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A potential new endemism: speciation of the common octopus, *Octopus vulgaris*, in the Desertas Islands, Cabo Verde?

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RESUMO

Cabo Verde é uma região biogeográfica única, onde a co-ocorrência de espécies temperadas e tropicais origina um número anormalmente alto de espécies endémicas. Os cefalópodes são peças centrais nas redes tróficas em todo o mundo, interagindo como predador/ presa e competindo com peixes por nichos ecológicos. O nosso objectivo foi avaliar como a topografia, a disponibilidade de presas e a pressão predatória nas ilhas Desertas moldaram o comportamento e a ecologia da população de *Octopus vulgaris*. Foram realizados censos visuais (subtidais e intertidais) na ilha de Santa Luzia (20 dias) e no ilhéu Raso (oito dias). Indivíduos de *O. vulgaris* foram encontrados apenas em áreas intertidais, durante a maré baixa, e a morfometria média da população foi de 35,6 ± 10,4 cm (comprimento total) e 175,0 ± 53 g (peso húmido). O tamanho acentuadamente reduzido de *O. vulgaris*, apenas parcialmente explicável pela regra de Bergmann, e a exclusão das áreas subtidais, parecem dever-se principalmente a fortes pressões predatórias e competição interespecífica por nichos limitados de habitat. As alterações comportamentais e morfométricas induzidas podem ser o produto da plasticidade de desenvolvimento, ou indicar alterações genéticas mais profundas, que retratariam um potencial fenómeno de especiação das populações de polvos que residem nas ilhas Desertas de Cabo Verde.

Palavras-chave: complexo de espécies, contexto ecológico, pressão predatória, topografia

ABSTRACT

Cabo Verde is a unique biogeographical region, where by mixing temperate and tropical characteristics an unusually high number of endemic species are reported. Cephalopods are central pieces of trophic networks worldwide, interacting as predator/ prey and competing with fish for ecological niches. We aimed to assess how the topography, prey availability, and predatory pressure of the Desertas Islands shaped the behaviour and ecology of the existing *Octopus vulgaris* population. Visual census (both underwater and on tidal rock pools) were performed on Santa Luzia Island (20 days) and Raso Islet (eight days). *Octopus vulgaris* individuals were found only in intertidal areas, during low tide, and mean population morphometry averaged 35.6 ± 10.4 cm (total length) and 175.0 ± 53 g (wet weight). The markedly reduced size of *O. vulgaris*, only partly explainable by Bergmann's rule, and exclusion from subtidal areas, appears to have been mainly driven by severe predatory pressure and strong inter-specific competition for limited habitat niches. The induced behavioural and morphometric alterations may be the product of developmental plasticity, or have arisen from deeper genetic alterations, which would portray a potential speciation phenomenon of octopus' populations residing on Cabo Verde's Desertas Islands.

Key-words: ecological context, predatory pressure, species complex, topography

INTRODUCTION

Cabo Verde has never been connected to mainland Africa and is comprised of 10 islands located approximately 450 km off the West African coast (Duda & Rolán 2005, Duarte & Romeiras 2009). In the northwesternmost section of the Windward Islands, São Vicente was connected with the Desertas during the Pleistocene, which are composed of Santa Luzia Island, and Branco and Raso Islets, nowadays separated by depths of ~200 m (Ancochea *et al.* 2015, Freitas *et al.* 2015). Supported by a recently acquired status of Natural Reserve and Marine Protected Area and associated reduced anthropogenic pressures, the Desertas are a privileged location for life to thrive (Anonymous 2014, Almeida *et al.* 2015). Special biogeographical characteristics (supporting temperate, subtropical and tropical organisms) enabled the speciation of an unusually high number of endemic species (e.g. Duda & Rolán 2005). Although one of the top 10 hotspots of marine biodiversity in the world (Almeida *et al.* 2015), the limited extension of the continental platform, highly dynamic oceanographic currents and restricted intertidal area, make the Desertas ecosystems extremely vulnerable to anthropogenic pressures, such as overfishing (Roberts *et al.* 2002).

Coleoid cephalopods, such as the shallow-water common octopus *Octopus vulgaris* (Cuvier, 1797), are cosmopolitan species known for their 'live-fast-die-young' life cycles and ability to adapt to several habitat and intra-habitat changes. The main factors influencing distributional patterns of a given population, at a local scale, are topography, availability of prey, and predatory risk (Mather & O'Dor 1991). For *O. vulgaris*, topography is a crucial ecological feature, given its benthic nature and background-matching behaviour (Hanlon & Messenger 1996). These animals are more associated with complex habitats, e.g. rocky and coral reefs, than simple structured ones, as sandy bottoms (Mather 1982).

Regarding trophic interactions, octopuses are known for influencing abundance and diversity within ecosystems, due to the

marked top-down and bottom-up pressures they exert (Packard 1972), being sought by a multitude of predators, including fish and mammals (Katsanevakis & Verriopoulos 2004), while exhibiting a high nutritive demands and voracious appetite (Katsanevakis & Verriopoulos 2006). Octopuses are frequently generalist and mobile predators, shaping their foraging decision-making process according to the characteristics of the prey (Wells 1978). Despite their flexibility, octopuses preferentially use chemotactile methods to hunt for prey in rock and coral crevices while hovering through the seabed (speculative hunting), while the visual senses are primed for predatory avoidance (camouflage matching) and ambushing prey that wanders close to their den (Mather & O'Dor 1991, Forsythe & Hanlon 1997).

As most cephalopods, *O. vulgaris* co-evolved with fish since their massive diversification, living mostly in vertebrate-dominated environments (Packard 1972). Therefore, cephalopods and fish are competitors for ecological niches, and the distribution and size of respective populations directly affect each other (Ambrose 1988, Taylor & Bennett 2008). The Desertas Island are, both from biotic and abiotic standpoints, unique habitats where the population status of these cephalopods is virtually unknown (Almeida *et al.* 2015). Thus, here we aimed to assess how the *O. vulgaris* population is distributed throughout the multilayered, biodiversity-rich environments of the Desertas. Moreover, we aimed to highlight the key roles that geographical isolation and topography of the Desertas Islands, as well as their unique ecological contexts, might have in variations of behaviour and ecology in *O. vulgaris*.

MATERIAL AND METHODS

Fieldwork for this study was performed in the Desertas Islands, Cabo Verde. On Santa Luzia Island (20 sampling days), the main areas covered were Praia de Francisco (front and rocky bottoms on both sides), Praia dos Achados, and Portinho, at the end of Praia de Palmo a Tostão (Fig. 1A). On Raso Islet (eight sampling days), only rocky substrate was observed, and the main location searched was Ponta de Casa (Fig. 1B). Branco Islet was not sampled, given its low accessibility and impracticable logistics. Combining both islands, sampling spanned approximately one month (10 September – 8 October 2017), and analyzed areas comprised sandy beaches and rocky shores.

Underwater, the preferred method used for searching for *O. vulgaris* and registering marine fauna was snorkeling (normally 0–15 m deep), in 2-h sampling sessions for 3–4 times a day. The researcher and volunteers followed a straight line from an edge of the are marked in red in Fig. 1, and performed continuous census until closing the square. In smaller areas, this procedure was repeated (2 to 3 times) until the 2h-limit was reached. Nevertheless, one dive resorting to SCUBA was also performed in the south coast of Raso (25 m), which enabled searching in deeper waters during a longer period. Snorkeling sampling lasted for 25 days and an averaged 6–8 hours per day, which added to a total effort of ~180 h of active search.

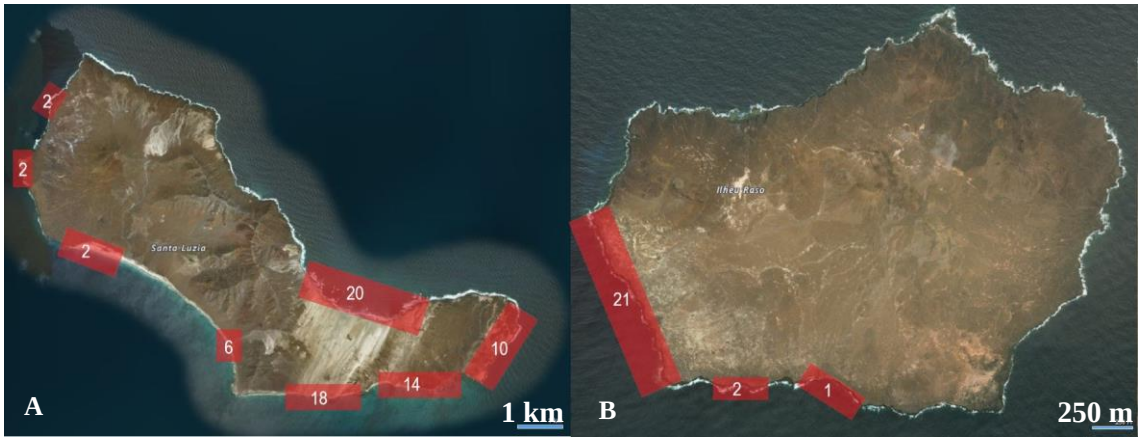

Fig. 1. Sampled areas in the Desertas, Cabo Verde (in red). **A)** Sampled areas on Santa Luzia Island (from upper left and counter-clockwise: Ponta de Algoder, Ponta Branca, Ponta de Água Doce, Ponta de Praia, Portinho, Pesqueiro da Salema, Praia de Francisco – Praia de Roque, and Ponta da Mãe Grande – Ponta de Creoulo; and **B)** on Raso Islet (from left to right: Ponta da Baleia – Ponta de Casa, Chã de Posende, and Ponta da Cruz). The numbers depict the amount of two-hour sessions performed on each location.

Rocky intertidal pools were surveyed by researchers and fishermen on Raso, both visually and using tools (i.e. spear) to prospect for animals in holes. On Santa Luzia, fisherman reports and dead individuals (locally used as bait for coastal fishing) were taken as evidence for the presence of *O. vulgaris* and their small-sizes (two different fishermen teams were interviewed about the distribution, habitat and size of octopus on both islands).

Six individuals, representatives of the population observed, were sampled for morphometric measurements, photographed (Morphobank project P3289) and stored afterwards in 96% ethanol at the University of Cabo Verde collections (UCV).

RESULTS

By snorkeling or SCUBA, no subtidal records of vagrant *O. vulgaris* were noted, either foraging or otherwise (i.e. in dens, camouflaging in rocks, etc.), after a total of 74 and 24 sampling two-hour sessions, on Santa Luzia and Raso, respectively. In fact, *O. vulgaris* were only detected in the intertidal rock pools during low tide in both islands. Specifically, 18 intertidal occurrences were recorded by fishermen on Santa Luzia, across the south side of the island, but mostly in the eastern section. Regarding Raso, 16 intertidal occurrences were recorded by fishermen and researchers in the southwestern section (Fig. 2).

Mean size and weight (± SD) of analyzed *O. vulgaris* individuals averaged 35.6 ± 10.4 cm and 175.0 ± 53 g (Table 1).

Fig. 2. *Octopus vulgaris* individual (UCV 2019/00011, see Table 1 for details) found in the intertidal rocky areas of Raso Islet (photo by Eduardo Sampaio).

Table 1. Morphometric measurements from six representative individuals of *O. vulgaris* collected on Raso Islet (Morphobank project P3289) and deposited at the University of Cabo Verde (UCV), with respective voucher and collection codes.

Voucher	Collection	Total Length (cm)	Weight (g)
UCV 2019/00009	OCTOCVD1	32.1	197
UCV 2019/00010	OCTOCVD2	41.2	193
UCV 2019/00011	OCTOCVD3	48.9	260
UCV 2019/00012	OCTOCVD4	28.0	65
UCV 2019/00013	OCTOCVD5	36.6	149
UCV 2019/00014	OCTOCVD6	30.1	91

DISCUSSION

Average size and weight of *O. vulgaris* were found to be remarkably lower to what was registered for other biogeographical regions, and such is referenced to be little changed over the year, by local fisherman (Salamansa and São Nicolau fishermen, per. comm.). Moreover, September is usually when individuals with larger sizes are found in other geographical reasons, given that it is their mating season (Katsanevakis & Verriopoulos, 2004), and there is no reason (up to this point) to think that this is not the case in Cabo

Verde. Reports from the Mediterranean Sea describe that this species can reach over 3 m of total length, and wet weights of 7 kg (Quetglas *et al.* 1998), and 6 kg in the Southern Indian Ocean (Guerra *et al.* 2010).

There are several hypotheses which may underpin this severe morphological reduction. First, there is a general biological rule that states that animal body size increases with latitude, as reduced surface to volume ratios provide more efficient heat conservation, whereas larger ratios in smaller individuals facilitate heat loss, and are thus selected near the tropics. Thought to be applicable only for endotherms (Bergmann 1847), later this rule was found to be pervasive for marine ectotherms (Atkinson 1994), including the majority of cephalopod classes (Rosa *et al.* 2012). Concomitantly, the smaller size relatively to European and Indian Ocean populations of *O. vulgaris* could be partially underpinned by Bergmann's rule. However, in a similar latitudinal gradient, *O. vulgaris* are reported to reach up to 6 kg in African mainland and neighbouring Senegal (Domain *et al*. 2000). Concurrently, the maximum weight reported for an individual octopus by fishermen on São Vicente Island was roughly 2 kg, and even that weight was considered well over what is found in the population of the Desertas Islands (this study, Salamansa and São Nicolau fishermen, pers. comm.). Thus, such a marked reduction in average size, especially in the Desertas, has probably been selected by additional biological/ ecological mechanisms.

Simultaneously, no *O. vulgaris* individuals were found foraging through subtidal areas in the Desertas Islands. As sampling was performed throughout the day (between approximately 8 a.m. and 19 p.m), we consider that sampling timing was not an issue for finding *O. vulgaris* foraging. This species is known to hunt during the day in other areas of the world (e.g. Europe and America), with multiple occurrences being described by both divers and snorkelers alike (Mather & O'Dor 1991). Moreover, dens with individuals were not found outside the intertidal area of both Santa Luzia and Raso. Since the availability of prey does not seem to be a constraint in the Desertas Islands (Almeida *et al.* 2015), predatory pressure even by fishermen and topography appear to be the main factors conditioning the species distribution. In fact, both Raso and Santa Luzia are characterized by a high presence of diurnal and nocturnal predators on rocky reefs (Fig. 3A and B). Moreover, other fish that are not regular predators of octopus, compete with them for space for habitat, such as dens and sheltered rock structures (Fig. 3C and D), which further strengthens the idea that octopuses would very rarely hunt out in the open, i.e. go on foraging bouts, and are as such driven towards the intertidal.

Despite the fact that our sampling reported no *O. vulgaris* in subtidal areas, the nearshore topography of these islands are quite different. While the coast of Raso is mostly circumvented by vertical rock walls which immediately drops to 20–30 m, Santa Luzia is heterogeneously characterized by gradual slopes down to 5–10 m for the first 15 m offshore, thus potentially providing a more suitable shelter for octopuses to inhabit and forage. However, given this more extended rocky substrate, Santa Luzia is also populated by carnivorous elasmobranchs (potentially being a nursery area) which are known to feed on cephalopods, such as the nurse shark, the guitarfish (Fig. 3E) and the black tip shark (Fig. 3F), dampening any topographical benefits. Rockpools are usually the home of small crabs, shrimps and mollusks, which are all part of the regular diet of octopus (Mather & O'Dor 1991). Conversely, small cryptic fish that are confined to these habitats (e.g. blennies), across tide changes during the day, do not possess the necessary size to prey on *O. vulgaris*, feeding mostly on similar smaller organisms, or are herbivorous. Moreover, *O. vulgaris* are known to possess the ability to change between rock pools in search for food, or to avoid potential predation, making these habitats considerably safer, compared to subtidal areas.

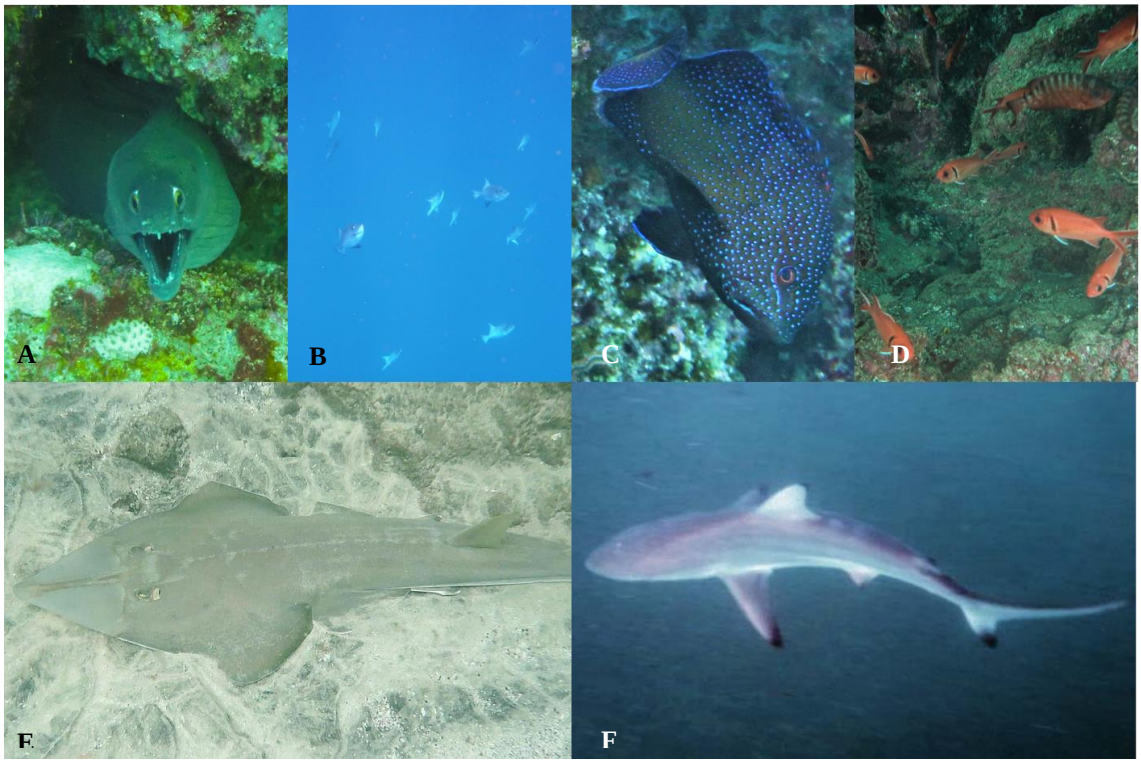

Fig. 3. Predators and competitors of *O. vulgaris* usually found adjacent to intertidal areas (shallow subtidal) of the Desertas Islands (photos by Eduardo Sampaio). **A)** Purplemouth moray *Gymnothorax vicinus*; **B)** ocean triggerfish *Canthidermis sufflamen*; **C)** bluespotted seabass *Cephalopholis taeniops;* **D)** blackbar soldierfish *Myripristis jacobus,* glasseye snapper *Heteropriacanthus cruentatus*, and Atlantic bigeye *Heteropriacanthus fulgens*; **E)** blackchin guitarfish *Glaucostegus cemiculus*; **F)** blacktip reef shark *Carcharhinus melanopterus*.

Considering all these facts, we argue that the population of *O. vulgaris* on the Desertas Islands has migrated almost exclusively to the intertidal area, which shaped behavioural and morphological adaptations. In this case, the octopus's 'drive to explore' cited by Mather & O'Dor (1991) may have been out-selected in favor of a more cautious approach, taking into account the intense predatory pressure and competition for suitable habitats within the rocky shores of the Desertas.

Future enquiries with a larger temporal coverage and DNA analyses should be planned to understand if what was found for this *O. vulgaris* population may derive from developmental plasticity, or if these peculiar ecological contexts have led to more profound changes, and potentially leading to a speciation phenomenon. If so, we may be looking at a newly found endemic species to Cabo Verde, which would attest to the biological heritage of these islands, fruit of its unique combination of biogeographic and ecological conditions.

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