

Den ecology of *Octopus vulgaris* Cuvier, 1797, on soft sediment: availability and types of shelter*

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SUMMARY: To avoid predation, octopuses select and actively modify shelters (also called dens) in the substratum, where they remain most of the time, especially during daylight hours. The main questions that this study deals with are: Is den availability a significant constraint for the distribution of *Octopus vulgaris* on soft sediment? What kind of dens does *O. vulgaris* use on soft sediment and what factors affect the selection of one type instead of another? With population density measurements by SCUBA diving and enrichment experiments with artificial dens, we concluded that the availability of solid materials necessary for den construction is a limiting factor for the distribution of *O. vulgaris* on soft sediment. *O. vulgaris* used four different types of den on soft sediment: "well" (a vertical hole in the sediment), "rock/stone" (the octopus uses a rock or a large stone to dig a cavity under it), "shell" (an empty shell is used), "human origin" (a solid material of human origin is used). The relative proportion of the four types of den in the areas studied was: 38.7% "human origin", 29.7% "well", 21.5% "rock/stone", 2.9% "shell". Also, 7.3% of the octopuses were found outside their den. The main types of den were found in different relative proportions in relation to the depth, the distance from shore, the octopus size and the granulometry of the sediment.

Key words: cephalopod, den ecology, marine debris, *Octopus vulgaris*, visual census.

RESUMEN: ECOLOGÍA DE REFUGIOS DE *OCTOPUS VULGARIS*, CUVIER 1797, EN SEDIMENTOS BLANDOS: DISPONIBILIDAD Y TIPOS DE REFUGIOS. – Para evitar la depredación, los pulpos seleccionan y modifican de forma activa sus refugios en el sustrato donde permanecen casi todo el tiempo, sobretodo durante las horas del día. Las principales preguntas de las que trata el presente estudio son: ¿Es la disponibilidad de los refugios una restricción importante para la distribución del *Octopus vulgaris* en el sedimento blando? ¿Qué clase de refugios utiliza *O. vulgaris* en el sedimento blando y qué factores afectan la selección de un tipo en lugar de otro? A partir de medidas de densidad de población hechas por submarinistas y de experimentos hechos con refugios artificiales, concluimos que la disponibilidad de los materiales sólidos necesarios para la construcción de refugios es un factor que limita la distribución del *O. vulgaris* en el sedimento blando. Se descubrió que *O. vulgaris* utiliza 4 tipos diferentes de refugios en el sedimento blando: "pozo" (un agujero vertical en el suelo blando), "roca/piedra" (el pulpo utiliza una roca o una piedra grande para cavar un agujero debajo de ellos), "concha" (utiliza una concha vacía), "origen humano" (utiliza un material sólido de origen humano). Las proporciones relativas de los 4 tipos de refugios en las zonas estudiadas son: 38.7% "origen humano", 29.7% "pozo", 21.5% "roca/piedra", 2.9% "concha" y 7.3% de los pulpos fueron encontrados fuera de sus refugios. Los principales tipos de refugios se encontraron en proporciones relativamente diferentes en relación con la profundidad, la distancia a la orilla del mar, el tamaño del pulpo y el tamaño de los gránulos del sedimento.

Palabras clave: cefalópodo, ecología de refugios, escombros marinos, pulpo, censo visual.

INTRODUCTION

Octopus vulgaris Cuvier 1797 is a truly coastal and sedentary species living between 0 and 200 m

depth. Its abundance decreases with depth and is nearly zero at the slope of the continental shelf. The species is perfectly adapted to living in very different biotopes: coral reefs, rocks, sandy and muddy bottom, and seagrass. It has a wide range of prey species, dependent to some extent on the local

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biotope, and appears to be unselective in prey choice (Nixon, 1986).

Because of their soft body, octopuses appear to be very vulnerable to predation, particularly from fish (Aronson, 1991) but also from marine mammals (dos Santos and Haimovici, 2001). Remains of octopuses are found in the stomachs of several fish species (Randall, 1967; Quast, 1971) and for a few, especially the moray eels, they form a large proportion of their diet. Aronson (1986) suggested that the lack of a fish predator population of *Octopus briareus* in Sweetings Pond, a salt-water lagoon, led directly to a very dense population (9/1000 m²) of octopuses. Ambrose (1988) speculated that the dense population of octopuses on Bird Rock (15.5/1000 m²) was a result of removal of fish predators by humans. To survive the pressure of visual predators (such as fish) many marine species that do not rely upon vision themselves adopt a nocturnal activity pattern. Octopuses' prey-catching method of speculative foraging (Yarnall, 1969; Chase and Wells, 1986), using chemical and tactile cues but not always visual ones, does not select them for either diurnal or nocturnal activity. The fact that *Octopus vulgaris* has selected a nocturnal activity pattern (Altman, 1967; Kayes, 1974, personal observations) may indicate a strong pressure by visual predators. If predation risk is high, the octopus may maximise efficiency not by optimising energy gain but by avoiding the risk of injury or death to ensure survival to reproduction (Mather and O'Dor, 1991).

To avoid predation, octopuses select and actively modify shelters (also called dens) in the substratum, where they remain most of the time, especially during daylight hours (Kayes, 1974; Mather, 1988). "Sleep" or rest probably serves to inactivate animals and keep them from the risk of predation when they do not need to be finding food (Meddis, 1975). The existence of appropriate shelters seems to be a significant constraint on octopus distribution, especially on soft sediment. On sandy or muddy bottoms octopuses need to find sufficient solid materials, such as rocks, stones, shells and litter of human origin to be used for the construction of their dens.

Use of shelter is documented for several octopus species. *Octopus joubini* in the sandy-bottom areas of northern Florida were confined to areas containing mollusc shells for homes (Mather, 1982). *Octopus briareus* in the Caribbean were unusually abundant in a salt-water lagoon with many shelters and few predators, and when areas were enriched with artificial dens local density increased (Aronson,

1986). Hartwick *et al.* (1988) compared two populations of *Octopus dofleini* in Clayuquot Sound, an inshore group with easy access to shelters and an offshore group with lesser access. Octopuses in the offshore group were both less abundant and more likely to show arm damage, which was probably a result of predation. *Octopus tetricus* densities were higher in patch reef habitats than broken and flat reefs and abundance increased with an increasing mean number of small boulders (Anderson, 1997). Iribarne (1990) studied the use of shelter by *Octopus tehuelchus* in a sandy bottom area in Argentina and suggested that shelters may be a limiting resource mainly for larger octopuses. Forsythe and Hanlon (1988) described *Octopus bimaculoides* as confined to sheltered areas under a pier and along the edge of a rocky outcrop. Beer bottles allow *Octopus rubescens* to utilise the sand/mud habitat in areas where natural dens are limited (Anderson *et al.*, 1999). Thus, shelter availability is very important for octopuses.

Little work has been done on the den ecology of *O. vulgaris*. In Bermuda, Mather studied the day-time activity of juvenile *O. vulgaris* (Mather, 1988) and home choice and modification by juvenile *O. vulgaris* (Mather, 1994) in shallow water (up to 2 m depth) and a rocky substratum. Recent papers, though, support the hypothesis that *O. vulgaris* is a species restricted to the Mediterranean and Eastern Atlantic coast (Mangold, 1998; Söller *et al.*, 2000). Although this species has been cited in Japan or the Western Atlantic (as in Mather's papers from Bermuda), these specimens are members of a species complex rather than real *O. vulgaris*. In the Mediterranean, Altman (1967) and Kayes (1974) have studied some aspects of den ecology, mainly daily activity patterns, in shallow waters. Despite this, many aspects of den ecology remain unknown. In particular, there is a lack of knowledge about shelter on soft sediment and for greater depths than shallow coastline. No study on den ecology of *O. vulgaris* has been carried out on soft sediment. Some aspects of the ecology of *O. vulgaris* have been studied in the Mediterranean and on soft sediment through several fishing surveys (Guerra, 1981; Sanchez and Obarti, 1993; Quetglas, 1998; Belcari *et al.*, 2002; Tsangridis *et al.*, 2002). However, there are many aspects, such as those dealt with in this paper, that cannot be studied through fishing surveys, and direct observation in the field is necessary. As a step towards a better understanding of the den ecology of *O. vulgaris*, the present study deals with

the following questions: (1) What kind of dens does *O. vulgaris* use in soft sediment areas? (2) What factors affect the selection of one type of shelter rather than another? (3) Is the availability of solid material (rocks, stones, shells, litter of human origin etc.) utilised for den construction a significant constraint for the distribution of *O. vulgaris* on soft sediment?

MATERIALS AND METHODS

To answer the aforementioned questions three different surveys were performed. All surveys were conducted with scuba diving in coastal areas and on soft sediment. The authors performed all the dives and no professional divers or volunteers were used.

Survey one

To check whether the availability of solid materials is a significant constraint for the distribution of *Octopus vulgaris* on soft sediment, population density was measured by visual census during scuba diving. The dives were made at 38 different sites in Greek coastal waters, grouped in 8 geographical sections as shown in Figure 1, and at depths of 0 to 25 m. The different sites were chosen so that some of them were completely “clean” in the sense that no solid material such as stones, rocks, large shells and litter was available (white circles in Fig. 1) and the others were abundant with such solid materials (black circles in Fig. 1). This survey was conducted between June 2001 and December 2001. To avoid the influence of seasonal variations on octopus abundance for our results, the monthly relative proportion of the two kinds of sites that were visited (‘clean’ and not ‘clean’) was held constant during the survey.

The octopuses were counted within 1600 m² 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 Mather’s (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 at each end. The two weights touched the substrate and, as the diver moved forward, traced a 50 m long and 2 m wide corridor (starting corridor). Then the diver started moving

parallel to the starting corridor in such a way that the one weight of the pipe traced 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 tangent corridors, thus forming a 50x2x16=1600 m² transect. During this procedure the diver recorded all the octopuses found inside each corridor and the *Octopus vulgaris* density was calculated for each site as individuals per 1000 m² (ind/1000 m²). Octopuses were never observed to leave their den due to the presence of the diver or due to the procedure described, so disturbance is assumed to be minimal. At some sites, more than one dive was made in different areas at different depths. One repetitive dive was made in every area on a different day. For each area the arithmetic mean of the two densities was taken as the *O. vulgaris* density in the area. The mean density of the areas with no solid material available (15 sites, 23 areas) was compared to the mean density of the areas with available solid material for den construction (23 sites, 33 areas).

Survey two

To further verify that the availability of solid materials is a significant constraint for the distribution of *Octopus vulgaris* on soft sediment, an enrichment experiment with artificial dens was made. We chose four sites (black triangles in Fig. 1), two with no solid material availability and more than 1 km away from hard bottom areas (sites S₁ and S₂) and two with plenty of solid material available for den construction (sites S₃ and S₄). At each site, four measurements of octopus density were made on different days in the same way as described for Survey One. During the first measurement of each site the border of the 1600 m² transect was outlined with rope that was left on the bottom during the experiment in order to survey the same area exactly. After the four measurements, at each site 30 PVC pots (15 of 10 cm diameter and 15 of 20 cm diameter) were placed in the outlined area and left there. The distribution of the pots on the transect area was as even as possible. After approximately one month, the octopus density was measured again four times at each site. As controls we used areas with similar characteristics and approximately 1.2-2.0 km from each experimental site, which were also used in Survey One (Fig 1). The controls were not chosen closer to the enrichment areas to minimise the possibility of octopuses’ migration between the experimental and

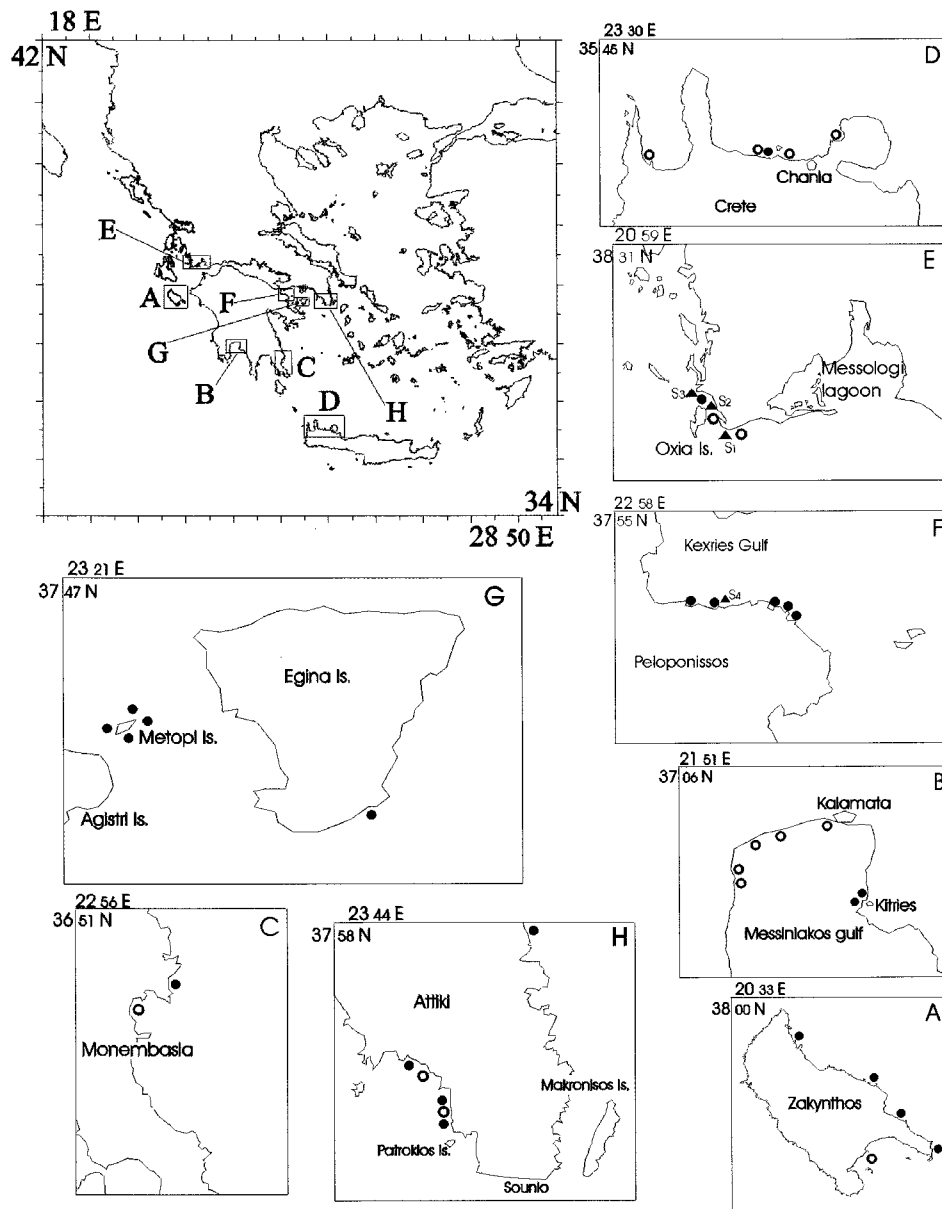


FIG. 1. – Location of the 8 geographical sections (A-H) and the 38 experimental sites. White circles represent sites with no solid material such as stones, rocks, large shells, litter etc. available. Black circles represent areas with abundance of solid material. Black triangles show sites for enrichment Survey Two.

control area. The mean density at each site without the PVC pots was compared with the corresponding density at the same site after placing the PVC pots. Survey Two lasted from September 2001 until December 2001. After the completion of the measurements at sites S₃ and S₄, the density of solid materials that may be utilised for den construction was counted during separate dives in the experimental areas.

Survey three

This survey was planned to find out: (1) what kind of dens *Octopus vulgaris* uses on soft sediment,

(2) the relative proportion of the different dens in relation to the size of the octopus, and (3) whether the type of den correlates to abiotic factors such as distance from shore, depth and granulometric characteristics of the sediment.

At the 23 sites of Figure 1, where solid materials were available for den construction, 174 dives with SCUBA were made at depths of 0 to 25 m between February 2001 and August 2002 and 344 octopuses were recorded. At each site several dives were made at different depths so that the whole depth range from 0 to 25 m was covered (wherever possible). Each site was visited either monthly (sections F and H) or quarterly (sections A, B, C, D, E, G). Each

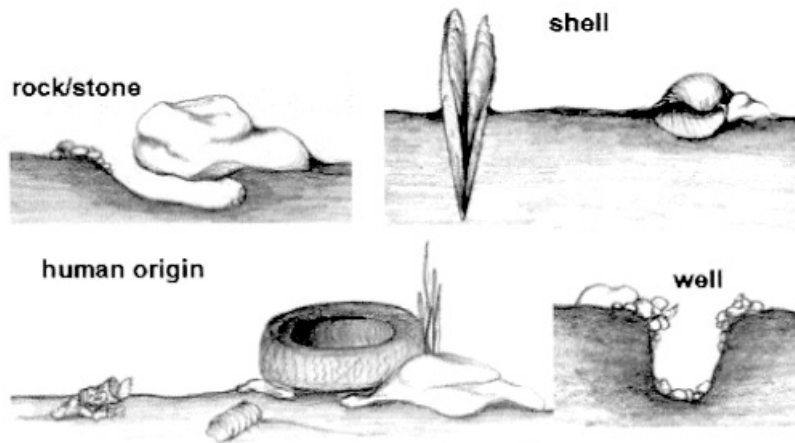


FIG. 2. – A sketch of the 4 different den types.

time the dive position was recorded at the point of entrance by aiming with the compass at fixed points and then the distance from shore was estimated using a map of the area. The dive areas were divided into two groups: group A included areas that were less than 50 m from the shore and group B included areas that were more than 50 m from the shore.

During each dive the researcher searched for octopuses, and whenever he found one he recorded the den type, the depth and the size class of the octopus. A sample of the surface sediment (upper 5 cm) was taken.

The depth, depth range and the dive duration were recorded with a dive computer (Sunto, model Vyper) with an accuracy of 0.1 m for the depth. Particle size analysis of the sediment sample was made according to Buchanan (1984), and for each sample the median diameter $Md\phi$ and the quartile deviation $QD\phi$ were calculated as measures of the central tendency and the degree of scatter of the granule size frequencies respectively. The classification of the median diameter $Md\phi$ was made according to the Wentworth scale (Wentworth, 1922), and the following 6 classes were used: very coarse sand ($-1 < Md\phi < 0$), coarse sand ($0 < Md\phi < 1$), medium sand ($1 < Md\phi < 2$), fine sand ($2 < Md\phi < 3$), very fine sand ($3 < Md\phi < 4$), and silt ($4 < Md\phi < 8$). The classification of the quartile deviation $QD\phi$ was as follows: well sorted ($QD\phi < 0.50$), moderately sorted ($0.50 < QD\phi < 1.00$) and poorly sorted ($1.00 < QD\phi$).

To estimate the size of the octopuses, 5 size classes were used: size 1 (< 50 gr), size 2 [50 gr, 200 gr], size 3 [200 gr, 500 gr], size 4 [500 gr, 2000 gr] and size 5 (> 2000 gr). The diver placed each octopus he encountered in one of these classes, by sight.

To reduce the classification error the authors practiced initially on more than 70 specimens that were used at the lab for other purposes, and before the onset of this survey five 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 placed in neighboring classes. This error was considered acceptable for the experimental needs.

Dens were divided into four different types (Fig. 2):

- “well”: the octopus digs a vertical hole in the soft sediment and reinforces the inner wall with stones, shells and other solid materials so that it is quite stable. Around the well rim the octopus also usually puts solid materials.

- “rock/stone”: the octopus uses a rock or a large stone to dig a cavity under it. The cavity usually has an inclined direction in relation to the horizontal but can sometimes be completely horizontal.

- “shell”: an empty shell, usually a *Pinna nobilis* or a *Tonna galea* shell, is used as a den.

- “human origin”: a solid material of human origin that forms a cavity such as empty bottles, plastic cups, buckets, barrels, tyres, pots, pipes, cans, shoes, etc. may be used as a den.

- “free”: octopuses that were found moving outside their den were recorded as “free”.

RESULTS

Survey one

In the 23 areas with no solid material available no octopus was found, so the mean density was zero. In the 33 areas with abundance of solid materials the

TABLE 1. – *Octopus* densities (ind/1000 m²) at the experimental sites and the controls of Survey two, before and after the enrichment with artificial dens. S₁, S₂, S₃, S₄ are the four experimental sites and C₁, C₂, C₃, C₄ the corresponding controls.

S1	C1	S2	C2	S3	C3	S4	C4
Before enrichment							
0.00	0.00	0.00	0.00	1.25	0.63	1.25	0.63
0.00	0.00	0.00	0.00	1.25	0.63	0.63	1.88
0.00	0.00	0.00	0.00	0.63	0.63	1.25	1.25
0.00	0.00	0.00	0.00	0.63	0.00	2.50	1.25
After enrichment							
0.63	0.00	3.75	0.00	1.88	0.63	2.50	1.88
1.25	0.00	5.00	0.00	3.13	0.63	1.25	0.63
1.25	0.00	2.50	0.00	3.13	0.63	1.88	1.25
0.63	0.00	4.38	0.00	2.50	0.63	1.88	1.88

densities ranged from 0 to 3.4 ind/1000 m², with a mean value of 1.35 ind/1000m² and a standard deviation of 0.98 ind/1000 m².

The mean density in areas with abundance of solid materials was significantly greater than the mean density in areas with no available solid materials (non-parametric Mann Whitney test, U=34.5, n₁=23, n₂=33, p<0.0001). It can therefore be concluded that the existence of solid materials in a soft sediment area is a significant factor for *Octopus vulgaris* density during daylight hours. This is a rather obvious conclusion since the density was zero in every “clean” area.

Survey two

The octopus densities at the experimental sites and the controls, before and after the enrichment

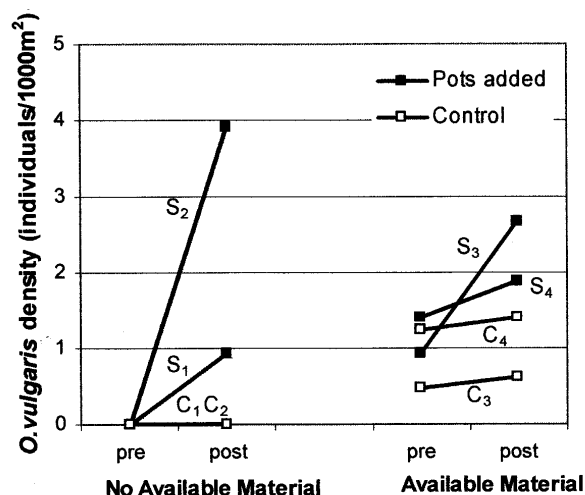


FIG. 3. – Results of enrichment Survey two. The mean octopus density at each experimental and control site, before and after the enrichment with artificial dens (pre and post correspondingly) is given.

with artificial dens, are given in Table 1. In Figure 3 the mean *Octopus vulgaris* density is shown at each of the four sites S₁, S₂, S₃, S₄ (black triangles in Fig. 1), before and after placing the pots. At the same graph the mean density in the control areas is shown.

At sites S₁ and S₂ the densities before the enrichment were zero at all times, as were the densities in the control areas. The density after the enrichment was significantly greater than zero (one sample t-test) both in S₁ (n=4, t=5.25, p=0.0067) and in S₂ (n=4, t=7.32, p=0.0026), so the enrichment was efficient.

At sites S₃ and S₄ the corresponding mean density of the control was deducted from each density measurement, in order to exclude possible seasonal (or other) variation of octopus density during the one-month period that each enrichment lasted. An F-test showed that we may assume equal variances both for S₃ (F=2.79, p=0.42) and S₄ (F=2.38, p=0.49), so two-sample t-tests were conducted to compare densities before and after enrichment. At site S₃, enrichment significantly increased octopus density (t=4.48, p=0.042), but it did not at site S₄ (t=0.67, p=0.5304). The density of solid materials that may be utilised for den construction was 6.3 items/1000 m² at S₃ and 31.4 items/1000 m² at S₄. At S₄ most of the items were of human origin (79%) while at site S₃ no items of human origin were found. The overabundance of solid materials at S₄ caused no statistically significant increase in octopus density after the enrichment. On the other hand, at S₃ with much less available material for den construction the enrichment caused a statistically significant increase in octopus density.

The hypothesis that the increase in octopus density (after control correction) depends on the experimental site was tested with an ANOVA test. Statistical significant differences were found in the increase of octopus density between sites (df=3, F=20.90, p<0.0001). A Tukey HSD multiple range test showed two homogenous groups (at 99% significant level) with site S₂ having statistically greater increase than the three other sites, which were grouped together.

Survey three

Most of the 344 octopuses that were recorded used litter of human origin as their den (Fig. 4). 7.3% of the octopuses were found outside their den. Of the octopuses that used litter of human origin as their den, 23% used plastic bottles (mainly mineral

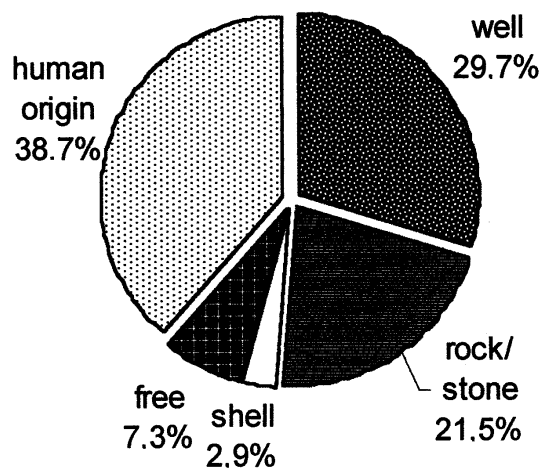


FIG. 4. – The relative proportion of the different types of dens occupied by the 344 octopuses recorded during Survey three. The 4 different den types are: “well” when the octopus digs a vertical hole in the soft sediment and reinforces the inner wall with solid materials; “rock/stone” when the octopus uses a rock or a large stone to dig a cavity under it; “shell” when an empty shell is used; “human origin” when a solid material of human origin that forms a cavity is used. The octopuses that were found moving far from their den were characterised as “free”.

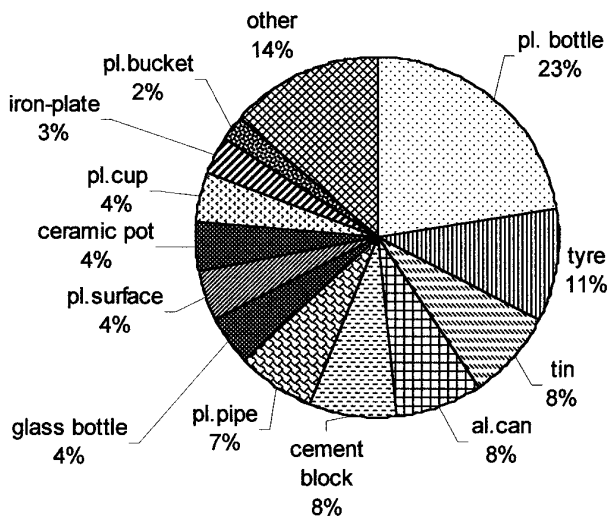


FIG. 5. – The 133 “human origin” dens that were recorded during Survey three are categorised by type of material. (pl.=plastic, al.=aluminium)

water bottles) and plastic litter in general consisted of 47% of the recorded dens (Fig. 5).

Six Chi-square tests were conducted to check whether the frequencies of occurrence of the several den types were independent of the following 6 variables: *Octopus vulgaris* size, depth, distance from shore, Mdφ, QDφ and geographical section. To satisfy the recommendation that the average expected frequency should be at least 6.0 when one is performing a chi-square analysis (Zar, 1996), the “shell” den type and “free” animals were not con-

sidered. For the same reasons the five size categories for octopuses were merged into just three: small (size 1 and 2), medium (size 3) and large (size 4 and 5); the “silt” and “very fine sand” Mdφ classes were not taken into account, nor were the geographical sections A, C and D.

The six contingency tables that were analysed by chi-square statistics are given in Table 2, where the categories in each case are given, together with the observed and expected values. By chi-square analysis of the contingency tables (Zar, 1996), we concluded that the Den Type is not independent of the Depth ($\chi^2=22.5$, Df=8, $p=0.0041$), the distance from shore ($\chi^2=22.1$, Df=2, $p<0.0001$), Mdφ ($\chi^2=20.9$, Df=6, $p=0.0019$), the geographical section ($\chi^2=64.9$, Df=8, $p<0.0001$) and *O. vulgaris* size ($\chi^2=12.3$, Df=4, $p=0.0151$). Den Type is independent of QDφ ($\chi^2=2.1$, Df=4, $p=0.7194$).

Shells were not used at all by large animals (Sizes 4 and 5). In shallow waters, mostly small octopuses were found, while larger animals were mainly found in deeper areas. It is worth mentioning

TABLE 2. – Contingency tables of Den Type frequencies in relation to octopus size, depth categories, Mdφ, QDφ, distance from shore and geographical section. In each cell the observed frequency is shown with the corresponding expected frequency in parenthesis.

	Den Type human origin	rock/stone	well
Octopus Size			
small	36 (41.3)	38 (34.3)	49 (47.3)
medium	23 (27.2)	28 (22.6)	30 (31.2)
large	30 (20.5)	8 (17.0)	23 (23.5)
Depth			
0-5 m	5 (9.4)	14 (7.8)	9 (10.8)
5-10 m	24 (30.2)	31 (25.1)	35 (34.6)
10-15 m	23 (21.2)	18 (17.6)	22 (24.2)
15-20 m	24 (16.8)	8 (14.0)	18 (19.2)
20-25 m	13 (11.4)	3 (9.5)	18 (13.1)
Mdφ			
very coarse sand	7 (12.4)	16 (12.2)	18 (16.4)
coarse sand	12 (17.6)	16 (17.2)	30 (23.2)
medium sand	5 (6.1)	8 (5.9)	7 (8.0)
fine sand	29 (17.0)	12 (16.6)	15 (22.4)
QDφ			
poorly sorted	31 (26.6)	22 (23.6)	28 (30.8)
moderately sorted	21 (24.9)	24 (22.2)	31 (28.9)
well sorted	11 (11.5)	10 (10.2)	14 (13.3)
Dist. from shore			
A (<50 m)	23 (28.9)	40 (24.0)	23 (33.1)
B (>50 m)	66 (60.1)	34 (50.0)	79 (68.9)
Geogr. Section			
B	15 (15.9)	7 (7.7)	13 (11.4)
E	27 (12.7)	0 (6.2)	1 (9.1)
F	77 (74.9)	41 (36.3)	47 (53.8)
G	2 (15.0)	6 (7.3)	25 (10.8)
H	7 (9.5)	8 (4.6)	6 (6.9)

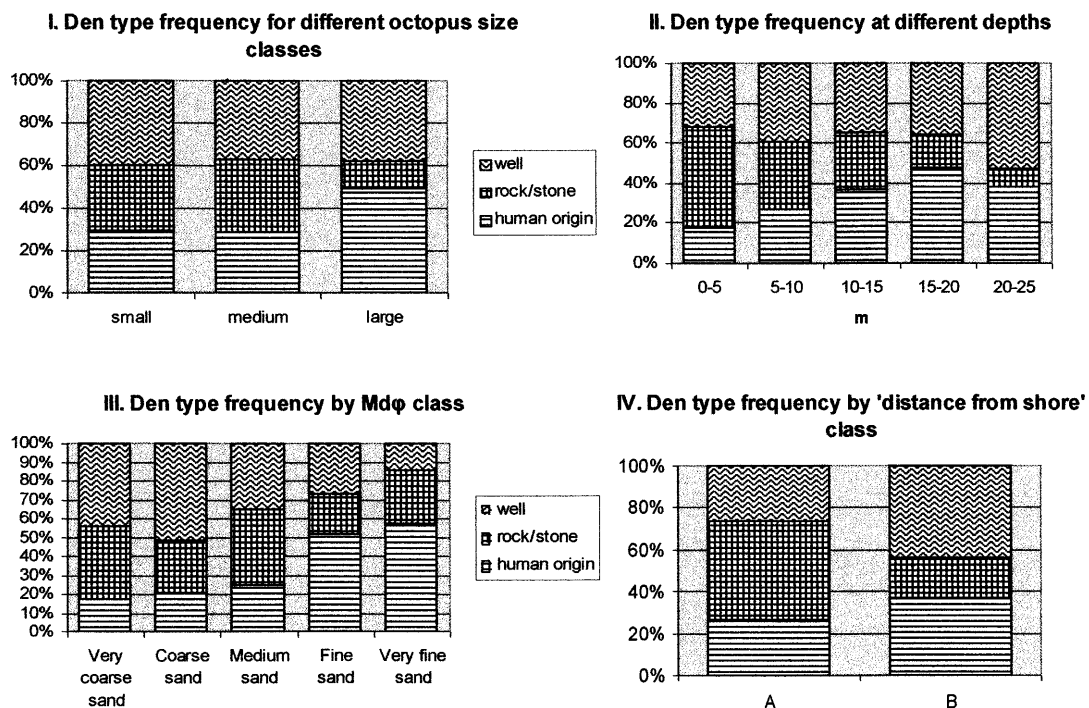


FIG. 6. – Den type frequencies in relation to *Octopus vulgaris* size, depth, distance from shore and the sediment's median grain diameter Mdφ.

that “Size 5” animals were not found at all in the 0–5 m zone, while 80% of them were deeper than 15 m. On the other hand, 82% of “Size 1” (<50gr) octopuses were found in less than 15 m-deep waters. “Wells” were used more on coarser sand than on fine sand and the opposite was true for “human origin” dens.

The deeper and further from the shore, the fewer dens were made under a rock or a large stone (Fig. 6, Charts II, IV). Large octopuses use “rock/stone” much less than the other size classes (Fig. 6, Chart I). From the 27 “Size 5” animals (>2000 kg) none was observed to utilise “rock/stone” as a den. One reason for the lower frequency of “rock/stone” dens for large octopuses is that they tend to dwell deeper than small/medium ones and the deeper and further away from shore the less available are rock/stone. Indeed, from the large octopuses found shallower than 15 m, 23% used “rock/stone” dens, while at depths of 15 to 25 m the corresponding frequency was only 3.5%. Still, this difference alone does not fully explain the greater frequency of “human” dens among large animals. Even if we consider only the records shallower than 15 m and run a chi-square test, we find that the frequency of the different types of dens is still different among large and small/medium octopuses ($p = 0.0369$, $\chi^2 = 10.22$, $df = 4$).

DISCUSSION

Our main conclusion is that on soft sediment, material that can be utilised for den construction is a limiting factor to the distribution of *O. vulgaris*. Even in areas with zero octopus densities, enrichment with artificial dens allowed the establishment of octopus populations (Fig. 3). No significant increase in density was only observed in area S_4 , which already had an overabundance of dens.

The likely dependence of octopus density on den availability has been documented for other octopus species such as *Octopus joubini* (Mather, 1982a, b), *O. briareus* (Aronson, 1986), *O. dofleini* (Hartwick *et al.*, 1988), *O. tehuatlchus* (Iribarne, 1990), *O. bimaculoides* (Forsythe and Hanlon, 1988), and *O. rubescens* (Anderson *et al.*, 1999). An enrichment experiment with artificial dens for *O. briareus* (Aronson, 1986) also increased local density.

Density increases with short-term enrichment such as that of Survey Two are due to immigration and do not alone establish that dens are globally limiting (Aronson, 1986). It is not obvious that enrichment with artificial dens on soft sediment would cause the overall octopus population to increase in the long term. A more even dispersal of the population between soft substrate and adjacent rocky areas

might happen without a net total population increase. But as the mobility of octopuses would increase (more dens periodically occupied by the same number of octopuses), it would be easier for them to exploit wider areas for food and den competition would also reduce. Eventually, a greater post settlement survival might occur (it has to be proved, though). To prove a global limitation of dens, a long-term, large-scale enrichment would be necessary. The combined results of Surveys One and Two, though, suggest that the existence of solid material appropriate for den construction is indeed a limiting factor.

The importance of the den is evident from the rather low frequency (7.3%) of recorded octopuses outside a protected shelter during daylight hours. This frequency is a good estimate of the percentage of daytime that octopuses spend outside their den and it is close to the value (11%) estimated by Mather (1988) during a full daytime observation of four juvenile octopuses over a five-week span in a near-shore environment in Bermuda.

As during daylight hours no free octopus was observed in "clean" areas, it is suggested that octopuses hunt in these areas during long night trips from adjacent areas (rocky or soft bottom with available dens) and may migrate when they find an appropriate den. This is consistent with the observation that *Octopus vulgaris* makes short trips during the day and much longer excursions during the night (Altman, 1967; Kayes, 1974). One month was more than enough for octopuses to immigrate to experimental sites S_1 and S_2 , and at S_2 the density achieved was very high compared to the densities of Survey One. Fishery studies with pots or traps (Sanchez and Obarti, 1993; Whitaker *et al.*, 1991) have also documented that artificial dens become occupied within a few days. No migration can be proved, however, since there is no way to find out whether the octopuses were already resident in the area in non-artificial dens or they migrated from other areas far away. On the other hand, by visual census we were able to ascertain the non-existence of shelters and octopuses at sites S_1 and S_2 before the enrichment and to conclude that long-distance migrations do happen.

The effectiveness of an enrichment of an area with artificial dens depends on the density of solid material necessary for den construction. Consequently, the catching efficiency of pot fishing is dependent on the fishing site and the abundance of materials used for den construction. A low catch of a pot fishing survey is not strong evidence of a low

octopus density in the area, as a high octopus density is also quite possible if there is a great abundance of materials that can be used for den construction. Furthermore, many of the octopuses (or even all) caught by pot fishing may have immigrated from neighbouring areas, so the pot fishing catch does not necessarily represent the octopus abundance in the specific area fished but rather in a much wider region. Animals branded by Itami (1964) and recaptured after 3, 38 and 40 days had travelled 31, 30 and 50 km respectively. The degree of immigration might also be very variable. Mather (1994) found that octopuses occupied dens for short periods (average 10 days), stayed longer in areas where preferred prey was available and a 'Win-Stay' foraging strategy is suggested (Mather and O'Dor, 1991). Therefore, the availability of food affects immigration intensity and consequently affects the efficiency of pot fishing. Moreover, moonlight and the lunar cycle may significantly affect octopus mobility. Voight (1992) has found that full moonlight significantly reduced the mobility of *Octopus digueti* and proposed as a possible explanation either the increase in an individual's vulnerability to predation or the increase in an octopus's foraging efficiency, reducing its need to travel long distances and seek new shelter. Since the intensity of moonlight affects octopus mobility, cloudy weather, depth or seawater turbidity may affect it also. So, octopus mobility and consequently immigration are quite variable and may depend on multiple factors, affecting pot-fishing efficiency in a very complicated way. Thus, pot fishing may not be used reliably to make spatial or temporal comparisons of octopus abundance or density estimations, and such results should be considered with caution.

Four basic types of den were found, as described above. The relative percentage of the different types of den in an area is a function of the availability of the corresponding solid materials. Near shore the availability of rocks and stones, which come mainly from land erosion, is much greater than far from the shore, where there may be no rocks and stones at all. As a consequence, "rock/stone" dens are more common near shore. The availability of "human origin" solid materials is quite variable among different areas. The density of marine benthic debris on the continental shelf and the seabed in the Mediterranean has been estimated by several studies to be from 0 up to some hundreds of thousands of items per km² (Galgani *et al.*, 1995a; Galgani *et al.*, 1995b; Galil *et al.*, 1995; Stefatos *et al.*, 1999; Gal-

gani *et al.*, 2000). Even greater densities were observed at some points along the coast (Galgani *et al.*, 2000). A considerable geographical variation in concentrations of debris is encountered, with peak abundance near metropolitan areas (Galgani *et al.*, 1995a), near areas with low circulation like inlets (Hess *et al.*, 1999; Galgani *et al.*, 2000), around the estuaries of rivers (Williams and Simmons, 1997), in areas with high shipping traffic (Stefatos *et al.*, 1999), in submarine canyons (Galgani *et al.*, 1995b) and in areas of high coastal fishing activities (personal observation). The density of debris is dependent on all the above (and maybe more) factors and this is why the relative frequency of “human origin” dens is so variable. For example, areas of Section E (Fig. 1) are off long sandy beaches and flat landmarks so that no rocks or stones are found on the sea-bottom. At the same time, these areas are highly fished and several potential dens of human origin are found on the bottom. On the other hand, four of the five areas of Section G are around an uninhabited island (Metopi) and almost no litter is found on the sea-bottom, so almost no “human origin” dens are encountered. Thus, it seems that the distribution pattern of marine litter may affect the distribution pattern of *O. vulgaris* on soft sediment, especially in areas with low availability of dens. Among the “human origin” dens, plastic bottles (mainly mineral water bottles) constitute almost one fourth, while plastics in general account for almost half of the dens (Fig. 5).

Small and medium octopuses (Fig. 6-Chart I) often seem to mostly built “wells” or use “rocks/stone” when available (in shallow waters near shore) rather than shelters of “human origin”. This could be explained by the high growth rates of small and medium animals, which create a continuous need for larger dens in order to fit. Both *Octopus dofleini* in the field (Hartwick *et al.*, 1978) and *O. joubini* in the laboratory (Mather, 1982a) chose homes of a volume roughly matching their size. “Rock/stone” or “wells” are easily convertible to greater volume; thus, small and medium octopuses could stay longer in these shelters. Mather (1994) observed that juvenile octopuses, not just initially but over many days of occupancy, regularly modify their homes by blowing or pushing sand out of the den and rearranging rocks or shells in front of them. On the other hand, in most cases “human origin” dens have a fixed cavity volume, so octopuses have to change den when they no longer fit. Longer stay in “rock/stone” and “wells” than in “human origin”

dens may be the reason for more records of these den types during this study. Larger octopuses have smaller growth rates or even negative ones near before and after spawning (Mangold, 1983). Therefore, the urge (if it comes) to change den due to tightness is after longer time intervals.

The median diameter (Md ϕ) of sand granules significantly affects the analogy of the different den types (Table 2, Fig. 6-Chart III), while the quartile deviation (QD ϕ) has no effect. “Wells” are used more on coarser sand than on fine sand and the opposite is true for “human origin” dens. One explanation might be that fine sand is more compact and difficult to excavate and octopuses may not be able to do so, or avoid using the energy needed to dig a well. On the other hand, coarse sand is much easier to excavate and takes much less energy for an octopus to dig a well.

CONCLUSION

Our results show that the availability of solid materials (rocks, stones, shells, litter of human origin, etc.) that are utilised for den construction is a significant constraint for the distribution of *Octopus vulgaris* on soft sediment. The main types of den (“wells”, “rock/stone”, “human origin”, “shells”) are found at different relative proportions according to the depth, the distance from shore, the octopus size and the size of the sand granules. Den availability seems to be a basic parameter in studying the distribution of *O. vulgaris*.

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