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A field guide to distinguishing *Octopus insularis* and *Octopus americanus* (Octopoda: Octopodidae)

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Shallow-water, benthic octopuses from the Caribbean, Gulf of Mexico and tropical western Atlantic have undergone extensive taxonomic expansion and revision over the last two decades (reviewed in Avendaño *et al.* 2020a). Many of the geographically-overlapping octopuses within this region were cryptic (*sensu* Bickford *et al.* 2007), with only subtle differences in habitats, morphology and body patterns that can make it difficult to distinguish between species, especially in the field (Avendaño *et al.* 2020a; Lima *et al.* 2020b). Moreover, considerable variation in morphology, behavior and body patterning exists within species (Leite *et al.* 2008; Amor *et al.* 2016; Avendaño *et al.* 2020a). The coexistence of species that appear similar and exhibit intra-species variation has resulted in a great deal of confusion as to the identity and habits of octopuses in these regions (Lima *et al.* 2017). Recent taxonomic and molecular studies have been instrumental in resolving this confusion (Amor *et al.* 2016) and represent critical early steps in elucidating the evolutionary course of the genus *Octopus*.

Previously, any large, non-ocellated octopus in the Caribbean, Gulf of Mexico or western Atlantic observed primarily during the day was referred to as *Octopus vulgaris* Cuvier, or as a member of the *O. vulgaris* complex (e.g., Norman 2003). However, *O. vulgaris* is now recognized as a cosmopolitan species group comprising at least six subtropical, tropical and temperate species (*O. vulgaris sensu stricto*, *O. vulgaris* Type III, *O. sinensis*, *O. tetricus*, *O. cf. tetricus*, and *O. americanus*; Amor *et al.* 2016, 2017, 2019; Avendaño *et al.* 2020a). In 2008, *O. insularis* Leite & Haimovici was named and described based on specimens from Brazil (Leite *et al.* 2008) and later shown to be morphologically distinct and genetically distant from the *O. vulgaris* species complex (Ritschard *et al.* 2019; Lima *et al.* 2020b). Over a decade later, a study reported *O. vulgaris* Type II (Amor et al. 2016) from Brazil and *O. vulgaris* Type I from Mexico and North America as a cryptic species within the *O. vulgaris* complex and suggested reinstating the name *O. americanus* Monfort (Avendano et al 2020). *Octopus insularis* and *O. americanus* look very similar, overlap geographically throughout much of Caribbean, Gulf of Mexico and the western Atlantic (Figure 1) and as a result are commonly mistaken for one another. Moreover, despite the re-designation of these two species as separate from *O. vulgaris*, this name is still often incorrectly applied to both *O. insularis* and *O. americanus* in the western Atlantic.

Accurate species identification and description is important for assessing population dynamics as well as for promoting conservation and sustainable fisheries (Lima *et al.* 2017). Both *O. insularis* and *O. americanus* are targeted in artisanal and commercial fisheries throughout their range (e.g., Sauer *et al.* 2020) and have been the focus of recent and on-going research in behavioral ecology and the effects of climate change (e.g., Ángeles-González *et al.* 2020; Lima *et al.* 2020a; Medeiros *et al.* 2020; Rosas-Luis *et al.* 2019). To facilitate further research with these two species, particularly fieldwork (e.g., abundance estimates, *in situ* behavioral assays), accurate field guides for species identification are needed. To this end, we describe three differences (two visual and one contextual) that can facilitate the identification of *O. insularis* and *O. americanus* in the field or from photographs and videos, eliminating the need to handle or sacrifice animals for species identification. These body pattern components and habitat features have been validated and utilized successfully for species differentiation in locations where the presence of both species was established genetically, including Brazil (Lima *et al.* 2017) and Mexico (González-Gómez *et al.* 2018). Unfortunately, these distinguishing characteristics are not widely known, and we highlight them here.

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FIGURE 1. The geographic ranges of *Octopus insularis* and *O. americanus*. The currently-recognized range of *O. americanus* is indicated in blue (from Avendano *et al.* 2020a), the currently-recognized range of *O. insularis* in orange (from Lima *et al.* 2017) and the proposed range extensions for *O. insularis* are indicated in green (this publication).

Differences in body pattern components

The most notable visual distinction between the two species is a difference in the ventral surface of the arms. *Octopus insularis* has a distinct configuration of dark purple/red/brown "patches" against a light background (Figure 2a). Leite & Mather (2008) named this component "red/white reticulate on ventral arms," and found it to be a species-specific feature present in every specimen examined. The contrast between the dark patches and light background can vary in intensity both over time in a single individual and across individuals (CEO, pers. obs.), but is usually visible *in situ* and readily-apparent in photographs and videos. By contrast, the ventral surface of the arms of *O. americanus* have more uniform coloring, ranging from orange to brown, with no well-defined dark "patches" or reticulation (Figure 2b; Avendaño *et al.* 2020a). This distinguishing characteristic has the advantage of being easy to discern, even if the octopus is inside its den.

A second difference between the two species is located in the area around the eye during each species' deimatic (sometimes called dymantic) display. This body pattern is evoked in octopuses and other cephalopods when they are startled or threatened, and consists of a paling of the mantle and arms and a darkening of the head around the eyes to varying degrees (Packard & Sanders 1971). In *O. insularis*, the deimatic display is comprised in part by a white eye and a encircling pale ring (appearing white or blue-green), often accompanied by a dark eye bar, within a broader, darkened area (Figure 3a; Leite & Mather 2008). By contrast, the deimatic display of *O. americanus* consists of a continuous darkening around the eyes - the eyes themselves are dark, as is the entire surrounding area (Figure 3b). While the deimatic body pattern is transient, it is often evoked both inside and outside the den by the approach of a diver or photographer, and thus commonly observed.



FIGURE 2. a.) *Octopus insularis* from Brazil (photo by Diogo Pagnoncelli/Projeto Cephalopoda). Arrow indicates the pattern of dark "patches" against the light background on the ventral arms that can be used to distinguish the species from b.) *Octopus americanus* from Brazil (photo by Fernando Moraes) with a uniform pattern on the ventral surface of the arms.



FIGURE 3. The deimatic display of a.) *O. insularis* includes a white eye, a light ring around the eye and often a distinct, dark eye bar within the darkened area (photo by TL, Brazil), while in the deimatic display of b.) *O. americanus*, the entire area around the eyes is darkened (photo by Fernando Moraes, Brazil).

We examined photographs and videos of 29 individual octopuses (15 *O. insularis* and 14 *O. americanus*) from genetically-identified populations in the Brazilian octopus fishery, where both species are common and co-occur in the same areas. These photographs and videos were taken in the specific conditions (temperature and depth) that each species is known to inhabit (see next section). The *O. insularis* and *O. americanus* individuals could be identified as such using one or both of the visual characteristics mentioned above: 55% individuals could be identified by the ventral arm surfaces alone, 14% by the deimatic display alone and 31% could be identified by both features. Specifically, dark patches on the ventral arm surface and a light ring around the eye during the deimatic display were never observed in *O. americanus*. Thus, these two features are both ubiquitous and species-specific, making them ideal visual indicators.

Differences in habitat

Habitat parameters that can be used in combination with each other to distinguish *O. insularis* from *O. americanus* (based on where an animal is encountered) are water temperature, depth and substrate type. *Octopus insularis* is reported as a tropical species with adults and juveniles inhabiting waters between 23 and 30°C (Leite *et al.* 2008) and paralarvae in water temperatures ranging between 24 and 29°C (Ángeles-González *et al.* 2020). By contrast, *O. americanus* is reported as a mainly subtropical and temperate species, with adults inhabiting waters between 18 and 25°C (Amado *et al.* 2015; Bastos 2018) and paralarvae in waters between 19 and 24°C (Ángeles-González *et al.* 2020).

Where the two species overlap in geographic range, juvenile and adult *O. insularis* tend to be found on shallower (0.5–40 m) reef and rocky substrates in warmer water (Leite *et al.* 2009; Rosas-Luis *et al.* 2019), while juvenile and adult

O. americanus are found up to 200 m in cooler waters on rock, rubble, shell beds or on the interface between rock and sand (Lima *et al.* 2017; Avendaño *et al.* 2020b). In subtropical regions, where shallow areas are typically less than 24°C throughout the year, *O. insularis* is less common, although its range may shift due to climate change (Ángeles-González et al. 2020; Lima et al. 2020a). The disparate habitat preferences of *O. insularis* and *O. americanus* likely allow the two species to partition the range in which they co-occur by temperature, substrate type and depth (Amado *et al.* 2015; Amor *et al.* 2016). It also explains why previously, the "Caribbean *O. vulgaris*" (Norman 2003) - really the conflated and misidentified *O. insularis* and *O. americanus* - was reported as having a geographic range that spanned tropical, subtropical and temperate waters.

Octopus insularis: New sightings and proposed geographic range expansion

The geographic range of *O. insularis* is currently recognized as extending from the coast of southern Brazil to as far north as Puerto Rico in the Caribbean to the east, and the Yucatan Peninsula in the Gulf of Mexico to the west (Avendaño *et al.* 2020a; Figure 1). However, we have collected photographs of 25 individual octopuses displaying the species-specific characteristics described above for *O. insularis* from locations farther north than this recognized range, including the Turks and Caicos Islands (11 individuals), south Florida (five individuals), the Bahamas (six individuals) and Bermuda (three individuals; Table 1, Figures 1 and 4). Because these individuals possess the characteristics described above for *O. insularis*, we recommend tentatively extending the recognized range of this species to include these areas until a formal genetic analysis can be conducted.



FIGURE 4. Representative photographs of *O. insularis* from regions north of its currently-recognized range. a.) In the Turks and Caicos Islands, showing dark patches on the ventral arms taken in <2 m of water at approximately 27°C (photo by CEO). b.) In south Florida, showing the dark patches on the ventral arms and deimatic display with the light ring around the eye and dark eye bar taken in 24 m of water at 29°C (photo by Mark Kosarin) c.) In the Bahamas, showing a deimatic display with the light ring around the eye and dark eye bar taken in 8 m of water at approximately 28°C (photo by Shane Gross). d.) In Bermuda, showing darks patches on ventral arms and captured in 1 m of water (photo by Nesta Wellman at the Bermuda Aquarium, Museum and Zoo).

TABLE 1. Individual O. insularis (n = 25) documented by photograph and/or video in four locations north of the species'
currently-recognized range. The column "Ventral arms only" refers to the number of individuals identified solely by the
presence of dark patches on the ventral arms; "Deimatic display only" refers to individuals identified solely by the pres-
ence of a light ring around the eye when the deimatic pattern is displayed; "Both" refers to individuals in which both
features (ventral arms and deimatic light eye ring) could be discerned.

	Ventral arms only	Deimatic display only	Both	Total # individuals photographed
Bermuda	3	0	0	3
Bahamas	4	1	1	6
South Florida	4	0	1	5
Turks and Caicos	7	3	1	11

Conclusion

The visual and contextual differences between *O. insularis* and *O. americanus* described and illustrated here with sideby-side photographs should enable researchers, divers, marine photographers and citizen scientists working in the field to easily distinguish between the species without the need for a tissue sample or close visual inspection. This should avert confusion in future literature, enable more accurate assessments of the two species' respective habits and ecology and facilitate the study of any geographic range shifts that occur as the result of climate change (see Ángeles-González *et al.* 2020; Lima *et al.* 2020a). We have summarized these differences as well as the recognized and hypothesized geographic range of each species in a printable field identification guide available as Supplemental Material.

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