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Age of spent *Octopus vulgaris* and stress mark analysis using beaks of wild individuals

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Abstract Age estimation of the cephalopod *Octopus vulgaris* by using beaks has improved in recent years, but maximum age and longevity in the wild have not been confirmed due to the low availability of senescent wild octopuses. In this study, a beak analysis of lateral wall surfaces (LWS) from 20 spent specimens confirmed the one-year lifecycle of the species in Central East Atlantic waters. Stress marks (checks) were clearly located in the daily increment sequence of rostrum sagittal sections (RSS). The highest daily variations in sea surface temperature (Δ T) that occurred during the last months of their lifetimes coincided with the locations of the marks on the beak, enabling confirmation of *O. vulgaris* beaks as life recorders for the first time. It also supports the daily deposition of RSS beak increments in the wild. Individuals were grouped into two main zones, at 20°N and 18°N respectively. Both groups showed different thermal check patterns, in accordance with the oceanographic differences. Two other checks (not coinciding with high values of Δ T) were observed in RSS at averages of 15 and 28 days before death, respectively, which were interpreted as responding to senescent-related events.

Keywords: *Octopus vulgaris,* age, beak microstructure, check increments, oceanography, Central East Atlantic.

Introduction

The common octopus *Octopus vulgaris* Cuvier, 1797 is an important exploited cephalopod species, with global catches reaching 41000 tonnes in 2010 (FAO, 2012). Age and growth studies are essential for the assessment and management of wild populations of harvested marine species. As with the majority of cephalopods, the common octopus has high and variable growth rates, a short lifecycle, and massive post-spawning mortality (Jackson, 1994; Semmes et al., 2004). Consequently, anatomic methods of ageing based on interpretation of growth increments in hard calcified structures (after validation of deposition periodicity) are the most accurate for this purpose (Dawe & Beck, 1992; Semmens et al., 2004). Assessment and management of marine populations have transitioned to more ecosystem-based approaches, and the need to understand ecological and oceanographic processes has been advanced through the analysis of daily microstructure in hard structures. Fish otoliths (e.g. Pannella, 1980; Campana, 1983; Kalish, 1992; Sponaugle, 2010) and cephalopod statoliths (e.g. Arkhipkin et al., 1999; Durholtz & Lipinski, 2000; Lipinski, 2001; Arkhipkin, 2005) have been tested as life recorders. Regarding beaks, this is the first study of wild *O. vulgaris*.

Beaks have been used for the ageing of O. vulgaris specimens (Raya & Hernández-González, 1998, Hernández-López et al., 2001; Perales-Raya et al., 2010; Canali et al., 2011; Cuccu et al., 2012) because statoliths are not suitable for ageing octopuses (Young, 1960; Lombarte et al., 2006; Perales-Raya et al., 2010). Daily deposition of beak increments has been previously supported (Hernández-López et al., 2001; Oosthuizen, 2003; Canali et al., 2011), although it still needs to be documented for specimens of all sizes/ages in order to validate the one-day-one-increment hypothesis in the species. Presently, both the internal lateral wall surfaces of beaks (LWS) and the rostrum sagittal sections (RSS) are used for ageing O. vulgaris. The former is more accurate for estimation of absolute ages because RSS seem to underestimate the number of increments due to tip erosion of the beak during feeding (Perales-Raya et al., 2010). However, the maximum age and longevity in the wild have not been confirmed because of the lack of senescent individuals. Availability of senescent wild octopuses is unusual due to the erratic behaviour of the animals at this stage, and their imminent death (Anderson et al., 2002). However, during the last two years a total of 20 spent individuals were identified during octopus biological sampling among more than 4000 specimens. Given that spent individuals are close to their natural death, this was an opportunity to study their beaks in order to estimate maximum age and lifecycle duration of the species in Central East Atlantic waters by using LWS.

In addition, the beaks were tested for their potential as life recorders. We observed in the RSS microstructure daily increments, and also checks (stress marks or discontinuities) that are very well identified in the sequence of daily increments. These checks may record periods of perturbation or stress in the octopus, as has been reported for fish otoliths where checks may reflect anomalous incorporation of either calcium, or protein, or both (Campana, 1983; Campana & Neilson, 1985). Having a sample of wild octopuses at the end of their lifetime with their capture coordinates, and taking into account that *O. vulgaris* is a benthic species with no reported adult migrations in the area (Domain et al., 2000), we tried to relate the checks observed in RSS with some internal or external factors. In this context, two hypotheses were considered: (a) Daily temperature variations have a direct effect on the deposition process as thermal checks, and (b) Biological-reproductive events related to senescence (e.g. mating, breeding eggs, stop feeding, etc.) occurred towards the end of the octopus's life can change the rate of deposition in the beaks. These events would be found amongst the increments corresponding to the last months of the animal's life.

Material and methods

The sample

The study was carried out with a sample of 20 spent individuals (5 males and 15 females), caught at depths from 36 to 235 m between April 2010 and March 2011 by the Spanish industrial freezer trawler fleet that operates in Mauritanian waters. Each octopus was preserved frozen and tagged with its catch date, depth and coordinates (Fig. 1). Based on the octopus locations, two main groups of animals were considered: the Northern Group (15 octopuses caught at 20°N) and the Southern Group (3 octopuses caught at 18°N). The other two specimens were not grouped because they corresponded to different coordinates with different temperature variations. Dorsal mantle length (DML), body weight (BW), sex and maturity stages (based on a 5 maturity stages scale) were determined for each defrosted specimen. All the sample data are presented in Table 1. The morphological characters of the post-spawning (spent) stage for both sexes were based on Inejih (2000), and illustrated in Fig. 2. Beaks were removed, cleaned and preserved in distilled water at 5°C in labeled vials.

Figure 1. Locations of the twenty spent *O. vulgaris* caught off the Mauritanian coast during 2010-2011 (black spots).



Figure 2. Spent reproductive organs of *O. vulgaris* males (A) and females (B). The definition of the spent stage is based on Inejih (2000).



Table	e 1. Sampling	information	of the spent	O. vulgaris	captured	between	April 2010	0 and Marc	h 2011.	M: male,
F: fen	nale.									

	Octopus	Catch date	Catch depth (m)	BW (g)	Sex
Northern Group	1	22-Jul-10	48	1718.6	F
(20°N)	2	08-Sep-10	60	499.5	F
	3	16-Sep-10	60	584.9	F
	4	04-Dec-10	40	1015.1	F
	5	08-Dec-10	60	1276.4	F
	6	09-Dec-10	36	1732.2	F
	7	11-Dec-10	60	1086.3	F
	8	12-Dec-10	62	663.0	F
	9	17-Dec-10	43	2292.2	Μ
	10	17-Dec-10	44	1808.0	Μ
	11	04-Jan-11	60	362.7	F
	12	06-Jan-11	62	2236.1	Μ
	13	08-Jan-11	65	836.0	F
	14	18-Jan-11	42	667.9	F
	15	21-Jan-11	40	1591.1	F
Southern Group	16	10-Apr-10	235	575.9	F
(18°N)	17	05-Jan-11	62	1822.9	Μ
	18	21-Mar-11	138	5325.1	Μ
17°N	19	05-Aug-10	62	1395.5	F
19°N	20	12-Apr-10	138	2536.9	F

Estimation of absolute ages and lifecycle

Age of the specimens was estimated by counting the daily increments in the inner surface in the LWS, by using vertical epi-illumination light and magnifications of 100-150X with an image analysis system. The full technique is described by Perales-Raya et al. (2010). The total number of increments for each octopus was counted twice on the LWS by an experienced reader. Coefficients of variation (CV) of the estimated ages allowed assessment of the precision between readings. CV was calculated as the ratio of the standard deviation over the mean (Campana, 2001):

CV (%) =
$$100 \times \sqrt{(R1-R)^2 + (R2-R)^2} / R$$

R1 and R2 being the number of increments from the first and the second reading respectively, and R the mean number of increments from both readings.

Hatching dates were back-calculated (Dawe & Beck, 1992) by using the estimated age and the catch date, drawing a "life line" for each individual. By considering the mean sea surface temperature (SST) during the previous months before hatching at each octopus location and the embryonic periods assigned to a mean temperature (Mangold, 1983), the approximated spawning day was estimated.

Observation of stress marks or checks

Stress marks were observed in the RSS (for both groups North and South) by an experienced reader, after mounting and polishing the rostrum area of the beak with the technique described by Raya & Hernández-González (1998), and improved by Perales-Raya et al. (2010). A thermal check was considered only when increments from death to the check were clearly visible. To avoid low accuracy of daily increment counts, only checks located less than five months before death were considered. When checks were coincident with days of major values of ΔT (daily SST variations: $\Delta T_{day i} = SST_{day i} - SST_{day i-1}$), they were located in the "life lines" of each octopus.

Other checks that were laid down within the last two months of life but did not coincided with a high ΔT , were also taken into account to detect a possible pattern related to other factors such as reproductive/biotic events of senescence. Some checks have been also observed in the LWS, but we used the RSS because the last daily increments at the edge area of the LWS are difficult to count with precision. Conversely, the daily increments laid down within the last months of life are easier to identify and count in RSS.

Temperature data

Because *in situ* bottom temperatures, where the octopuses were caught, are not available, high resolution data (0.25°) in the area from World Ocean Atlas 2005 (WOA05) by Boyer et al. (2005) were used to confirm that SST changes can be used as a proportional estimation of changes in bottom temperatures for octopuses that live up to 75 m depth. Daily high-resolution SST time series (from the NOAA-THREDDS Data Server, 2012) were used to obtain daily ΔT for each catch location of all spent octopuses. As Reynolds et al. (2007) reported, these SST time series are obtained by an optimum interpolation method that uses Advanced Very High Resolution Radiometer (AVHRR) infrared satellite SST data, in combination with *in situ* surface data from ships and buoys. They include a large-scale adjustment of satellite biases with respect to the *in situ* data. The analyses have a spatial grid resolution of 0.25°. Graphs with mean values of ΔT were obtained for each group.

Results

Absolute ages and lifecycle

The mean CV obtained from the LWS readings was 1.99 ± 0.64 with 95% confidence. These results indicate that both readings were similar, therefore either could be selected. R1 was used for age estimation. The ages of the spent *O. vulgaris* ranged from 194 days (584.9 g) to 322 days (1718.6 g), which indicate a lifecycle of around one year. Regarding weights, spent individuals ranged from 362.7 g (a female of 254 days) to 5325.1 g (a male of 303 days). Results showed a high individual variability, both in weight and age of the spent octopuses (Table 2).

Table 2. Age (number of increments in the lateral wall surface of beak) obtained for each *O. vulgaris*, coefficients of variation CV (%) between readings and back-calculated hatching date. Estimated embryonic period (in days), as a function of temperature (from Mangold, 1983), and estimated spawning dates.

	Octopus	Age (days)	CV (%)	Hatching date	Estimated embryonic period	Estimated spawning date
Northern	1	322	2.914	03-Sep-09	20	14-Aug-09
Group	2	209	2.329	11-Feb-10	50	23-Dic-09
(20°N)	3	194	3.899	06-Mar-10	50	15-Jan-10
	4	253	4.335	26-Mar-10	50	04-Feb-10
	5	200	0.000	22-May-10	50	02-Apr-10
	6	228	0.309	25-Apr-10	50	06-Mar-10
	7	312	1.790	02-Feb-10	50	14-Dic-09
	8	254	0.840	02-Apr-10	50	11-Feb-10
	9	214	0.664	17-May-10	50	28-Mar-10
	10	250	3.852	11-Apr-10	50	20-Feb-10
	11	254	4.599	25-Apr-10	50	06-Mar-10
	12	267	1.312	14-Apr-10	50	23-Feb-10
	13	274	1.040	09-Apr-10	50	18-Feb-10
	14	291	1.205	02-Apr-10	50	11-Feb-10
	15	259	2.941	07-May-10	50	18-Mar-10
Southern	16	231	3.580	22-Aug-09	20	02-Aug-09
Group	17	233	0.905	17-May-10	50	28-Mar-10
(18°N)	18	303	0.233	22-May-10	50	02-Apr-10
17°N	19	264	1.589	14-Nov-09	20	25-Oct-09
19°N	20	217	1.611	07-Nov-09	20	18-Aug-09

Back-calculations from death in Table 2 indicated that most of the hatchings occurred during spring (N=16) and autumn (N=4). Regarding estimated spawning periods, two groups were observed: a winter-spring spawned group, with mean SST of 19°C and incubation time of around 50 days, and a summer-autumn spawned group with mean SST of 25.7°C and incubation time of around 20 days.

Stress marks or checks

The absolute ΔT values recorded as stress thermal marks in the RSS ranged from 1.36°C to 2.43°C (Table 3). They were detected up to 142 days before death and registered in the RSS microstructure as darker increments (Fig. 3).

Table 3. Values and dates of the main peaks of Sea Surface Temperature variations (Δ T) for the two main areas considered off the Mauritanian coast (Northern Group around 20°N and Southern Group around 18°N).

	∆T peak	Date	ΔT (°C)
Northern	Ι	29-Oct-10	+2.11
Group	II	26-Oct-10	-1.63
	III	18-Oct-10	+1.48
	IV	30-Sep-10	-1.71
	V	25-Aug-10	+1.40
	VI	16-Aug-10	+1.91
	VII	05-Apr-10	-1.60
Southern	VIII	12-Sep-10	+1.36
Group	IX	16-Aug-10	+2.42

Figure 3. Arrows indicate stress checks (darker increments) corresponding to dates with noticeable sea surface temperature variations, among the daily increments in the central area of the rostrum sagittal sections (200X) of *O. vulgaris* beak.



Seven dates, corresponding to the highest ΔT values of the period, were identified in the RSS as checks in the Northern Group (Fig. 4), and two dates in the Southern Group (Fig. 5). At around 20°N, where the Northern Group was caught, the ΔT graph shows a period of high values in August-October 2010. ΔT peak number I (29th October 2010) and number VI (16th August 2010) corresponded to the most frequent and clear thermal checks registered on the beaks. As it is observed in Fig. 4, some of the ΔT peaks did not produce a detectable stress mark in RSS. The temperature variation graph in the southern area (18°N) was different, with less temperature variations during the same period. Both areas had a ΔT peak on 16 August 2010, registered on all beaks in which this date fell within the last five months of life, with exceptions in octopuses 12, 13. In the individuals 16 and 18, checks related to ΔT peaks were not found, which could be explained by either the lack of thermal peaks at depths where they lived (235 and 138 m) or by their occurrence before the last five months of life.

Figure 4. "Lines of life" (horizontal bars) for each spent *O. vulgaris* of the Northern Group (20°N), where white vertical lines correspond to stress checks on the beak (A). Graph of daily sea surface temperature variation (Δ T), where Roman numerals identify the main temperature changes (B).



Figure 5. "Lines of life" (horizontal bars) for each spent *O. vulgaris* of the Southern Group (18°N), where white vertical lines correspond to stress checks on the beak (A). Graph of daily sea surface temperature variation (Δ T), where Roman numerals identify the main temperature changes (B).



On the other hand, two checks (not matched with high values of ΔT) were observed in RSS during the 50 days before death in 17 individuals (Fig. 6). Both checks corresponded to an average of 15 and 28 days before death respectively. The exceptions were 3 specimens with only one check (Fig. 7). Octopus number 2 is a particular case, because both checks matched high ΔT dates. These two checks were considered to be related to senescent events because spent individuals are close to death. No differences were observed between sex and geographical locations.

Figure 6. Black arrow corresponds to death, and white arrows indicate stress marks that were observed in the two months before death, among the daily increments on the rostrum sagittal sections (200X) of a spent *O. vulgaris* beak.



Figure 7. First (black) and second check (grey) observed on the rostrum sagittal sections of the beaks, attributed to metabolic changes related to *O. vulgaris* senescence. When only one check was found, it was represented by a white rectangle.



Discussion

Senescent animals are close to death but their expected longevity may be a little longer than the obtained age estimates, thus reaching one year of age. Therefore, maximum ages obtained for the spent *O. vulgaris* are consistent with the one-year lifecycle proposed for the species in this area (Fernández-Núñez et al., 1996; Raya & Hernández-González, 1998; Jouffre et al., 2000).

Studies including spent octopuses in the wild are scarce, probably because such animals are difficult to catch (Domain et al., 2000). For earlier life stages, high individual variability for *O. vulgaris* growth has been reported, where several biotic and abiotic factors (such as temperature and feeding) influence individual growth rates (Semmens et al., 2004; André et al., 2009; Canali et al., 2011; Cuccu et al., 2012, among others). In the analysed sample, several senescent females were found weighing less than 600 g (the smallest at only 362.7 g),

whereas the lowest weight of a spent male was 1822.9 g. Although the sample is small, it seems that males reach greater weights before their final decline than females, as was reported in Senegal by Domain et al. (2000). It is known that males reach maturity at lower weights than females, as described for the West African coast (Bravo de Laguna, 1988; Dia, 1988; Fernández-Núñez et al., 1996; Inejih, 2000, among others). Recent studies including age at maturity of octopuses in West Mediterranean waters by using beak readings (Cuccu et al., 2012) found that males reached mature stages younger and smaller (average 141 days and 225 g) than females (average 227 days and 675 g). The authors found similar mean values of sizes and ages in the mature stage, although minimum values for males were lower (190 g and 161 days) than for females (310 g and 210 days). Therefore, the process of maturation in males starts earlier and at lower sizes, as demonstrated in other cephalopods (e.g. Jackson & Yeatman, 1996). However, the absence of a crucial energy-consuming event in males (such as spawning and brooding eggs) could be a reason for the greater weights achieved at the end of their lifetimes.

Sample size is not enough to obtain definitive conclusions, but the back-calculated hatchling dates for the spent individuals (spring and autumn) are consistent with the results obtained by Inejih (2000) for the species at the Mauritanian coast. That study concluded that *O. vulgaris* spawns throughout the year with two spawning peaks in winter-spring and autumn. The estimated spawning dates in the present study (Table 2) are in agreement with these spawning peaks.

The thermal checks registered daily variations at surface of around 2°C, which indicates how sensitive the beak deposition microstructure could be to oceanographic variations. In fish, environmental conditions affect their physiology and it is reflected in the growth rates of the hard structures, varying increment widths that form stress marks (Volk et al., 1999; Morales-Nin, 2000, among others). In cephalopods, several authors have related increment width variations with temperature oscillations in statoliths (e.g. Durholtz & Lipinski, 2000; Jackson & Moltschaniwskyj, 2001; Villanueva et al., 2003; Arkhipkin, 2005) and beaks (Canali et al., 2011). For the beaks, these authors found checks in LWS beaks after thermal shock variations of around 15°C in captivity. Our results indicate that beaks are capable of registering lower temperature oscillations in the wild. However, specific surveys to obtain more precise data of the environmental conditions of the caught octopuses would contribute to determine the ranges of daily temperature variations that beaks are able to register.

The coincidence between thermal check locations in the RSS and dates of high ΔT supports the daily deposition of increments in wild *O. vulgaris* beaks. Therefore, ΔT check

deposition could be used as a natural tag, avoiding the complexity of validation experiments based on capture and recapture (Lipinski, 1998; Domain et al., 2000). Field age validations in cephalopods are scarce but, as mentioned by Lipinski (1998), this is the most important source of data in any validation exercise. Differences found in the thermal check deposition between the Northern (20°N) and Southern (18°N) groups could be explained by different oceanographic conditions, and probably genetic differences between both areas. Waters around 20°N at the Northwest African coast form a pronounced hydro-climatological transition area (the Cape Verde Frontal Zone) between the cool upwelling waters in the north, and the warm coastal waters of tropical origin in the south (Martínez-Marrero et al., 2008). The seasonal interruption of upwelling south of 20°N reduces the regional temperature anomalies (Mittelstaedt, 1991). The Northern Group lived in this transition zone, with high thermal fluctuations in autumn that did not happen at 18°N (location of the Southern Group) for the same period (see Figures 4 and 5). Murphy et al. (2002) found genetic differences in octopus samples from both locations.

We suggest that the last checks before capture in these spent octopuses were related to senescent events because they showed a deposition pattern, and did not match with high thermal fluctuations. These checks were not observed before in our studies of beak microstructure of non-spent individuals. It is known that a dramatic hormonal change triggers the spawning process in octopuses, directly related to protein metabolism (O'Dor and Wells, 1978; Hunt and Nixon, 1981), and it is likely that it leaves a print on the chitin-protein complex of the beak microstructure. Arkhipkin et al. (1999) and Arkhipkin (2005) reported stress checks in peripheral zone of males and females of *Illex coindetii* statoliths. The authors suggested that the first check was coincident with the start of maturation in both sexes, and subsequent checks were induced by stress stimuli during mating events. Our results also found no sex differences in the check deposition. Octopuses with only one "senescent check" may be explained by different reasons. Although there is no information, it could be that another check was not observed for technical limitations, or was not laid down yet.

We conclude that microstructure anomalies observed on beak sections in *O. vulgaris* can indicate environmental events and, therefore, beaks could be used as life recorders. Also the coincidence between known events and check location in the beak supports the daily deposition of increments in the wild. Further analysis in this field would provide a better understanding of environmental/biological anomalies in cephalopod beak microstructure as a response to ecological and oceanographic processes occurring during their lifetime. This would be a critical tool for evaluating the life history of cephalopods in an ecosystem context

and could enable predictions of individual and population responses to internal/external changes.

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References

- Anderson, R. C., J. B. Wood & R. A. Byrne, 2002. Octopus senescence: the beginning of the end. Journal of Applied Animal Welfare Science 5: 275-283.
- André, J., E. P. M. Grist, J.M. Semmens, G. T. Pecl & S. Segawa, 2009. Effects of temperature on energetic and the growth pattern of benthic octopuses. Marine Ecology Progress Series 374: 167-179.
- Arkhipkin, A. I., P. Jereb & S. Ragonese, 1999. Checks in the statolith microstructure of the short-finned squid, *Illex coindetii* from the Strait of Sicily (Central Mediterranean). Journal of the Marine Biological Association of the U.K. 79: 1091-1096.
- Arkhipkin, A. I., 2005. Statoliths as "black boxes" (life recorders) in squid. Marine and Freshwater Research 56: 573-583.
- Boyer, T.P., J.I. Antonov, H.E. Garcia, D.R. Johnson, R.A. Locarnini, A.V. Mishonov, M.T. Pitcher, O.K. Baranova & I.V. Smolyar, 2006. World Ocean Database 2005. In S. Levitus (ed), NOAA Atlas NESDIS 60, U.S. Government Printing Office, Washington, D.C. DVDs.
- Bravo de Laguna, J., 1988. Managing an international multispecies fishery: the Saharan trawl fishery for cephalopods. In Caddy, J. F. (eds), Marine invertebrate fisheries: their assessment and management. Wiley-Interscience Publication: 591-612.
- Campana, S. E., 1983. Calcium deposition and otoliths check formation during periods of stress in coho salmon, Onchorynchus kisutch. Comparative Biochemistry and Physiology 75: 215-220.
- Campana, S. E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59: 197-242.
- Campana, S. E. & J. D. Neilson, 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42: 1014-1032.
- Canali, E., G. Ponte, P. Belcari, F. Rocha & G. Fiorito, 2011. Evaluating age in *Octopus vulgaris*: estimation, validation and seasonal differences. Marine Ecology Progress Series 441: 141-149.
- Cuccu, D., M. Mereu, A. Cau, P. Pesci & A. Cau, 2012. Reproductive development versus estimated age and size in wild Mediterranean population of *Octopus vulgaris* (Cephalopoda: Octopodidae). Journal of the Marine Biological Association of the U. K. Early view: 1-7.
- Dia, M. A., 1988. Biologie et exploitation du poulpe *Octopus vulgaris* (Cuvier, 1797) des côtes mauritaniennes. Thèse de Docteur, Université de Bretagne Occidentale, Brest, France.
- Dawe, E. G & P. C. Beck, 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES C.M. 1992/K: 33.
- Domain, F., D. Jouffre & A. Caverivière, 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. Journal of the Marine Biological Association of the U. K. 80: 699-705.

- Durholtz, M. D. & M. R. Lipinski, 2000. Influence of temperature on the microstructure of statoliths of the thumbstall squid *Lolliguncula brevis*. Marine Biology 136: 1029-1037.
- FAO, 2012. Species fact sheets, *Octopus vulgaris* (Lamarck, 1798). United Nations Food and Agriculture Organization [available on internet at http://www.fao.org/fishery/species/3571/en]. Accessed November 2012.
- Fernández-Núñez, M. M., C. L. Hernández-González, C. P. Raya & E. Balguerías, 1996. Reproductive biology of *Octopus vulgaris* Cuvier, 1797 from north-western African coast (21°N-26°N). ICES C.M. 1996/K: 15.
- Hernández-López, J. L., J. J. Castro-Hernández & V. Hernández-García, 2001. Age determined from the daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fishery Bulletin 99: 679-684.
- Hunt, S. & M. Nixon, 1981. A comparative study of protein composition in the chitin-protein complexes of the beak, pen, sucker disc, radula and oesophageal cuticle of Cephalopods. Comparative Biochemistry and Physiology. Part B. Biochemistry and Molecular Biology 68: 535-546.
- Inejih, C. O., 2000. Dynamique Spatio-temporelle et biologie du poulpe (*Octopus vulgaris*) dans les eaux mauritaniennes: modélisation de l'abondance et aménagement des pêcheries. Thèse de Docteur, Université de Bretagne Occidentale, Brest, France.
- Jackson, G. D., 1994. Application and future potential of statoliths increment analysis in squids and sepioids. Canadian Journal of Fisheries and Aquatic Sciences 51: 2612-2625.
- Jackson, G. D. & J. Yeatman, 1996. Variation in size and age at maturity in *Photololigo* (Mollusca: Cephalopoda) from the northwest shelf of Australia. Fishery Bulletin 94: 59-65.
- Jackson, G. D. & N. A. Moltschaniwskyj, 2001. The influence of ration level on growth and statolith increment width of the tropical squid *Sepoteuthis lessoniana* (Cephalopoda: Loliginidae): an experimental approach. Marine Biology 138: 819-825.
- Jouffre, D., C. A. Inejih, & M. Simier, 2000. Cycle biologique du poulpe (*Octopus vulgaris*) au large du Cap-Blanc (Mauritanie). In Gascuel, D., P. Chavance, N. Bez, N. & A. Biseau (eds), Les espaces de l'halieutique. Éditions IRD, Paris: 243-267.
- Kalish, J.M., 1992. Formation of a stress-induced chemical check fish otoliths. Journal of Experimental Marine Biology and Ecology 162: 265-277.
- Lipinski, M. R., 2001. Statoliths as archives of cephalopod life cycle: a search for universal rules. Folia Malacologica 9: 115-123.
- Lipinski M. R., M. D. Durholtz & L. G. Underhill, 1998. Field validation of age readings from the statoliths of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) and an assessment of associated errors. ICES Journal of Marine Science 55: 240-257.
- Lombarte, A., M. M. Rufino & P. Sánchez, 2006. Statolith identification of Mediterranean Octopodidae, Sepiidae, Loliginidae, Ommastrephidae and Enoploteuthidae base don warp analyses. Journal of the Marine Biological Association of the U.K. 86: 767-771.
- Mangold, K., 1983. *Octopus vulgaris*. In Boyle, P. R. (eds), Cephalopod Life Cycles (I): Species Accounts. Academic Press, Orlando: 335-363.
- Martínez-Marrero, A., A. Rodríguez-Santana, A. Hernández-Guerra, E. Fraile-Nuez, F. López-Laatzen, P. Vélez-Belchí & G. Parrilla, 2008. Distribution of water masses and diapycnal mixing in the Cape Verde Frontal Zone. Geophysical Research Letters 35, L07609, doi:10.1029/2008GL033229.

- Mittelstaedt, E., 1991. The ocean boundary along the northwest African coast: circulation and oceanographic properties at the sea surface. Progress in Oceanography 26: 307-355.
- Morales-Nin, 2000. Review of the growth regulation processes of otolith daily increment formation. Fisheries Research 46: 53-67.
- Murphy, J. M., E. Balguerías, L. N. Key & P. R. Boyle, 2002. Microsatellite DNA markers discriminate between two *Octopus vulgaris* (Cephalopoda: Octopoda) fisheries along the northwest African coast. Bulletin of Marine Science 71: 545-553.
- NOAA-THREDDS Data Server, 2012. http://www.ncdc.noaa.gov/thredds/catalog/oisst/NetCDF/AVHRR/ catalog.html. Accessed June 2012.
- Oosthuizen, A., 2003. A development and management framework for a new *Octopus vulgaris* fishery in South Africa. PhD Rhodes University, Grahamstown, South Africa.
- O'Dor, R. K. & J. M. Wells., 1978. Reproduction Versus Somatic Growth: Hormonal Control in *Octopus vulgaris*. The Journal of Experimental Biology 77: 15-31.
- Pannella, G., 1980. Growth patterns in fish sagittae. In Rhoads, D. C. & R. A. Lutz (eds), Skeletal growth of aquatic organisms; biological records of environmental change. Plenum Press, New York: 519-560.
- Perales-Raya, C., A. Bartolomé, M. T. García-Santamaría, P. Pascual-Alayón & E. Almansa, 2010. Age estimation obtained from analysis of octopus (*Octopus vulgaris* Cuvier, 1797) beaks: improvements and comparisons. Fisheries Research 106: 171-176.
- Raya, C. & C. L. Hernández-González, 1998. Growth lines within the beak microstructure of the Octopus Octopus vulgaris Cuvier, 1797. In Payne, A. I. L., M. R. Lipinski, M. R. Clarke & M. A. C. Roeleveld (eds), Cephalopod biodiversity, Ecology and Evolution. South African Journal of Marine Science 20: 135-142.
- Reynolds, R.W., T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey & M. G. Schlax, 2007. Daily High-Resolution-Blended Analyses for Sea Surface Temperature. Journal of Climate 20: 5473-5496.
- Semmens, J.M., G. T. Pecl, R. Villanueva, D. Jouffre, I. Sobrino, J. B. Wood & P. R. Rigby, 2004. Understanding octopus growth: patterns, variability and physiology. Marine Freshwater Research 55: 367-377.
- Spounagle, S., 2010. Otolith microstructure reveals ecological and oceanographic processes important to ecosystem-based management. Environmental Biology of Fishes 89: 221-238.
- Villanueva, R., A. Arkhipkin, P. Jereb, E. Lefkaditou, M. R. Lipinski, C. Perales-Raya, J. Riba & F. Rocha, 2003. Embryonic life of the loliginid squid *Loligo vulgaris*: comparison between statoliths of Atlantic and Mediterranean populations. Marine Ecology Progress Series 253: 197-208.
- Volk, E.C., S. L. Schroder & J. J. Grimm, 1999. Otolith thermal marking. Fisheries Research 43: 205-219.
- Young, J.Z., 1960. The statocysts of *Octopus vulgaris*. Proceedings of the Royal Society of London. Series B, Biological Sciences 152: 3-29.