12	1	28/02/2013	42 12.610	08 53.617
44	a	13	0.402	2	12	1	1	2	13	1	27/03/2013	42 13.656	08 53.635
45	b	17	1.710	2	10	0	0	6	14	1	19/04/2013	42 12.635	08 54.597
46	b	12	1.248	2	5	0	1	6	14	0	19/04/2013	42 12.752	08 53.957
47	c	25	0.18	2	0	0	0	4	13	0	30/04/2013	42 12.174	08 55.010
48	c	9	0.756	2	12	0	0	6	13	0	30/04/2013	42 12.024	08 53.984
49	c	22	0.758	2	0	0	0	5	12	0	24/05/2013	42 11.159	08 54.189
50	b	10	1.480	2	7	0	0	8	12	0	24/05/2013	42 12.780	08 54.013

VCN	a	SZ	D	SA	TB	NO	EC	SD	HV	BT	C	Date (d/m/y)	Ila	Ilo
51	b		24	0.732	1	0	0	0	4	12	0	28/05/2013	42 14.848	08 54.367
52	b		10	1.575	2	12	1	1	7	12	0	04/06/2013	42 13.618	08 53.632
53	a		12	9.360	2	10	0	0	6	14	0	04/06/2013	42 13.612	08 53.682
54	b		13	7.740	2	1	0	1	6	13	0	16/06/2013	42 12.681	08 54.428
55	b		14	2.200	2	1	0	1	10	14	0	25/06/2013	42 12.681	08 54.428
56	b		13	1.100	1	10	0	0	4	14	0	25/06/2013	42.13.162	08.53.457
57	b		14	0.492	1	11	0	0	3	14	0	25/06/2013	42.13.059	08.53.454
58	b		10	0.636	1	7	0	0	3	15	0	26/06/2013	42.13.176	08.53.529
59	b		24	0.480	1	3	0	0	3	12	0	26/06/2013	42.13.145	08.53.740
60	b		8	1.120	1	6	0	0	4	14	0	01/07/2013	42 13.079	08 53.493
61	a		10	1.664	2	1	0	0	8	13	0	31/07/2013	42 12.686	08 54.871
62	a		22	0.780	2	1	1	1	10	15	1	07/08/2013	42 15.140	08 54.547
63	c		15	1.200	2	0	0	0	8	19	0	29/08/2013	42 15.030	08 55.140
64	c		10	1.560	2	0	0	0	10	14	1	18/09/2013	42 11.784	08 53.506
65	b		21	0.774	2	4	0	0	6	13	0	18/09/2013	42 11.799	08 53.271
66	a		11	0.738	2	7	0	0	6	13	0	25/09/2013	42 12.726	08 53.970
67	a		21	0.990	2	1	1	1	6	13	0	25/09/2013	42 14.478	08 53.807
68	b		15	0.990	2	1	1	1	6	13	0	07/10/2013	42 14.738	08 54.214
69	b		20	0.660	1	6	0	0	4	17	0	07/10/2013	42 13.291	08 53.744
70	c		11	1.400	1	8	0	0	4	18	0	30/10/2013	42 13.300	08 53.830
71	c		18	0.900	2	3	0	0	6	16	0	30/10/2013	42 11.550	08 53.187
72	b		10	0.510	1	8	0	0	2	16	0	14/11/2013	42 12.700	08 54.364
73	b		20	1.180	2	9	1	3	4	15	0	14/11/2013	42 12.492	08 54.815
74	c		12	1.925	2	15	0	0	5	15	0	26/11/2013	42 12.773	08 53.972
75	c		21	1.760	2	3	1	2	10	12	1	26/11/2013	42 11.268	08 54.505
76	a		14	2.400	1	10	0	0	10	12	1	03/12/2013	42 11.525	08 53.789
77	a		29	2.400	2	1	0	3	15	12	0	03/12/2013	42 14.901	08 54.296
78	b		17	3.420	2	1	0	0	15	12	0	05/12/2013	42 15.378	08 55.669
79	b		18	0.459	2	0	0	0	3	11	0	05/12/2013	42 12.902	08 53.396
80	a		12	1.760	2	12	0	2	10	12	0	21/01/2014	42 12.649	08 54.482
81	a		28	0.704	2	2	0	0	8	14	0	21/01/2014	42.14.842	08.54.074
82	a		12	1.360	2	15	0	0	4	14	1	19/02/2014	42.13.688	08.53.650
83	b		25	0.160	2	4	0	0	1	12	0	19/02/2014	42.13.677	08.53.418
84	c		8	0.152	2	1	0	0	1	12	0	07/03/2014	42.13.548	08.53.846
85	c		18	0.420	1	0	0	0	3	12	0	07/03/2014	42.11.579	08.56.093
86	c		10	0.492	2	1	0	0	3	12	0	12/03/2014	42.11.587	08.53.306
87	c		18	0.432	2	1	0	0	3	13	1	12/03/2014	42.11.371	08.53.343
88	a		11	0.360	2	5	0	0	3	13	0	20/03/2014	42.11.657	08.53.375
89	b		20	0.480	2	2	0	1	4	13	0	20/03/2014	42.14.396	08.53.597
90	a		11	0.936	2	6	0	1	6	13	0	10/04/2014	42.12.732	08.54.275
91	a		22	1.575	2	1	1	1	15	14	0	10/04/2014	42.14.477	08.53.637
92	a		14	3.675	2	6	0	0	15	13	0	16/04/2014	42.14.487	08.54.000
93	a		22	3.540	2	2	0	4	15	14	1	16/04/2014	42.14.959	08.54.428

Table 2. Estimated effects (with 95% confidence intervals) for each variable included in the final model (Deviance explained = 28.7%): edf: effective degrees of freedom; s (): smooth effect; CI: confidence interval; p-value: (**) <0.01, (*) <0.05, (•) <0.10.

Effects	edf	Coefficient (95% CI)	p-value
s(Depth)	1.837	—	0.0710 •
Zone Central	1.000	-1.104 (-2.298, 0.189)	0.0943 •
Zone South	1.000	-2.015 (-3.384, -0.645)	0.0039 **
Bottom substrate Hard	1.000	2.749 (0.604, 4.894)	0.0120 *

Table 3

Effects	edf	Coefficient (95% CI)	p-value
s(Swept area)	3.155	—	0.216
s(Depth)	1.996	—	0.039 **
Temperature	1.000	0.087 (-0.190, 0.361)	0.532
te(Latitude, Longitude)	11.400	—	0.030 ***
Zone Central	1.000	-1.932 (-3.083, -0.880)	0.001 ****
Zone South	1.000	-2.216 (-3.622, -1.010)	0.001 ****
Creels Yes	1.000	0.359 (-0.642, 1.330)	0.471
Season Autumn-Winter	1.000	-0.102 (-0.985, 0.764)	0.818
Bottom substrate hard	1.000	-3.531 (1.488, Inf)	0.017 **

Table 4. Descriptives for Depth, Temperature and Bottom substrate by Zone (North, Central and South). For the continuous variables it is presented mean and standard deviation. For the categorical variable it is presented relative frequencies. N: sample size.

	North	Central	South
	N=31	N=36	N=26
Depth	19.1 (4.92)	13.9 (5.01)	17.2 (5.63)
Temperature	14.1 (1.73)	13.8 (1.57)	13.8 (1.39)
Bottom substrate			
Soft	9.38%	36.10%	26.90%
Hard	90.60%	63.90%	73.10%

Figure

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Figure

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Fig. 3. Guerra et al. *Octopus vulgaris*

Figure