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Short Communication

Behavioural observations of the common octopus *Octopus vulgaris* in Baía dos Tigres, southern Angola

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Observations on the behaviour of the common octopus *Octopus vulgaris* were made during daytime and night-time sampling on an unexploited rocky reef habitat in Baía dos Tigres, southern Angola. The relative numerical abundance sampled was 0.47 octopus person^{-1} h^{-1} during the day and 5.33 octopus person^{-1} h^{-1} during the night, suggesting that the population under study was nocturnal. The activity patterns differed between sizes of octopus. Small octopus (<20 cm total length [TL]) were observed roaming during the night, whereas the large individuals (>20 cm TL) generally fed in their dens. This ontogenetic behavioural shift may be due to tidal constraints or could be a strategy to avoid cannibalism. Octopus inhabiting a shallow, small-boulder substratum made extensive modifications to their habitat, excavating dens of up to 1 m deep in the sand below the boulders. These dens were not visible during the day as the octopus appeared to retract the small boulders over their den entrances. This unique behavioural strategy is thought to be a means to reduce predation and reduce light intensity during the day. Octopus were not observed in the small-boulder habitat during the five hours of daytime sampling. With nocturnal activity and extensive habitat modification, it is likely that avoidance of predation may be an important driver influencing the behaviour of the octopus population under study.

Keywords: activity patterns, cephalopod, den ecology, habitat modification

Introduction

The common octopus *Octopus vulgaris* (Cuvier 1797) is a shallow-water cephalopod species that inhabits coastal rocky areas or reefs. It is the most studied and widely distributed species in its genus. This species has a short lifespan and a rapid growth rate of over 5% of body weight per day (García and Valverde 2006, Ibáñez and Keyl 2010). It is semelparous, with females laying large strings of eggs that they attach to the substrata in their dens (Hernández-García et al. 2002). There is a paucity of information on the preferred habitat and behaviour of *O. vulgaris* in its natural environment (Anderson 1997, Meisel et al. 2006). The species has been classified as highly mobile, yet resident individuals may exhibit high levels of territoriality. Its mobility allows it to move efficiently between a wide range of suitable habitats (Katsanevakis and Verriopoulos 2004). Octopus make use of both tactile and visual senses to forage, feed and seek suitable shelter (Forsythe and Hanlon 1997, Carvalho and Sousa Reis 2003, Rodríguez-Rúa et al. 2005). They are active feeders that seek out prey such as crustaceans, sessile molluscs and small fish (Forsythe and Hanlon 1997, Boyle and Rodhouse 2005), as well as their smaller conspecifics (Ibáñez and Keyl 2010).

The majority of behavioural ecology studies on octopus have been on captive individuals. However, the activity patterns (Mather 1988), foraging strategies and aspects of the movement behaviour (Mather and O'Dor 1991) of juvenile *O. vulgaris* in the wild were described for an exploited population in Bermuda. Because intertidal octopus stocks are exploited by recreational, subsistence and artisanal fisheries (e.g. Oosthuizen and Smale 2003, Sauer et al. 2011), there are few opportunities to study the behavioural ecology of unexploited populations. An opportunity arose to study various behavioural patterns in an unexploited population in Baía dos Tigres, a large (~200 km^2) coastal embayment situated on an isolated stretch of the southern Angolan coast (Figure 1). This study provides information on the population size structure, aspects of the movement behaviour, activity patterns and foraging strategies of *O. vulgaris* in this largely unstudied coastal embayment.

Methods and materials

Study site

Baía dos Tigres is relatively shallow (~12 m mean depth) with predominantly sandy and muddy substrata, and patches of rocky reef along the north-eastern shore. The study site is an isolated reef (16°36' S, 11°44' E) that extends approximately 500 m along the shoreline (Figure 2). Similar to other reef areas along this shoreline, the nearshore region (0–20 m offshore) comprises small boulders (10–50 cm in diameter) (referred to here as SB habitat) resting on sandy sediment. This habitat hosts a range of invertebrates including

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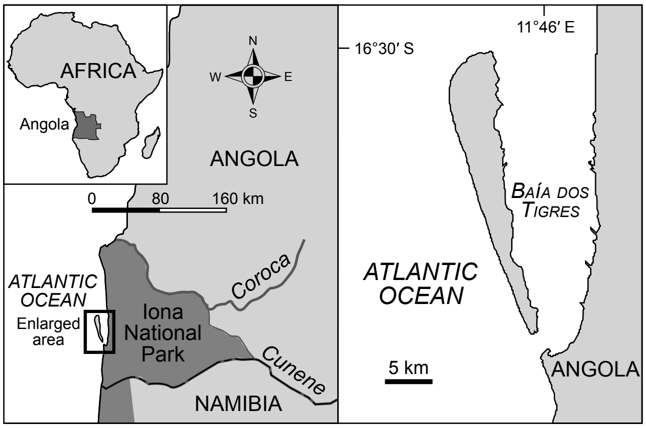

Figure 1: Map showing the location of the study site, Baía dos Tigres, and places mentioned in the text

Figure 2: The small-boulder and large-boulder habitats on a rocky reef along the north-eastern shore of Baía dos Tigres

molluscs such as large mussels *Perna perna* and limpets *Helcion dunkneri* (Figure 3). Beyond 20 m offshore, the small boulders are replaced with larger boulders (40–80 cm diameter) (LB habitat) with interspersed exposed reefs and limited sand. Two large reef complexes, with several rocky overhangs on their edges, extend through both the SB and LB habitats for approximately 40 m out into the bay.

Sampling

The study was undertaken in July 2012 while collecting octopus specimens for a comparative morphological and genetic study between South African and Angolan *O. vulgaris*. In order to locate specimens, three researchers conducted a roving census in the SB and LB habitats. Each individual was equipped with an octopus gaff comprising a 1 m wooden or aluminium rod, fitted at one end with an 8/0 fishing hook and a coloured plastic skirt. The starting location and the paths taken by each individual were random. The first roving census was conducted over a period of five hours during the day, from low tide at 08:30 to well into the incoming tide at 13:30. The second census took place at night over a similar tide sequence, between 21:00 and 00:30 (3.5 h); however, only the SB habitat was sampled during this census. Data recorded included the time searched, the number of octopus captured and the area of capture (SB or LB) of each individual. Details on the habitat,

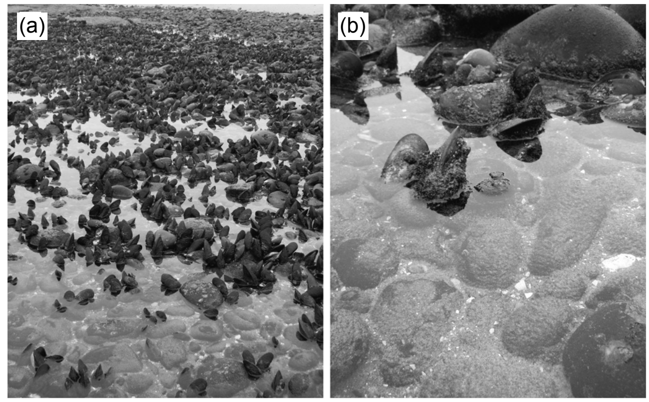

Figure 3: Typical small-boulder habitat at the Baía dos Tigres study site showing (a) the high densities of mussels and (b) small boulders lying in a bed of sand

depth of den and activity of the octopus were noted. In order to reduce the impact of tentacle coiling on measurement accuracy, TL was obtained by adding the length of the dorsal mantle (DML), head (HL) and the longest arm (AL). DML was defined as the length from the dorsal midpoint between the eyes to the tip of the mantle, whilst HL was measured from the midpoint between the eyes to the point of attachment between the first left and right arm. AL was classified as the length from the beak to the tip of the longest arm.

Results and discussion

The relative abundance of octopus was 10 times lower during the daytime (0.5 octopus person^{-1} h^{-1}) than during the night-time (5.3 octopus person^{-1} h^{-1}) sampling event. By way of comparison, in the sheltered coastal areas of the Eastern Cape province, South Africa, the abundance of *O. vulgaris* sampled during the daytime was 1.7 octopus person^{-1} h^{-1} (Oosthuizen and Smale 2003). The marked difference between the daytime and night-time catch per unit effort (CPUE) in Baía dos Tigres suggests that the *O. vulgaris* population at that location is nocturnal. Elsewhere, *O. vulgaris* has been classified in the Mediterranean as a nocturnal species (Meisel et al. 2003), whereas studies conducted in the Caribbean Sea and North Atlantic Ocean suggest a diurnal activity pattern (Mather 1988, Meisel et al. 2006). Similar to other intertidal organisms, *O. vulgaris* is subject to extreme environmental variation on a daily basis. Meisel et al. (2006) suggested that variation in light intensity is an important driver of behaviour in *O. vulgaris* and that individuals and populations may shift between diurnal and nocturnal states. Cobb et al. (1995) identified light as an important cue for many cephalopods that inhabit the photic region of the ocean.

Predation pressure is also an important driver of ecological and coleoid behavioural evolution, and it may be a key factor shaping the population as a whole (Rosenzweig 1991). Octopus abundance in the Caribbean was shown to be restricted by the high diversity of predators within the region (Aronson 1991), and a negative relationship between the abundance of predatory fish and octopus population size was found along the coasts of South-East Asia, the Adriatic and the North-West Atlantic (Aronson 1991). Octopus are able to make use of strategies such as adaptive colouration to reduce daytime predation (Mather 1988, Meisel et al. 2003, 2006), and nocturnal behaviour has often been observed in areas with extreme predation pressure (Gibson 2003, Katsanevakis and Verriopoulos 2004).

Octopus vulgaris is an important dietary item of the Cape fur seal *Arctocephalus pusillus pusillus* (De Bruyn et al. 2005), bottlenose dolphin *Tursiops truncatus* (Blanco et al. 2001) and the spotted gully shark *Triakis megalopterus* (Smale and Goosen 1999), all of which occur in Baía dos Tigres (Croxall and Prince 1996). Simmons et al. (2006) reported large numbers of *A. p. pusillus* in Baía dos Tigres and Dyer (2007) observed *T. truncatus* during a short stay in the bay. During our study a large school of these dolphins was observed approximately 100 m from the shore. Both *A. p. pusillus* and *T. truncatus* are known to be active and to feed during the day (Harzen 2002, Miller et al. 2010). Given that much of the fauna in Baía dos Tigres is unexploited, it is most likely that high levels of predation pressure are driving the observed nocturnal behavioural pattern in *O. vulgaris*.

There was a substantial difference in the distribution of octopus between daytime and night-time sampling. During daytime sampling, none were found in the SB area and seven were located in the LB area. Those sampled in the LB area were in water >40 cm deep and were relatively large (>20 cm TL). Six exhibited either sleeping or resting activity, as described by Mather (1988), and one was observed modifying the sandy substrate near the den entrance. In contrast, during night-time sampling a total of 56 octopus inhabited the shallow (<20 cm) SB area. The large number of dens containing octopus that were observed in the SB area during night-time sampling indicated that these individuals were present during daytime sampling but had not been observed by the sampling team.

Several *Octopus* species actively modify their surrounding habitat in order to increase their level of protection (Anderson 1997, Katsanevakis and Verriopoulos 2004). The use of dens is an important survival strategy for a number of octopod species, and is thought to play a role in influencing their distribution (Mather 1994). Octopus dens generally consist of crevices in rocks, available shells and other accessible spaces found on reefs or in rocky benthic environments (Mather 1982, Boyle 1990, Anderson 1997). The use of dens and their cryptic colouration often make octopus difficult to detect. The den entrances in the SB area were relatively small, and when disturbed many of the octopus immediately covered the entrances with small boulders. The reasons for small den entrances in the SB area may be twofold. Firstly, small entrances are thought to provide higher levels of protection for octopus (Aronson 1986, Anderson 1997). As soft-bodied animals, they are capable of squeezing through very small gaps to gain access to their dens, which are then inaccessible to predators (Mather 1994). Secondly, octopus may also prefer small entrances to reduce the light penetration into their dens; early reports of *O. vulgaris* behaviour suggest that individuals modify their dens to reduce light penetration (de Haan 1926 in Iribane 1990). This behaviour has also been reported for *O. tehuelchus* (Iribarne 1990), but no other studies have reported den covering during the daytime. The efficacy of the observed den modification behaviour, from a predation perspective, was demonstrated when no octopus were found in another similar environment approximately 1 km north which was sampled by the research team the next day, despite the knowledge of the den 'camouflage' behaviour.

Forsythe and Hanlon (1997) suggested that sandy, shallow waters with small rocks did not provide suitable habitat for octopus, given that they generally prefer rock crevices and spaces between rocks and reef. *Octopus vulgaris* in Baía dos Tigres were, however, able to utilise the SB area by making extensive habitat modifications and often created dens in the sand underneath the small boulders. Katsanevakis and Verriopoulos (2004) found that the excavation of holes under rocks was an important strategy for *O. vulgaris* inhabiting softer sediments. This behaviour has also been reported for other octopus species including *O. briareus*, *O. bimaculatus* and *O. tetricus* (Ambrose 1982, Aronson 1986, Anderson 1997). Other species such as *O. joubini* use shells as dens in sandy habitats (Mather 1982), although there was no evidence of this for the species under study. Octopus create dens in sandy habitats using the interbranchial webs between their well-developed arms and by expelling strong currents through their siphons (Ambrose 1982, Aronson 1986, Katsanevakis and Verriopoulos 2004). Many of the dens examined in our study were large and deeper than 1 m, therefore requiring the expenditure of a considerable amount of energy to construct them. Rosenzweig (1991) suggested that population dynamics and habitat selection are closely interconnected in any species. The author found a negative correlation between population density and habitat selectivity, suggesting that habitat selection is less important in areas that are close to carrying capacity and that the diversity of habitat used is seen to increase with an increase in population density. The lack of rocky reef habitat in Baía dos Tigres, coupled with the apparently high population density on the available rocky habitats, suggests that the population of *O. vulgaris* is forced to expend large amounts of energy on constructing dens in what could be considered an unfavourable, shallow, small-boulder environment. Food availability and quality have major implications for the cost of foraging by any species (Weimerskirch et al. 2003). An increased abundance of quality prey decreases the costs associated with foraging activities, thereby allowing the allocation of energy and time to alternative activities (Weimerskirch et al. 2003). As a result of the high abundance of prey species within the SB area, octopus in Baía dos Tigres are able to invest a considerable amount of energy in den modification, and effectively increase the chances of survival.

All of the smaller octopus (<20 cm TL, <370 g) were observed out of their dens during the night-time sampling. The majority (~90%) of the larger individuals (>20 cm TL, >370 g) were, however, found in their dens at night, where they were feeding, predominantly on mussels. This behaviour suggests that the larger individuals had been foraging earlier in the evening, when the tide was high. Variation in daily activity patterns could be a function of ecological interactions, cyclic environmental processes, or a combination of both. Environmental changes associated with tidal rhythmicity are of particular importance to octopus inhabiting the intertidal region, and are often linked to changes in their activity (Mather 1988). The differences observed in the activity patterns between large and small octopus may be associated with their different depth requirements (Gibson 2003). Large octopus would likely retreat into their dens as the tide falls, due to restrictions associated with body size and water depth (Félix-Hackradt et al. 2010). The deep dens, which can be up to 1 m deep in the SB habitat, therefore allow larger octopus to maintain their position on the reef, even on the low tide. This strategy eliminates the horizontal migrations that are normally driven by tidal fluctuations (Speirs et al. 2002) and would reduce the risk of predation associated with moving off the SB area into deeper water.

Variation in activity patterns is an important behavioural adaptation to reduce competition between conspecifics, especially in unexploited, high-density populations (Meisel et al. 2003). Size-segregated feeding behaviour could develop within a population as a result of the presence of size-based hierarchies or the avoidance of competition and cannibalism. In captivity, several octopus species, including *O. cyanea* (Yarnall 1969), *O. joubini* (Mather 1982), *O. rubescens* (Dorsey 1976 cited in Iribane 1990), *O. vulgaris* (Boyle 1980) and *Eledone moschata* (Mather 1985) formed dominance hierarchies, which were partially based on size. These dominance hierarchies often determined access to food in captive environments, with small individuals often being food-deprived. There is less evidence for dominance hierarchies in the wild. For example, *O. joubini* seem to be solitary, perhaps asocial, when they have unlimited space (Mather 1982). Smith and Griffiths (2002) suggested that inter-cohort variation in activity patterns is a tactic to avoid inter-cohort cannibalism, and that smaller *O. vulgaris* were more active during the day, whereas large individuals were more active in the evening. Cannibalism is a common feature in *O. vulgaris* (Smith and Griffiths 2002, Ibáñez and Keyl 2010) and this behaviour is thought to play a major role in regulating population densities, decreasing intra-cohort competition and enhancing growth rates (Ibáñez and Keyl 2010). Cannibalism generally increases at high population densities (Ibáñez and Keyl 2010). The high density of octopus in the SB environment (more than five individuals were observed within a 10 m^2 area in some places) may have led to either social hierarchy or cannibalism, or a combination of the two, to act as drivers for size-segregated feeding in this unexploited population.

While this study has provided some insight into the behaviour of an unexploited *O. vulgaris* population, a more quantitative and experimental approach would be required to uncouple the underlying reasons for the development of these behaviours. Manipulative experimental studies could be used to explore further aspects of the behavioural ecology, including the influence of light and predators. The results of this and other studies do, however, suggest that the common octopus is a highly adaptable species, with the ability to change and use complex behavioural strategies to adapt to a variety of habitats.

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