Spatial considerations for the Dakhla stock of *Octopus vulgaris*: indicators, patterns, and fisheries interactions

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The common octopus (*Octopus vulgaris*) is the target species of the cephalopod fishery that exploits two stocks, Dakhla and Cap Blanc, off southern Morocco (26°N 21°N), an area commonly referred to as the Saharan Bank. *Octopus vulgaris* is also one of the most abundant demersal species in this highly productive area, and plays a key role in the upwelling ecosystem. Spatial patterns of the main phases of the *Octopus vulgaris* life cycle of the Dakhla stock are described, using trawl surveys carried out twice a year from 1998 to 2003. Using geostatistics and spatial indicators, mature females and juveniles are analysed and mapped to characterize the main features of the spawning and recruitment phases. There are clear distinctions between the spatial patterns of the spawning and recruitment phases: juveniles are more coastal, less spatially dispersed, more anisotropically distributed, and more patchy. Our results suggest that the spatial pattern of the *Octopus vulgaris* Dakhla stock is different from that of the same species in other ecosystems such as the Mediterranean. GIS reveals that the spawning and with important resource management implications.

Keywords: accessibility indices, cephalopod fishery, Dakhla stock, geostatistics, GIS, *Octopus vulgaris*, recruitment, spatial indicators, spatial patterns, spawning.

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Introduction

The common octopus (Octopus vulgaris), a coastal cosmopolitan species, is abundant around the whole Northwest African coast (Guerra, 1981), from 10°N to 26°N (Hatanaka, 1979). The northern stock, also known as the Saharan Bank stock, is biologically very productive because of the upwelling system, and the area is recognized to be one of the richest fishing grounds in the world and supporting an intense fishery (Balguerías et al., 2002). Over the past three decades, O. vulgaris has often been the most abundant of >100 species of the demersal community exploited in the region. According to Balguerías et al. (2000), the reason was probably the heavy trawling activity that removed the species' main predators and competitors. Despite its importance in terms of abundance and productivity, and its key role in the ecosystem, the ecology of O. vulgaris is not well known. In particular, better understanding of the spatial aspects of its ecology would help to explain its interactions with other components of the upwelling ecosystem foodweb, and ultimately improve stock assessment and fisheries management.

Hatanaka (1979) distinguished two stocks within the fishing grounds off Morocco, the Dakhla stock (north of $22^{\circ}00'N$) and the Cap Blanc stock (between $22^{\circ}N$ and $19^{\circ}30'N$; Figure 1). His analysis, based on $30' \times 30'$ annual catches of Japanese trawlers operating from 1964 to 1975 was the basis for current understanding of the spatial distribution of *O. vulgaris* and its seasonal and annual variability. However, spatial patterns inferred from

commercial catch data, which are biased by the prevalent fishing strategy, do not reflect the intrinsic characteristics of the spatial patterns in the O. vulgaris life cycle. To eliminate such biases, a demersal stock assessment and monitoring programme was initiated in 1980 by the Institut National de Recherche Halieutique (INRH, Casablanca, Morocco) with the objective of quantitatively evaluating the status of the stocks and the impacts of fishing (Idelhaj, 1984a). The surveys permitted unbiased observations of annual and seasonal fluctuations of abundance, as well as observation of spawning and recruitment peaks reported by Hatanaka (1979). The main spawning peak is in spring (February-May), and a secondary one in autumn (October-December); recruitment peaks in autumn (September-November) and to a lesser extent in spring. However, the analyses are based on spatially aggregated data and do not describe the spatial characteristics of the development stages of octopus.

Until the early 1990s, *O. vulgaris* was fished by EU (until the end of 1999) and Moroccan freezer trawlers using two types of gear, the so-called "Spanish trawl" and "Korean trawl". Nowadays, the cephalopod fishery has three sectors: industrial, artisanal (wooden boats using passive selective gears like pots and hand jigs), and coastal (ice-trawlers using an "atomic trawl"). As a consequence of the development of inland-based infrastructure and high prices, the last two sectors have burgeoned since 1993. They now account for more than half the nominal catches (INRH, 2002), and competition between the three

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Figure 1. (a) The study area, and (b) the two *O. vulgaris* stocks on Moroccan cephalopod fishing grounds.

sectors is intense, so in an attempt to manage the stock sustainably and because it is difficult to reduce fishing effort, a global quota system was implemented for each sector in 2002. Implementation of this system immediately led to a "race" for the resource, each sector trying to catch more than the others in the least time. Another consequence of the competition was disagreement on fishing areas. Because there are spatial interactions between the sectors, permanent conflicts persist and make the management system very complex. These conflicts underscore the need for the scientific community to appraise better the spatial patterns of the *O. vulgaris* life cycle.

To this end, a regional project led by the FAO was initiated in 1996 to characterize the spatio-temporal variations of demersal resources, and to define spatial and temporal management units on a biological basis (FAO, 1996). The project has demonstrated an area of good recruitment north of Dakhla (around 24.5° N) and has allowed the impact of the small-scale fishery on the parent stock to be evaluated by overlapping the area of activity of small-scale boats on the seasonal distribution maps of the spawning adult octopus (Taconet *et al.*, 2000).

In this context, the objective of this study is to update previous work, using simple indicators to improve the description of the spatial pattern of the *O. vulgaris* life cycle and particularly of the Dakhla stock spawning and recruitment phases in spring and autumn. The spatial pattern is also compared and contrasted with that described for other areas (Canary Islands and the Mediterranean). Finally, the accessibility and sensitivity of the parent stock to the industrial and the artisanal fleets is re-evaluated.

Material and methods Data surveys

Data are derived from the 1998–2003 monitoring programme trawl surveys carried out since 1980 by the INRH. A latitudinal profile of the mean standardized densities involving all surveys since 1984 (Boumaaz *et al.*, 1997) has been developed. Since 1998, two surveys (RV "Charif al Idrissi"; grt 397 and 1100 hp; "Spanish" type bottom trawl, Idelhaj, 1982, adapted for cephalopods) have been carried out each year covering the continental

shelf between 20°50/N and 26°N, from the coast to 100 m deep (Figure 2). A geostatistical stratified random sampling design (Conan *et al.*, 1988) has been applied (Figure 2), each sample being located randomly inside a cell of 11×11 nautical miles. The average number of hauls per survey is 90, at an average rate of seven tows per day. New technology has allowed the area swept to be computed on the basis of horizontal trawl opening and towing speed. Hauls generally lasted 30 min, and average area swept was 65 000 m², except between 1998 and 2000, when haul duration was reduced to 12 min and average area swept to 25 000 m². Octopus yields were divided by swept area and expressed in terms of density, i.e. number of octopus per unit area (nautical mile²).

Using the estimated mean area swept from the 1998–2003 surveys, data from the 1984–1998 period were converted into *O. vulgaris* densities. All data (1984–2003) were pooled, standardized by the survey average density, and averaged over rectangles of 2×2 nautical miles. This process was used under the assumption that standardization reduces the influence of the surveys on resulting densities, so generating a latitudinal profile of octopus densities from which the study area could be selected.

During the surveys, the catch of each tow was weighed and measured, and the sex and stage of maturity were noted. Four female stages were identified (Idelhaj, 1984b), stages 2–4 being mature (Boumaaz *et al.*, 1997). In the study area, spring is the main spawning season and autumn the main recruitment season, so the spatial pattern of spawning was inferred from the density of mature females during spring surveys (Table 1), expressed as the number of mature females (no_{mf}) per square nautical mile. The recruitment pattern is depicted as the density of juveniles during autumn surveys (Table 1), expressed as the number of juveniles (no_{juv}) per square nautical mile, juveniles being assumed to be the small commercial size categories, i.e. categories Tako 8 and Tako 9 according to Japanese classification (Boumaaz *et al.*, 1997). Landing these categories is prohibited by Moroccan fishery legislation.



Figure 2. Stratified random sampling: random location of the trawls in cells of 11 \times 11 nautical miles.

 Table 1. Dates of the surveys carried out between 1998 and 2003.

| Year | Autumn surveys Month | Spring surveys Month | |
|------|-------------------------|-------------------------|--|
| 1998 | October | - | |
| 1999 | October | April | |
| 2000 | October | March | |
| 2001 | September | March | |
| 2002 | September | March | |
| 2003 | September | April | |

Spatial indicators

Because of the spatial heterogeneity in densities and its interaction with the geometry of the study area (e.g. density decreases towards its offshore border), statistics per individual were used (Bez and Rivoirard, 2001). In this framework, which is derived from transitive geostatistics (Matheron, 1970), the key concept is to move from unweighted to weighted statistics where the weights are proportional to the number of individuals present at any location. As recommended for irregular sampling designs (Bez and Rivoirard, 2001), we also weighted the various statistics by the surface of influence S_i of each sample $i \in [1,N]$, where N is the number of samples available for each survey. Octopus density (e.g. the number of mature females, no_{mf} per square nautical mile) was interpreted as a regionalized variable z(x), x denoting a point in geographical space. Sample values are denoted z_i .

The average position of the population (\bar{x}) was estimated by the centre of gravity of fishing locations weighted by octopus density (Bez and Rivoirard, 2000):

$$\bar{x} = \frac{\sum_{i=1}^{N} S_i z_i x_i}{\sum_{i=1}^{N} S_i z_i}.$$
(1)

The spatial dispersion (I) was estimated by the inertia (expressed in nautical mile²):

$$I = \frac{\sum_{i=1}^{N} S_i z_i (x_i - \bar{x})^2}{\sum_{i=1}^{N} S_i z_i}.$$
 (2)

This inertia was split into orthogonal directions, the first direction explaining the maximum inertia, and the second being orthogonal to it. Such decomposition is the same as the result of a principal components analysis of sample coordinates weighted by density (i.e. the coordinates of individuals). This decomposition was performed in an ortho-normal metric system, so the axes were perpendicular one to the other in the system. When back-transformed in the geographical system, some distortions (small in this analysis because latitudes are small) left the two axes no longer orthogonal. For purposes of representation, the respective sizes of the axes were determined so that the ellipse surface they define was equal to the inertia (the longer the axes, the stronger the inertia).

The ratio of the smallest axis to the largest was used as a proxy for quantifying isotropy, i.e. the existence of preferred directions. When individuals are distributed in all directions and there is no preference, the two axes have the same length and the index of isotropy is 1. In contrast, when individuals are dispersed along a single axis, the index is 0. The index of aggregation, I_a (Bez and Rivoirard, 2001), expressed in inverse units of surface, i.e. nautical mile⁻², was used to measure the statistical heterogeneity of sample values (it is not, *per se*, a spatial indicator):

$$I_{a} = \frac{\sum_{i=1}^{N} S_{i} z_{i}^{2}}{\left(\sum_{i=1}^{N} S_{i} z_{i}\right)^{2}}.$$
(3)

Finally, mean depth per octopus (depth) was quantified by

$$\overline{\text{depth}} = \frac{\sum_{i=1}^{N} S_i z_i \text{depth}_i}{\sum_{i=1}^{N} S_i z_i},$$
(4)

and depth inertia in the population (I_{depth}) by

$$I_{\text{depth}} = \frac{\sum_{i=1}^{N} S_i z_i (\text{depth}_i - \overline{\text{depth}})^2}{\sum_{i=1}^{N} S_i z_i}.$$
 (5)

Results are represented as time-series of the mean depth \pm the square root of the inertia. Where appropriate, the difference between the indices obtained for the spawning and recruitment stages was tested using a non-parametric Wilcoxon–Mann–Whitney test (H₀: corresponding to equal median values). As *O. vulgaris* live for just 1 year, the patterns observed for the spawning and recruitment stages are not independent, so we used paired tests and provide the corresponding *p*-values.

Mapping

As acknowledged for many other species, octopus density distributions are skewed; a few large values at specific locations make any stationary hypothesis unacceptable. Octopus density is also highly dependent on the geometry of the field, indicating that habitat geometry could be the main driver of spatial structure (i.e. autocorrelation) in the species; a preliminary study on octopus (not reported in detail here, but unpublished) indicated such dependence. The octopus autocorrelation function and habitat geometry are therefore strongly connected. This led us to use a transitive geostatistical approach (Matheron, 1989; Bez *et al.*, 1995), in which (transitive) covariogram models represent in rows the inner structure of octopus and its habitat geometry, the two being indistinguishable.

The covariogram (Matheron, 1970; Bez, 2002) of the regionalized variable z(x) is the function of a distance vector *h*, expressed here in nautical miles, equal to

$$g(h) = \int z(x)z(x+h)\mathrm{d}x,\tag{6}$$

and the relative covariogram used here $[g_r(h)]$ is defined by

$$g_r(h) = \frac{g(h)}{Q^2},\tag{7}$$

where Q is the total abundance, itself defined as $Q = \int z(x) dx$. The relative covariogram is expressed in inverse units of surface, i.e. nautical mile⁻². It decreases universally from a maximum value $g_r(0)$, the index of aggregation, to 0 at far distance, referred to as the range, and quantifies the maximum diameter of the population distribution area in a specific direction.

To estimate the covariogram, we used the approach suggested by Bez *et al.* (1995) for stratified random sampling. Directions of computation are given in trigonometric angles, so hereafter "shoreline direction" corresponds roughly to 60° and "depth direction" to 150° . Distances were computed after coordinates were projected by simple cosine transformation in a rectangular reference system. Empirical relative covariograms were fitted automatically by non-linear regressions minimizing the sum-of-square residuals. The models used are constructed of a discontinuous component (8; also referred to as the nugget effect) to take into account the discontinuity at zero distance, and a continuous component of several nested spherical functions (9):

$$\operatorname{nugget}(h) = \begin{cases} 1 \text{ when } h = 0\\ 0 \text{ when } h \neq 0 \end{cases},$$
(8)

spherical(h) =
$$\begin{cases} 1 - h^3/2a^3 + 3h/2a & \text{when } h < a \\ 0 & \text{when } h > a \end{cases}$$
(9)

Mapping was done by interpolating between samples in a moving circular neighbourhood (of radius 36 nautical miles in this case). The weights assigned to the samples are selected to minimize global estimation variance and are computed by the covariogram models. Such interpolation is also known as transitive kriging.

Interactions between fishing areas and the spawning stock

To estimate the accessibility of the artisanal and the industrial fleets to the parent stock, we calculated the overlap between the spawning areas and the potential fishing areas (Figure 3), yielding accessibility indices. The spawning area (S_R) was defined as the area where mature female density (no_{mf}) exceeded 100 per



Figure 3. Potential fishing area for the artisanal and industrial sectors off Morocco.

nautical mile²:

$$S_R = \int 1_{z(x)>100} \mathrm{d}x,$$
 (10)

where $l_{z(x)>100}$ represents the indicator equal to 1 where z(x) > 100 mature females (no_{mf}) per nautical mile².

Artisanal fishing areas (S_A) were defined as the combination of circles of 20 nautical mile radius centred on landing sites, and the industrial fishing area (S_I) as the area offshore of the 12 nautical mile line without known rocky areas (Figure 3). By definition, S_A and S_I were fixed arbitrarily according to management rules (for the industrial fleet), and information on the landings made by INRH during sampling surveys for the artisanal fleet, and S_R changed from year to year. We then calculated the ratio of the overlapping area as a percentage of the spawning area, $S_R \cap S_A / S_R$ and $S_R \cap S_I / S_R$. Owing to the uneven spatial distribution of octopus, we also calculated the percentage of total mature female abundance inside the two fishing areas by integrating spatially the kriging maps over the corresponding areas:

$$Q(S_{\rm A}) = \frac{\int_{S_{\rm A}} z^k(x) \mathrm{d}x}{Q}$$
 and $Q(S_{\rm I}) = \frac{\int_{S_{\rm I}} z^k(x) \mathrm{d}x}{Q}$

where $z^k(x)$ represents the kriging values, and Q the total abundance of mature females inside density area 100 mature females (no_{mf}) per nautical mile².

Results

The two stocks and the Dakhla stock area

The geographical profile based on all available data (Figure 4) shows a clear octopus density discontinuity between two areas, consistent with a two-stock hypothesis, the two separated by a transition area between $22^{\circ}30'$ N and 23° N (Cap Barbas). We arbitrarily chose a limit at $22^{\circ}43'$ N to select data which we assigned to the Dakhla stock. As the Cap Blanc stock is represented by too few samples and is possibly a northern component of a stock extending from the south, it is not considered further here, and we focus our attention on the Dakhla stock.

Time-series of spatial indicators

For the study period, the time-series of spatial inertia (Figure 5) indicates that mature females were on average twice as dispersed as juveniles (p = 0.03). The convergence of the two life stage



Figure 4. Latitudinal profile of average octopus densities off Morocco, 1984-2003.

Figure 5. Time-series of (left) inertia (per nautical mile²) and (right) indices of isotropy for juveniles (J) and mature females (F). Symbol sizes are proportional to abundance.

trends to a similar dispersion level in 2003 is mainly attributable to the extremely low O. vulgaris abundance during the final autumn survey and the consequential dominance of areas of low concentration. Both juvenile and mature female densities were strongly anisotropic (indices of isotropy <0.55; Figure 5), mainly because of the shape of the continental shelf they inhabit and the variability in O. vulgaris density, which tends to be smaller in a direction parallel to the shore than perpendicular to it. Indices of isotropy were smaller for juvenile than for mature females (p = 0.09), and decreased over the study period, down to 0.3 in 2003. The difference in the indices of isotropy is consistent with the idea of diffusion of the concentrated juvenile stage to a more widely spatially distributed mature female stage. Indices of aggregation (Figure 6, Table 2) for juvenile density were on average $(7 \times 10^{-4} \text{ nautical mile}^{-2})$ higher than for mature females $(3.6 \times 10^{-4} \text{ nautical mile}^{-2}; p = 0.09)$. Juvenile densities were greatest in shallow water (20-40 m), and mature females more prevalent between 20 and 100 m (p = 0.03; Figure 6). Although time-series abundances are represented by symbols is proportional to size, abundance is not taken into account in computing the *p*-values. Finally, ellipsoids representing the centre of gravity and dispersion of the individual octopus show the systematic coastal preference of juveniles compared with the more dispersed and offshore distribution of mature females (Figure 7).

To summarize (Table 2), juveniles are more coastally distributed (shown by the centre of gravity), less spatially dispersed (inertia), more anisotropically distributed (index of isotropy), and more patchy (index of aggregation).

Spatial distribution and its variability

Kriging maps derived from juvenile surveys (Figure 8) showed, for most years, large concentrations of juveniles near the coast, mainly in the area 24–25°N. Occasionally too, there was a concentration of juvenile octopus south of Dakhla (around 23°30'N), but at lower density than in the northern area. The relative importance

mile⁻²) and (right) mean depth \pm square root of depth inertia for juveniles (J) and mature females (F). For the indices of aggregation, symbol sizes are proportional to abundance.

Figure 6. Time-series of (left) indices of aggregation $(10^{-4} \text{ nautical})$

Table 2. Average value of the spatial indices over the period 1998 – 2004 for juvenile and mature female densities of *Octopus vulgaris*.

| Parameter | Mature females | Juveniles |
|---|----------------|-----------|
| Mean depth (m) | 52 | 32 |
| Depth inertia (m²) | 609 | 131 |
| Index of isotropy | 0.49 | 0.37 |
| Index of aggregation $(10^{-4} \text{ nautical mile}^{-2})$ | 3.6 | 7 |
| Inertia (per nautical mile ²) | 2 519 | 1 372 |

of the southern area increased when northern density decreased. This phenomenon is very clear for autumn 2003.

In contrast, kriging maps of mature female density showed great annual variability in spawning areas over the period 1999–2003 (Figure 9). The maps revealed that mature female densities were sometimes widely distributed over the shelf (2000–2002), but sometimes localized either in the southern part of the survey area (1999) or in its northern part (2003). In the last two cases, the pattern of densities was less dispersed and more aggregated (with areas of high concentration), similar to the pattern for juveniles. Comparing the empirical covariograms by depth (Figure 10) emphasized the fact that the spatial structure of mature females (spring surveys) was less stable from year to year than that of juveniles (autumn surveys).

Artisanal fishery vs. industrial fishery

Accessibility indices estimated for the artisanal and industrial fleets showed that the spawning stock was more accessible to the industrial fleet than to the artisanal fleet, except in 1999 (Table 3, Figure 11). For that year, 98% of the parental stock was within the artisanal fishing area and just 4% inside the industrial fishing area, mainly because of the stock's apparently unusual





Figure 7. Centroids and ellipsoids of inertia for juvenile (bold continuous lines) and mature female (dashed lines) octopus for the Dakhla stock, 1998–2003.

Longitude

compact, coastal distribution (Table 3). For all other years, the accessibility indices for the industrial fleet were in the range 60-93% and for the artisanal fleet in the range 29-43%. For four years out of five studied, therefore, the accessibility indices for the parent (spawning) stock were higher for the industrial fleet.

Discussion

The transition area between the Cap Blanc and Dakhla stocks is discussed in Balguerías *et al.* (2002), using fishery data, and by Murphy *et al.* (2002), using genetic analyses, and is confirmed here on the basis of the entire time-series of available surveys. The transition area is characterized by a very low presence of *O. vulgaris* and by physical characteristics such as the width of the continental shelf and the timing of maximum upwelling

intensity (Roy, 1991). Between Cap Blanc and Cap Barbas (Figure 2), the upwelled waters partially contain South Atlantic Central Water (SACW), which distinguishes the area from the northern Dakhla region and makes it among the most productive parts of the continental shelf off Northwest Africa (Minas *et al.*, 1982; Jacques and Treguer, 1986).

For the Dakhla area, the results show a clear distinction between spatial areas of spawning and recruitment. Spawning took place over the whole continental shelf up to 100 m deep, with sometimes more spawning close to the coast, whereas recruitment seemed systematically to be concentrated at the coast, shallower than 50 m. Further, the area used for spawning was highly variable annually throughout the study period between 1998 and 2003, whereas the areas of recruitment were more stable.

We therefore present a hypothesis for the spatial patterns of O. vulgaris in Moroccan waters. The species spawns over the whole continental shelf; although there is not as yet direct scientific evidence of the distribution of paralarvae, the broad distribution of spawning suggests that O. vulgaris paralarvae will be found all over the continental shelf. Recruitment seems to be exclusively coastal; the reason for this is not clear, but it could involve transport to and retention in favourable areas, and/or passive selection of those favourable areas. However, it is very likely that recruitment success is strongly dependent on environmental conditions during the pelagic larval stage (Balguerías et al., 2002), which is fairly long (about two months). Indeed, such a link was demonstrated by Demarq and Faure (2000), who demonstrated the link between indices of retention and the extent of O. vulgaris recruitment off Mauritania and Senegal, and by Balguerías et al. (2002), who showed that high catch rates of O. vulgaris coincided with low temperature, which is itself indicative of strong upwelling. During the recruitment season in autumn, most of the O. vulgaris stock is concentrated in coastal upwelled waters, so presumably the juveniles disperse towards deeper water (Hatanaka, 1979) before ultimately settling (an ontogenic migration). For this hypothesis to be confirmed, however, the ontogenic migration of octopus needs to be confirmed by independent study.

The life cycle of *O. vulgaris* off Morocco seems to be different from that of the same species off the Canary Islands (Hernandez-Garcia *et al.*, 1997). According to those authors, maximum catches correspond to concentrations of adult animals, which are recorded near the coast during the spawning



Figure 8. Kriging maps of the spatial distribution of juvenile O. vulgaris densities (no_{juv} per nautical mile²) during autumn of 1998-2003.





Figure 9. Kriging maps of the spatial distribution of mature female *Octopus vulgaris* densities (no_{mf} per nautical mile²) during spring of 1999 – 2003.

periods of April/May and from September to November. Such high concentrations of *O. vulgaris* at the coast during a spawning season would be supported by a coastward spawning migration (mature animals moving from deeper water towards the coast to spawn). The same spatial pattern, i.e. a concentration of spawners near the coast and an extensive large distribution of recruits, is observed and described by Quetglas *et al.* (1998) and Sanchez and Obarti (1993) for the Mediterranean *O. vulgaris* population. In Spanish waters deeper than 50 m, octopus do not exceed some 11–12 cm mantle length, whereas in shallower



Figure 10. Bands of empirical relative covariogram fluctuations computed perpendicular to the coast. Comparison between the covariograms of juvenile densities in autumn (dark) and mature female matures densities in spring (grey). The *x*-axis represents the distance (*h*) in nautical mile and the *y*-axis the covariogram in 10^{-4} nautical mile⁻².

| Table 3. | Accessibility | indices of | the spawnir | ng stock of | f octopus 1 | to |
|-----------|----------------|---------------|-------------|-------------|-------------|----|
| the indus | trial and arti | isanal fleets | | | | |

| Survey | S _R (per nautical mile ²) | S _I (%) | S _A (%) | Q | Q (S ₁) | Q (S _A) |
|---------------|--|--------------------|--------------------|-----------|---------------------|---------------------|
| April 1999 | 291 | 6% | 99% | 46 286 | 4% | 98% |
| March 2000 | 4 485 | 63% | 37% | 620 829 | 60% | 40% |
| March 2001 | 7 990 | 67% | 33% | 2 107 808 | 62% | 43% |
| March 2002 | 4 542 | 67% | 39% | 694 090 | 65% | 40% |
| April 2003 | 710 | 91% | 30% | 91 542 | 93% | 29% |
| Mean | 3 604 | 59% | 48% | 712 111 | 57% | 50% |
| | | | | | | |

Accessibility indices are estimated by overlapping the spawning (S_R) and fishing areas (S_I for industrial fleet, S_A for artisanal fleet). Accessibility indices are also calculated in term of abundance within the overlapping areas.

waters, such a size falls at the lower limit of the length frequency distribution observed. According to Quetglas *et al.* (1998), the pattern is explained by a coastward spawning migration from off-shore. In summary, therefore, there appear to be different spatial patterns of *O. vulgaris* distribution (Figure 12): in the Moroccan coastal upwelling system, a large spawning spatial distribution is supported by coastal recruitment and ontogenic migration; in the Mediterranean and Canary Islands systems, recruitment is spatially more diffuse and coastal spawning is associated with a spawning migration towards the coast.

In this context, the conflict between the artisanal and industrial fishing sectors working on the Dakhla stock needs to be revisited. Traditionally such a conflict is based mainly on two issues. First, the pot, the main fishing gear used by artisanal fishers (Srour, 1992), is considered by the industrial sector to be targeting spawning animals with eggs, on a selective basis. However, analysis of the maturity stage of catches taken by pots for scientific purposes off



Figure 11. Potential areas for industrial and artisanal fishing activities, and the spawning areas (where the mature female, no_{mf} density exceeded 100 per nautical mile²) overlapping with these potential fishing areas.

Mauritania showed that pots do not target just spawning animals (Jouffre *et al.*, 2002). The pot would be a species-selective gear for *O. vulgaris*, but a non-selective one for size. Second, the artisanal fishery, which operates inside 20 nautical miles from the coast, is also blamed by the industrial sector for targeting and destroying spawning stocks because it is traditionally believed that mature octopus migrate towards the coast to spawn, as in the Mediterranean (Mangold-Wirz, 1963). Converging to the main artisanal fleet fishing grounds, mature females would then be over-exploited by that sector. Such a pattern is, however, still unsupported in Mauritanian waters (Caverivière *et al.*, 2000), and is not supported by our results in the case of the Dakhla stock. Indeed, in the case of the Dakhla stock, as

Spatial patterns of Octopus vulgaris



Figure 12. Schematic representation of the spatial pattern of *O. vulgaris* in the Moroccan coastal upwelling system, compared with the same for the Mediterranean and Canary Islands system.

shown by the average values of the accessibility indices (Table 3), half the spawning stock is available to the artisanal fleet within its coastal fishing grounds, and 57% of the spawning stock is available to the industrial fleet on its offshore fishing grounds. These results agree with the seasonal synoptic maps (for 1984–1995) of Taconet *et al.* (2000), who estimated that half the parent stock was accessible to the artisanal sector. Although the parent stock was on average equally available to the artisanal fleet and to the industrial fleet over the study period, year-on-year fluctuations of the accessibility indices showed that, from 2000 to 2003, the spawning stock was more available to the industrial fleet, and that it was not exposed to greater fishing pressure by the artisanal sector than by the industrial sector.

If we consider that the octopus life cycle ends with an ontogenic migration that allows juveniles to colonize the shelf from their recruitment area (the hypothesis advanced here), the main developmental stage sensitive to fishing pressure would be the coastal juvenile stage, because it represents the bulk of the annual octopus stock. From this argument, juveniles concentrated near the coast during the recruitment period would need to receive some protection from fishing by all sectors, allowing them to colonize the shelf area widely. Currently, Moroccan fishing regulations do not allow fishing during September and October to protect recruitment. Taking into account the dynamics of the dispersion process for juveniles from their recruitment areas, this fishing regulation would ideally be complemented by a measure allowing the fishery to be opened in a staged manner, both spatially, from offshore towards the coastal recruitment areas, i.e. opposite to ontogenic migration, and temporally, i.e. small parts of the fishery at a time. Such measures would allow fishing first to take place in areas far from the source of recruitment, i.e. on animals that had time to grow and disperse.

In conclusion, we believe that this study has provided spatial insight into the life cycle of *O. vulgaris*. The spatial distribution pattern has been outlined and a modified approach suggested for exploitation of octopus off Morocco. Our belief is that currently the parent stock could potentially be overfished as much by the industrial fishery as by the artisanal fishery, if not more. In addition, we conclude that coastal *O. vulgaris* recruitment is crucial and should receive enhanced protection from exploitation. Comparison of the spatial pattern of octopus in the Dakhla area with spatial patterns of the same species in other areas has revealed clear differences which are likely to be linked to local hydrodynamic conditions. Therefore, a study of physical processes such as enrichment, concentration, and transport would enhance our understanding of the various strategies adopted by species such as octopus in the different areas.

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