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The cuttlefish *Sepia officinalis*
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ECOLOGY OF *SEPIA OFFICINALIS*

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ABSTRACT. – This article comprises an up-dated review of the processes influencing the distribution and abundance of the common cuttlefish *Sepia officinalis*, the interactions between the species and the main variables of the environment in which it lives and its trophic, demographic and behavioural ecology.

The geographical distribution of the common cuttlefish, *Sepia officinalis* L., 1758 covers the Mediterranean Sea and the waters of the Eastern Atlantic from southern Norway and northern England to the northwestern coast of Africa. The species also lives in Madeira and in the Canary Islands (Khromov *et al.* 1998). The geographical distribution of *S. officinalis* and *Sepia hierredda* Rang, 1837 in the eastern Central Atlantic shows that these species are sympatric. The southern boundary of *S. officinalis* coincides approximately with the border between Mauritania and Senegal (16ºN) and the northern limit of *S. hierredda* is at Cape Blanc (21ºN) (Guerra *et al.* 2001).

Factors influencing the distribution and abundance of Sepia officinalis

S. officinalis is a nekto-benthic species occurring predominantly on sandy and muddy bottoms from the coastline (2-3 m depth) to approximately 200 m depth, with the greatest abundance in the upper 100 m. Life in inshore waters exposes this species to hydrologically unstable conditions, and because of this *S. officinalis* is relatively tolerant to variations in salinity. Animals have been observed in coastal lagoons at a salinity of 27 PSU in the Mediterranean (Mangold-Wirz 1963). Observations from the Western Mediterranean and the NW Atlantic have shown that juveniles and adults can survive for some time at salinities 18±2 PSU if slowly acclimatized (Boletzky 1983, Guerra & Castro 1988). In culture tanks both embryonic development and growth of young cuttlefish usually occurs between 37±3 PSU (Domingues *et al.* 2001). However, Paulij *et al.* (1990) observed that some embryos of *S. officinalis* from eggs collected in the SW Netherlands hatched at a salinity of 26.5 PSU, but no hatching occurred below 23.9 PSU, and below 22.4 PSU embryos with morphological malformations were found.

Experiments with *S. officinalis* showed that shells of large animals implode between 150 and 200 m, whereas advanced embryonic specimens and newly hatched animals implode between 50 and 100 m. The larger individuals are occasionally caught at depths greater than the implosion depth of the juvenile shell parts. They apparently avoid implosion of the early shell portions by refilling these first-formed chambers with cameral liquid later in life (Ward & Boletzky 1984).

The temperature limits of the species range from 10ºC to 30ºC. At temperatures below 10ºC the individuals do not feed, stay inactive and die in a couple of days (Richard 1971, Bettencourt 2000). Hatchlings and young *S. officinalis* were successfully cultured in tanks with an open sea water system in which temperature reached 30ºC (Domingues *et al.* 2001), and indeed the species lives in the lagoon system of the Ria Formosa (South Portugal), where temperature reaches 27±3ºC in summer (Domingues *et al.* 2002). Oxygen affinity expressed by P_{50} (partial pressure of gas at which the blood remains 50% saturated) as a function of temperature for *S. officinalis* showed that it increased from 12 mm Hg at 5ºC to near 38 at 17ºC, the slope of the linear regression being relatively low. This is an indication that the species does not have the ability to accommodate large or small temperature ranges in its natural habitat (Brix *et al.* 1994). Recent findings by Melzner *et al.* (2004) supported the hypothesis of an oxygen limitation due to thermal tolerance (upper limit at about 26º C) caused by limited capacity and a loss in coordination of the components of the oxygen delivery system.

Johansen *et al.* (1982) studied the O_2 uptake in relation to body weight and concluded that the common cuttlefish is not very tolerant to low oxygen concentrations. Low oxygen concentrations can account for the absence or low abundance of *S. officinalis*. Thus, a comparison between the cuttlefish fisheries in the upwelling areas off the NW African coast and the Northern Benguela current undertaken by Guerra & Sánchez (1985) suggested continuous euthrophic scenarios in shallow waters in the cores of the southern upwelling (25-28ºS).

This is where low oxygen concentrations are common, and they appear to be the most important limiting factor for the development of cuttlefish populations.

The physiological processes for buoyancy in the cuttlebone of *S. officinalis* determine their role as major bioenergetic consumers. As indicated by Webber *et al.* (2000), buoyancy and activity of *S. officinalis* are typically higher at night (VO_2 from 93 to 120 mg O_2 kg^{-1} h^{-1}) than during the day (VO_2 between 77 and 93). Within the depth limits imposed by shell implosion, the cuttlefish is less energetically expensive with depth than any fish. Thus, it can competitively occupy top niches in the trophic web of shallow waters that involve daily vertical migrations.

Landing per unit effort of cuttlefish from a time series of 18 years in SW Spain indicated that the abundance of this species did not show a correlation with rainfall rates, river discharges and sea surface temperature (Sobrino *et al.* 2002). This reinforces the view that the common cuttlefish exhibit high physiological flexibility, which allows a great ability to endure changing environments, not only during its adult phase but also at early juvenile stages (Sobrino *et al.* 2002). Jorge and Sobral (2004) indicated that strong precipitation had a negative influence on the cuttlefish abundance in the Ría de Aveiro (Central Portugal) and that, on the contrary, the cumulative effect of high values of solar radiation, temperature of the air, water transparency and salinity near the bottom seemed to positively influence the catches of this species.

Toxic effects of heavy metals can negatively influence the distribution and abundance of *S. officinalis*. As the species is a primary food source for many predators and also for human consumption, it is a potential threat for higher trophic levels (Bustamante *et al*. 2002). Concentration and distribution of heavy metals in tissues of *S. officinalis* have observed high and selective bioaccumulation (Miramand & Bentley 1992). Ecotoxicological studies using bioassays from isolated digestive gland cells demonstrated that some heavy metals (Cu, Zn and Ag) induced high disturbance of enzymatic systems (Le Bihan *et al.* 2004). The impact of these metals on survival and growth of eggs and juvenile cuttlefish can be very negative (Koueta pers comm). Culture experiments at different stages of the life cycle of *S. officinalis* using Zn and Cd tracers with sea water, sediments and food as uptake pathways showed that food is the likely primary track for bioaccumulation, and that the digestive gland plays a major role in the subsequent storage and presumed detoxification of these elements regardless of the uptake pathway (Bustamante *et al.* 2002). Malformed common cuttlefish caught in the Bay of Arcachon could be a product of the teratogenic effects of the antifouling compound TBT (Schipp & Boletzky 1998).

S. officinalis does not form shoals neither in the wild nor in the laboratory, but in culture they tolerate one another except under extreme food deprivation. This tolerance is higher in young animals than in subadult and adult ones (Hanlon & Messenger 1996). A feeding hierarchy first appearing after 4 months, which stabilizes after 5 months, has been found in this species (Warnke 1994). Captive-rearing experiments indicated that behaviour of *S. officinalis* was strongly affected by housing conditions and suggested that this species is probably semi-solitary under natural conditions (Boal *et al.* 1999). The results obtained when studying the effects of crowding in cuttlefish cultured at different densities are somewhat contradictory. This could be due to the difficulty of comparing experiments undertaken under different conditions. Experiments completed by Domingues *et al.* (2003) showed that cuttlefish cultured in isolation had higher growth and survival rates that the ones maintained at relatively high densities, even when stressed. The authors observed agonistic behaviour related with competition for space with higher densities in thanks, indicating that density, or lack of space, appear to be more limiting than isolation.

To date, very few interspecific associations (excluding parasitism) have been reported for this species. Bacterial populations associated with *S. officinalis* have been localized mainly in the accessory nidamental glands, the renal appendages and the shell epithelium. The accessory nidamental glands show an intense orange-red coloration in mature females, and this colour is due to carotenoid pigments, which occur in symbiotic bacteria (Van Den Braden *et al.* 1980). Five symbiotic bacterial taxa (*Agrobacterium*, *Roseobacter*, *Rhodobium-Xanthobacter*, *Sporochtya* and *Clostridium*) were identified in the tubules of the accessory nidamental glands, and three taxa of Pseudomonacae were located in the renal appendages and the shell epithelium. All these bacteria, except Gram-positive ones, were also present in embryos, suggesting vertical transmission, i.e. maternal transmission at egg stage (Grigioni & Boucher-Rodoni 2002).

The copepod *Metaxymolgus longicaudata* has also been found to be associated with this cuttlefish, but its role was not elucidated (Ho 1983). Small specimens (mantle length, ML<65 mm) of *S. officinalis* and adult *S. elegans* (ML 45-65 mm) exhibited diets with similar prey types, although in different proportions. This may suggest a trophic competition between the two species at that size range (Castro & Guerra 1990).

Apparent replacement of finfish by *Octopus vulgaris* and *S. officinalis* in the Sahara Bank (21ºN-26ºN) since the 1960s was attributed to a change in the ecosystem due to overexploitation of finfish. Balguerias *et al.* (2000) re-evaluated the history of these fisheries and suggested that the changes in the faunistic composition of the communities were caused by a combination of factors, including economic initiatives as well as oceanographic variations and competition for food. This ultimately favoured benthic cephalopod populations at the cost of most finfish populations.

The present-day geographical distribution pattern of the Sepiidae may have been generated by a complex mosaic of factors involving palaeo-oceanographical changes (Neige 2003). Some attempts were made to clarify the taxonomic status of the genus *Sepia* L., 1758, which comprises approximately 100 species. Khromov *et al.* (1998) proposed a subdivision of the genus into six species complexes, which are not to be viewed as phylogenetic entities. Khromov (1998) suggested that five main stages could be seen in Sepiid radiation. One of the scenarios proposed by Khromov suggested that the *Sepia* sensu stricto forms (to which *S. officinalis* belongs) emerged in the Palaeogene (70 to 40 MYA). Khromov's scenario also suggested that these forms underwent a relatively recent radiation starting from the warm waters of the Tethyan Sea, and that the Western Mediterranean and Southern Atlantic European forms colonized the west coast of Africa. Recent studies on the biogeography of Sepiidae showed two radiation patterns: one to the southern African coasts, and the other to the 'East Indian' area. The southern African pattern is characterized by high disparity for very different species richness values. This pattern may be caused by the coexistence of two independent phylogenetic clusters of species, one from the Atlantic and the other from the Indian Ocean. This has to be viewed in the paleogeographical context of the Eocene (60-40 MYA), where the Tethyan Sea was still open at its eastern end providing a connection between Europe, on the one hand, and the Indian Ocean and east African coast, on the other. At the end of the Eocene, this eastern corridor between the Mediterranean and western India disappeared, involving a huge transformation in possible routes for cuttlefish migration. This could have produced two clusters of species, one in Europe and along the west African coast, the other in the Indian Ocean and along the east African coast. Mixing of these two clusters in southern Africa may have produced the present pattern (Neige 2003).

Allozyme (Pérez-Losada *et al.* 1999) and microsatellite markers (Pérez-Losada *et al.* 2002) display a highly significant subpopulation structuring of *S. officinalis* around the Iberian Peninsula, consistent with an isolation-by-distance model of low levels of gene flow. Distinct and significant clinal changes in allele frequencies between the Atlantic and the Mediterranean samples indicated, however, that these results might also be consistent with an alternative model of secondary contact and introgression between previously isolated and divergent populations. A pronounced 'step' change between SW Mediterranean samples associated with the Almería-Oran front suggest that this oceanographic feature may represent a contemporary barrier to gene flow.

Seasonal migrations between shallow and deeper waters are a well-known ecological feature of *S. officinalis*. In the Western Mediterranean populations a general tendency for the animals to migrate inshore in spring and summer for reproduction and move offshore in autumn was observed, although not all the animals migrate at the same time, size and age (Mangold 1966). These migrations are over different distances, from a few dozens to several hundred nautical miles, and represent an important displacement of biomass, which has also been observed in other regions (Richard 1971, Najaï 1983, Boucaud-Camou & Boismery 1991, Coelho & Martins 1991, Le Goff & Daguzan 1991b, Guerra & Castro 1988, Jorge & Sobral 2004). As pointed out by Boucaud-Camou & Boismery (1991), autumn *S. officinalis* offshore migration in winter in the English Channel is mainly influenced not only by cooling of the littoral waters, but also by day-length reduction and decreased light intensity, which are other factors influencing maturation and spawning (Boletzky 1983, Boucaud-Camou *et al.* 1991). Thus, the relatively deep milder waters at the central axis of the Channel seem to constitute the common hibernation area to all cuttlefishes in the Channel, which they leave at the end of the winter. Spring inshore displacements are mainly due to an increase of the temperature in littoral waters. These displacements were shown by tagging experiments (Boucaud-Camou & Boismery 1991), but this spatial and temporal pattern is also supported by the analysis of geo-referenced data measured at both sides of the English Channel (Dunn 1999, Denis & Robin 2001, Royer 2002, Wang *et al.* 2003). The role of strength of the Atlantic currents into the west part of the English Channel and the south part of the Celtic Sea was found to be the dominant influence on the timing of cuttlefish migration to these areas. Thus, the local abundance was positively correlated to sea surface temperature, with cuttlefish expanding their distribution further north in the spawning seasons in warm years and shifting in cool waters. The centre of high abundance in offshore deep water shifts north in warm winters and south in cool winters (Wang *et al.* 2003).

Trophic ecology

The diet of *S. officinalis* includes crustaceans, bony fishes, molluscs, polychaetes and nemertean worms (Nixon 1987, Castro & Guerra 1990, Pinczon du Sel *et al.* 2000). Species composition within these prey groups depends upon the respective species composition and availability in each ecosystem. Main crustacean prey items are mysids, shrimps, prawns, and crabs, but *S. officinalis* also feeds upon amphipods, isopods, and ostracods. The most important bony fishes found in the diet of the species were gobies, sand eels, whiting and wrasses, but cuttlefish can also prey upon some flatfishes. Among the cephalopods main food items include various sepiolids and sepiids species. Large cuttlefish are also cannibals, capturing and eating smaller individuals. Other small prey found in the stomach of this species, like bryozoans, foraminifera, bivalve molluscs and insects should be regarded with caution, because they can be the prey of prey, or accidentally ingested prey (Castro & Guerra 1990). *S. officinalis* shows a wide range of diets and should therefore be considered as a trophic opportunist. The species feeds exclusively on living animals, but in the laboratory it has been fed with different kind of surimi and pelleted diets, and non-living food (Castro *et al.* 1993, Koueta & Boucaud-Camou 1999, Perrin 2004). Significant ontogenetic changes in the diet of the species with the progressive replacement of crustaceans by fishes have been found (Castro & Guerra 1990). Ontogenetic changes in the prey size of this species are also well documented (Blanc *et al.* 1999, Blanc & Daguzan 2000). There were, however, no differences in feeding habits of male and female *S. officinalis* at any size, the feeding intensity of females increasing with sexual maturity, and no seasonal changes in diet were found (Castro & Guerra 1990).

An attempt to establish the trophic position of *S. officinalis* in an estuarine community (a *Zostera* meadow in San Simón inlet, Ría de Vigo) was undertaken by Filgueira and Castro (2002) based on the analysis of the stable isotopes C^{13} and N^{15} in its muscle and from sympatric organisms. Significant decreases in $\delta^{13}C$ and $\delta^{15}N$ were found related with cuttlefish size (15-195 mm ML) when these values were converted to trophic level. These results disagree with an expected increase in values corresponding to trophic level with predator size, and are in contradiction with previous knowledge of the common cuttlefish feeding ecology. These authors proposed a working hypothesis based on spawning migration. As cuttlefish approach maturity, they migrate to shallow waters, such as those of San Simón inlet, for spawning. Then, the smallest mature animals used in this study (60 mm ML for males and 80 mm ML for females) would probably not have left San Simón inlet yet, their isotopic composition representing the local food web. The largest animals present in San Simón were probably coming back from deeper waters, having an isotopic composition that does not depend initially on the local food web. Moreover, as the metabolic rate of large animals is lower than that of smaller ones, they would keep for longer time the isotopic signals from deeper waters before its body composition is in equilibrium with that of the shallow area. If the food web of San Simón shows higher delta (δ) isotopic values than that from outside, a predator, such as cuttlefish, growing in that habitat, should show a heavier isotopic composition than a predator outside this area. Therefore, C and N isotopic composition of cuttlefish from San Simón would be inadequate for estimating its trophic level, and for testing the hypothesis that the trophic level of a predator increases with body size, because large and small animals could belong to different trophic webs.

Analyses using carbon- and oxygen-isotope composition [$\delta^{13}C$ (CO_3^{2-}) and $\delta^{18}O$ (CO_3^{2-}), respectively] in the cuttlebone aragonite of wild and cultivated specimens of *S. officinalis* from NW Spain showed that seasonal changes in isotopic temperature revealed by these analyses agreed with changes in surrounding sea water temperature: $CaCO_3$ was deposited in the cuttlebone all year round, a maximum life span of 2 years, a yearly spawning season, and the existence of variable growth rates among and within individuals can be inferred from isotopic temperatures (Bettencourt & Guerra 1999).

The tentacles of *S. officinalis*, when ejected, reach the prey in less than 15 milliseconds at 25ºC. Prey is dealt with summarily. Thus, prawns are paralysed and bitten within six seconds of capture and crabs are paralysed in about ten seconds. The immobilisation of prey is provoked by neurotoxins secreted by the posterior salivary glands (Hanlon & Messenger 1996). If it exists, external digestion of prey seems to be very weak and many pieces of exoskeleton are ingested (Guerra *et al.* 1988).

Despite the small size of the mouth, cuttlefish can seize relatively large prey with their prehensile arms and tentacles. This, together with voracity, versatile feeding habits, and a highly evolved sensory system, allows them to occupy a broad trophic niche. Furthermore, migrations enable *S. officinalis* populations to exploit the temporal and spatial variability of productive systems and fluctuating populations of prey (Rodhouse & Nigmatullin 1996). Visual detection of prey involves movement, contrast, size, shape and orientation. The visual attack in this ambush predator when facing a prawn exhibits three phases: attention, positioning, and seizure (Hanlon & Messenger 1996). Data collected in two 24 h sampling operations carried out in August and February in the Ría de Vigo (NW Spain) suggested a 24 h feeding pattern for this species where most of the feeding occurred during darkness (Castro & Guerra 1989). Such a feeding pattern has been also described in South Brittany (Pinczon du Sel *et al.* 2000) and in the Ría Formosa lagoon (Quintela & Andrade 2002). These results suggest that *S. officinalis*, apart from visual detection, may also detect some prey by light emitted from their light organs, and that chemo- and mechanoreception (via statocysts and/or the lateral line analogue) cannot be ruled out. Predation of non-luminous prey can be also facilitated by dinoflagellate luminescence (Fleisher & Case 1995).

Common cuttlefish have high absorption efficiency, which explains high growth rates and relatively low production of faeces. Forsythe *et al.* (1994) estimated a conversion efficiency of 59% in animals cultivated at 24°C and fed with shrimps, which showed a growth rate of 6.5 and a feeding rate of 11.0 (both rates in% body mass per day).

With very few exceptions, there are no fishes that are specialist cephalopod predators. Among the elasmobranches, lower beaks of *S. officinalis* were found in the stomach content of *Prionace glauca* (Clarke & Steven 1974). *S. officinalis* also occurred in the stomachs of *Scyliorhinus canicula, Mustelus mustelus* (Morte *et al.* 1997) and *Galeus melastomus* (Velasco *et al.* 2001). Among teleostei, it occurred in the stomach contents of *Merluccius merluccius* (Larrañeta 1970, Velasco *et al.* 2001). Hatchling and juvenile common cuttlefish are preyed upon by *Serranus cabrilla* in *Posidonia* grass areas of the Mediterranean (Hanlon & Messenger 1988). The species *Pollachius pollachius* exerts great predatory pressure on young cuttlefish in the French waters of north Brittany (Le Mao 1985). In the Bay of Biscay, Velasco *et al.* (2001) found *S. officinalis* in the stomach contents of *Pagelus acarne, Aspitrigla cuculus, A. obscura, Lophius piscatorius, L. budegassa, Trisopterus luscus*, *Lepidorhombus whiffiagonis* and *L. boscii.* Young cuttlefish were observed in the stomach contents of *Dicentrarchus labrax*, *Labrus bergylta*, *Spondyliosoma cantharus* and *Conger conger* in Morbihan Bay (Blanc & Daguzan 1999).

A total of 12 specimens of *S. officinalis* were found in a Risso's dolphin (*Grampus griseus*) (Clarke & Pascoe 1985). To date, the species has not been clearly identified in the stomach contents of other marine mammals, except in monk seals (*Monachus monachus*) from the Aegean Sea (Salman *et al.* 2001). However, some remains identified as *Sepia* sp, *Sepia* spp or simply Sepiidae were observed in the harbour porpoise (*Phocoena phocoena*), and in the dolphins *Tursiops truncatus*, *Delphinus delphis* and *Stenella coeruleoalba* (Santos 1998).

It has been suggested that the ecological niche of a cephalopod species is more important in determining its risk of parasite infection than its phylogeny, and that *S. officinalis* should be included in one ecological coastal group (González *et al.* 2003). The virus-like particles found in the stomach epithelium of wild *S. officinalis* have a structure similar to vertebrate 'Retrovirus' (Hanlon & Forsythe 1990). Cultured in the laboratory, this species showed susceptibility to a highly virulent systemic infection by bacteria (*Pseudomonas* and *Vibrio*), which does not appear to be related to external injury (Hanlon & Forsythe 1990). Diseases may be caused by other protistans and metazoans such as fungi, coccidians, microsporidians, ciliates, dicyemids, diageneans, cestodes, nematodes, brachyurans, copepods and isopods (Hochberg 1990). Many of these parasites are transmitted through the food web. Sexual stages of the coccidian *Aggregata eberthi* occur in the digestive tract of *S. officinalis*, and asexual stages infect the digestive tract of crustaceans. The complete life cycle of *A. eberthi* in NE Atlantic was only achieved when experimental infections showed that the prawns *Palaemon elegans* and *P. adpersus* are the intermediate hosts for this parasite (Gestal *et al.* 2002a).

Demographic ecology

Considering its reproductive traits, *S. officinalis* has been included in the group termed 'Intermittent terminal spawning' (Rocha *et al.* 2001). This reproductive pattern is characterized by the fact that all species included spawn once, ovulation is group-synchronous, spawning is monocyclic, egg lying occurs in separate batches, and somatic growth does not generally take place between spawning events. In such a species, spawning period tends to be relatively long. The main spawning season of *S. officinalis* in the Western Mediterranean and the Gulf of Tunis covers spring and summer, but winter spawning has also been observed (Mangold-Wirz 1963, Najaï 1983). The spawning period extends from early spring and late summer in south and central Portugal and both the Atlantic and Mediterranean coast of South Spain, with a spawning peak in June and July (Villa 1998, Tirado *et al.* 2003, Jorge & Sobral 2004). The spawning season of this species within the downed estuarine valleys in NW of the Iberian Peninsula extends from early spring to late summer, but winter spawning has also been recorded (Guerra & Castro 1988). The spawning season in the Bay of Biscay and the Gulf of Morbihan lasts for six months, from mid-March to late June (Le Goff & Daguzan 1991a). Along both the north and the south coast of the English Channel the spawning season of *S. officinalis* extends from February to July (Dunn 1999, Royer 2002, Wang *et al.* 2003). Environmental factors (much milder winter conditions in some areas than in others) probably account for most of the variations observed in *S. officinalis* spawning times (Boletzky 1983). It also has been observed that a restriction of food intake in early life may delay maturation and extend life span in this species (Boletzky 1979).

Studies on fecundity carried out by Laptikhovsky *et al.* (2003) showed that the potential fecundity (PF) of advanced maturing and mature pre-spawning *S. officinalis* in the Aegean Sea varies from

3,700 to 8,000 (mean 5,871) oocytes, whereas the number of large yolk oocytes increase with ML from 130 to 839. These authors also observed that spawning females have a PF of some 1,000-3,000 eggs below that of pre-spawning females. This provides evidence that intermittent spawning, which occurs in captivity (Boletzky 1987), is a normal process in natural habitats, suggesting that common cuttlefish females release a number of eggs equivalent to about 50% of PF during spawning, although many individual variants are possible under wild conditions.

S. officinalis generally lays eggs at depths rarely greater than 30 or 40 m. The eggs are attached in clusters to various plants, sessile animals such as tube worms, or dead structures such as drowned trees, cables or nets. No parental care has been reported in this species, but no major predation pressure on the eggs has been observed. The length of embryonic development is temperature dependent (Boletzky 1983). Hatchlings of this species have a mantle length that may vary from 6 to 9 mm, and are strikingly similar to adults both in morphology and basic behaviour. Hatching generally occurs at a stage sufficiently advanced to enhance active feeding within hours after hatching. Young cuttlefishes can adapt to very low food intake and maintain growth rates much lower than normal. This provides a margin of safety allowing animals to survive under unfavourable conditions (Boletzky 1983).

Common cuttlefish live for approximately two years, although some male individuals may attain a greater age. Females die shortly after spawning, although this event can extend over several weeks or even months in the laboratory. Mass mortality, after the spawning season, has been observed in the French and Spanish Atlantic coasts (Richard 1971 and pers obs), but nothing of comparable intensity is known in the Mediterranean (Boletzky 1983).

There can be several causes of death among the common cuttlefish in a population: removal by fishing, predation, diseases, accident, etc., each with its own rate. It is a usual practice in population dynamic studies to consider a division into only two types: fishing, and natural mortality, which includes everything else. Each kind of mortality has it own instantaneous rate (Ricker 1975). In an ideal scenario, the natural mortality could be differentiated by different causes. In practice, this is, however, very difficult. Preliminary results of a management exercise of *S. officinalis* gillnet fishery in San Simón inlet for the period 1997-2001 demonstrated that monthly instantaneous rate of natural mortality (M) over a six-month period (from November to April) ranged from 2.27 to 3.38, the mean being 2.70 (Outeirial 2002, Rocha & Guerra unpubl). These values were estimated by different methods exclusively based on the biological parameters obtained by Guerra & Castro (1988) and Bettencourt (2000) from the *S. officinalis* populations within the Galician Rías, and are similar to those calculated by Emam (1994) in the *Sepia prashadi* exploited population from the Gulf of Suez. The concept of an "instantaneous" rate can be troublesome to readerships not familiar with population dynamics. There is, however, an excellent explanation of this concept in Ricker (1975). The mean value of M estimated for the *S. officinalis* of San Simon inlet corresponds to an annual mortality rate (A) of approximately 93% of the total number of individuals of a given population, which is very high. That mortality rate suggests a catastrophic post-spawning mortality, which has been corroborated in the species by both field and laboratory observations. However, when M is used in different stock assessment methods (Pierce & Guerra 1994) its value ranges from 0.1 to 0.6. The remaining mortality is due to fishing (F).

S. officinalis constitutes part of the diet of many marine predators at different stages of their life cycle, but natural mortality rates caused by predation have not yet been evaluated. Although various parasites are known in juvenile and adult *S. officinalis*, most of them do not appear to be important as a natural mortality factor at pre-reproductive stages (Hochberg 1990). Nevertheless, a detrimental effect on gastrointestinal function by high digestive tract infections with *Aggregata eberthi* might result in a decrease or malfunction of absorption enzymes (Gestal *et al.* 2002b).

How many units of population conforms *S. officinalis* within its area of distribution is something still unknown. However, from an exploitation point of view, cuttlefish concentrations within the English Channel are considered as a management unit. This is mainly due to the fact that catch per unit effort is lower in the adjacent waters of the Bay of Biscay and the Celtic Sea than in the English Channel (Denis & Robin 2001).

Common cuttlefish can exhibit variations in its life cycle along its geographic range. Around the Iberian Peninsula and in the Mediterranean Sea, spawning female sizes range from 90 to 320 mm ML. This suggests the presence of two-year classes of breeders in the population, and the population structure of *S. officinalis* may superficially look simple, with seldom more than two annual cohorts or a cycle of alternating shorter and longer generations, at least as far as the female individuals are concerned (Boletzky 1983). However, as cuttlefish may attain sexual maturity at very different sizes, spawning occurs over a long time period when compared to life span, the duration of egg development is dependent on temperature, and its growth is very much depending on environmental factors (Bouchaud & Daguzan 1990, Forsythe *et al.* 1994, Clarke *et al.* 1989, Dunn 1999, Bettencourt 2000, Domingues *et al.* 2002, Koueta & Boucaud-Camou 2003). Recruitment of successive broods reveals subgroups, cohorts or 'micro-cohorts', whose age at recruitment varies significantly between seasons and cohorts, demonstrating different growth rates among them, and there are large interannual variations in recruitment (Challier *et al*. 2002, Challier 2005), so a more complex demographic pattern is underlined. Factors affecting recruitment are, therefore, of key importance in understanding the population dynamics of this species (Challier 2005).

A consistent biannual life cycle has been described in the English Channel (Dunn 1999, Royer 2002). Hatchlings born from July to September grow rapidly, and the juveniles migrate from the inshore nursery grounds in late autumn to overwintering grounds in deeper waters. The following spring they return inshore, and begin to exhibit the first signs of sexual maturation. Males start to mature at a mean ML of about 100 mm, and most are mature by September (about 13 months old). Female maturation begins slightly later, and takes longer, with the final stages of female maturation occurring during the following winter. After a second offshore migration to overwintering grounds the adult cuttlefish (approximately 18 months old) return inshore in the spring to spawn and then die. In south Brittany, some of the juveniles born from mid-March to late June begin their sexual development as early as November for males and late December for females. These precocious individuals require only one year to complete their life cycle, and constitute small size breeders (80-100 mm ML). However, most individuals reproduce after a second offshore-inshore migration, they constitute a second group of breeders (130-350 mm ML). These two-year classes of breeding cuttlefish are not reproductively separated (Gauvrit *et al.* 1998).

Behavioural ecology

The seasonal migrations between shallow and deeper waters bring *S. officinalis* into contact with various types of soft and rocky bottoms. The ability of small juveniles to attach themselves to a hard substrate may be very important because it allows them to withstand strong water movement without being carried away. These animals are able to bury themselves in soft bottoms, and the behavioural pattern of this sand covering is well established at hatching (Boletzky 1983).

The entire morphology of this species reflects adaptation to life near or on the bottom in a very complex environment. Moreover, *S. officinalis* has a considerable repertoire of defensive strategies involving a large number of chromatic, textural and postural components (Hanlon & Messenger 1996). Detailed studies on defence sequences of young and adult *S. officinalis* show complicated and different behavioural patterns. However, these tactics were mainly observed under laboratory conditions and, therefore, caution must be invoked when extrapolating to wild conditions (Hanlon & Messenger 1996). Dickel *et al* (2000) provided evidence that the environment during the 2nd and/or 3rd months of life was crucial to the ontogenetic development of memory in *S. officinalis*.

The reproductive behaviour in this species is well known (Hanlon & Messenger 1996). A single pair can mate several times in succession, sometimes intermixed with egg lying. Under culture conditions temporary mate guarding by the male has been observed. However, when guarding relaxes, other mature males can copulate with the female. Therefore, there is evidence of promiscuity, at least in the laboratory, where some results obtained using microsatellite DNA (Guerra unpubl data) and from behavioural studies (Hanlon *et al.* 1999) provide evidence that sperm competition may be a major feature of the mating behaviour in this species.

Some general ecological remarks

S. officinalis has life-cycle characteristics known in other coleoid cephalopods: early sexual maturation, extended spawning season, breeding once, catholic predator habits, rapid growth with variable growth rates depending on environmental factors, short life-span, little overlap of generations, and complex recruitment. However, in contrast to other species, mainly those that are pelagic throughout their life cycle (e.g. ommastrephid squids) or those with planktonic paralarval stages (e.g. some octopods), *S. officinalis* is not so vulnerable to predation and environmental variables. This is mainly due to the fact that the new hatchlings of this species are almost miniature adults, both in morphology and behaviour, and also because their physiological layout is highly flexible (Nixon & Mangold 1998). In consequence, this species does not show as much unpredictability of distribution and density as other cephalopod species (Boyle & Boletzky 1996).

As all cephalopods, *S. officinalis* shows relatively low levels of genetic variation (Sanjuan *et al*. 1996, Shaw & Pérez-Losada 2000), and its population dynamics appears to be influenced principally by phenotypic plasticity in response to environmental variability, and the maintenance of this diversity balances the risks of mortality factors combining at any one time to cause periodic extinctions (Boyle & Boletzky 1996). The change in the faunistic composition of the communities observed in the Sahara Bank showed that major ecological perturbations, such as environmental shifts or imposed effects such as commercial fishing, have an important impact on *S. officinalis* and other cephalopod populations (Boyle & Boletzky 1996).

Whether or not *S. officinalis* fits into the generalizable *r*-or *K*-strategies, and in view of the doubts expressed by Stearns (1992) on the value of these strategies to the interpretation of life histories, a theoretical framework for cephalopod life cycle is perhaps premature (Boyle & Rodhouse 2005). It is best to consider that this species shows a complex set of covarying traits which constitute both strategies throughout its life cycle, as indicated by Calow (1987).

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