

Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean



Stefanie Keller*, Maria Valls, Manuel Hidalgo, Antoni Quetglas

Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, 07015 Palma de Mallorca, Spain

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ABSTRACT

The cuttlefish *Sepia officinalis* constitutes an important fishery resource in the Mediterranean, where it is exploited by both the bottom trawl and small-scale fleet. However, there is currently scarce information on the Mediterranean stocks, since most studies on the population dynamics of this species have been undertaken in the northeast Atlantic. In this work we first analysed different aspects of the cuttlefish life-history from the western Mediterranean such as population structure, reproduction and the trade-offs between somatic condition and reproduction investments. Secondly, we investigated the effects of different environmental parameters (e.g. climate indices, sea surface temperature (SST), rainfall, chlorophyll-a concentration (Chla) and moon phase) on these populations, analysing several landing time series spanning the last 45 years. Our results revealed that Mediterranean cuttlefish populations exhibit strong seasonal variations owing to a reproductive migration towards coastal waters. The positive relationships between somatic and reproductive condition pointed to an income breeder strategy; this was reinforced by the percentage of empty stomachs, which was lowest just before the reproductive period peak. Despite the putative high sensitivity of cephalopod populations to external abiotic factors, our results showed that Mediterranean cuttlefish populations were not affected by most of the environmental parameters investigated. Significant effects were found for SST and a local climatic index, but no or very weak influences were evident for other parameters such as large-scale climatic phenomena (e.g. North Atlantic Oscillation, Mediterranean Oscillation) or other locally-related variables (e.g. rainfall, Chla). Our results revealed a shift in the cuttlefish population dynamics in the early 1980s, which could be related to important changes in the local hydroclimatology reported by previous authors.

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1. Introduction

Cephalopods play a pivotal role in marine food webs, both as voracious consumers and major prey of many predators, spanning from fishes to whales (Piatkowski et al., 2001; Rosas-Luis et al., 2008). Many cephalopod species are also important living marine resources, supporting relevant fisheries worldwide (FAO, 2012). Therefore, fluctuations in cephalopod abundances due to natural (climate) or anthropogenic (harvesting) perturbations have significant implications for both commercial landings and marine ecosystems through both direct or indirect effects on different trophic levels (Pech and Jackson, 2008; Andre et al., 2010). The impacts of such perturbations are furthermore aggravated by the high sensitivity of cephalopods to environmental conditions. Indeed, most

cephalopod species are characterized by high growth rates and short life cycles (1–2 years), making their population sizes very dependent on the success of spawning and recruitment (Boyle and Rodhouse, 2005). Whereas juveniles and adults are primarily affected by fishing exploitation, early life stages (paralarvae and recruits) are strongly influenced by environmental factors such as oceanic currents, temperature or food availability (Waluda et al., 1999; Dawe et al., 2000). According to recent reviews (Semmens et al., 2007; Pierce et al., 2008), the most investigated factors influencing cephalopod abundance and distribution include global climatic phenomena, temperature, productivity and rainfall. Large-scale climatic indices such as the North Atlantic Oscillation (NAO) have been shown to affect cephalopod populations from the European Seas (Sims et al., 2001; Pierce and Boyle, 2003; Otero et al., 2005). On the other hand, the effects of the global-scale index El Niño Southern Oscillation (ENSO) have been detected not only in the southeast Pacific waters where this phenomenon occurs

* Corresponding author.

E-mail address: stefanie.keller@ba.ieo.es (S. Keller).

(Waluda et al., 2004) but also in areas far away from its action centre (Quetglas et al., 2013). The availability of remotely-sensed ocean data during the last decade facilitated investigating the effects of some surface parameters on cephalopods, most notably sea surface temperature and surface primary production (Arvanitidis et al., 2002; Georgakarakos et al., 2002; Wang et al., 2003). Other works have focused on local weather-related variables such as rainfall, winds or river discharges (Lloret et al., 2001; Sobrino et al., 2002). Finally, a few studies have analyzed the influence of the moon cycle on some jigging squid fisheries (Chen et al., 2006; Cabanellas-Reboredo et al., 2012).

Since ancient times, the cuttlefish *Sepia officinalis* Linnaeus, 1758 has been an important living resource in the Mediterranean Sea, where fishermen take advantage of the seasonal movements of large individuals to coastal waters for mating and spawning (Mangold-Wirz, 1963; Boletzky, 1983). Despite the importance of cuttlefish as a fishery resource, only a study of Belcari et al. (2002) analyzes the exploitation patterns of the species in the western, central and eastern Mediterranean in detail. Concerning the western basin, existing multi-species fishery studies containing information on *Sepia* include a preliminary bioeconomic analysis of a trammel net fishery (Merino et al., 2008) and a study on the harvesting and climate effects on the inter-annual variability of population abundances (Quetglas et al., 2013). Regarding the ecology and population dynamics of cuttlefish, most works have been conducted in the northeast Atlantic, the majority of them in waters of the Bay of Biscay and the English Channel (e.g. Denis and Robin, 2001; Wang et al., 2003; Royer et al., 2006), but also off the Portuguese coast (Fonseca et al., 2008). Although there are many results from laboratory studies (Boletzky and Hanlon, 1983; Boletzky, 1987; Clarke et al., 1989; Forsythe et al., 1994), few studies have been undertaken in the Mediterranean. Apart from the comprehensive work of Mangold-Wirz (1963), there is a study on the reproductive biology of *Sepia* from the Aegean Sea (Önsoy and Salman, 2005) and a fecundity study by (Laptikhovskiy et al., 2003).

In the Balearic Islands (western Mediterranean), cuttlefish is exploited by both the bottom trawl and the small-scale fleet. While bottom trawlers capture the species as a by-catch on continental shelf grounds deeper than 50 m all year round (Quetglas et al., 2000), cuttlefish supports an important seasonal small-scale trammel net fishery taking place in coastal waters (Merino et al., 2008). The main objective of this work was to analyze both intra-annual and inter-annual population dynamics of cuttlefish in the western Mediterranean. With this aim, we first analyzed different aspects of the cuttlefish life-history (population structure, reproduction and the trade-offs between somatic condition and investment in reproduction) influencing the intra-annual population dynamics in the study area. In addition, we investigated the effects of different environmental parameters (e.g. climate indices, sea surface temperature, rainfall and moon phase) on the seasonal and inter-annual variation of the population abundance, analysing time series of landings embracing the last 45 years to shed new light on the natural drivers shaping the population dynamics of the species.

2. Material and methods

To investigate life-history related aspects, monthly biological sampling was carried out during the seasonal small-scale trammel net fishery (January–July) in two consecutive years (2007, 2008). Additionally, biological samples from annual spring (June) scientific trawl surveys (2004–2011) were included in the calculation of the length weight relationship. To obtain monthly size distributions for the trawl fraction, we performed monthly size frequency sampling aboard commercial bottom trawlers between 2000 and 2011. A total of 949 (505 males, 444 females) and 2247 individuals were

analyzed in the biological and size sampling, respectively. During the biological sampling, the following measurements were taken: sex, mantle length (ML, to the nearest mm), total and eviscerated weight (TW and EW, respectively, both to the nearest 0.1 g), gonad weight (GW), digestive gland weight (DGW) and stomach weight (all to the nearest 0.01 g).

To determine the relationship between ML and TW, the parameters of the power formula $TW = a(ML)^b$ were calculated for females, males and for the total. The slopes and the intercepts were compared between sexes applying an analysis of covariance (ANCOVA) to the log-transformed linear relationships. The size-frequency distributions of the small-scale and the bottom trawl fractions were obtained in order to compare their size structure. To determine intra-annual differences in the proportion of males and females in the population, the sex-ratio was analyzed monthly and differences were tested by using the Chi-square test. Sexual development was determined through the monthly evolution of the gonadosomatic index ($GSI = 100 \cdot GW / (TW - GW)$). To infer relationships between reproduction and food intake, the monthly evolution of both the digestive gland index ($DGI = 100 \cdot DGW / (TW - DGW)$) and the percentage of empty stomachs (emptiness index, EMI) were computed.

For the investigation of individual body condition and the relationship between somatic and reproductive investment, reduced major axis regression (RMA; Bohonak and van der Linde, 2004) was used. This regression technique was developed for cases where the independent variable is measured with error, because in such a case the slope estimation calculated using ordinary least square regression methods is biased (Sokal and Rohlf, 1995). After regression equations were calculated for log-transformed ML-EW and ML-GW relationships, residuals were obtained and standardized by dividing each by the standard deviation of the predicted values. These residuals provide a size-independent measure for comparing the relative condition of somatic and gonad tissues, considering that individuals with heavier tissues for their length (higher residuals) are in better condition (Hayes and Shonkwiler, 2001). Hence, ML-EW and ML-GW residuals were used as indicators of somatic condition (SC) and reproductive condition (RC) respectively. To determine trade-offs in energy allocation, SC was modeled against the explanatory variables month, size (ML) and RC. Although data were size-corrected for linear effects, ML was still included in the model to analyze its non-linear effect. As multiple variables were analyzed and non-linear relationships were expected, generalized additive models (GAMs) were applied.

In order to investigate the effects of environmental conditions on cuttlefish populations, two time series of landings at different temporal scales were analyzed: 1) monthly total landings (pooled bottom trawl and small-scale) from 1965 to 2011; and 2) daily catches per vessel between 2000 and 2011. All cuttlefish landing data were supplied by the fish auction wharf of Mallorca. Landings were used as a proxy of abundance owing to the fact that: 1) discards are negligible; 2) landings and CPUE's are highly correlated (see Quetglas et al. 2013); and 3) landings and effort are not correlated (see Pierce et al., 1994) (Fig. 1). We modelled the effects of climatic indices at different spatial scales together with several local environmental parameters on cuttlefish landings. The large-scale North Atlantic Oscillation (NAO) measures the difference in the normalized sea-level pressure between the Azores and Iceland (Hurrell, 1995) and influences the climate variability in the Mediterranean Sea. Two Mediterranean climate indices were also used: the Mediterranean Oscillation Index (MOI), which indicates the normalized pressure difference between Gibraltar's Northern Frontier and Lod Airport in Israel (Palutikof, 2003), and the Western Mediterranean Oscillation index (WeMO) representing pressure

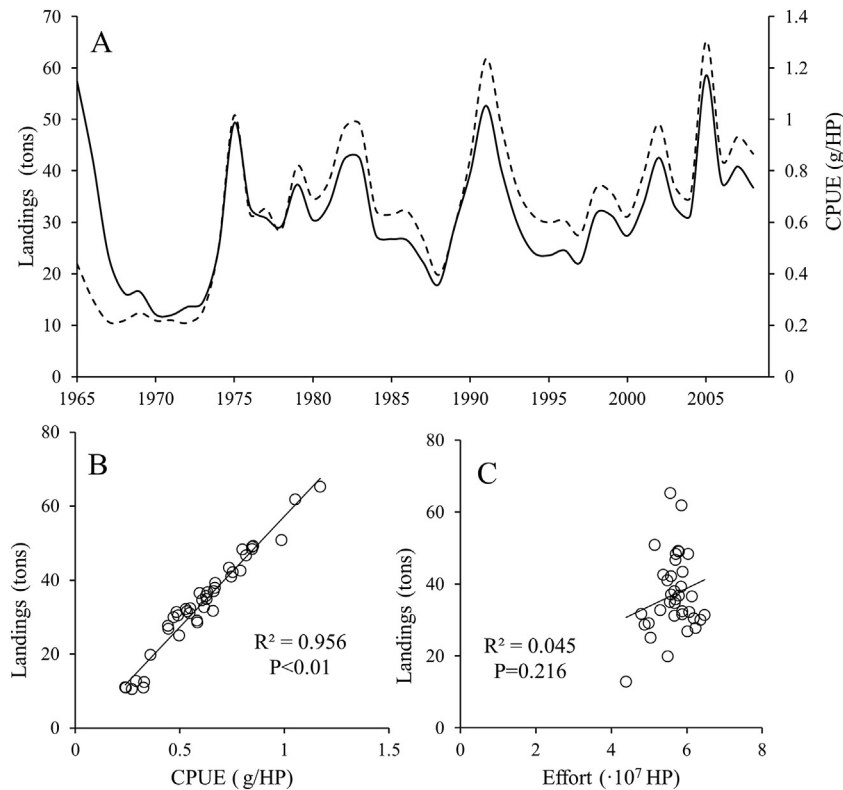


Fig. 1. Time series of cuttlefish (*Sepia officinalis*) landings (continuous line) and catch per unit effort (CPUE; dotted line) from the Balearic Islands (western Mediterranean) during 1965–2009 (A); relationships of cuttlefish landings against CPUE (B) and fishing effort (C) with the corresponding linear fits.

differences between Padua in Italy and Cádiz in Spain (Martin-Vide and Lopez-Bustins, 2006). At a smaller spatial scale, a local climatic index (LCI) already used in the study area (Fernández de Puelles and Molinero, 2007; Hidalgo et al., 2011) was analyzed. This index quantifies the regional hydroclimatic variability around the Balearic Islands synthesizing the following variables by means of the first axis of a PCA (for details, see Molinero et al., 2005): monthly anomaly fields of surface air temperature, sea surface temperature, atmospheric sea level pressure, 500 hPa geopotential height and precipitation records (Kalnay et al., 1996). High LCI values are associated with higher temperatures, drier conditions and weaker winds compared to low LCI values.

The local environmental variables analyzed included the monthly mean sea surface temperature (SST), which was obtained from two sources: a) modelled SST data from 1965 until today (SSTa); and b) satellite-derived data from 2000 to 2009 for the area where the main fishery of *Sepia* takes place (SSTb). Chlorophyll-a concentration (Chla) was used as a proxy for food availability and was modelled using different time lags (1, 2 and 3 months) to account for the time required for energy transfers between trophic levels. Additionally, rainfall data from the study area was included in the analysis. To avoid the seasonal pattern being reflected in the variables SST, Chla and Rainfall, anomaly data was used, calculated as the residuals obtained by modeling SST/Chla/Rainfall versus Month and Year. Below we refer to these anomalies when mentioning these model parameters. Finally, the lunar cycle was accounted for. Moon phases were calculated as daily sine-transformed fraction of the moon illuminated (Kuparinen et al., 2010), with values oscillating between 1 (full moon) and –1 (new moon). The lunar cycle was treated as a factor of four levels accounting for lunar phases from new moon (1) to full moon (4). As the lunar influence might be more evident during the reproduction

period when animals might be more sensitive to external conditions (see Wingfield and Sapolsky, 2003), the interaction between lunar phase and season was modeled. In this case, and to simplify the interaction term, season was treated as a factor with two levels, first and second semester, accounting for the reproduction and non-reproduction periods, respectively. The variable year was included in the models to take into account density-related dynamics independent from the environmental processes. To test its influence, we first checked that results of models with and without year gave similar results. Secondly, year was modeled against each environmental parameter separately and in all cases it never explained more than 17.3% of the variance.

Table 1

Main characteristics (time series, time scale, explanatory variables) of the three different models fitted in this study along with the sources of the datasets used. NAO: North Atlantic Oscillation; MOI: Mediterranean Oscillation Index; WeMO: Western Mediterranean Oscillation; SST_a and SST_b: modeled and satellite-derived Sea Surface Temperature anomaly, respectively; LCI: Local Climate Index; Chla: chlorophyll-a concentration anomaly.

	Time series	Time scale	Explanatory variables
Model I	1965–2009	Monthly	Year, month, NAO ^a , MOI ^b , WeMO ^c , LCI ^d , rainfall ^e , SST _a ^d
Model II	2000–2009	Monthly	Year, month, SST _b ^f , Chla ^f , rainfall ^e
Model III	2000–2010	Weekly	Year, semester, moon phase ^g , rainfall ^e

^a http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html.

^b <http://www.cru.uea.ac.uk/cru/data/moi/>.

^c <http://www.ub.edu/gc/English/wemo.htm>.

^d <http://www.esrl.noaa.gov/psd/data/reanalysis/reanalysis.shtml>.

^e <http://www.aemet.es/es/web/serviciosclimaticos/datosclimatologicos/valoresclimatologicos>.

^f http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month.

^g <http://aa.usno.navy.mil/data/docs/MoonFraction.php>.

The effects of environmental parameters on cuttlefish landings were also analyzed with GAMs. Since the data available covered different time series and temporal scales, three models were fitted. These three models, together with the data sources of all environmental parameters, are shown in Table 1. After testing for collinearity of parameters by analyzing linear pairwise correlation coefficients and calculating the variance inflation factor (VIF), a stepwise approach was adopted to select the best model. First, non-significant variables were removed one by one unless their removal resulted in a higher Akaike information criterion (AIC). Afterwards, significant variables were excluded whenever their removal resulted in a better model fit according to the minimization of the generalized cross-validation criterion (GCV) and the AIC. The response variable (landings) and the explanatory variable rainfall were log-transformed to obtain normalized distributions. All GAM analyses performed in this study were carried out with the R package (version 2.15.1; <http://www.r-project.org/>) using the mgcv library. For all GAMS, residuals were checked for homogeneity of variance, absence of temporal (inter-annual) autocorrelation and violation of normality assumptions.

3. Results

3.1. Life-history traits

The ANCOVA revealed significant differences ($p < 0.001$) between sexes in the length–weight relationships (females: $a = 3 \cdot 10^{-4}$, $b = 2.812$, $R^2 = 0.983$; males: $a = 5 \cdot 10^{-4}$, $b = 2.695$, $R^2 = 0.982$). Males outnumbered females between February and April ($p < 0.05$, χ^2 -test). Cuttlefish sizes from the small-scale fishery ranged from 8 to 24 cm ML and showed a main modal size at 10–11 cm ML and a minor mode at 19–20 cm ML, while individuals from the bottom trawl fishery ranged from 4 to 21 cm ML and showed a main modal size at 12–13 cm ML (Fig. 2A). In both fisheries, the landings displayed a clear seasonal trend (Fig. 2B), with small-scale landings peaking in March before plummeting down until August and remaining very low until December. By contrast, bottom trawl catches peaked in February and decreased down to

July, increasing markedly afterwards. Mean monthly sizes showed the same pattern, increasing from January (~12.5 cm ML) to March (~14.5 cm ML) and decreasing until July (~10.5 cm ML) in the small-scale fishery (Fig. 2C). Individuals from the bottom trawl fleet decreased from mean sizes of 13.5 cm ML during January down to 10.5 cm ML in August, increasing progressively up to 11.5–12.5 cm ML in October–December (Fig. 2D).

The mean gonadosomatic index (GSI) in females increased from January to March, remained at the highest values (~5%) between March and May, and decreased in June–July (Fig. 3A); in males, however, the GSI did not show important changes. Digestive gland index (DGI) values were always higher for females than for males. While the mean DGI decreased with time in males, such a decrease was only evident since April in females (Fig. 3B). Although in general the Emptiness Index (EMI) was higher in males than in females (Fig. 3C), the mean values showed a similar increasing trend from February to June in both sexes; it is of note, however, that EMI values decreased markedly between January and February.

The body condition analysis revealed important differences between sexes (Fig. 4). The only common pattern was the increase of somatic condition (SC) with increasing reproductive condition (RC), although the relationship was markedly more linear and confident in males than in females. The temporal pattern of SC differed by sex: while the seasonal effect was most positive in January and became less positive with time in females, it was low in February and reached a maximum in May in males. In both sexes, the SC decreased with increasing size to about 15 cm ML, from where on it increased with increasing size.

3.2. Environmental effects

Once the significant variables for each of the three models considered were selected, different GAMs were run to obtain the best fit based on the lowest GCV and AIC (Table 2). When analyzing model I (monthly data from 1965 to 2009), we did not find significant effects of either large scale climatic index (NAO, MOI or WeMO), the SST or the rainfall, and the final trials included year, month and LCI; the best fit was obtained combining the effects of

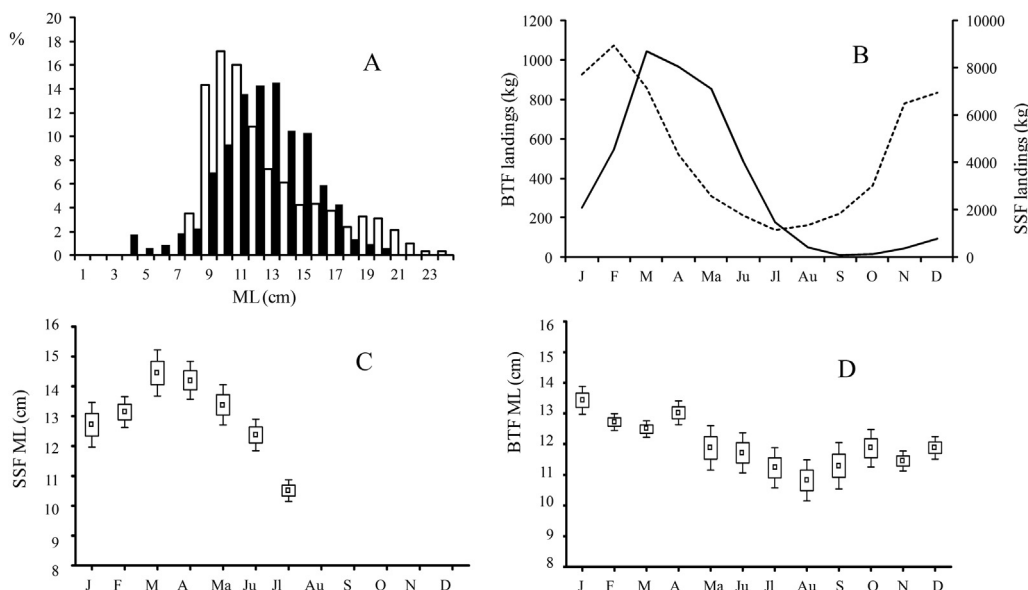


Fig. 2. Cuttlefish (*Sepia officinalis*) populations caught by the bottom trawl (BTF) and small-scale (SSF) fleets from the Balearic Islands (western Mediterranean) during 2000–2011: A) Total size-frequency distributions (SSF: white; BTF: black); B) monthly landings (SSF: dotted line; BTF: continuous line); and mean sizes \pm SD and the 95% CI (whiskers) of the SSF (C) and BTF (D). BTF and SSF distributions were obtained using individuals taken during January–December and January–July, respectively.

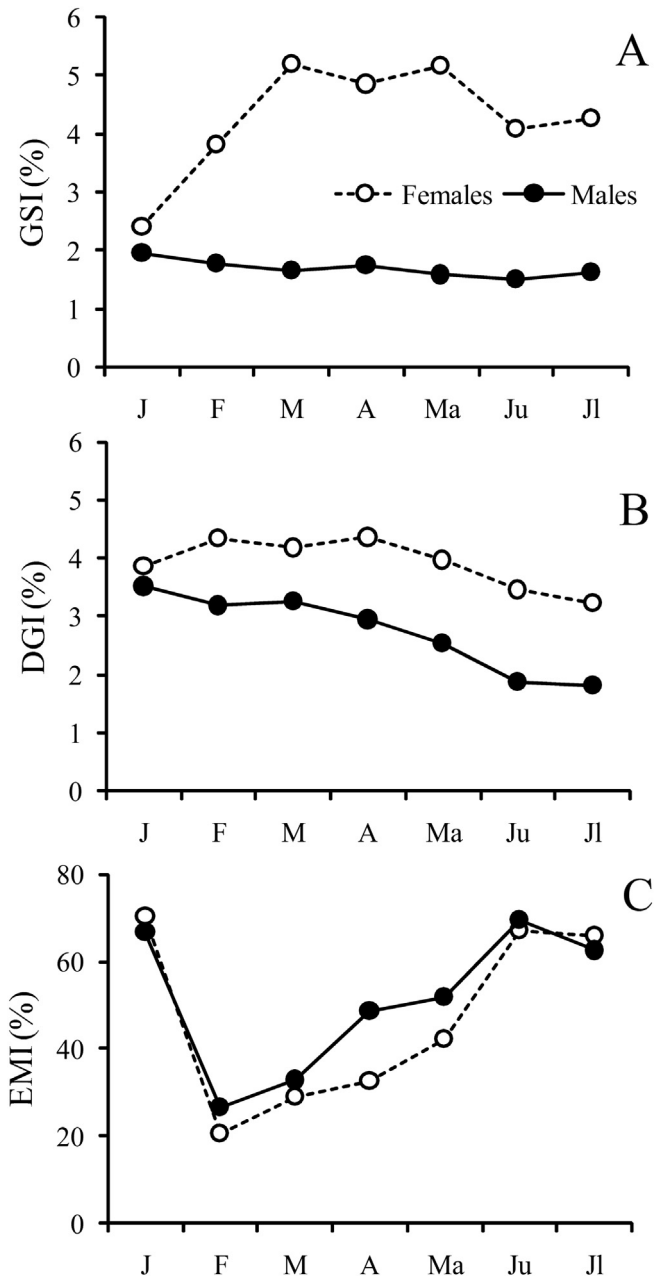


Fig. 3. Monthly development of the gonadosomatic (GSI), digestive gland (DGI) and emptiness (EMI) indices of cuttlefish caught by the small-scale fleet from the Balearic Islands (western Mediterranean) during the fishing season (January to July), separated by sex.

year and month by means of a bivariate smoother. Landings increased with increasing LCI (Fig. 5A). The bivariate smoother revealed the appearance of a clear periodicity of about 10 years since the early 1980s characterized by an alternating seasonal dynamics (Fig. 5B). During periods of high abundance, the seasonal cycle is mainly dependent on the very high catches in spring with values close to the season average in autumn. By contrast, during periods of low abundance, spring values are close to the season average with very low catches in autumn shaping the seasonal pattern.

The final model II (monthly data from 2000 to 2009) included year as a factor and month, LCI and SST_b as covariates, since the effects of Chl_a and rainfall were not significant. The model

displayed an increasing trend in landings from 2000 to 2005 followed by a progressive decrease afterwards (Fig. 5C). The effect of month (Fig. 5D) depicted the strong intra-annual cycle with maximum values in spring and minimum values in autumn as already shown in Fig. 2B and the SST anomaly was positively correlated with landings. The partial linear effect of LCI is not shown because it resulted in a very similar graph to the one shown for model I.

Model III (weekly data from 2000 to 2010) revealed that the best model included year as factor, rainfall and semester. Rainfall displayed a negative and nonlinear effect with very light rainfall triggering a negative influence on the cuttlefish landings (Fig. 5F). The effect of year is not depicted because it is similar to that shown for model II; the factor semester is not shown as it provides the same information as the effect of month in model II. No significant interaction was found between semester and lunar cycle. Although landings differed slightly during new and full moon compared to the second moon phase (Fig. 5G), the effect was very weak and moon phase was therefore not included in the final model.

4. Discussion

Our study shows how the life-history dynamics of cuttlefish in the western Mediterranean is phenologically adapted to cope with the seasonal environmental variability that is ultimately reflected in their landings. As a result of its fast growth rate and short life-span, cephalopods display a wide capacity for life-history and population plasticity (Pecl and Jackson, 2008). In spite of this, there are currently few studies analyzing the effect of environmental conditions on Mediterranean cephalopod populations (e.g. Lloret et al., 2001; Lefkaditou et al., 2008; Cabanellas-Reboredo et al., 2012; Quetglas et al., 2013). Such analyses are especially important in the Mediterranean, an area highly susceptible to the climate change (Parry, 2000; Coma et al. 2009) and supporting intense fishing exploitation rates (Colloca et al., 2011), where synergistic effects between climate and anthropogenic uses will likely exacerbate climate-induced changes (Quetglas et al., 2013).

Owing to the physiological plasticity of cephalopods, differences in cuttlefish life-history traits are expected in populations from areas with contrasting oceanographic conditions, such as the northeast Atlantic and the Mediterranean. Indeed, northeast Atlantic populations have larger modal sizes (for the trawling and small-scale fisheries respectively: 17 and 23 cm ML, Dunn, 1999; 16 and 12 cm ML, Coelho and Martins, 1991) than Mediterranean populations (8–12 and 10–14 cm ML, Belcari et al., 2002; 13 and 10 cm ML, this study). Differences also arise for the sex-ratio, which favored males during January–April in our study, but was balanced in the eastern Mediterranean (Önsoy and Salman, 2005) or showed annual changes in the northeast Atlantic (Coelho and Martins, 1991). However, Dunn (1999) found that the sex-ratio was balanced in northeast Atlantic populations from the trawl fleet, but favored males in those from the small-scale fleet. Consequently, differences in the proportion of sexes depending on the exploited fishing grounds, as we found in our samples, could indicate lag times in the seasonal movements between males and females. Indeed, based on the fact that males outnumbered females in July, Mangold-Wirz (1963) concluded that females leave the coastal waters earlier than males. The main reproductive period does not show important differences between the Mediterranean (March–June, Önsoy and Salman, 2005; April–June, Mangold-Wirz, 1963; March–May, this study) and the Bay of Biscay (March–June, LeGoff and Daguzan, 1991), whereas it spanned from February to July in the English Channel (Dunn, 1999). In the Mediterranean, as well as in estuarine valleys on the northwestern Spanish Atlantic coast,

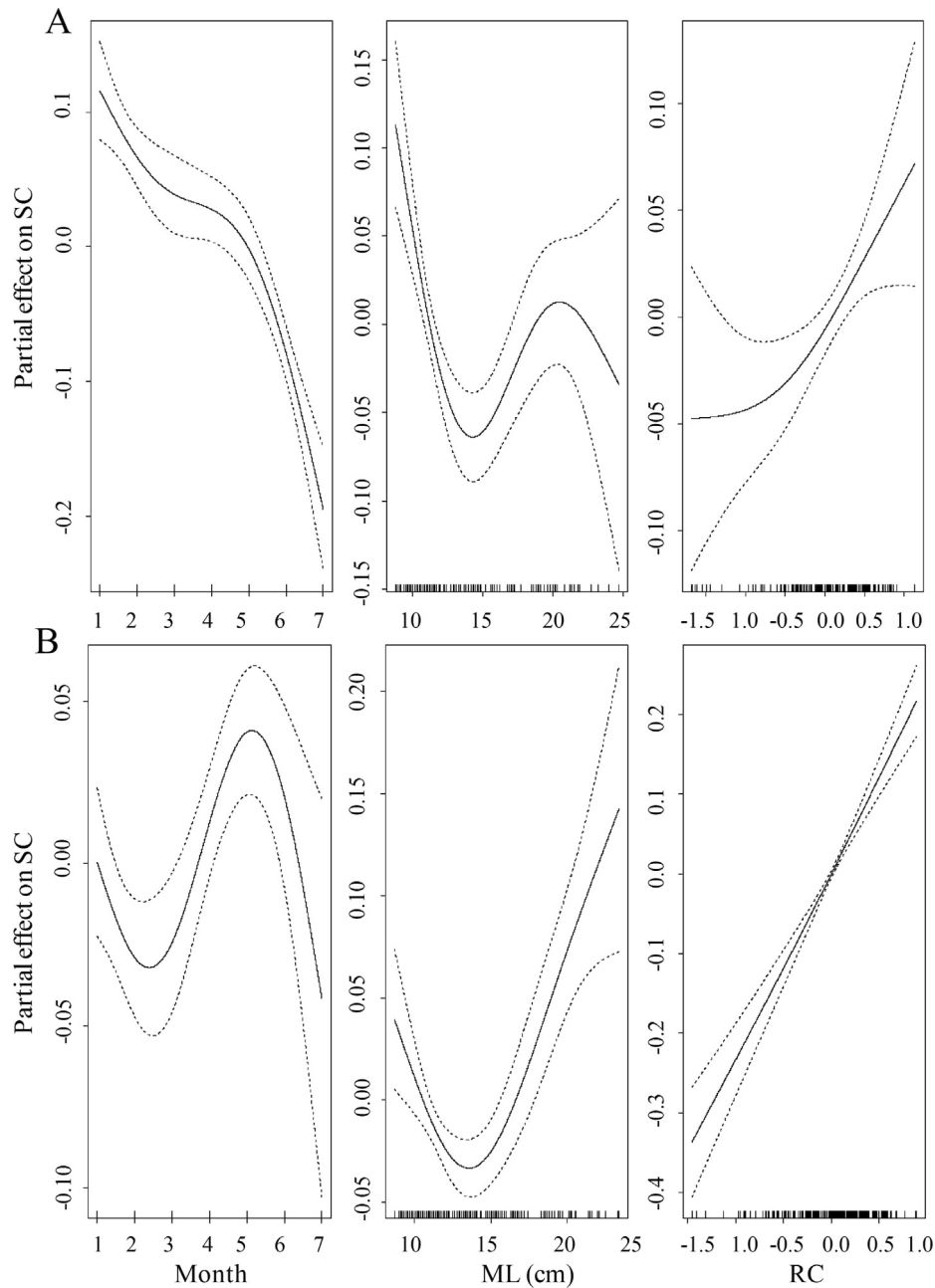


Fig. 4. Generalized additive model (GAM) outputs showing the effects of month, size (ML) and reproductive condition (RC) on somatic condition (SC) of females (A) and males (B) cuttlefish from the Balearic Islands (western Mediterranean). Solid lines indicate the fitted partial effects, whereas broken lines are the 95% confidence intervals.

Table 2
Selection of the best fit for each of the three models considered in this study (see Table 1). For comparative purposes, the two/three best fits are shown for each model. The final model (shown in bold) is the one having the lowest generalized cross validation (GCV) and Akaike information criteria (AIC) while explaining the same (or more) percentage of the deviance (%DE). LCI: local climatic index; SST_a and SST_b: modeled and satellite-derived Sea Surface Temperature anomaly, respectively; MP: moon phase; SM: semester; N: sample size.

	Response variable ~ explanatory variables	%DE	N	GCV	AIC
Model I	Log Landings ~ s(Year, Month) + s(LCI)	82.6	540	0.204	673
	Log Landings ~ Year + s(Month) + s(LCI) + s(SST _a)	73.9	540	0.321	914
	Log Landings ~ s(Year) + s(Month) + s(LCI) + s(SST _a)	67.1	540	0.373	1002
Model II	Log Landings ~ Year + s(Month) + s(LCI) + s(SST _b)	94.1	117	0.109	71
	Log Landings ~ s(Year) + s(Month) + s(LCI) + s(SST _b)	93.1	117	0.122	86
Model III	Log Landings ~ Year + SM + s(log(rain + 1))	51.7	2752	0.916	7570
	Log Landings ~ Year + SM + MP + s(log(rain + 1))	51.7	2752	0.917	7573
	Log Landings ~ Year + s(log(rain + 1)) + MP + SM + MPxSM	51.7	2752	0.919	7578

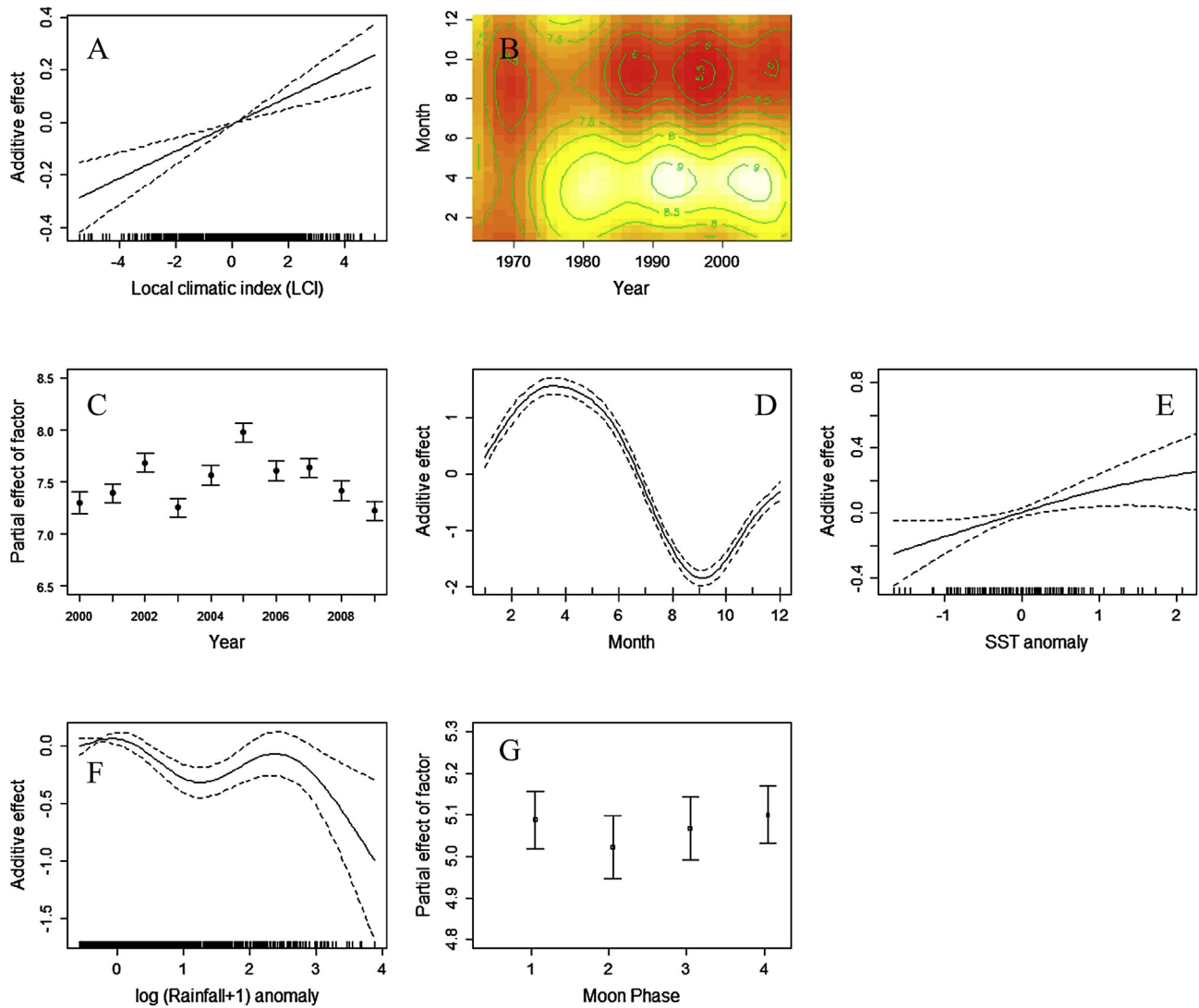


Fig. 5. Outputs of the three generalized additive models (GAMs) fitted in this study (see Table 2). Graphs show the partial additive effects of different explanatory variables on cuttlefish landings (in log scale) from the Balearic Islands (western Mediterranean). The explanatory variables modeled are: A) Local Climatic Index (LCI); B) bivariate effect of year and month; C) year; D) month; E) SST anomaly; F) log (rainfall + 1) anomaly; and G) moon phase, from new moon (1) to full moon (4). Although depicted here, the effect of the moon phase was very weak and therefore not included in the final model. In figure B, deep red colors represent the lowest influence on the response variable, lighter colors represent higher influence. For the continuous effect (LCI, month, SST anomaly, rainfall anomaly), solid lines indicate the fitted partial effects and broken lines the 95% confidence intervals (CI). For factors (year, moon phase), the mean \pm the Standard Error are given. To avoid repetition, partial effects of year and LCI are only plotted once, although they occur in different models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

winter spawning has also been observed (Mangold-Wirz, 1963; Guerra, 2006).

The annual evolution of landings of both the trawl and small-scale fisheries from our results gives interesting insights into spatial movements between the coastal waters (small scale fleet) and the shelf grounds deeper than 50 m (trawl fleet). The landings showed a strong seasonality with peaks in February (trawl fishery) and March (artisanal fishery), followed by a gradual decrease; only in the trawl fishery, landings increased again from July on. The lag time between the trawl and small-scale landing peaks indicates that the bulk of the cuttlefish migration takes place in March, whereas the lack of small-scale catches from July on marks the end of the reproductive period. The landing peaks coincide with those found by previous studies undertaken both in the Mediterranean (Belcari et al., 2002) and the English Channel (Dunn, 1999). In the Catalan Sea, Mangold-Wirz (1963) reported a peak in June, whereas Lloret and Leonart (2002) found a rather different pattern with catches showing low seasonality and peaking in winter

(November–January). In agreement with previous studies (Mangold-Wirz, 1963; Önsöy and Salman, 2005), the increase of the population mean size up to March and the subsequent decrease reveal the arrival of large, mature individuals and their subsequent disappearance from the fishing grounds after mating. Recruitment would take place during late summer, as suggest the increase of both the monthly mean size and the landings from August onwards. Such timing agrees with the growth rates and development times given by Richard (1971), who suggested a period ranging from 4.5 to 7 months, depending on the water temperature, between egg laying and recruitment of 5 cm ML cuttlefishes. This points to a synchronization between external conditions and recruitment taking place when environmental conditions, such as food availability, are optimal for offspring growth, a crucial prerequisite for the persistence of populations in oligotrophic systems such as the Mediterranean Sea (Hidalgo et al., 2011; Quetglas et al., 2011).

Cephalopod investments in reproduction are very high, especially in females: whereas gonad weight can reach up to 20–30% of

the female body weight, the values for males rarely exceed 5% (Forsythe and Van Heukelem, 1987). Consequently, strong relationships between reproduction and body condition are expected (Gabr et al., 1999a; Quetglas et al., 2011). Body condition depends either on energy stores or current food intakes (capital and income breeders, respectively; Roff, 2002). In the first case, energy is directly obtained from mantle tissues which serve as storing sources. These trade-offs are usually evident in species storing energy reserves while immature, which they later use for gonad growth during the maturation process. In the second case, gonads develop directly from a food source, which is used for somatic growth before maturation but directed to the gonads afterwards. Both the capital breeding (Gabr et al., 1999b; Jackson et al., 2004) and income breeding (Gabr et al., 1999a; Pecl and Moltchanivskyj, 2006; Quetglas et al., 2011) strategies have been reported in cephalopods. Although less frequent, these two strategies can also be combined (Laptikhovskiy and Nigmatullin, 1993). The positive relationships between somatic and reproductive condition that we found in both sexes points to an income breeder strategy, since trade-offs between stored reserves in somatic and reproductive tissues are inferred from negative relationships (Roff, 2002). This conclusion is further supported by the percentage of empty stomachs, which was lowest (20–25%) in February, just before the reproductive period peak (March to May), but then increased to about 65% at the end of that period. The positive relationship between somatic and reproductive condition implies that cuttlefish in good condition typically possess better reproductive condition (Pecl and Moltchanivskyj, 2006). In female cuttlefish, such positive relationship might be regulated through the reabsorption of oocytes (Laptikhovskiy et al., 2003).

In line with the aforementioned differences between sexes in reproductive investments, we found contrasting effects of month and size on the somatic condition in males and females. Whereas the somatic condition in females was highest before the reproductive period and decreased steadily with time, it increased since February up to a marked peak in May and decreased afterwards in males. Such contrasting responses might be due to the much higher energy requirements for gonad development in females compared to males. Although food intakes (EMI) showed the same trend for both sexes, the lower energy demands in males allow concomitant improvements of both the somatic and reproductive condition, while females allocate most food input to gonad growth, improving their reproductive condition. This also explains the effect of size on the somatic condition of large-sized (>15 cm ML) animals, which showed a strong increasing pattern for males but was hardly significant for females. In fact, a slowdown of growth during maturation, much more accentuated in females than in males, has been reported in several cephalopod species (Mangold-Wirz, 1963; Boyle and Rodhouse, 2005).

As a result of its high sensitivity to environmental conditions, cephalopods are considered good ecological indicators of both natural and human induced variations in marine ecosystems (Andre et al., 2010). Most available studies dealing with environmental effects on cephalopod populations analyzed the influence of climatic phenomena at large spatial scales (e.g. El Niño-Southern Oscillation, North Atlantic Oscillation, Mediterranean Oscillation), remotely sensed ocean data (e.g. sea surface temperature, chlorophyll-a) or local weather-related parameters like rainfall, river discharges and winds (for recent reviews, see Semmens et al., 2007; Pierce et al., 2008). Cephalopod responses to NAO seem to be species-specific: whereas positive NAO values (high winter temperatures and reduced precipitation over Europe; Hurrell, 1995) were related to high abundances and precocious maturation of *Loligo forbesii* in northeast Atlantic waters (Pierce et al., 2005), negative NAO values were associated with high abundances of *Illex*

illecebrosus in the northwest Atlantic (Dawe et al., 2000). In Mediterranean latitudes, the NAO has also been reported to influence fishes (Massuti et al., 2008), crustaceans (Maynou, 2008) and cephalopods (Orsi-Relini et al., 2006). Even the global-scale ENSO index has recently been found to affect Mediterranean cephalopod populations, such as *Sepia officinalis*, *Loligo vulgaris* and *Octopus vulgaris* (Quetglas et al., 2013). In this study, however, we did not find evidence for an influence of large-scale climatic phenomena such as the NAO, WeMO or MOI on *Sepia* landings. In contrast, the local climatic index (LCI) significantly affected the cuttlefish landings from the Balearic Islands. The influence of the LCI in this area has already been reported for zooplankton (Fernández de Puelles and Molinero, 2007) and benthopelagic fishes such as hake (Hidalgo et al., 2011). Our results also revealed a clear periodicity of about 10 years in the population dynamics of cuttlefish since the early 1980s. There is mounting evidence that the regional hydroclimatic conditions in the western Mediterranean changed noticeably through the 1980s, leading to higher temperatures and hydrographic pressures, less precipitation and weaker winds, which affected the population dynamics of many marine organisms within the trophic webs (Fernández de Puelles and Molinero, 2007; Molinero et al., 2008; Hidalgo et al., 2011; Quetglas et al., 2013). However, the responses to such changes seem to be species-dependent: whereas the shift in the early 1980s induced stronger seasonality in our cuttlefish populations, it in turn led to the disappearance of the seasonality observed for hake until these years (Hidalgo et al., 2009). The high dependence of cephalopods on the environmental conditions, together with their short life cycle and their high adaptability to new ecological scenarios (Pecl and Jackson, 2008), may have triggered the strong change in the monthly landings pattern observed in our results around the early 1980s.

Remotely sensed data have been used in a variety of cephalopod studies and a comprehensive review of cephalopod–environment interactions in European Seas evidenced that the effect of SST varies according to species and areas (Pierce et al., 2008). For example, Wang et al. (2003) found the centre of high squid abundance in the English Channel to be in warmer waters, which is similar to our results of higher availability of cuttlefish at above-average temperatures. Other authors found positive and negative correlations between *Loligo* abundance and SST in the North Sea depending on the season (Waluda and Pierce, 1998). While we obtained a significant positive relationship between SST and cuttlefish landings, no relationship was found for populations from the Gulf of Cadiz (Sobrinho et al., 2002). According to Georgakarakos et al. (2002), the correlation of cephalopod abundances with SST depends on the productivity. Although increased food availability generally has a positive effect on cephalopod growth and abundance (Arvanitidis et al., 2002; Valavanis et al., 2002), there was no significant relationships between the chlorophyll-a concentration and cuttlefish landings.

Local weather-related parameters and the lunar cycle do not seem to strongly affect cuttlefish populations either. In the Gulf of Cadiz, Sobrinho et al. (2002) did not find relationships between trawl landings and rainfall or river discharges. In the western Mediterranean, Lloret et al. (2001) found no or very weak correlations between cuttlefish landings and river run-offs or a wind mixing index. Similarly, our results showed very weak effects of rainfall on weekly landing data from 2000 to 2010. Although there is evidence for lunar influences on some squid species, the results are contrasting and the mechanisms unknown. For loliginid squids, some studies reported increased catches during full moon (Lloret and Leonart, 2002; Young et al., 2006; Postuma and Gasalla, 2010) but others close to new moon (Schön et al., 2002; Cabanellas-Reboredo et al., 2012). We found effects of both full and new

moon, but such effects were marginal compared to the other covariates.

In summary, our results show that despite the high sensitivity of cephalopod populations to external abiotic factors, cuttlefish *Sepia officinalis* from the western Mediterranean was not affected by many of the environmental parameters investigated. We only found significant effects of SST and the local climatic index (LCI), whereas no influences were obtained of other parameters such as large-scale climatic phenomena (NAO, MOI, WeMO) or some of the key locally-related variables like rainfall or primary productivity (Chla concentration). This might be explained by the high adaptability of cuttlefish to environmental changes throughout different life stages (Sobrinho et al., 2002) and to local hydroclimatic conditions. In fact, our work revealed a shift in the population dynamics during the early 1980s coinciding with important changes in the hydrodynamic conditions in our study area. Finally, we also showed that Mediterranean cuttlefish populations exhibit strong seasonal variations related with the reproductive movements to coastal waters, where the species constitutes an important commercial resource for local small-scale fisheries. In spite of such importance, long term monitoring and fisheries assessment and management in the Mediterranean are missing. Our work is a first step to provide information on cuttlefish life-history and stock dynamics as a knowledge base for future management measures to be implemented in the Mediterranean.

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