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Abundance of *Octopus vulgaris* on soft sediment*

STELIOS KATSANEVAKIS and GEORGE VERRIOPOULOS

Department of Zoology-Marine Biology, School of Biology, National and Kapodistrian University of Athens, Panepistimioupolis, Athens 15784, Greece. E-mail: skatsan@biol.uoa.gr

SUMMARY: Until now the distribution and abundance of *Octopus vulgaris* had been investigated in the main fishing areas of the species only by fishing surveys. The catching efficiency of fishing gear is variable and depends on several aspects of the animal's behaviour and life history as well as on the type of the gear and the environmental characteristics of the area surveyed. A good alternative for studying the abundance of octopus is by visual census. The population density of *O. vulgaris* was measured by visual census with scuba diving. The survey was conducted in coastal areas of Greece and on soft sediment. *O. vulgaris* density ranged from 0 to 6.88 individuals/1000m^2 and the mean density values of this study were much higher than those mentioned in other papers. Octopus density was significantly associated with season. Densities of octopuses lower than 500 g were higher in coarse sediments than in finer ones. The density of large octopuses (> 500 g) increased with depth. Octopuses larger than 200 g tended to dwell deeper during the period of intense thermocline than during the no-thermocline period.

Key words: cephalopod, visual census, population density, fishing gear efficiency, thermocline, *Octopus vulgaris*.

RESUMEN: ABUNDANCIA DE *OCTOPUS VULGARIS* EN SEDIMENTO BLANDO. – La distribución y abundancia de *Octopus vulgaris* ha sido investigada en las principales áreas de pesca de la especie únicamente mediante estudios de pesca. La eficacia de su captura por medio de aparejos de pesca es variable y depende de algunos aspectos del comportamiento animal y de su vida, así como del tipo de aparejo y de las características medioambientales del área estudiada. Una buena alternativa para el estudio de la abundancia del pulpo es por medio del censo visual. La densidad de población de *O. vulgaris* fue medida por submarinistas mediante censos visuales. Las zonas estudiadas se situaron en sedimentos blandos de zonas costeras de Grecia. La densidad de *O. vulgaris* varió de 0 a 6.88 unidades/1000m? con promedios mucho mayores a los mencionados en otros escritos. La densidad de los pulpos estaba significativamente relacionada con la estación. La densidad de los pulpos de tamaño menor de 500 g fue mayor en sedimentos groseros que en sedimentos más blandos. La densidad de pulpos grandes (> 500 g) aumentó en función de la profundidad. Los pulpos mayores de 200 g se hallaron en áreas más profundas durante el periodo de intensa termoclina.

Palabras clave: cefalópodo, censo visual, densidad de población, eficacia del aparejo de pesca, termoclina, *Octopus vulgaris*.

INTRODUCTION

The common octopus, *Octopus vulgaris*, is one of the most widely studied cephalopods. It is a species of great scientific and commercial importance and its culture is an area of increasing interest. It is a coastal and sedentary species, living mostly between 0 and 100 m depth; it is scarce at depths between 100 and 200 m and is only occasionally found at greater depths (Guerra, 1981; Belcari *et al*., 2002). In very shallow water, *O. vulgaris* is mostly an inhabitant of coral reefs or rocks, but in many areas it is equally or even more abundant over sandy and muddy bottoms or in seagrass beds (Mangold, 1983).

The distribution and abundance of *O. vulgaris* have been investigated in the main fishing areas of

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the species either by trawl surveys (Guerra, 1981; Tursi and D'Onghia, 1992; Costa and Fernandes, 1993; Fonseca and Campos, 2002; Smale *et al.*, 1993; Quetglas *et al.*, 1998; Sánchez *et al.*, 1998; Quetglas *et al.*, 2000; Belcari *et al.*, 2002) or by pot and trap surveys (Whitaker *et al.*, 1991; Sánchez and Obarti, 1993; Hernández-Garcia *et al.*, 1998). All fishing gear is to some extent selective. Pots are size selective, as octopuses tend to choose dens of a volume roughly matching their size (Hartwick *et al.*, 1978; Mather, 1982a; Iribarne, 1990). In trawl surveys, small animals may pass through large-mesh nets easily, although the plasticity of the octopus body may allow even larger animals to escape. The efficiency of a trawl depends on the type of dens that the octopuses use in the surveyed area. The relative proportion of the various den types varies in relation to depth, distance from shore, octopus size and sediment granulometry (Katsanevakis and Verriopoulos, 2004), so the catching efficiency of a trawl varies from area to area and reliable octopus density estimations are difficult.

An alternative method for studying the abundance of *O. vulgaris* is by visual census during SCUBA dives. Visual census is used extensively to measure the abundance of aquatic animals, mainly benthic organisms (Edgar and Barrett, 1997; Jorgensen and Gulliksen, 2001), but also for more mobile animals like neritic fish (Chabanet *et al.*, 1995; De Girolamo and Mazzoldi, 2001; Guidetti *et al.*, 2002; Pet-Soede *et al.*, 2001). The different types of dens encountered on soft sediment (Katsanevakis and Verriopoulos, 2004) are very easily located visually and failure to spot octopuses is minimised.

Altman (1967) conducted a pioneering diving survey and studied the diurnal pattern and behavior of the common octopus, by visual observations in the wild; he too highlighted the problems of this type of investigation. Since then, the daytime activity (Kayes, 1974; Mather, 1988), 'home' choice and modification by juveniles (Mather, 1994) and den ecology (Katsanevakis and Verriopoulos, 2004) of *O. vulgaris* have been studied by visual census. Several ecological aspects of other octopus species have also been studied by visual census: foraging by *Octopus cyanea* (Forsythe and Hanlon, 1997), habitat selection and shelter use by *Octopus tetricus* (Anderson, 1997), den ecology of *Octopus briareus* in a marine lake (Aronson, 1986) and shelter use by *Octopus tehuelchus* (Iribarne, 1990). Scheel (2002) conducted a SCUBA survey to study habitat characteristics and the abundance of the giant Pacific octopus, *Enteroctopus dofleini*. Certain aspects of the population biology of *Octopus vulgaris* (maturity, spawning period, average size at spawning, seasonal size variation, sex ratio) have been studied in a SCUBA survey in South Africa (Smith and Griffiths, 2002). However, the population density of *Octopus vulgaris* has not been estimated by visual census on soft sediment until now. In this study the abundance of *O. vulgaris* on soft sediment in coastal areas of the eastern Mediterranean is estimated and correlated with environmental factors.

MATERIALS AND METHODS

The population density of *Octopus vulgaris* was measured by visual census with scuba diving. The authors made all the dives and no professional divers or volunteers were used. All surveys were conducted in coastal areas and on soft sediment. The dives were made at 23 different sites in Greek coastal waters, grouped in 7 geographical sections as shown in Figure 1, and at depths from 0 to 25 m.

The octopuses were counted within 1600 m^2 transects (50x32 m). Early trials indicated that smaller transects yielded too many zero values and larger transects were unfeasible due to violation of no decompression dive limits. The rectangular 50x32 m area was outlined in a way similar to that described by Mather (1982b). The diver began moving parallel to the long side of the rectangular area, holding, horizontally and perpendicular to his movement direction, a 2 m long PVC pipe of 40 mm diameter with two 1 kg weights hanging from each end. The two weights touched the substrate and, as the diver moved forward, traced a 50 m long and 2 m wide corridor (the starting corridor). Then the diver started moving parallel to the starting corridor in such a way that one of the weights hanging from the pipe traced over one of the tracks of the starting corridor and the other weight traced a new track forming a second corridor, and so on. In this way the diver created 16 parallel and consecutive corridors, thus forming a 50 x 2 x 16 = 1600 m^2 transect.

During this procedure the diver recorded all the octopuses found inside each corridor and the size of each octopus was estimated. To estimate the size of the octopuses, 3 size classes were used: small (< 200 g), medium [200 g, 500 g], and large (> 500 g). The diver classified every octopus he found into one of

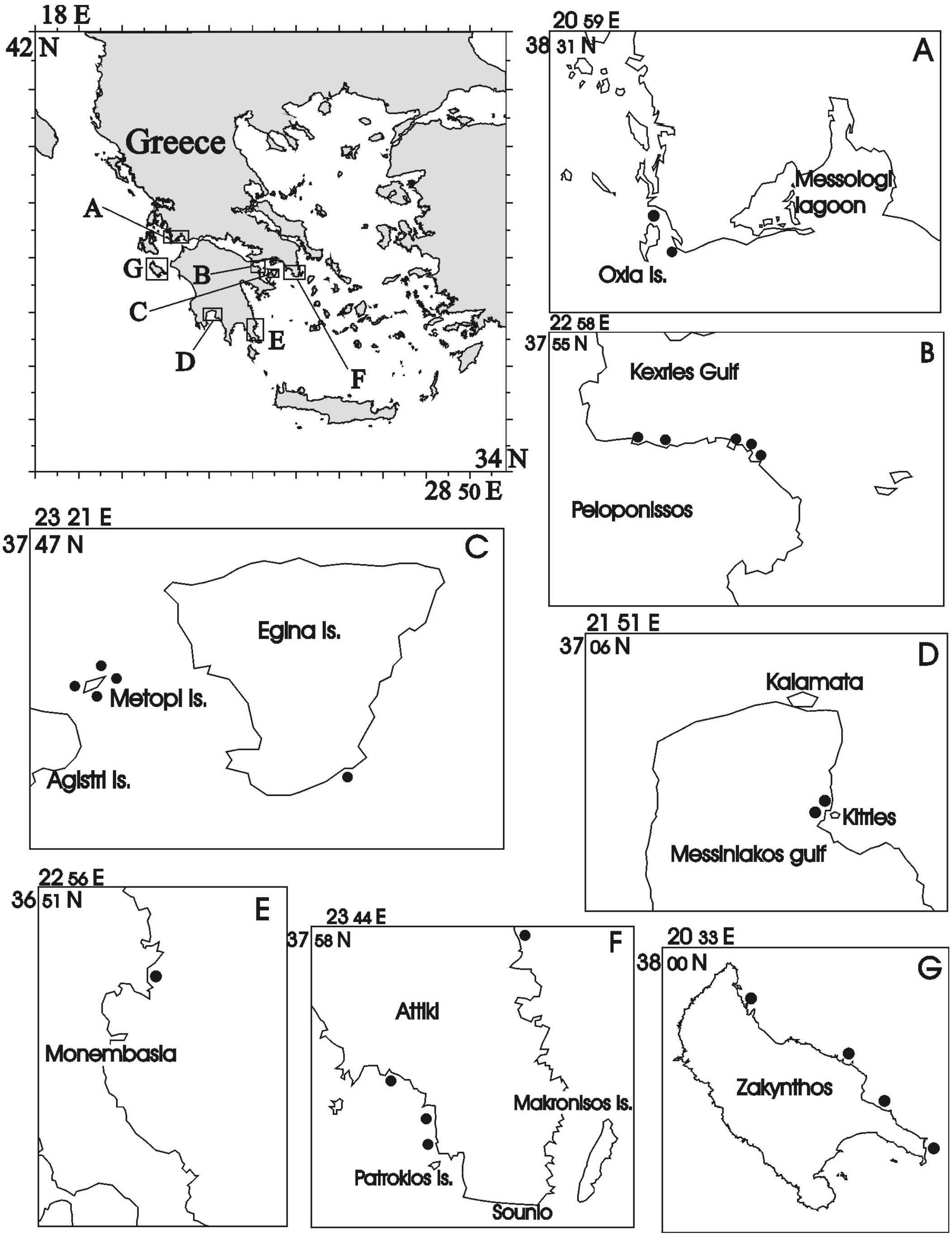

FIG. 1. – Location of the 23 sites of the survey, grouped in 7 geographical sections (A-G).

these classes by sight. To reduce the classification error the authors practiced initially on more than 70 specimens that were used in the lab for other purposes, and before the onset of this survey 5 test dives were made in which, after classifying 23 animals, the diver collected them and weighed them on shore. 18 out of 23 were classified correctly (78%) and the other 5 were classified into neighbouring classes. This error was considered acceptable for the experimental needs. The *O. vulgaris* density was calculated for each site and for each size class as individuals per 1000 m^2.

The depth range of each transect (maximum-minimum depth) was recorded with a dive computer (Sunto, model Vyper) with an accuracy of 0.1 m, and in every case it was less than 5 m. The mean value of the minimum and maximum depth of each transect was considered as the transect depth (*D*).

A 250 ml sample of the surface sediment (upper 5 cm) was taken from each transect. Particle size analysis of the sediment sample was made according to Buchanan (1984) and for each sample the median diameter, Mdϕ, and the quartile deviation, QDϕ, were calculated as measures of the central tendency and the degree of scatter of the granule size frequencies respectively. A 500 ml water sample was taken at maximum depth and, after the dive, salinity was measured using a WTW type TetraCon 325 salinometer with an accuracy of $0.1^{o}/_{oo}$.

The water temperature was recorded during each dive with an electronic temperature recorder integrated in a dive watch (Citizen Promaster) with an accuracy of 0.1°C. The difference between the temperature at 5 m and at 25 m was used as a measure of the intensity of the thermocline: when this difference was less than 1°C the thermocline was considered insignificant and when it was more than 1°C it was considered significant. A dummy variable *Th* was used to indicate the existence of significant thermocline: $Th = 1$ when there is a significant thermocline or else $Th = -1$.

At each site, several transects at different depth ranges were surveyed. Each site was visited either monthly (sections F and H) or quarterly (sections A, B, C, D, E, G). This study was conducted between July 2001 and June 2003, and a total of 199 density measurements were made.

General Linear Model (GLM) methods were used (Glantz and Slinker, 2001) to identify the association between octopus densities (of each size class and total) and the observed environmental variables. Specifically, four General Linear Models of the following form were calculated using the least squares method and assuming a normal error distribution:

$$[\text{Density (i)}]^{1/2} = b_0 + b_1S_1 + b_2S_2 + b_3S_3 + b_4Md\phi + b_5QD\phi + b_6(D - D_m) + b_7Th \cdot (D - D_m) \quad (1)$$

The index *i* in *Density* is ‘sm’ for ‘small’ size class, ‘me’ for ‘medium’, ‘La’ for ‘Large’ and ‘T’ for ‘Total’. Densities were square root transformed in order to stabilise variance and produce fairly straight lines on the normal probability plots (Glantz and Slinker, 2001); untransformed densities produced curves on the normal probability plot with one inflection, indicating that the distribution of the residuals was skewed. Squared root transformation is particularly effective when data are counts (Glantz and Slinker 2001) as in our case. Variables S_1, S_2, S_3 are dummy variables used to encode the effect of season, following the ‘effects coding’ approach according to Glantz and Slinker (2001). Specifically, in autumn, S_1=1 and S_2=S_3=0, in summer, S_2=1 and S_1=S_3=0, in spring, S_3=1 and S_1=S_2=0, and in winter, S_1=S_2=S_3=-1. When the data are unbalanced, as in our case, ‘effects coding’ is essential for obtaining the correct sums of squares in the model (Glantz and Slinker, 2001). As depth appears in two terms of the model, centering the data by subtracting the mean depth D_m greatly reduces the structural multicollinearity associated with these terms (Glantz and Slinker, 2001); thus $(D - D_m)$ is used instead of *D*. The term $Th \cdot (D - D_m)$ is entered in the model to find out whether the bathymetric distribution of octopuses during the intense thermocline period differs in comparison to the period of no significant thermocline. The ‘Statistica v5.5’ (Statsoft, Inc) software was used for the analysis. Marginal Sums of Squares (Type III) were used to test the significance of each regression coefficient and the Student-Newman-Keuls test for multiple comparisons (Glantz and Slinker, 2001). In all four GLMs, a residual analysis was conducted according to Glantz and Slinker (2001) to check whether the results were consistent with the model assumptions.

RESULTS

Octopus vulgaris density ranged from 0 to 6.88 ind/1000m^2. Salinity in the surveyed areas was relatively constant and varied between 38.5 and $39.0^{o}/_{oo}$. Mdφ varied from –1.5 to 4.6 and QDϕ from 0.2 to 1.95.

After the square root transformation of densities, the residuals plotted against any independent variable or against the observed dependent variables showed no deviation from the constant variance assumption and the normal probability plots of the residuals were reasonably linear, indicating no substantial deviation from normality. The residuals showed no trend, curve or other systematic variation and in the scatterplots of the transformed densities against any of the independent variables there was no indication of nonlinearity; thus the linearity assumption inherent in the GLM model may be considered valid. There was no studentised residual greater than 3.0, except in the *Density(La)* model, where there was one such residual (=3.36). In no cases was there a leverage value greater than 3 times the average leverage or data points with unusually large values of Cook’s distance (no Cook’s distance

TABLE 1. – Summary of the results of fitting 4 general linear statistical models relating the octopus densities of each size class (sm-small, me-medium, La-large) and the total densities (T) to 5 predictive environmental factors (* p<0.05, ** p<0.01, *** p<0.001).

GLM - Dependent variable: Density (sm)

Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value	
Season	14.9	3	4.96	18.48	0.0000	***
Mdϕ	1.19	1	1.19	4.44	0.0364	*
QDϕ	0.51	1	0.51	1.89	0.1709	
$D\text{-}D_m$	0.49	1	0.49	1.83	0.1777	
$Th(D\text{-}D_m)$	0.03	1	0.03	0.12	0.7312	
Model	18.88	7	2.70	10.04	0.0000	***
Residual	51.29	191	0.27			
adj-R^2:	24.2%					
st.error:	0.518					

GLM - Dependent variable: Density (me)

Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value	
Season	5.33	3	1.78	8.39	0.0000	***
Mdϕ	2.39	1	2.39	11.29	0.0009	***
QDϕ	0.12	1	0.12	0.55	0.4577	
$D\text{-}D_m$	0.46	1	0.46	2.17	0.1423	
$Th(D\text{-}D_m)$	0.98	1	0.98	4.63	0.0326	*
Model	9.27	7	1.32	6.24	0.0000	***
Residual	40.51	191	0.21			
adj-R^2:	15.6%					
st.error:	0.461					

GLM - Dependent variable: Density(La)

Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value	
Season	2.77	3	0.92	3.51	0.0163	*
Mdϕ	0.002	1	0.002	0.01	0.9243	
QDϕ	0.06	1	0.06	0.22	0.6430	
$D\text{-}D_m$	5.16	1	5.16	19.62	0.0000	***
$Th(D\text{-}D_m)$	1.14	1	1.14	4.32	0.0390	*
Model	10.02	7	1.43	5.44	0.0000	***
Residual	50.25	191	0.26			
adj-R^2:	13.6%					
st.error:	0.513					

GLM - Dependent variable: Density (T)

Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value	
Season	10.36	3	3.45	9.47	0.0000	***
Mdϕ	2.29	1	2.29	6.28	0.0130	*
QDϕ	0.12	1	0.12	0.32	0.5738	
$D\text{-}D_m$	2.65	1	2.65	7.27	0.0077	**
$Th(D\text{-}D_m)$	0.67	1	0.67	1.83	0.1780	
Model	15.12	7	2.16	5.92	0.0000	***
Residual	69.65	191	0.36			
adj-R^2:	14.8%					
st.error:	0.604					

TABLE 2. – The coefficients of the 4 general linear statistical models predicting the octopus densities for each size class (sm-small, me-medium, La-large) and total density (T) according to Equation 1.

	b0	b1	b2	b3	b4	b5	b6	b7
Density(sm)	0.458	-0.235	0.410	-0.179	-0.0638	0.121	-0.0097	-0.0022
Density(me)	0.477	0.112	0.193	-0.190	-0.0904	0.058	0.0094	0.0121
Density(La)	0.535	0.042	-0.160	-0.047	-0.0028	-0.040	0.0313	0.0130
Density(T)	1.128	-0.076	0.308	-0.271	-0.0885	0.057	0.0224	0.0100

greater than 0.0045); thus there were no outliers or influential points.

The results of fitting the GLMs described by Equation 1 are presented in Table 1 and the coefficients b_i of Equation 1 in Table 2. All four models were highly significant. All densities (sm, me, La, T) were significantly associated with season. The multiple comparison tests (Table 3) showed that the density of small octopuses was significantly greater in the summer than in other seasons, for medium octopuses in the summer and autumn rather than in winter and spring, and for large octopuses in winter rather than in summer (Fig. 2). Total density peaked in summer, mainly because of the increased density of small octopuses. Densities of small and medium octopuses, as well as total density, were significantly associated with Mdφ (Table 1); specifically, the b_4 coefficient of Mdϕ was significantly negative in these models (Table 2), indicating that the finer the sediments, the less abundant small and medium-sized octopuses were. The grain size of the sediment was not significantly associated with the density of large octopuses. QDϕ was not a significant factor in any model (Table 1). Depth was a significant factor for large octopus densities as well as total densities (Table 1); the b_6 depth coefficient

TABLE 3. – The results of Student-Newman-Keuls multiple comparison tests among octopus densities for the 4 different seasons. The homogenous groups are identified using columns of X's. Within each column, the seasons containing X's form a group of means within which there are no statistically significant differences (95% confidence level) in octopus densities.

	Small		Medium		Large		Total		
Winter	X		X			X		X	
Spring	X		X		X	X	X		
Summer		X		X	X				X
Autumn	X			X	X	X	X	X	

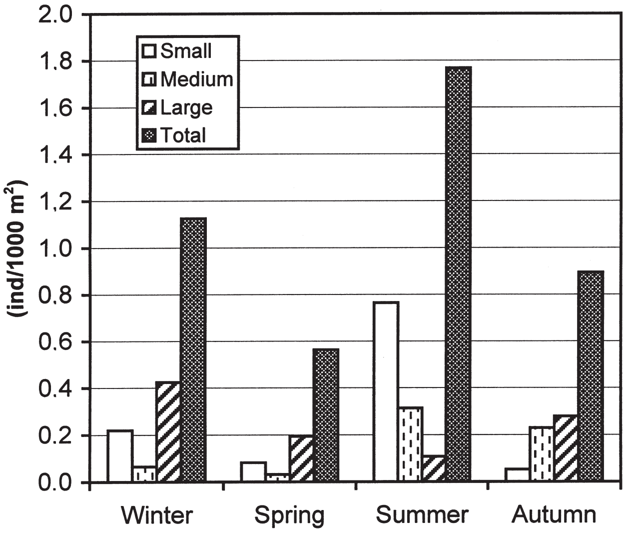

FIG. 2. – The seasonal variation of octopus density. Densities for each size class and total densities were calculated from Equation 1 at the mean depth Dm = 12.83 m and using the mean $Md\phi$ and $QD\phi$ values ($Md\phi_m$ = 1.90, $QD\phi_m$ = 1.06) and the bi coefficients as estimated by the General Linear Models (Table 2).

was positive in these cases (Table 2), indicating increasing densities of large octopuses and total densities, with increasing depth (in the range 0-25 m). The $Th{\cdot}(D - D_m)$ factor was significant in the models of medium and large octopus densities (Table 1); the corresponding b_7 coefficient was significantly positive in these models (Table 2), indicating that during the period of intense thermocline, medium and large octopuses tend to dwell deeper (and thus in cooler water) than when there is no significant thermocline.

DISCUSSION

In trawl surveys the abundance of octopuses is usually given as 'individuals caught per hour of trawling'. Most trawl survey papers (Costa and Fernandes, 1993; Quetglas *et al.*, 1998; Quetglas *et al.*, 2000; Sánchez *et al.*, 1998; Smale *et al.*, 1993; Tursi and D'Onghia, 1992) do not discuss density or provide information (haul duration, horizontal opening at wings, trawling speed) for converting catch per hour into density. However, the information provided by Guerra (1981) and Fonseca and Campos (2002) is sufficient for such calculations and Belcari *et al.* (2002) provide direct density estimations. The mean *Octopus vulgaris* density off the northwest coast of Africa (Guerra, 1981) at depths between 14 m and 362 m was 0.09 ind/1000m^2 and ranged between 0 and 0.51 ind/1000 m^2, while at depths shallower than 25 m (comparable to our study) the mean density was 0.17 ind/1000 m^2. Off the northern coast of Portugal (Fonseca and Campos, 2002) and at depths between 46 m and 124 m, the mean density was 0.263 ind/1000 m^2 and the density range was 0.154-0.495 ind/1000 m^2. In a wide area of the Mediterranean basin and at depths between 10 and 50 m, the octopus density varied between 0 and 0.884 ind/1000 m^2 (Belcari *et al.*, 2002). Specifically, in the east Ionian Sea and Argosaronicos region (also surveyed by our study), at depths between 10 and 50 m the octopus density ranged between 0 and 0.154 ind/1000 m^2, with a mean density of 0.063 ind/1000 m^2 (Belcari *et al.*, 2002). These mean densities are much lower than all the mean seasonal densities of this study (Fig. 2), and the highest density recorded in this study is 13.5, 13.9 and 7.8 times higher than the highest densities found by Guerra (1981), Fonseca and Campos (2002) and Belcari *et al.* (2002) respectively.

This difference is partly explained by a possible low catching efficiency of trawls with respect to *Octopus vulgaris*. Similar conclusions have been made regarding *Nephrops norvegicus* (a mud-burrowing decapod), whose catching efficiency by trawls is greatly dependent on the time of the day, the season (Chapman, 1980) and other environmental factors. A survey by Tuck *et al.* (1997) found a trawling catching efficiency of *N. norvegicus* varying between 10.5 and 59.3%. Trawl surveys are generally regarded as an unreliable method for assessing *Nephrops* stocks (Bailey *et al.*, 1993). A large percentage of *O. vulgaris* live in 'wells' in the soft sediment (Katsanevakis and Verriopoulos, 2004), which is quite a similar case to that of *N. norvegicus,* and the variability in trawling catching efficiency with respect to octopuses is probably a significant constraint in abundance estimations as well. Another reason for our high octopus density values could be a comparatively greater abundance of potential dens in the areas of our study. Our study was conducted in areas very close to the shore while the trawl surveys were probably conducted in areas more distant from the shore. Far from the shore, solid materials (stones, rocks, litter etc.) that are necessary for den construction are usually less abundant, and this has proven to be a limiting factor for *O. vulgaris* abundance (Katsanevakis and Verriopoulos, 2004). Furthermore, 'wells' used as dens tend to be more common in areas far from the shore and octopuses living in 'wells' are comparatively more difficult to capture by trawls.

During the period of intense thermocline (late spring-summer), medium and large octopuses tend to dwell deeper than when there is no significant thermocline. A similar observation has been made for *Octopus digueti* in the northern Gulf of California (Voight, 1992) where, during the high peak of temperature, mature individuals seem to abandon the intertidal population, leaving only immature octopuses. It is quite possible that in the summer large octopuses were stimulated to abandon the shallow and warm areas and seek cooler areas in deeper waters, thus reducing the energy cost of higher metabolism. On the other hand, smaller octopuses do not seem to be affected by the thermocline. It is not unusual for young poikilotherms to prefer warmer temperatures than their intraspecific adults, perhaps in order to achieve greater growth rates and thus shorten the period during which they are more vulnerable to predation. In cephalopods, even small differences (1-2 °C) in temperature during the first three months of post hatching life could greatly accelerate growth and significantly reduce the time required to reach adult size (Forsythe, 1993; Hatfield, 2000). Similar thermocline-induced size (and age) separation has been documented for several species such as pollock *Theragra chalcogramma* (Swartzman *et al.*, 1994) or perch *Perca fluviatilis* (Imbrock *et al.*, 1996).

A seasonal variation in *Octopus vulgaris* abundance was found, which is related to the short life span and rapid population turnover of the species. Small octopuses had peak densities in summer, indicating that this is the period when the new cohorts arise in the benthos. Embryonic development ranges from 125 days to 22 days at temperatures between 13 °C and 25 °C respectively (Mangold, 1983), while at a mean water temperature of around 25 °C hatchlings settle after 33-40 days (Itami *et al.*, 1963). Thus, for the summer peak in small octopuses it is estimated that there is a major spawning period during spring. The main reproductive period of *O. vulgaris* has been estimated to be from January to July along the Spanish Mediterranean coast by Sánchez and Obarti (1993), from January to July with a peak in April off the Canary Islands by Hernández-García *et al.* (2002), and at the end of spring to summer along the Catalan coastline by Guerra (1977). The peak in density of small octopuses in summer is followed by a peak in density of medium octopuses during summer-autumn and by a peak in density of large animals during winter (Fig. 2). The density of large octopuses fell during spring and further declined, reaching a minimum, during summer. Spawning is followed by death and therefore the decline in the densities of large animals after the winter peak is probably due to natural mortality, which is a second indication of a main spawning period during spring. Sánchez and Obarti (1993), after a survey with clay pots along the Spanish Mediterranean coast, stated that octopuses weighing about 500 g (which are the smallest caught with clay pots) appear in September and October and that large specimens disappear from July onwards, which is in agreement with our data (Fig. 2).

Compared to trawl or pot and trap surveys, a visual census has many advantages, as the records are independent of catching effort. The various types of den encountered on soft sediment (Katsanevakis and Verriopoulos, 2004) are very easily located visually and failure to spot them is probably rare, except for very small sizes (<15 gr); thus only the 'small' size class was probably underestimated. Octopuses did not appear to be affected by the diver's presence and no octopuses were observed to leave their den due to the diver's presence. The disadvantages of a scuba diving visual census method are the depth limitations due to breathing gas sufficiency and decompression sickness and the comparatively greater time and labour requirements.

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REFERENCES

Altman, J.S. – 1967. The behavior of *Octopus vulgaris* Lam. In its natural habitat: a pilot study. *Report of the Underwater Association of Malta:1966-1967*, pp. 77-83.

Anderson, T.J. – 1997. Habitat selection and shelter use by *Octopus tetricus*. *Mar. Ecol.- Prog. Ser.*, 150: 137-148.

Aronson, R.B. – 1986. Life history and den ecology of *Octopus briareus* Robson in a marine lake. *J. Exp. Mar. Biol. Ecol.*, 95: 37-56.

Bailey, N., C.J. Chapman, J. Kinnear, D. Bova and A. Weetman. – 1993. Estimation of *Nephrops* stock biomass on the Fladeb Ground by TV survey. ICES C.M. 1993/K:34,9.

Belcari, P., D. Cuccu, M. González, A. Srairi and P. Vidoris. – 2002. Distribution and abundance of *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopoda) in the Mediterranean Sea. *Sci. Mar.*, 66(Suppl. 2): 157-166.

Buchanan, J.B. – 1984. Sediment Analysis. *In:* N.A. Holme and A.D. McIntyre (eds.) *Methods for the study of Marine Benthos*, pp. 41-65, Blackwell.

Chabanet, P., V. Dufour and R. Galzin. – 1995. Disturbance impact on reef fish communities in Reunion Island (Indian Ocean). *J. Exp. Mar. Biol. Ecol.*, 188: 29-48.

Chapman, C.J. – 1980. Ecology of juvenile and adult *Nephrops*. *In:* S. Cobb and B. Philips (eds.), *The biology and Management of Lobsters, Vol II,* pp. 143-178, Academic Press, New York.

Costa, P.A.S. and F.C. Fernandes. – 1993. Seasonal and spatial changes of cephalopods caught in the Cabo Frio (Brazil) upwelling ecosystem. *Bull. Mar. Sci.*, 52: 751-759.

De Girolamo, M. and C. Mazzoldi. – 2001. The application of visual census on Mediterranean rocky habitats. *Mar. Environ. Res.,* 51: 1-16.

Edgar G.J. and N.S. Barrett. – 1997. Short term monitoring of biotic change in Tasmanian marine reserves. *J. Exp. Mar. Biol. Ecol.*, 213: 261-279.

Fonseca, P. and A. Campos. – 2002. Bottom trawl codend selectivity for cephalopods in portuguese continental waters. *Fish. Res.*, 59: 263-271.

Forsythe, J.W. – 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In:* T. Okutani, R.K. O'Dor, T. Kubodera (eds.), *Recent advances in fisheries biology*, pp. 133-143, Tokai University Press, Tokyo.

Forsythe, J.W. and R.T. Hanlon. – 1997. Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. *J. Exp. Mar. Biol. Ecol.,* 209: 15-31.

Glantz, S.A. and B.K. Slinker. – 2001. Primer of applied regression and analysis of variance, 2nd ed. McGraw-Hill, New-York.

Guerra, A. – 1977. *Estudio sobre la biologia y estructura de las poblaciones del pulpo común (Octopus vulgaris) de la costa noroccidental africana*. PhD thesis, Univ. Barcelona.

Guerra, A. – 1981. Spatial distribution pattern of *Octopus vulgaris*. *J. Zool.,* 195: 133-146.

Guidetti, P., G. Fanelli, S. Fraschetti, A. Terlizzi and F. Boero. – 2002. Coastal fish indicate human-induced changes in the Mediterranean littoral. *Mar. Environ. Res.*, 53: 77-94.

Hartwick, E.B., P.A. Breen and L. Tulloch. – 1978. A removal experiment with *Octopus dofleini* (Wulker). *J. Fish. Res. Board*, 35: 1492-1495.

Hatfield, E.M.C. – 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). *Fish. Res.*, 47: 27-40.

Hernández-García, V., J.L. Hernández-López and J.J. Castro. – 1998. The octopus (*Octopus vulgaris*) in the small-scale trap fishery off the Canary Islands (Central-East Atlantic). *Fish. Res.*, 35: 183-189.

Hernández-Garcia, V., J.L. Hernández-Lopez and J.J. Castro-Hdez. – 2002. On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. *Fish. Res.*, 57: 197-203.

Imbrock, F., A. Appenzeller and R. Eckmann. – 1996. Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and in situ observations. *J. Fish. Biol.*, 49: 1-13.

Iribarne, O.O. – 1990. Use of shelter by the small Patagonian octopus *Octopus tehuelchus*: availability, selection and effects on fecundity. *Mar. Ecol.- Prog. Ser.*, 66: 251-258.

Itami, K., Y. Izawa, S. Maeda and K. Nakai. – 1963. Notes on the laboratory culture of the *octopus* larvae. *Bull. Jap. Soc. Scient. Fish.*, 29: 514-520.

Jorgensen, L.L. and B. Gulliksen. – 2001. Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. *Polar Biol.*, 24: 113-121.

Katsanevakis, S. and G. Verriopoulos. – 2004. Den ecology of *Octopus vulgaris* on soft sediment: availability and types of shelter. *Sci. Mar.*, 68(1): 147-157.

Kayes, R.J. – 1974. The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Mar. Behav. Physiol.,* 2: 337-343.

Mangold, K. – 1983. *Octopus vulgaris*. *In:* P.R.Boyle (ed.), *Cephalopod Life Cycles Volume I Species Accounts*, pp. 335-364, Academic Press, New York.

Mather, J.A. – 1982a. Choice and competition: their effects on occupancy of shell homes by *Octopus joubini*. *Mar. Behav. Physiol.,* 8: 285-293.

Mather, J.A. – 1982b. Factors affecting the spatial distribution of natural populations of *Octopus joubini* Robson. *Anim. Behav.*, 30: 1166-1170.

Mather, J.A. – 1988. Daytime activity of juvenile *Octopus vulgaris* in Bermuda. *Malacologia*, 29: 69-76.

Mather, J.A. – 1994. 'Home' choice and modification by juvenile *Octopus vulgaris* (Mollusca: Cephalopoda): specialized intelligence and tool use? *J. Zool.*, 233: 359-368.

Pet-Soede, C., W.L.T. van Densen, J.S. Pet and M.A.M Machiels. – 2001. Impact of Indonesian coral reef fisheries on fish community structure and the resultant catch composition. *Fish. Res.*, 51: 35-51.

Quetglas, A., F. Alemany, A. Carbonell, P. Merella and P. Sánchez. – 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, Western Mediterranean). *Fish. Res.*, 36: 237-249.

Quetglas, A., A. Carbonell and P. Sánchez. – 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (North-Western Mediterranean). Biological aspects of some deep-sea species. *Estuar. Coast. Shelf. Sci.*, 50: 739-749.

Sánchez, P. and R. Obarti. – 1993. The biology of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean Coast. *In:* T. Okutani, R.K. O'Dor and T. Kubodera (eds.), *Recent Advances in Fisheries Biology*, pp. 477-487, Tokai University Press, Tokyo.

Sánchez, P., P. Belcari and P. Sartor. – 1998. Composition and spatial distribution of cephalopods in two north-western Mediterranean areas. *In:* A.I.L. Payne, M.R. Lipinski, M.R. Clarke and M.A.C. Roeleveld (eds.), *Cephalopod Biodiversity, Ecology and Evolution. S. Afr. J. Mar. Sci.,* 20: 17-24.

Scheel, D. – 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. *Mar. Ecol. - P. S. Z. N. I*, 23: 185-206.

Smale, M.J., B.A. Roel, A. Badenhorst and J.G. Field. – 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. *J. Fish. Biol.*, 43(Suppl A): 169-191.

Smith, C.D. and C.L. Griffiths - 2002. Aspects of the population biology of *Octopus vulgaris* in False Bay, South Africa. *S. Afr. J. Mar. Sci.*, 24: 185-192.

Swartzman, G., W. Stuetzle, K. Kulman and M. Powojowski. – 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. *ICES J. Mar. Sci.*, 51: 481-492.

Tuck, I.D., C.J. Chapman, R.J.A. Atkinson, N. Bailey and R.S.M. Smith. – 1997. A comparison of methods for stock assessment of the Norway lobster, *Nephrops norvegicus*, in the Fifth of Clyde. *Fish. Res.*, 32: 89-100.

Tursi, A. and G. D'Onghia. – 1992. Cephalopods of the Ionian Sea (Mediterranean Sea). *Oebalia*, XVIII: 25-43.

Voight, J.R. – 1992. Movement, injuries and growth of members of a natural population of the Pacific pygmy octopus, *Octopus digueti*. *J. Zool.,* 228: 247-263.

Whitaker, J.D., L.B. DeLancey and J.E. Jenkins. – 1991. Aspects of the biology and fishery potential for *Octopus vulgaris* off the coast of South Carolina. *Bull. Mar. Sci.*, 49(1-2): 482-493.

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