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FACTORS AFFECTING THE SPATIAL DISTRIBUTION OF NATURAL POPULATIONS OF *OCTOPUS JOUBINI* ROBSON

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Abstract. Observations were made on the density and distribution of *Octopus joubini* in its natural environment. The average density of octopuses was 1/33 m^2 but their distribution was clumped. This distribution correlated significantly with the distribution of molluscan shells in which they hid. In addition, octopuses were attracted to sites that had been enriched with extra empty gastropod shells. Since site stability was not observed and they were not repelled from one another when placed at a high density, octopuses were probably not spaced by social pressure. Small crab species, the normal prey of *O. joubini*, were at a very high density of 30/m^2, and food abundance probably did not limit octopus number. The main factor affecting distribution of this population of octopuses may be predator pressure acting through the availability of places to hide.

Social behaviour, normally studied in the natural environment, can be drastically altered by the spatial restrictions imposed by the laboratory (Leyhausen 1979). Because of the restrictions and the difficulty of keeping cephalopods in a laboratory situation, the study of social behaviour in these animals is minimal. Octopuses are intelligent animals with keen sensory perception (Wells 1978), making it difficult to study them in their natural environment without disrupting them. Moreover, they are often large and metabolically sensitive, requiring large tanks to remain in good condition in captivity. Thus studies of interactions of individuals in the laboratory are also difficult.

In their natural ocean habitat most species of *Octopus* are solitary (Guerra 1981) and are described in popular accounts as territorial. They use crevices in the rock, empty shells, or spaces in a reef face as homes from which they go out to catch prey and to which they return to eat and rest (Boycott 1954; Woods 1965; Altman 1967). Despite their solitary habit, octopuses have homes very close together and they have not been seen defending territories (Kayes 1974).

In captivity, the two *Octopus* species observed have shown dominance rather than territoriality. *Octopus cyanea*, kept in large outdoor ponds, did not defend occupied areas; instead, they appeared to set up a dominance hierarchy (Yarnall 1969). This type of social organization was more obvious with groups of *Octopus joubini* (Mather 1980), a species that is easy to keep in a laboratory situation (von Boletzky & von Boletzky 1969; Thomas & Opresko 1973; Forsythe & Hanlon 1980) because it is so small (15 g at maturity). When three to five *O. joubini* were kept in a 1 m^2 tank, they formed a size-based dominance hierarchy and this hierarchy determined access to homes and to food (Mather 1980).

The area in which these octopuses were confined probably caused crowding, and crowding can alter social behaviour. Social animals are often seen on a continuum from solitary territory holding (evenly spaced and exclusionary) to group formation and hierarchy within a group (clumped and not site-specific) (Wilson 1975). Crowding can cause the organization of individuals to move along the continuum, making a normally territorial species hierarchical, as in cats (Leyhausen 1965, 1979) and canaries (Shoemaker 1939). Thus there could be unobserved territoriality in the sea and dominance in the lab, or an artificial hierarchy imposed by crowding on octopuses that were normally a social.

To assess these two possibilities, I observed *O. joubini* in its normal habitat with two questions in mind. First, what is the normal density and natural spacing pattern in the sea? Second, what factors (such as prey availability, social spacing, and access to hiding places) might influence this pattern of distribution? The present study addresses both these questions by finding information on spacing of octopuses in the natural environment.

Methods

Field observations and experimental manipulations were carried out by diving in October, 1979, in St. Joseph Bay, Northern Florida, near

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Black's Island. This shallow bay, a mixture of open sand and *Thalassia* grass beds, supports a rich and diverse fauna, but *O. joubini* is the only octopus species present (Eidemiller 1972). Since individuals shelter all day in empty mollusc shells (at 1 to 3 m depth), they were easy to locate by divers. In St Joseph Bay *O. joubini* is an annual species hatched in May (Mather 1972), so all were of a similar age. It is a nocturnal species, inactive in the daytime, not moving about and seldom feeding.

1. Intra-individual Distances and Distribution

To measure both the density of octopuses and their spatial distribution with relation to one another, they were located within a large area. Two sample areas were examined, each in a single day, during daytime when all octopuses were stationary. Areas were pre-selected for presence of several octopuses (the areas may have had higher than average densities of octopuses, but were thus of interest for the patterns of distribution). First, divers laid down a 33 × 33 m quadrat of twine on the sand bottom. Then they placed two metal 1 m^2 frames side-by-side at one corner of the grid. They noted (1) the presence of octopuses, (2) shell type in which any octopus was found, (3) shells with internal volume as large as that of an adult octopus and (4) bottom type (sand or grass). Then each turned the metal frame so that it enclosed an adjacent square metre using the twine edge of the quadrat as a guide, and repeated the observation. In this manner a 2 × 33 m strip was sampled. The divers returned, moved the edge of the grid in 2 m, and repeated the process. One sample was 18 × 33 m and the other was 14 × 33 m. To ascertain whether the distribution of the octopuses in the two sample areas (1a and 1b) was random, I employed Pielou's (1959) method, using point-to-nearest-neighbour distances and density. This was computed using $\alpha = Dw$, where D is density and w is the mean of the squares of the nearest-neighbour distance. To ascertain whether octopus density was related to density of appropriate shells, both number of octopuses and number of shells were calculated for each 4 m^2 section of both samples. For each shell number I calculated a percentage probability that the area would be occupied by an octopus. The correlation between number of shells and probability of locating an octopus in the area was then calculated.

Because these sampled areas were presumed relatively crowded, another area was selected to measure inter-individual distances for comparison. Each of several divers, working outward in a different direction, located octopuses and conducted a circle search around each. The distance to their nearest neighbour was recorded to the nearest metre up to 5 m, or as > 5 m. By this method, distances were found for 20 octopuses.

2. Relocation of Octopuses to Measure Site Fidelity

Three different areas, each 5 × 6 m, were marked off with twine. Octopuses within were removed from the water, individual characteristics were noted for reidentification, and they were returned to the same site, Characters used for identification were size (S, M, L), sex(♂ testis is visible at the posterior end of the body), and pattern of wounded and regenerating arms. The areas from which the octopuses were removed, were rechecked daily from 9 October to 23 October. Several of the octopuses left the area after the initial disruption, and were excluded from this study. Two individuals present in the control areas of section (4) of the study were included in this group since they were also observed, bringing the total N to 6.

3. Dispersal after Increased Octopus Density

Two areas, each 2 × 5 m, were crowded with 20 octopuses each (2/m^2). They were revisited each day, one for 11 days and another for 6, and the number of octopuses present was recorded.

4. Attraction of Octopuses to Areas with Excess Shells

This study used five areas, also 10 m^2 and outlined with twine. Twenty marked gastropod shells were placed in each of two of the areas (*Busycon* sp, *Strombus pugilis*, *Fasciolaria tulipa*, and *Melongena corona*), and 20 marked bivalve shells (*Trachycardium egmontanum* cockles) in one on October 13 to increase shell density. Two were left unaltered as controls. Every area was visited daily for 10 days, weather permitting, to check for octopuses.

5. Prey Availability

Prey availability was checked at six locations spaced widely around Black's Island. At each location a 1-m^2 frame was placed on the bottom and all organisms within it were removed by hand and placed in buckets. They were sorted and the number of individuals of species known to be potential prey was tallied.

Results

1. Distribution

In the two sample areas, 19 and 13 octopuses were found, at an average density of 1/31.3 m^2 and 1/35.5 m^2. The values obtained for Pielou's test of distribution were $\alpha = 1.6286$ for sample la and $\alpha = 2.12$ for sample 1b. Each is outside the 99% confidence interval for $N = 20$; the animals were not randomly dispersed, and the direction of this difference indicates that they were aggregated.

Other data taken from these sampling areas suggest factors that influence octopus distribution. One factor is substrate: sand or grass. Octopus density in these areas was 1/138 m^2 in sand, and 1/29.4 m^2 in grass. These differences were not significant in a chi-squared test, although there is a trend towards fewer animals in sandy areas (see Fig. 1).

Presence of shells in which to hide (*O. joubini* does not burrow in sand) is another factor that may affect distribution. There was an excess of shells available in the areas described previously (0.7/m^2). There was a significant relation (Pearson product-moment correlation 0.7787; $P < 0.01$, $df = 8$) between the number of shells and octopuses (Fig. 2). The unevenness of octopus distribution may thus be a result of uneven distribution of shells in which they shelter (there are 0.21/m^2 in sand, 0.81/m^2 in grass). The distance to nearest neighbour was higher outside the sampled areas than within them (see Table I), but mean distance could not be calculated because nearest neighbours outside the sampled areas were not always located.

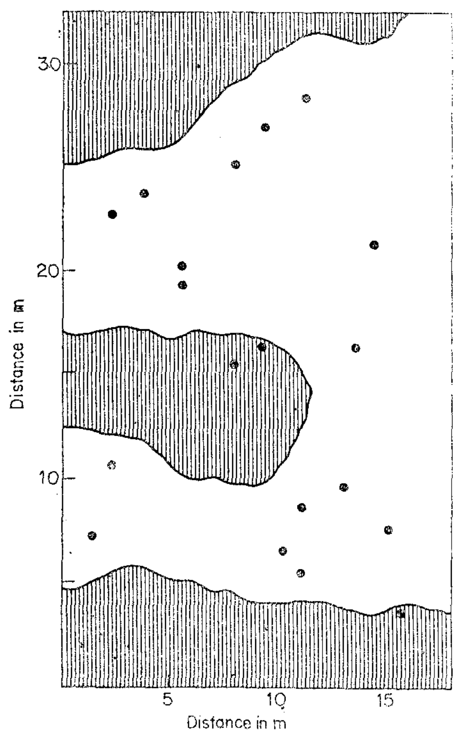

Fig. 1. A diagram of quadrat la, which was surveyed for individuals of *O. joubini* during one day. The area is 18×33 m; areas of sand (no *Thalassia* grass) are shaded and a black dot represents the location of each octopus $N = 19$).

2. Site Fidelity

Six individuals were identified and monitored in unaltered marked areas. Mean duration of stay was 3.7 days, standard deviation 2.3 days, and no octopus left and returned. This short-term and variable length of stay suggests neither a pattern of transiency nor one of long-term site stability.

3. Dispersal after Increased Density

The two groups of octopuses dispersed only gradually after their crowding. The first group, observed for 11 days, reached apparent stability at 1/1.6 m^2 after 7 days. The second reached that density after 6 days (Fig. 3).

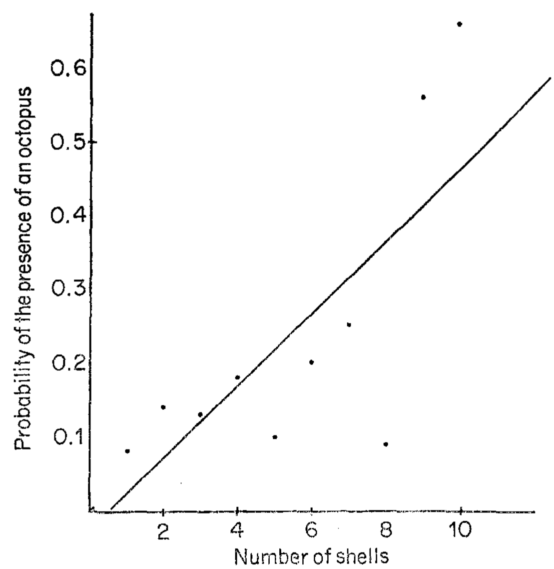

Fig. 2. The relationship between the number of empty molluscan shells in a 4-m^2 quadrat and the presence of an individual *O. joubini*.

4. Attraction to Shells

The density of octopuses in the two control areas began as 1/20 m^2 (similar to 'natural' density) and never exceeded this. The density in the three experimental areas began at 1/30 m^2. No octopuses were attracted to the area possessing an excess of cockle shells. Octopuses came to and left the areas with excessive gastropod shells, but the maximum density for one was 1/3.3 m^2 and for the other was 1/2m^2. The shells were also used by other animals. At the end of the 2-week period only 18 of the 40 marked gastropod shells were present in or near the experimental areas. One was observed far from its original position with a hermit crab in it, and others were probably also removed by these animals (*O. joubini* could move the shells with difficulty). Thus there were interspecific as well as intraspecific effects on shell occupancy (Mather, in press).

5. Prey Availability

In the six areas sampled, there was an average of 15 *Pagurus* sp. hermit crabs and 15 small Xanthid crabs, *O. joubini's* preferred prey, per m^2. There was also an average of 42 small bivalves (small *Anadara lienosa floridana*, *Chione cancellata* and *Glycymeris* sp.) and 123 mussels (*Modiolus americanus*) per m^2. *Octopus joubini* will sometimes accept small bivalves as prey (Mather 1972).

Discussion

Results of the study suggest a number of factors that may influence the distribution of *O. joubini.* The octopuses did not show the even distribution, place fidelity, or exclusion of conspecifics that is normally associated with a territorial species. There were many individuals of their preferred prey species available, so food was probably not limiting their numbers in this area. The octopuses were aggregated, but since likelihood of their presence correlated well with availability of many shells in which to hide, this aggregation is probably a result of environment and not of attraction to conspecifics. Predator pressure may act to restrict the presence of octopuses to the areas that have shells.

Despite some clumping, *O. joubini* appears to have little or no natural social spacing. Individuals were sometimes found right beside one another and sometimes far apart. They moved into the desirable shell homes provided for them to create a density several times higher than that observed in the samples in section 1. When artificially crowded in their natural habitat, these octopuses dispersed slowly and attained a fairly stable density, again one much higher than the density in the samples from experiment 1, a week after crowding. *Pachygrapsus* shore crabs which were crowded dispersed within 3 h so that only three, the number naturally found in the experimental location, remained, whether the crowded group numbered 5, 10, 15 or 20 (Bovbjerg 1960). *O. joubini*, in contrast, appears unresponsive to crowding and may have no social organization. Information from field studies of other octopus species suggests that this may be true for other species of *Octopus. Octopus vulgaris* (Woods 1965; Altman 1967; Kayes 1974; Guerra 1981) *Octopus bimaculatus* (Ambrose), and *Octopus dofleini* (Hartwick & Thorarinsson 1978; Hartwick et al. 1978) also were solitary but showed no signs of even spacing or place fidelity.

These results from the field can be compared with those from laboratory studies. The density of *O. joubini* in St. Joseph Bay was 1/30 m^2,

Table I. Distance to Nearest Neighbour for Individual *Octopus joubini* in Quadrats 1a, 1b and in an Outside Area (Total $N = 52$)

	Distance to neighbour (m)					
	0–1	1–2	2–3	3–4	4–5	5+
Sample area 1a	0	6	7	2	2	2
1b	2	0	7	2	0	2
Other	2	2	2	4	3	7

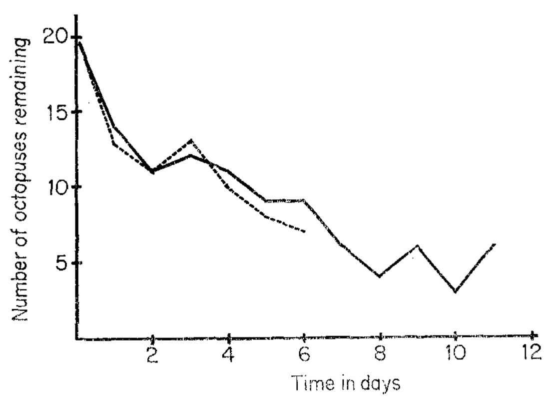

Fig. 3. Density of *O. joubini* over a period of days subsequent to initial crowding at a density of 2/m^2. The solid and dashed lines represent two different groups, each of 20 individuals.

much less than the 3 to 5/m^2 experimental density produced by Mather (1980). In the bay, distances between individuals seemed to depend on chance and availability of shelter. There may be no social pressures towards spacing, and thus in the laboratory octopuses' behaviour may not be drastically altered by confinement.

The clumped spacing pattern in the bay does not suggest territoriality, as territorial animals would likely be evenly dispersed. Since octopuses also were not actively repelled from one another and did not stay at the same location, they were probably not territorial. The hierarchical social pattern seen in the laboratory likely results from crowding of an asocial species, not crowding of a territorial one. This pattern is true also for hermit crabs (Reese 1966). This idea of the animals as asocial is supported by the simplicity of octopus aggressive interactions, which often consist of avoidance (Mather 1980), or a single touch (Yarnall 1969), and only rarely of a display like the sucker display of *O. vulgaris* (Packard 1961). This simplicity contrasts with the well-developed threats and displays of many other animals and suggests that octopuses do not encounter one another very often. However, only detailed records of the movements of several individuals in the field would confirm this. Such a study is in progress and will be described in the future.

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