Using artificial devices for identifying spawning preferences of the European squid: Usefulness and limitations

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Abstract

Sustainable management of exploited stocks demands, among others issues, to identify the spawning spatio-temporal patterns and eventually to protect the spawning grounds of the target species. Squid seems to aggregate at this crucial period of the life-history, which implies increasing vulnerability to fishing. Unlike those of other loliginid species, the spawning preferences of the European squid are largely unknown because finding egg clutches of this species in the wild is challenging. Validated records from research programs are virtually inexistent but unsystematic records from, for example fisherman, suggest that squid spawns regularly on artificial structures. Here, we report for first time a description of the spatio-temporal pattern of squid spawning on artificial devices (ADs). Thirty ADs were deployed over one year at a marine reserve (Cabrera National Park). ADs were distributed covering the three main types of benthic habitat, and ranging from 5 to 50 m depth. ADs were sampled monthly. Three main patters have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning would peak in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. It is debatable to extrapolate these patterns to those actually takes place in natural conditions. However, given the heavy fishing effort exerted on squid and data scarcity, the precautionary approach supports to take data from ADs as a starting point for advising sustainable management. Assuming that spawning at ADs and at the wild are correlated, the first pattern may be related to the faster marine currents that prevail on sandy bottoms or the lower abundance of potential predators in these habitats. The second pattern may be related with the typical phytoplankton-zooplankton cascade that, in the Western Mediterranean, takes place just preceding spring. While the third pattern is in accordance with the hypothesis that squid may undergo a spawning migration.

Keywords: Marine Protected Area; *Loligo vulgaris*; Egg Clutches; Essential Fish Habitats; Spawning Migrations

1. Introduction

Habitat degradation and overfishing may cause severe decline in some exploited living marine resources (Worm et al., 2006). Cephalopods are important target species for fisheries worldwide (Boyle and Rodhouse, 2005), thus stocks are potentially susceptible to overfishing (Pierce and Guerra, 1994). As in the cases of other short-lived species, squid abundance experiences important between-year variability and depends on environmental variability (e.g., temperature; Pierce et al., 2008), which complicates management.

In an effort to promote sustainable fisheries, different management strategies have been implemented to reduce fishing mortality, mainly through fishing limitations. Conventional regulations consist in limiting days-at-sea, closing areas, closing seasons and implementing gear restrictions (Morales-Nin et al., 2010). However, in some cases, this conventional approach has been ineffective (Hutchings, 2000). Therefore, integrating species-specific fishing limitations with a broader management strategy has been proposed (Roberts et al., 2005). This new paradigm implies, for example, that the biology and ecology of the species to be protected should be considered to achieve a successful regulatory implementation. For example, the movement characteristics of a species should be known to determine the optimal extension of a marine protected area (Walters, 2000; Taylor and Mills, 2013). To address such integrated management strategy, previous research has indicated the importance of identifying and eventually protecting essential fish habitats (EFHs; Rosenberg et al., 2000). An EFH is the habitat identified as essential to the requirements of a species at any critical stage of the life history. EFHs would require special protection for improving stock status and ensuring long-term sustainability (Valavanis and Smith, 2007). Therefore, the protection of EFHs is a challenge and should be considered when managing fisheries (Benaka, 1999).

Population dynamics of most short-lived species are characterized by important spatio-temporal variability, which, in the specific case of cephalopod fisheries, complicates the implementation of any management option (Pierce and Guerra, 1994; Boyle and Rodhouse, 2005). Nevertheless, sustainable development of the South African squid fishery was achieved after identifying and protecting some preferential spawning areas of the chokka squid, *Loligo reynaudii* (Augustyn and Roel, 1998), which supports the potential usefulness of characterizing EFHs of cephalopods.

The European squid, *Loligo vulgaris* Lamarck (1798), experiences considerable fishing pressure. This valued resource is one of the most exploited cephalopods in European waters (Pierce et al., 2010). In the Mediterranean Sea, the European squid is targeted by the trawl fishery (González and Sánchez, 2002), the artisanal fishery (hand-line-jigging with attraction lights and seine fishing; Guerra et al., 1994; Lefkadltou et al., 1998; Cabanellas-Reboredo et al., 2011; Ulaş and Aydin, 2011) and the recreational fishery (Cabanellas-Reboredo et al., 2014). A large recreational jigging effort concentrates at specific grounds (inshore waters at 20-35 m depth; Cabanellas-Reboredo et al., 2014) during the reproductive season of this species (winter-spring; Šifner and Vrgoč, 2004). Previous reports have suggested that the pattern depicted by the recreational fleet may be related to inshore-offshore spawning migrations of this species (Cabanellas-Reboredo et al., 2012a; Cabanellas-Reboredo et al., 2014). Squid may undergo these spawning migrations in an attempt to maximize spawning success (Villanueva et al., 2003; Cabanellas-Reboredo et al., 2012a) by optimizing embryonic development (e.g., seeking an optimal temperature range; Şen, 2005). Inshore spawning aggregations are highly vulnerable to fishing (Boyle and Rodhouse 2005). Therefore, fishing mortality is expected to intensify during a critical period in the squid life-history (Pierce and Guerra, 1994; Boyle and Rodhouse, 2005). The identification of spawning areas could play an important role in ensuring the stock sustainability as is the case of the above-mentioned *L. reynaudii* (Augustyn and Roel, 1998; Cochrane et al., 2014). Unfortunately, unlike other exploited loliginid species (e.g., *Loligo reynaudii* or *Loligo opalescens*) whose spawning grounds have been well identified, delimited and characterized (Sauer et al., 1993; Foote et al., 2006), data on explicit observations of the spatio-temporal spawning patterns of *L. vulgaris* are not available.

L. vulgaris females have been reported to lay eggs in clusters attached to different hard substrates or branched sessile organisms (Jereb and Roper, 2010). However, to find squid eggs at the wild seems to be very challenging. The study area considered here is a National Park, thus a large number of systematic scientific sampling programs (scuba diving visual censuses) have been completed but reports of egg clutches are merely anecdotic (Vázquez-Luis et al., Submitted). Conversely, non validated or unsystematic reports of egg clutches attached to fishing gears and other artificial structures (e.g., ropes of acoustic tracking structures; Cabanellas-Reboredo et al., 2012b) are relatively frequent. When detecting natural egg clutches is difficult or impossible, the use of artificial substrates has been suggested as an alternative sampling methodology (e.g., in the case of *Perca fluviatilis*; Gillet et al., 2013) and they has been already used in the case of *L. vulgaris* (Villa et al., 1997).

Here we reported for first time a description of the spatio-temporal pattern of squid spawning on artificial devices (ADs). Three main patters have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning peak takes place in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. The interpretation of the data obtained with ADs is not straightforward because the patterns observed may be biased in relation to the natural patterns. However, in the case of no data and applying a precautionary approach to a heavily exploited resource, the use of ADs may be a valuable starting point for implementing effective management measures.

2. Materials and methods

2.1 Study area

This study was conducted at Cabrera Archipelago National Park (CNP) (Balearic Islands, NW Mediterranean; Fig. 1). The CNP is a combination of nineteen small islands that form one of the largest marine reserves in the Mediterranean, with a coastline of 54 km and 87 km^2 of marine protected area.

Fishing started very early at Cabrera, with archaeological evidence of fish salting during Roman times (Frontera et al., 1993). Fishing activity, especially recreational fishing, was important from the 1960s (Massutí, 1991). After the enforcement of the marine reserve in 1991, a total of 80 small-scale boats were registered to fish in CNP waters (Coll et al., 1999). However, the current fishing effort is unknown (although most likely smaller) because these boats also operate outside the CNP. The main activity of these small-scale boats is trammel net fishing, but they may also fish for squid using hand-line-jigging with attraction lights. Trawling and recreational fishing are banned within the CNP.

2.2. Sampling strategy

Thirty ADs (Fig. 2A) were randomly deployed in the three main benthic habitat types (phanerogams, sandy and rocky bottoms) and covering a depth range from 5 to 50 meters (Fig. 1).

ADs were recovered monthly, and the egg clutches attached to the structures were collected and counted (Fig. 2C-D). The sampling frequency was based on the embryonic development of *L. vulgaris*, which lasts approximately one month (Şen, 2005). Samples were collected from June 2012 to June 2013, with the exception of February due to rough weather. The smooth gooseneck barnacle, *Lepas anatifera* Linnaeus (1758), was found on a relatively large number of ADs buoys (Fig. 2B). The presence/absence of this barnacle was also recorded. The egg clutches were removed to avoid over-counting in the subsequent sampling period, and ADs were replaced in the same position after sampling.

2.3. Data analysis

The goal of the analysis was to identify the environmental variables explaining the number of egg clutches on an AD and use these variables to predict the expected number of eggs clutches on an AD located at any point of the MPA and at any time of year. Raw data of the potential explanatory variables were obtained from diverse sources and they are at different spatial scales. Therefore, the input data for the analyses were first prepared (*raster* library of the R package and ArcGIS 9.2 ESRI) to fit them to a common statistical unit (AD-Month). Then, a Zero-Inflated Poisson (ZIP) model was used to model the response variable (number of egg clutches by AD and per month) as a linear combination of the potential explanatory variables (Habitat Type, Depth and Sea Surface Temperature; see below).

2.3.1. Predictive variables

Depth (*D*) and Habitat Type (*HT*) were obtained from the data produced by a LIFE project (Posidonia-LIFE map, Government of Balearic Islands; http://lifeposidonia.caib.es/user/home.htm), which provided information at a fine scale (5 m^2). The 24 benthic habitats characterized were grouped into three main types: 1) sandy bottoms (*HTS*), 2) rocky bottoms (*HTR*) and 3) bottoms covered by phanerogams (*HTP*) (Table 1).

Daily Sea Surface Temperature (*SST* in °C) was obtained from the MyOcean website (http://www.myocean.eu/) with a spatial resolution of 1 km^2.

2.3.2. Zero-Inflated Poisson Model

A preliminary inspection of the response variable (*EggClutches*$_{ij}$; number of egg clutches at the i^{th} AD and in the j^{th} sampling period) corroborates the non-normal distribution of the data. The apparent excess of zero values suggests that actual counts may result from the mixing of a Poisson distribution and a binomial distribution. Such a binomial distribution determines the probability of obtaining a false zero (i.e., spawners are present at the area around a specific AD at the time of sampling, but the AD does not record the spawning activity of these squid; Martin et al., 2005). This type of data can be analyzed using a ZIP model (Zuur et al., 2012). The fact that all ADs are sampled at the same day implies an additional analytical complexity, because samples from the same day can not be considered independent. Therefore, the explanatory variables of Habitat Type (Sandy *HBT*, Rocky *HTR* and phanerogams *HTF*), Depth (*D*) and Sea Surface Temperature (*SST*) were considered fixed variables, but the sampling period (*Month*) was added as a random effect. The binomial portion of the mixed ZIP model was simply:

$$W_{ij} \sim \text{Binomial}(\pi),$$

where W_{ij} can be either 0 or 1.

The Poisson portion was:

$$\begin{aligned}
&\mu e\!f\!f_{ij} = W_{ij}\mu_{ij}\\
&ObEC_{ij} \sim \text{Poisson}(\mu e\!f\!f_{ij})\\
&Log(\mu_{ij}) = \beta_0 + \beta_1 HTS_i + \beta_2 HTR_i + \beta_3 D_i + \beta_4 SST_{ij} + \beta_5 D_i SST_{ij} + MonthEffect_j\\
&MonthEffect_j \sim \text{Normal}(0,\sigma),
\end{aligned}$$

where i denotes the 30 ADs, j the number of sampling dates (11) and $ObEC_{ij}$ the observed number of egg clutches. It is important to note that when W_{ij} is zero, the effective mean of the Poisson process ($\mu e\!f\!f_{ij}$) is zero as well; thus, the actual observed number of egg clutches ($ObEC_{ij}$) is zero (i.e., a false zero). Otherwise (W_{ij} =1), $\mu e\!f\!f_{ij}$ depends on the linear combination of the explanatory variables.

Currently, no closed statistical package allows fitting such a ZIP model when including random effects. Therefore, this model was fitted using the Bayesian machinery as implemented in JAGS (http://mcmc-jags.sourceforge.net/) and using the *R2jags* library (http://cran.r-project.org/web/packages/R2jags/index.html) from the R package (http://www.r-project.org/ v2.15-2), with the following priors (mean and tolerance are indicated in brackets):

$$\beta_0 \; to \; \beta_5 \sim \text{Normal}(0, 10^{-6})$$
$$\text{logit}(\pi) \sim \text{Normal}(0, 10^{-6})$$
$$\sigma_{MonthEffect} \sim \text{Gamma}(0.01, 0.001),$$

where π (the prevalence of false zero values) is within the interval between 0 and 1. The conventional tools for assessing proper mixing of the Monte Carlo Markov chains (MCMC), convergence and lack of autocorrelation (burning interval = 500; number of chains = 3; valid sample size after thinning per chain = 1000), were used.

After model fitting, the model residuals were inspected to check over-dispersion (comparing the final model with the fully saturated model, as suggested by Zuur et al. 2012). The occurrence of an identifiable effect of any putative explanatory variable was evaluated based on 95% Bayesian credibility intervals (CI) for βs (and whether these intervals included zero).

Moreover, to improve the interpretation of the results, the fitted ZIP parameters were used to predict the expected number of egg clutches around the entire spatial scenario (Cabrera National Park) and for any moment of the seasonal cycle considered. A spatial framework was defined by a grid of 381 cells of 500 x 500 m. The eastern part of Cabrera National Park was not included in the predictions to avoid extrapolation at areas with scarce or no observations. One thousand bootstrap simulations were run to estimate the expected numbers of egg clutches and its variability (95% credibility intervals). Then, the mean expected values for each cell were mapped.

2.3.3. Complementary variables

To improve the interpretation of the results, some complementary variables were examined. These variables were not included in the ZIP model because they were not available for the entire spatial scenario or are available at coarse temporal scale, and thus could not be used with predictive purposes, and/or they are highly correlated with the variables included in the model (thus, avoiding potential collinearity problems). These complementary variables were presence/absence of *L. anatifera* on the AD buoys and Sea Surface Chlorophyll. The presence/absence of a filter-feeder species (*L. anatifera*) was used as a proxy (bioindicator) of zones where marine currents ensured food availability, which may improve the recruitment success of filter-feeder species (Inatsuchi et al., 2010). The effects of Habitat Type and Depth on the presence/absence (cumulated along the entire study period) of this barnacle were tested using a Generalized Linear Model (GLM) as implemented in the *lme4* library of the R package.

The other complementary variable that was considered was Sea Surface Chlorophyll (SSC; mg m^{-3}). To explore any type of relationship between squid spawning and primary production, the monthly average values (daily values are very incomplete) of this variable were downloaded from the MyOcean website with a spatial resolution of 1 km^2.

3. Results

Some egg clutches were recorded at some ADs throughout the entire year, but egg count reached a maximum peak in spring (May) with a gradual decrease afterwards (Fig. 3). The lowest number of egg clutches was recorded between October-January. Therefore, the spawning activity of *L. vulgaris* seems to extend all year-round.

A total of 242 egg clutches were recorded, of which 72.3% were attached to ADs located on sandy bottoms (Fig. 3 and 4). ADs located on rocky bottoms recorded 23.5% of the total egg clutches. The eggs attached to ADs deployed on phanerogams accounted 4.2% only. Moreover, egg clutches were only recorded between depths of 18 and 50 meters. No eggs were recorded from 5 to 17 meters depth. AD#27 (Fig. 1) was the shallowest AD (18 meters depth) with egg clutches (Fig. 4).

The estimated values for the ZIP model parameters are summarized in Table 2. These results demonstrated an effect of habitat type on the spawning preferences of *L. vulgaris*. More egg clutches tend to be found on ADs located on the sandy bottom and, to a lesser extent, on rocky bottoms (Table 2). The expected number of egg clutches on phanerogam bottoms was smaller (note that this effect was included in the grand mean β_0 in Table 2). Concerning depth, the number of expected egg clutches increased at deeper ADs.

SST alone had not a relevant effect on squid spawning preferences (95% CI included zero; Table 2). However, the interaction between SST and Depth suggested a relevant effect (Table 2 and Fig. 5): During warm months (e.g., September), egg clutches only appeared on ADs deployed in deeper waters (40-50 meters depth). Conversely, during cold months (e.g., February), egg clutches also appeared in shallower waters (18-39 meters depth; Fig. 5).

In regards to the complementary variables, we found a significant relationship between the presence/absence of *L. anatifera* with Depth and Habitat Type variables. *L. anatifera* tend to be present at deeper ADs and at ADs located on sandy bottoms (GLM results *p*-value <0.05). The temporal pattern of the SSC showed a clear peak at the end of winter (maximum values in March) but remained at a low levels during the rest of the year (Fig. 3).

4. Discussion

Here, we reported for first time a description of the spatio-temporal pattern of squid spawning on artificial devices. Three main patters have been evidenced: i) squid would prefer sandy bottoms for spawning, ii) spawning would peak in spring, and iii) squid would expand their spawning areas to shallower waters during the coldest months. However, the interpretation of the data obtained with ADs is not straightforward because the patterns observed may be biased in relation to the natural patterns. A number of hypotheses are possible. First, the chance of spawning on an AD is similar than on a natural substrate but clutches are cryptic and, therefore, not easily recorded by scuba divers. Second, the eggs clutches that should be laid in a large area around an AD are all attached to the AD (sink effect). Third, the strength of the sink effect depends on habitat or season, thus inducing bias. Forth, squid are induced to spawn by the mere presence of an AD even at inadequate habitat or season.

The available evidences are weak and all concerning fish. First, eggs counted by scuba divers on natural substrates and on artificial structures are different but correlated in *Perca fluviatilis* (Gillet et al., 2013), which would be against the third and fourth hypotheses. Second, depending on the site, fish may shift to spawn from natural to nearly located artificial substrates after AD deployment (sink effect) or egg number may remain similar (Hickford and Schiel, 2013).

Note that both the first and the second hypothesis do not invalidate the patterns found because egg abundance on AD would be relative estimates of the egg abundance at natural conditions, and therefore natural and AD abundance would remain well correlated. Nevertheless, the interpretation of the patterns found should be done with caution until the third and forth hypotheses were not rejected. In the meantime, given that squid is a heavily exploited resource, and provided that virtually no data are available in spite that a large number of scuba diving visual censuses have been completed, a precautionary approach could be adopted and the spatio-temporal pattern depicted by ADs may be considered as a valuable starting point for identifying and characterizing the possible spawning EFHs and preferred spawning seasons of the European squid, *L. vulgaris.*

The first pattern found in this study showed that the European squid preferentially choose ADs located on sandy bottoms for spawning (Table 2). This pattern may be the result of biased strength of the sink effect mentioned above. It is well known that most loliginid species frequently attach eggs on ropes, nets, traps and other fishing gears when these artificial structures are available (Hanlon and Messenger, 1996; Jereb and Roper, 2010). Few natural substrates would be available in sandy bottoms, thus ADs may be more effective to collect eggs. Conversely, rocky bottoms and phanerogams offer more potential natural substrates for egg attachment, thus ADs may be less effective.

Alternatively to the existence of a biased sink effect, squid preference for ADs located on sandy bottoms may reflect genuine habitat selection. In that case, this pattern might arise because a potential squid predator, *Epinephelus marginatus,* is very abundant in the CNP but is mainly restricted to rocky bottoms (Reñones et al., 1997; Reñones et al., 1999). It has been reported that predator presence may induce disruptions of egg deposition and cause the absence of chokka squid (*L. reynaudii*) from a priori adequate spawning grounds (Smale et al., 2001). It is also possible that the presence of predators was not the only factor that triggered a positive selection for the sandy bottoms as preferential spawning habitat. The positive relationship between sandy bottom and the presence of the filter-feeder *L. anatifera* suggests that sandy areas may have more favourable environmental conditions (food availability and currents; Inatsuchi et al., 2010), which it turn, may enhances survival of squid paralarvae (Roberts and van den Berg, 2002; Roberts et al., 2005; Martins et al., 2013).

Spawning at sandy habitats is not be a general pattern for squid. At one hand, it has been reported that other squids (*L. opalescens* and *L. reynaudii*) spawn on sandy bottoms (McGowan, 1954; Sauer et al., 1993). Moreover, in the same geographic region (Central and NW Mediterranean sea), sandy and muddy bottoms have also been suggested as potential spawning areas for *L. vulgaris* (Valavanis et al., 2002; Sánchez et al., 2008). Conversely, gravel and rocky bottoms are preferred to spawn by another related species, *L. forbesi* (Smith et al., 2013).

Regarding to the second pattern found, *L. vulgaris* maximum spawning activity at ADs (May) occurred two months after the chlorophyll peak (March; Fig. 3). An increase in the number of egg clutches of *L. vulgaris* has previously been reported during periods of higher zooplankton abundance (Villa et al., 1997). At Cabrera National Park, after the primary production peak in March, the mesozooplankton biomass reaches maximum concentrations in May (Álvarez et al., 2012), suggesting that the spawning peak of squid (May) could be adjusted to maximize food availability (mesozooplankton) for paralarvae (Fig. 3). It has been suggested that the European squid may modulate the seasonal timing of reproductive effort (Guerra and Rocha, 1994; Moreno et al., 1994; Arkhipkin, 1995; Šifner and Vrgoč, 2004) according to the specific environmental conditions of different geographical areas (Moreno et al., 2002; Boavida-Portugal et al., 2005).

The European squid seems to show some spawning activity all-year-round (Šifner and Vrgoč, 2004) but temperature has been repeatedly related with the strength of the spawning activity (Sauer et al., 1991; Roberts, 1998; Pierce et al., 2008). However, SST alone did not show a relevant effect on the temporal spawning pattern of *L. vulgaris* at Cabrera National Park, where at least some egg clutches were recorded all year-round. Conversely, the interaction between SST and Depth was clearly relevant. The relevant effect of this interaction is compatible with the existence of an offshore to inshore spawning migration during the coldest months. The outcome of such a migration would produce a spatial pattern similar to the one suggested by the model predictions (Fig. 5). *L. vulgaris* may spawn at deep waters throughout the year, but at cold months (when inshore waters reach lower temperature values), squid can spawn too at inshore waters. The hypothesis of inshore-offshore spawning migrations has been previously suggested by other studies in the Mediterranean Sea (Tinbergen and Verwey, 1945; Sánchez and Guerra, 1994; Valavanis et al., 2002; Cabanellas-Reboredo et al., 2012a).

Additional but indirect evidence for the hypothesis of spawning migration emerges from the spatio-temporal pattern of fishing effort of the recreational squid jigging fishery. Recreational squid fishing is restricted at inshore waters (20-35 meters depth), but only during the cold season (Cabanellas-Reboredo et al., 2014). Accordingly, it has been suggested that European squid seek spatio-temporal windows within which the bottom temperature optimizes spawning success (Cabanellas-Reboredo et al., 2012a, b). Reproductive success seems to be maximized within a relatively narrow range of sea temperatures, which is 12 to 17°C for *L. vulgaris* (Villanueva et al., 2003), and such a narrow temperature range maximizes hatching success (Şen, 2005, Rosa12). Therefore, depending on the sea temperature, squid may move from deeper waters to inshore waters. The existence of spawning migrations has been proposed for other loliginid species; for example, *L. reynaudii* in South Africa, where the temperature is one of the main environmental variables involved in the inshore spawning migration of this species (Sauer et al., 1991; Roberts, 1998).

Resource management of cephalopods has been performed with different measures such as a minimum legal size, the establishment of closed seasons, catch quotas and fishing power limitation (Pierce and Guerra, 1994; Augustyn and Roel, 1998; Rodhouse, 2001; Boyle and Rodhouse, 2005; Otero et al., 2005). However, perhaps due to their specific biological characteristics (very short life cycle, single lifetime breeding, and high turnover rate of annual biomass; Boyle and Rodhouse, 2005), conventional management techniques have not worked appropriately with cephalopods (Pierce and Guerra, 1994), nor have been effective in preventing the acute abundance decrease of some stocks in Galicia and elsewhere (Guerra et al., 2010). Another possible protection measure is to limit access to the resource by means of marine protected areas (MPAs). However, MPAs seem to be ineffective when protecting highly mobile species (Kramer and Chapman, 1999; Nowlis and Roberts, 1999; Gerber et al., 2003; Afonso et al., 2009; Claudet et al., 2010; Abecasis et al., 2013), which seems to be the case for *L. vulgaris* (Cabanellas-Reboredo et al., 2012b). MPAs may still play a role in protecting *L. vulgaris* populations' reproductive output, provided that they encompass appropriate spawning grounds. Recently, the protection of preferential reproductive EFHs for another cephalopod, *Octopus vulgaris*, has been proposed (Moreno et al., 2014; Guerra et al., Submitted).

In agreement with the results reported here, relatively small areas (e.g., those bounded by red circles in Fig. 1) could be especially favourable for spawning. Therefore, identifying and protecting these areas could enhance squid stock in places where it was necessary. However, as expected, most of the fishing effort is concentrated in these areas as well (Frontera et al., 1993) because fishermen are taking advantage of higher abundance and catches at EFHs. A compromise solution could be to protect EFHs only during the peak spawning in spring (spatio-temporal closure), but the trade-off between the short-term decrease in captures and long-term enhancement of the stock should be solved prior to suggest any specific measure.

The placement of artificial surfaces for cuttlefish spawning using cuttlefish traps has been suggested to avoid egg losses (Blanc and Daguzan, 1998). However, ADs could promote egg laying at inappropriate sites. Therefore, after demonstrating that the availability of adequate substratum may be a limiting factor for squid spawning and that egg clutches laid on artificial structures are at least as successful as those laid at natural substrates, the usefulness of placing ADs at sandy bottoms could be explored as a complementary management measure, as it has already been implemented to improve spawning at degraded habitats (Hickford and Schiel, 2013).

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Tables

Table 1. Reclassification of the Habitat types from the LIFE project characterization.

Habitat types	LIFE Project habitat classification
Sandy bottoms ***HTS***	Fine sand, Coarse sand, Poorly calibrated sand, Coralligenous, Dispersed coralligenous, Coastal dendritic, Precoralligenous, Dispersed precoralligenous
Rocky bottoms ***HTR***	Dispersed sciaphilous community, Littoral rock sciaphilous community, Infralittoral rock photophilic community, Dispersed photophilic community, *Peyssonnelia* coastal detrital, *Vidalia* coastal detrital, Pebbles coastal detrital, Precoralligenous on hard bottom
Phanerogams ***HTP***	Dense *Cymodocea*, Dispersed *Cymodocea*, Isolated phanerogams, Phanerogams with batches, Continuous phanerogams, Degraded phanerogams, Rocky phanerogams, *Cymodocea-Caulerpa* grassland

Table 2. Summary statistics for the posterior distributions of fixed and random effects. Relevant fixed effects are highlighted in grey.

	Parameters	**Description**	**Mean**	**SD**	**Bayesian Credibility Intervals**		
					2.5%	**Median**	**97.5%**
	π	False zero parameter	0.281	0.078	0.135	0.278	0.434
Fixed factors	β_0	Grand mean	-2.445	0.609	-3.800	-2.390	-1.355
	HTS	Habitat type sandy	1.772	0.388	1.056	1.747	2.605
	HTR	Habitat type rocky	1.016	0.403	0.271	0.989	1.883
	D	Depth	-0.076	0.008	-0.093	-0.076	-0.060
	SST	Sea Surface Temperature	-0.126	0.099	-0.321	-0.126	0.056
	D*SST	Interaction Depth*Sea Surface Temperature	-0.007	0.002	-0.011	-0.007	-0.004
Random	σ_γ	*Month* effect	1.331	0.475	0.739	1.242	2.445

Figure legends

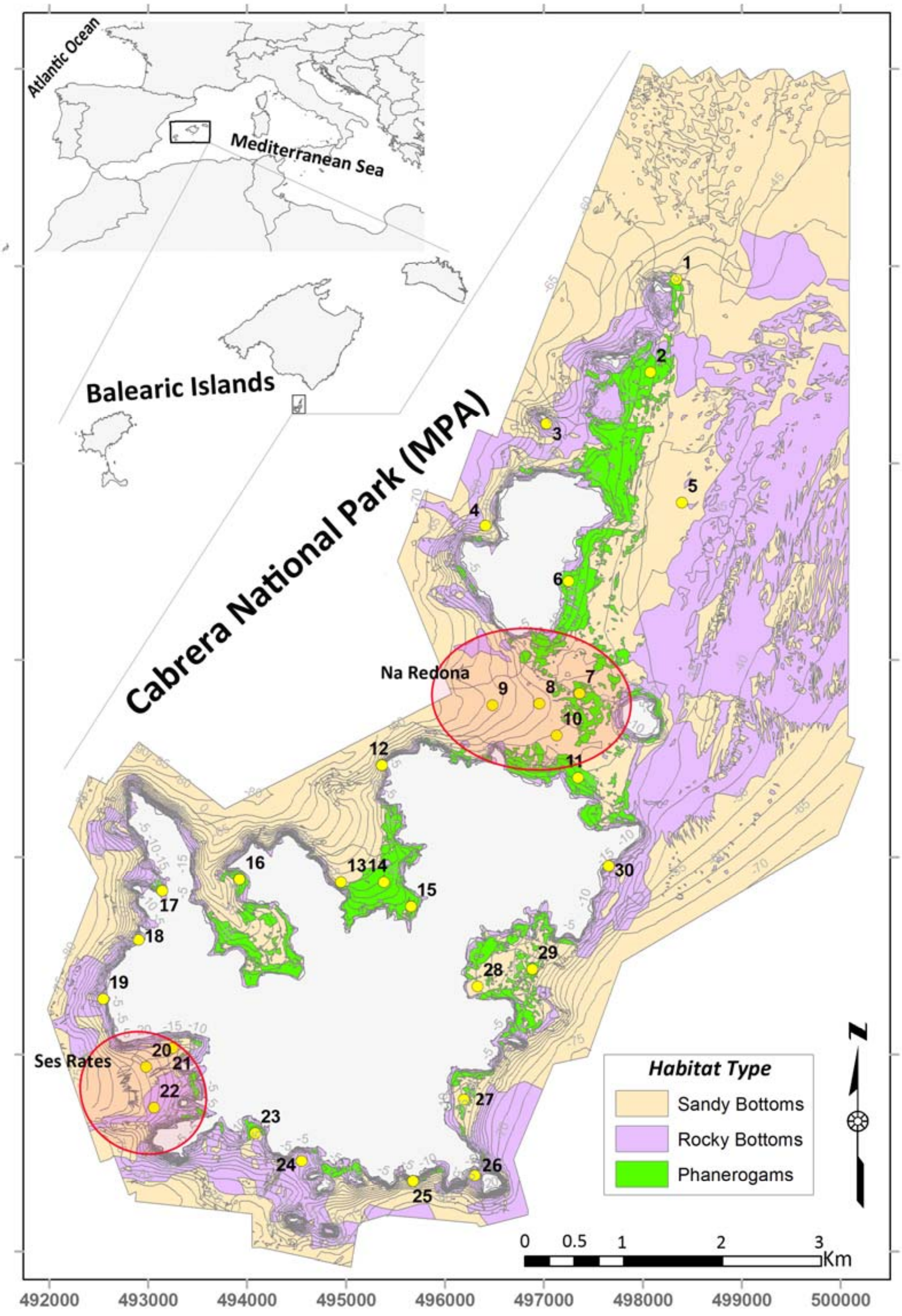

Fig. 1 Location of the study area and distribution of artificial devices (ADs) on the three main benthic habitats around Cabrera National Park. Na Redona and Ses Rates locations are highlighted by red circles. Isobaths are designated at 5 m intervals.

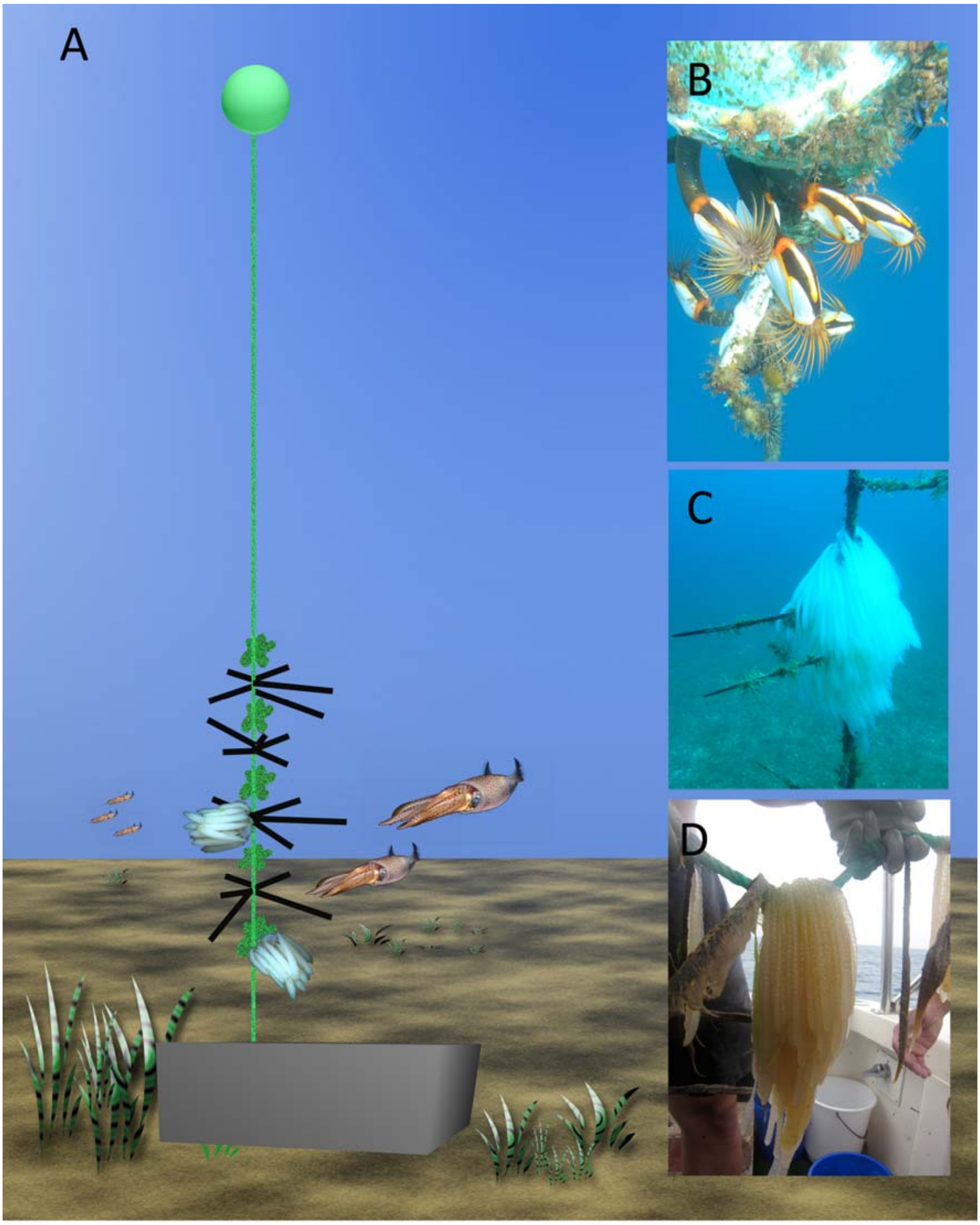

Fig. 2 Artificial devices (ADs) for *Loligo vulgaris*. A) Structure of the AD formed by a rope (Ø 1.2 cm), a buoy to keep the rope extended and a weight on the bottom to fix the structure in place. The first two meters of rope from the bottom contain 5 knots and plastic flanges (16) placed among these knots (to increase the attachment surface). B) Recruitment of several individuals of *Lepas anatifera* on an AD buoy. C) The egg clutches attached to the rope or flanges. D) Detail of the egg clutches recovered on board.

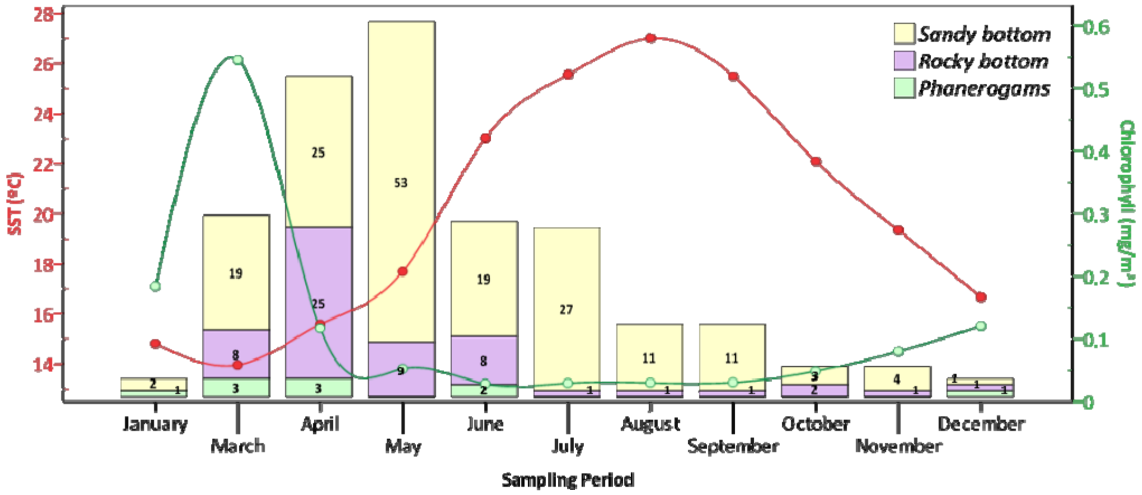

Fig. 3 *Loligo vulgaris* spawning activity (cumulated number of egg clutches per month) related to benthic habitat (colours of the bars), sea surface temperature (SST, red line) and sea surface chlorophyll (SSC, green line). Note the absence of February due to logistical problems during the sampling process.

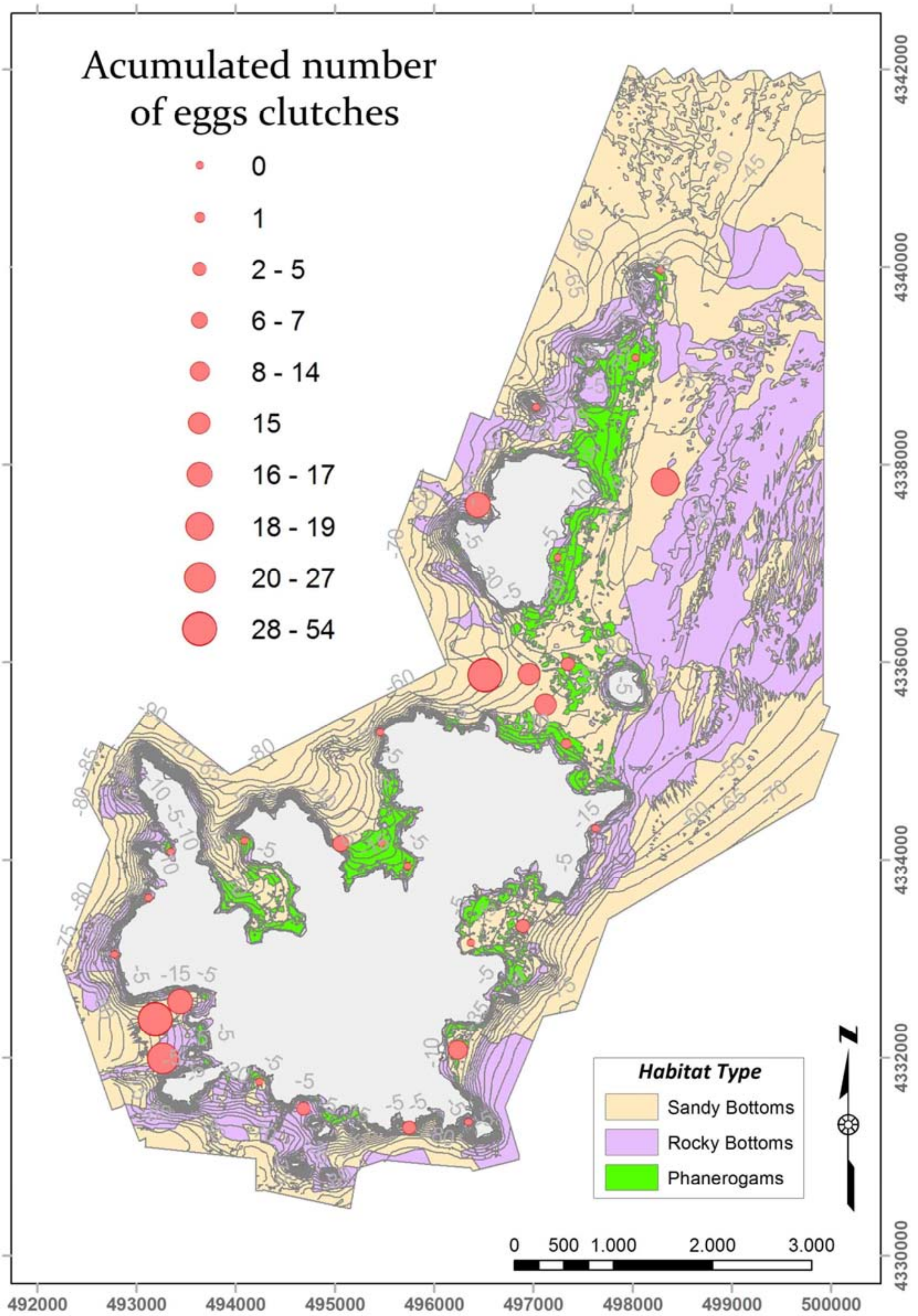

Fig. 4 *Loligo vulgaris*. Spatial distribution of the accumulated number of egg clutches by an artificial device (AD).

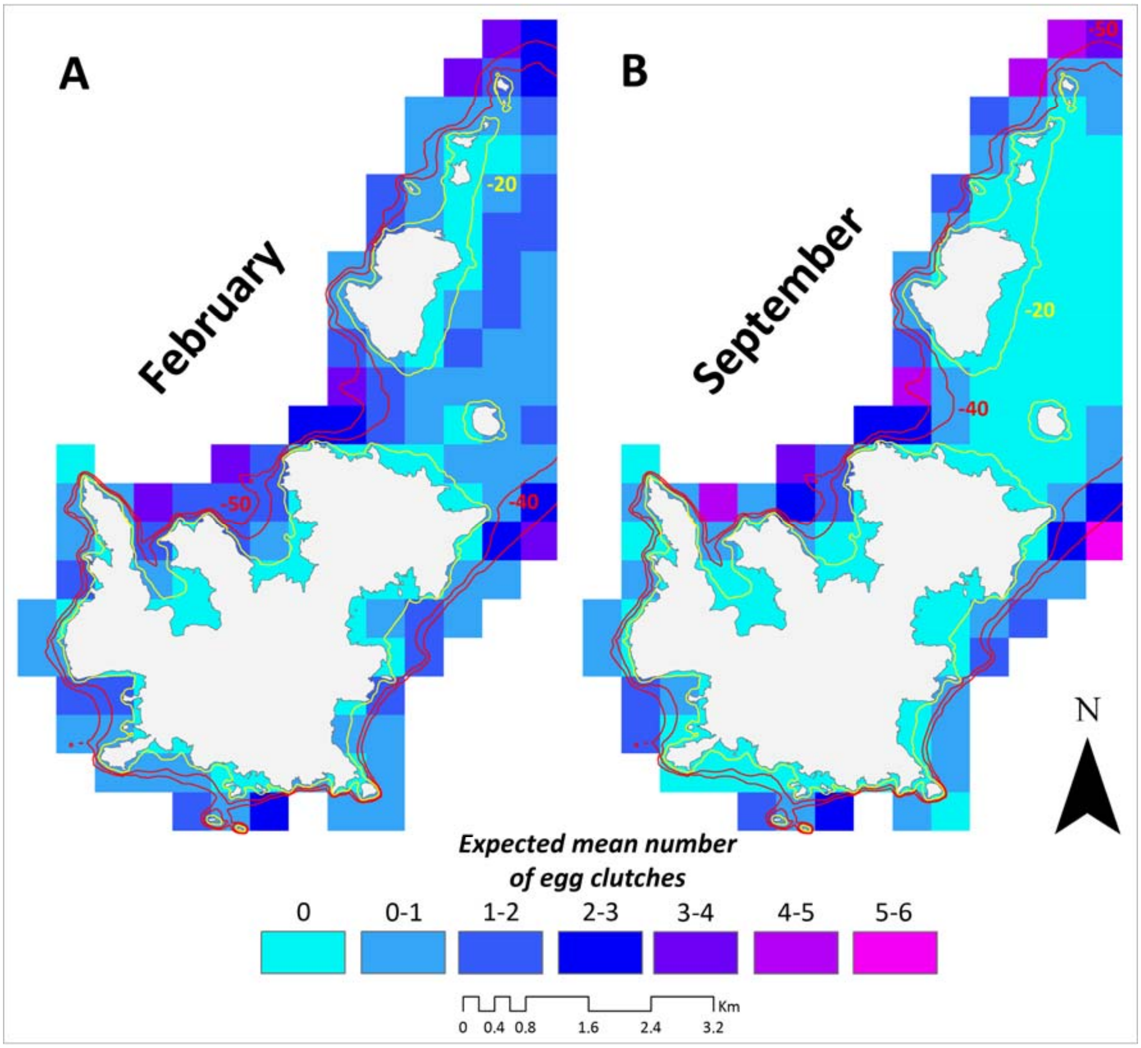

Fig. 5 Maps predicting the expected mean number of egg clutches of *Loligo vulgaris* in a: A) cold month and B) warm month. Isobaths at 40 and 50 m depth are represented by red lines. The isobath at 20 m depth is represented by a yellow line.

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