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Octopus arm flexibility facilitates complex behaviors in diverse natural environments

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Octopus arms are among the most flexible of biological structures, yet the full range of arm flexibility has not been investigated in detail, for example in varied benthic marine habitats where structural complexity far exceeds that of lab trials. This field study quantified arm flexibility with a hierarchical analysis of octopus behaviors, arm actions, and arm deformations used throughout diverse natural habitats. Twenty-five videos of naturally behaving octopuses were analyzed from 5 Caribbean sites and 1 site in Spain. Octopus behaviors were delineated into 12 arm actions, consisting of 4 possible arm deformations (shorten, elongate, bend, or torsion). Overall, 3,907 arm action occurrences demonstrated that all arms could execute each action. Anterior arms performed more actions than posterior arms, while there were no differences between left and right arms. Furthermore, 6,871 arm deformation occurrences indicated that all 4 arm deformations were used across all actions; however, the frequencies of these deformations varied by arm region (proximal, medial, distal). The combination of deformations and arm actions implemented to achieve complex behaviors illustrates extreme arm flexibility and coordination during a wide range of arm functions. Such demonstrations of flexibility may help inform ethologists, sensory ecologists, neuroscientists, and engineers designing soft robotic appendages.

Keywords Cephalopods, Behavioral ecology, Muscular hydrostats, *Octopus vulgaris*, Soft robotics

The elaborate behaviors of cephalopods, especially those of temperate and tropic shallow-water benthic octopuses inhabiting a range of environments, continues to spark curiosity and scientific exploration. Octopus arms (and suckers) constitute most of their body mass, playing a crucial role in nearly all of their behaviors such as locomotion, prey capture, den construction, postural camouflage, mimicry, signaling, and reproduction[1–3]. The octopus's extensive peripheral nervous system (PNS) and muscular hydrostatic arms allow for extensive flexibility and dexterity to achieve such a large behavioral repertoire[4,5].

The octopus nervous system is hierarchically organized and largely decentralized such that the PNS possesses the greatest number of neurons, most of which are in the arms and suckers, illustrating considerable importance in obtaining chemical and tactile information from the environment[6]. The muscular hydrostatic structure of the arms consists of a densely packed three-dimensional arrangement of four muscle groups (transverse, longitudinal, oblique, and circular) and connective tissue surrounding the axial nerve cord of each arm, responsible for both support and movement[4,5,7–9]. The orientation, arrangement, and interactions of these muscle groups allow the arm to shorten, elongate, bend, and twist (i.e., torsion)[10], and all of an octopus's arm movements are implemented by one or more of these deformations.

As a result of these neural and muscular adaptations, octopus arms exhibit seemingly limitless degrees of freedom lending to their extraordinary versatility to produce complex behaviors in seconds[2,11]. For these reasons, octopus arms have attracted attention over the last decade from the fields of animal behavior, neuroscience, biomechanics, and as a source of inspiration for soft robotics[8,12–15]. Several studies have investigated octopus arm flexibility, but these studies focused on an individual arm deformation, isolated arm actions (also referred to as "arm movements") or full behaviors, or were conducted in a laboratory setting[8,11,14–18]. Although there has been extensive research on octopus arm flexibility, it is still not fully understood how octopuses use their arms under natural conditions. An early ethogram of arm actions from several octopus species[2,19], and recent research focused on a single arm action ("slap")[20], are the only studies to describe arm actions in wild octopuses.

The aim of this study was to characterize arm flexibility in naturally-behaving octopuses in the wild by focusing on the qualitative aspects of arm actions and arm deformations, rather than the quantitative range of

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motion[17]. We established a hierarchical analysis to delineate octopus behaviors into discrete arm actions and then subsequently into specific arm deformations. We constructed a detailed ethogram with the hierarchical analysis components (i.e., animal behaviors, arm actions, and deformations) after observing wild octopuses in a range of environments. Since octopuses use specific behaviors on different substrate types[21], we recorded sequences of octopus behaviors throughout a range of shallow water habitats, thus enabling us to more thoroughly understand how arm actions and arm deformations are collectively used to produce a larger repertoire of behaviors.

Methods
Field Locations
Figure 1 illustrates a sample of the varied and complex ecohabitats from which the data were acquired. These included shell rubble, sand plains with algae, seagrass beds, coral rubble, live coral reefs, as well as combinations of these habitats (i.e., heterogenous environment "mixed") all in shallow well-lit waters of ca. 1-10 m depth. Field videos were collected by experienced divers (RTH and COB) from 25 freely-moving octopuses (mantle length: 10 to 17 cm) between 2007 and 2015 and across six field sites: Vigo, Spain (n = 3), south Florida (n = 11), Puerto Rico (n = 6), Cayman Islands (n = 3), Saba Island, Netherlands Antilles (n = 1), and Bonaire, Netherlands Antilles (n = 1). Specific field sites were visited multiple years to record additional individual octopuses as these species have short lifespans and are likely not to be recorded over multiple years. Octopuses were habituated to the divers' presence and were foraging naturally. Species recorded in these videos included *Octopus vulgaris* sensu stricto (Vigo) and closely related species, the recently reinstated *O. americanus* (part of the *O. vulgaris* species complex: Caribbean Sea and western Atlantic Ocean locations), and *O. insularis* (Caribbean Sea)[22–24]. These species are of relatively the same size and similar body and arm morphology and inhabit reef environments, rock, shells, sand, seagrass and algae[25,26].

Hierarchical analysis ethogram
Figure 2 is a hierarchically organized ethogram constructed from detailed reviewing of 120 min of field video that visualized octopuses in multiple behavioral states (e.g., foraging, threatening, escaping) to record a wide range of natural behaviors. From these videos, 15 animal behaviors were selected and 12 distinct arm actions constituting these behaviors were defined, as well as the 4 deformations that made up each of these actions (Fig. 2). Our ethogram built upon established definitions of behaviors, actions, and deformations from the existing literature[2,3,5,11,20,27]. The terms "arm action" and "arm movement" have been used synonymously in the literature to describe arm maneuvers. Here, the term "arm action" was used throughout the paper to refer to octopus arm movements. Deformation definitions were adopted from Kennedy et al. (2020).

Video analysis of arm actions and deformations
Arm actions were scored and related to a specific behavior by analyzing 1-min video clips that were selected from each of the 25 field videos (total duration 25 min from 25 octopuses). Field videos ranged in duration; each 1-min of video was carefully selected to allow observation of each arm with similar frequency. Normal replay speed was used to score overall behaviors in each video clip. Videos were then analyzed frame-by-frame to score arm actions associated with each animal behavior observed in each 1-min video clip. Various combinations of these actions not only occurred on the same arm, but on different arms simultaneously during complex

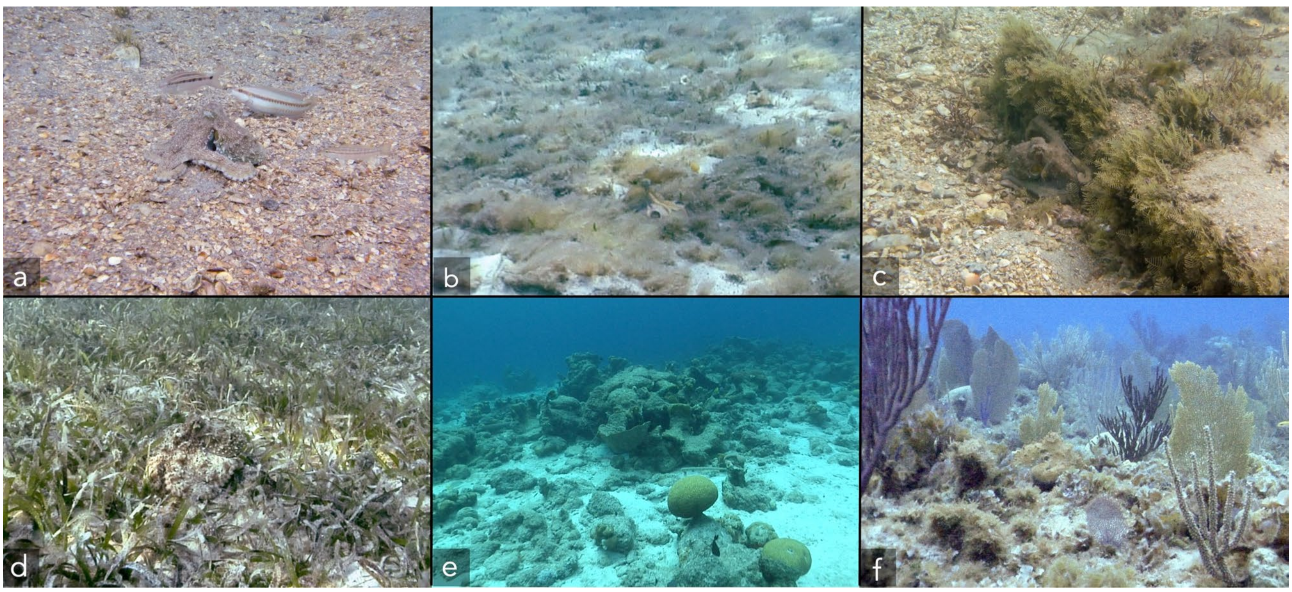

Fig. 1. Representative examples of ecohabitats from field sites. (**a**) shell rubble, (**b**) sand/algae, (**c**) mixed substrate, (**d**) seagrass, (**e**) coral boulders, (**f**) coral reef. Videos were collected from 25 naturally behaving octopuses across 6 field sites.

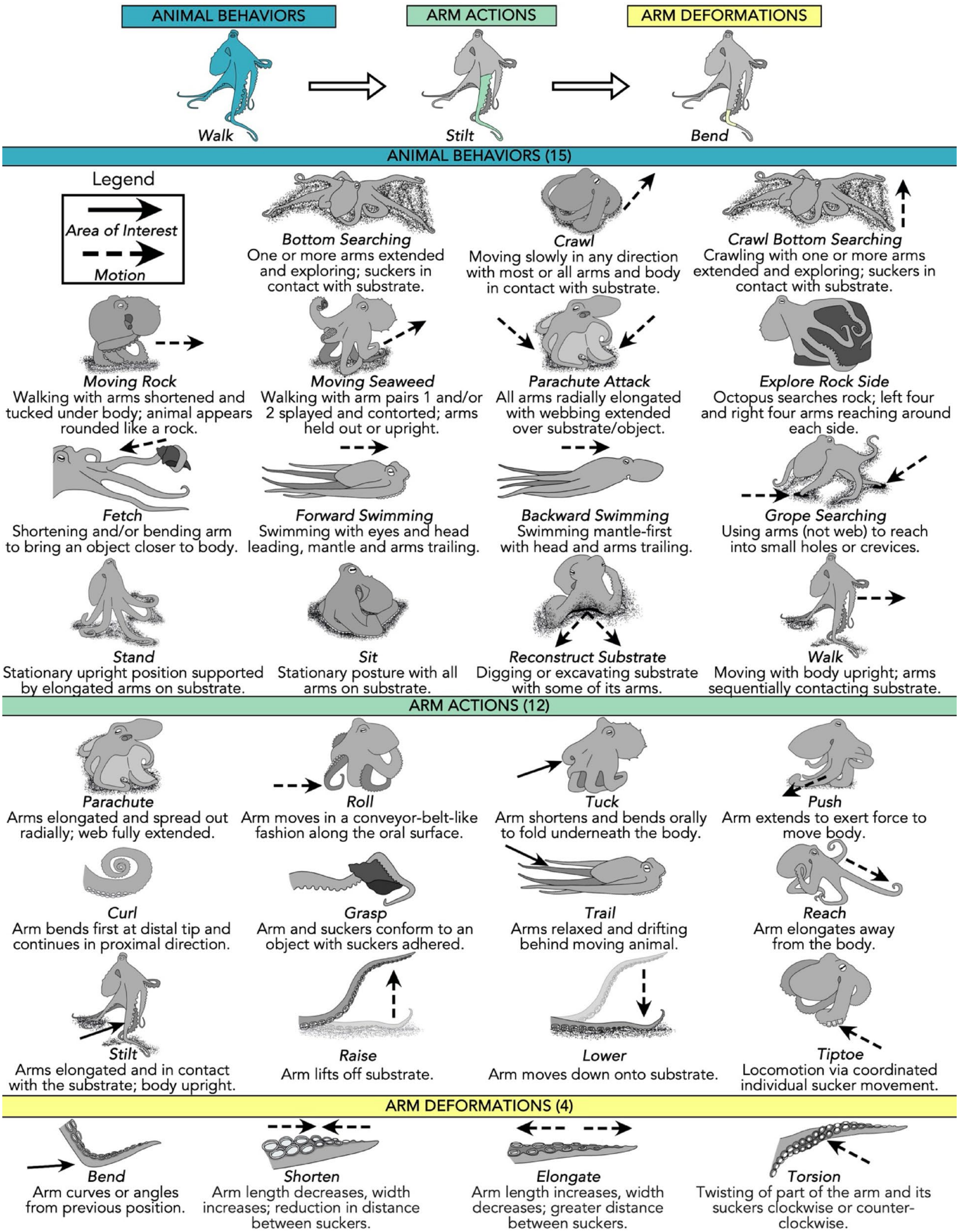

Fig. 2. An ethogram of octopus behaviors, arm actions, and arm deformations. A hierarchical analysis was used to delineate complex behaviors into arm actions. Arm actions were deconstructed into 4 distinct arm deformations. Species used in the construction of this ethogram included: *Octopus vulgaris* sensu stricto, *O. americanus*, and *O. insularis*.

behaviors. Thus, each left (L) and right (R) arm (1–4) was observed and scored individually for each video (i.e., reviewing the video clip 8 times to score each individual arm). The following criteria were developed for scoring arm actions: (1) all 3 arm regions (proximal, medial, and distal) were visible in the video; regrowing arms were not scored, (2) the arm being scored (each L and R arm 1–4) was in the field of view for at least 90% of the 1-min video segment, and (3) observations were not inhibited by poor water quality or by fauna and flora that blocked a clear view of the octopus. If an action on 1 arm continued into the next behavior, it was scored as a new action associated with that behavior.

Once arm actions were scored, they were further deconstructed into the 4 deformations: bend, shorten, elongate, and torsion (Fig. 2). To score the deformations of each arm action, 1 occurrence of each action from each 1-min video clip was randomly selected as the representative action. This was done for each of the 25 videos (25 individual octopuses) to ensure that deformations were scored for all arm actions and that each arm action was scored multiple times from different octopus individuals. Additionally, the occurrence of the 4 deformations were scored along each specific arm region (proximal, medial, distal). Videos were then analyzed frame-by-frame to score deformations associated with each arm action observed.

Before scoring the behaviors, actions, and deformations, a subset of 5 short behavior video clips were used to calculate inter-observer reliability using a Pearson correlation coefficient[28], averaged with Fisher Z's transformations[29,30]. Observers met the criteria of >80% reliability before scoring videos used in this study. Observers also frequently met as a group to confirm scoring methods.

Statistical analyses

The number of occurrences for each arm action across each of the behaviors was first visually observed through a heat map followed by descriptive statistics for the frequency of each arm action. The 5 most frequently occurring actions were further examined to test for differences between: left vs right arms, anterior (arms 1 and 2) vs posterior arms (arms 3 and 4), and individual arm pairs (i.e., left and right arm pairs: 1 vs 2 vs 3 vs 4). All arm pair combinations for each action were statistically tested using Mann-Whitney U tests with FDR corrections.

The next step in the hierarchal analysis determined the number of occurrences of each deformation (bend, shorten, elongate, and torsion) that constituted each arm action. The overall frequency of each deformation was compared for each arm action using a Kruskal-Wallis one-way ANOVA with post hoc Dunn's multiple comparisons. After comparing deformations across arm actions, the total number of deformations used in each arm region (i.e., proximal, medial, distal) was examined by a one-way ANOVA, followed by Tukey's post hoc tests. Lastly, to test for significant differences for each deformation across arm regions a Kruskal-Wallis one-way ANOVA followed by Dunn's multiple comparison tests was performed.

Laboratory versus field comparison

Our results for deformations were also compared to our previous laboratory study (n = 10 wild-caught *Octopus bimaculoides*) to determine accuracy and potential artifacts in studying deformations and octopus arm flexibility[17]. For side-by-side comparisons, this study's deformation data were characterized according to the protocol outlined in Kennedy et al. 2020. To summarize, all visual occurrences of the 4 deformations were recorded as: (1) bend (arm curves or angles from previous position), (2) shorten (distance between suckers decreases with a decrease in arm length and an increase in arm width), (3) elongate (distance between suckers increases with an increase in arm length and a decrease in arm width), and (4) torsion (twisting of arm clockwise or counter-clockwise) (Fig. 2). Results from both studies are compared and discussed.

Results

Arm actions

Twelve arm actions were identified from 15 behaviors with a total of 3,907 actions recorded from 25 wild octopuses (total 25 min, 1-min per octopus) across 6 field sites with varying ecohabitats. The majority of these actions were observed across multiple behaviors. Many actions were observed during the behaviors of crawl (11/12 actions), crawl speculative bottom searching (10/12 actions), moving seaweed (8/12 actions), and parachute attack (8/12), while few actions were observed for backward swimming (3/12 actions), grope (3/12 actions), and fetch (2/12 actions) (Fig. 3a). While recording actions for each arm, it was noted that for a single behavior, multiple arm actions could occur simultaneously on the same arm and/or on adjacent arms (Fig. 3b). Five of these arm actions accounted for 78% of the total arm actions recorded: reach 19%, raise 18%, lower 17%, tuck 14%, and curl 10% (Fig. 4a). These 5 actions were also used across the majority of behaviors (Fig. 3a). Actions observed less frequently included parachute, roll, grasp, stilt, and tiptoe (Fig. 4a).

Overall, the right and left arms performed relatively the same number of actions (49%, 51%, respectively). When observing individual arm action occurrences for the five most frequently occurring actions, Mann-Whitney U tests with FDR correction indicated no significant difference between left and right arms (Fig. 4b, reach: $U_4 = 302.0$, $P = 0.844$; raise: $U_4 = 306.5$, $P = 0.912$; lower: $U_4 = 297.0$, $P = 0.769$; tuck: $U_4 = 305.0$, $P = 0.889$; curl: $U_4 = 292.5$, $P = 0.703$). Comparisons for left vs right arms for all 12 arm actions can be viewed in Supplementary Information (Figure S1a).

Arm actions differed when comparing the 5 most frequently occurring actions between anterior arm pairs (1 and 2) and posterior arm pairs (3 and 4) (Fig. 4c). Anterior arms were used an average of 64% and posterior arms were used an average of 36% of the time. Anterior arms were used more frequently than posterior arms for reach ($U_4 = 172.0$, $P = 0.006$), raise ($U_4 = 182.5$, $P = 0.010$), lower ($U_4 = 175.0$, $P = 0.007$), and curl ($U_4 = 140.5$, $P < 0.001$). For a breakdown of each arm action: reach occurred 63% in anterior arms and 37% in posterior arms, raise occurred 64% in anterior arms and 36% in posterior arms, lower occurred 64% in anterior arms and 36% in posterior arms, tuck occurred 60% in anterior arms and 40% in posterior arms, and curl occurred 71% in anterior arms and 29% in posterior arms. Two actions were used more frequently by posterior arms than

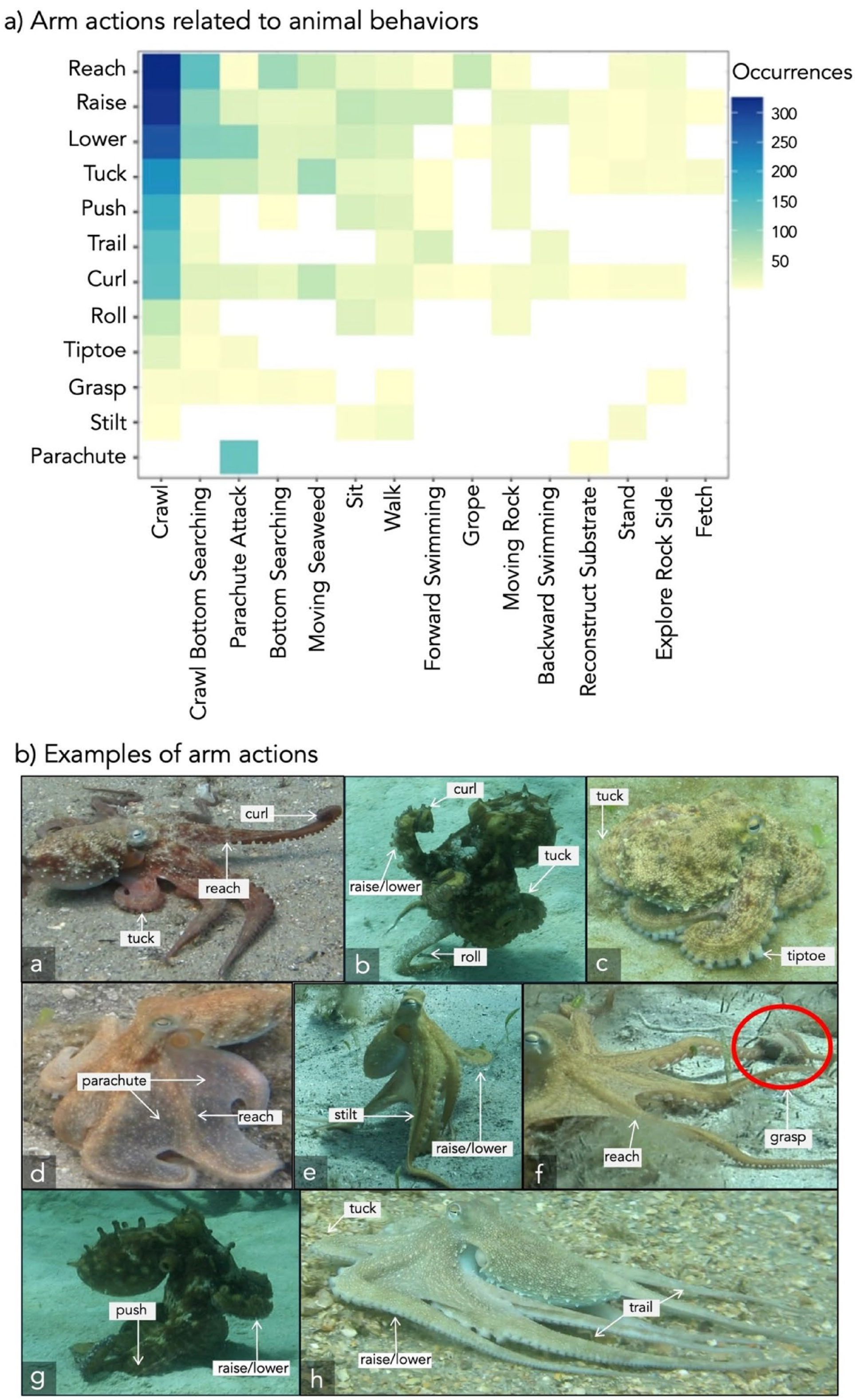

Fig. 3. Arm actions and their relationship to animal behaviors. (**a**) A heat map depicting the number of arm action occurrences for specific behaviors (n = 25 octopuses). (**b**) Examples of all 12 arm actions from wild octopuses; octopuses often used multiple arm actions on a single arm or multiple arms simultaneously.

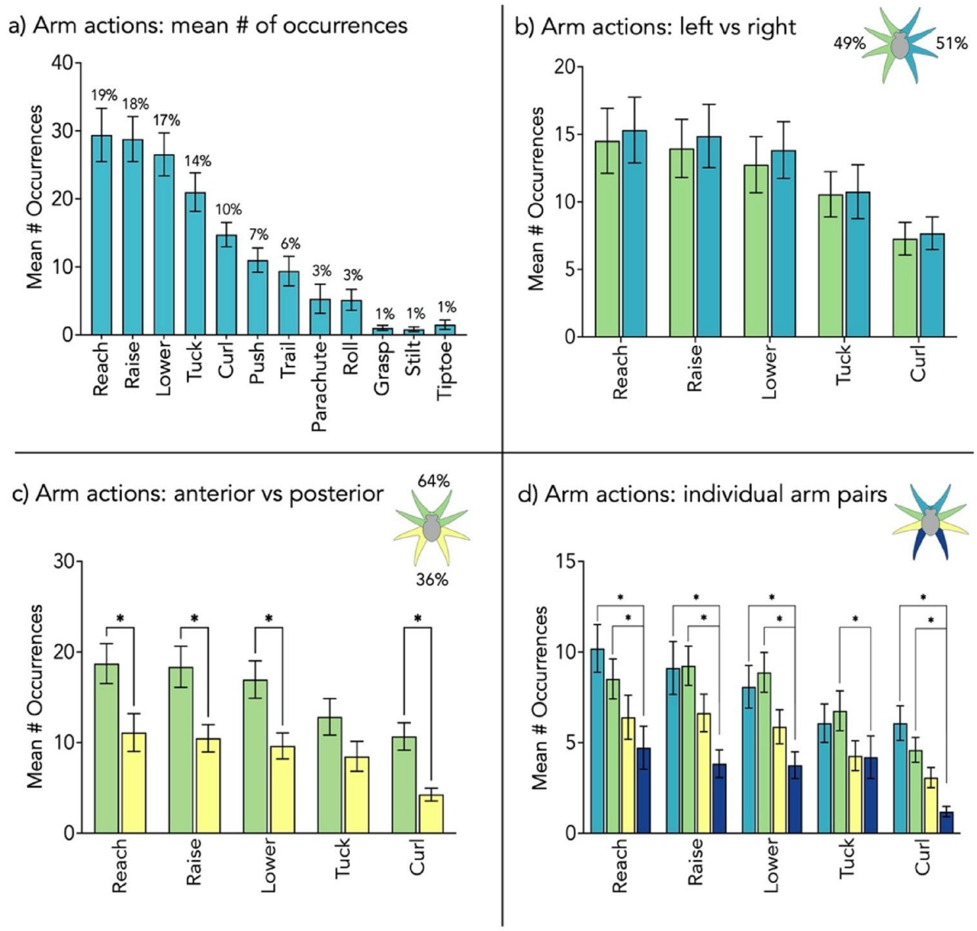

Fig. 4. Frequency and distribution of arm actions in naturally behaving octopuses. (**a**) Mean number of occurrences of all arm actions. Percentages above each bar indicate the overall percent occurrence of each action (rounded to the nearest %). Reach, raise, lower, and curl together accounted for 78% of all actions. (**b**) Mean number of occurrences of arm actions performed by the left versus right arms; arm actions were used with equal frequency on the left (49%) and right (51%) sides of the body (reach: $U_4 = 302.0$, $P = 0.844$; raise: $U_4 = 306.5$, $P = 0.912$; lower: $U_4 = 297.0$, $P = 0.769$; tuck: $U_4 = 305.0$, $P = 0.889$; curl: $U_4 = 292.5$, $P = 0.703$). (**c**) Anterior arms (64%) were used more frequently than posterior arms (36%) for reach ($U_4 = 172.0$, $P = 0.006$), raise ($U_4 = 182.5$, $P = 0.010$), lower ($U_4 = 175.0$, $P = 0.007$), and curl ($U_4 = 140.5$, $P < 0.001$). (**d**) Arm pairs 1 and 2 were used more frequently than arm pair 4 for reach (1 vs 4: $U_4 = 144.0$, $P < 0.001$; 2 vs 4: $U_4 = 166.5$, $P = 0.004$), raise (1 vs 4: $U_4 = 171.5$, $P = 0.005$; 2 vs 4: $U_4 = 130.0$, $P < 0.001$), lower (1 vs 4: $U_4 = 174.0$, $P = 0.006$; 2 vs 4: $U_4 = 133.5$, $P < 0.001$), and curl (1 vs 4: $U_4 = 98.5$, $P < 0.001$; 2 vs 4: $U_4 = 114.5$, $P < 0.001$), and arm pair 2 was also used more frequently than arm pair 4 for tuck ($U_4 = 210.0$, $P = 0.044$). Mann-Whitney U tests were used for all comparisons of the occurrences of the top 5 arm actions between: left versus right arms, anterior versus posterior arms, and individual arm pairs (n = 25 octopuses). Error bars indicate standard error of the mean. Asterisks depict statistically significant differences in frequency of actions.

anterior arms—stilt (posterior: 63%, anterior: 37%) and roll (posterior: 71%, anterior: 29%). These additional comparisons for anterior vs posterior arms can be viewed in Supplementary Information (Figure S1b).

There were differences in arm action occurrences between individual arm pairs (1–4) for the most commonly occurring 5 actions (Fig. 4d). Arm pairs 1 and 2 were used more frequently than arm pair 4 for reach (1 vs 4: $U_4 = 144.0$, $P < 0.001$; 2 vs 4: $U_4 = 166.5$, $P = 0.004$), raise (1 vs 4: $U_4 = 171.5$, $P = 0.005$; 2 vs 4: $U_4 = 130.0$, $P = < 0.001$), lower (1 vs 4: $U_4 = 174.0$, $P = 0.006$; 2 vs 4: $U_4 = 133.5$, $P < 0.001$), and curl (1 vs 4: $U_4 = 98.5$, $P < 0.001$; 2 vs 4: $U_4 = 114.5$, $P < 0.001$), and arm pair 2 was also used more frequently than arm pair 4 for tuck ($U_4 = 210.0$, $P = 0.044$). Comparisons for individual arm pairs (1- 4) for all 12 arm actions can be viewed in Supplementary Information (Figure S1c).

Arm deformations

A total of 6,781 arm deformations were recorded from the 25 individual octopuses. All 4 deformations (bend, shorten, elongate, and torsion) were observed in all 8 arms of the octopuses. Bend was the most frequently used (70%; 4,750 occurrences) followed by elongate (22%; 1,458 occurrences), shorten (6%; 410 occurrences) and torsion (2%; 63 occurrences). Bending was used with similar frequency across all arm actions (Kruskal-Wallis one-way ANOVA, $H_{11} = 9.90$, $P = 0.540$; Fig. 5a). Shorten was used more frequently for reach, raise, lower, tuck, and curl than for push, parachute, roll, grasp, stilt, and tiptoe (Kruskal-Wallis one-way ANOVA, $H_{11} = 147.1$, $P < 0.001$; Fig. 5b; Dunn's multiple comparison tests, $P < 0.05$, see Table S1 for specific Z-scores and adjusted P-values). Elongate was used more frequently for reach, raise, lower, and curl than for push, parachute, roll, grasp, stilt, and tiptoe (Kruskal-Wallis one-way ANOVA, $H_{11} = 129.7$, $P < 0.001$; Fig. 5c; Dunn's multiple comparison tests, $P < 0.05$, see Table S2 for specific Z-scores and adjusted P-values). Although torsion was used least often, the arm actions reach, raise, lower, and curl were used more often than push, parachute, roll, grasp, stilt, and tiptoe (Kruskal-Wallis one-way ANOVA, $H_{11} = 142.0$, $P < 0.001$; Fig. 5d; Dunn's multiple comparison tests, $P < 0.05$, see Table S3 for specific Z-scores and adjusted P-values).

There were significant differences in the number of deformations used in distal (47%), medial (35%) and proximal (18%) arm regions (Fig. 6a; one-way ANOVA, $F_2 = 27.79$, $P < 0.001$; Tukey's post hoc tests adjusted $P < 0.001$). There were also significantly different numbers of occurrences for each type of deformation

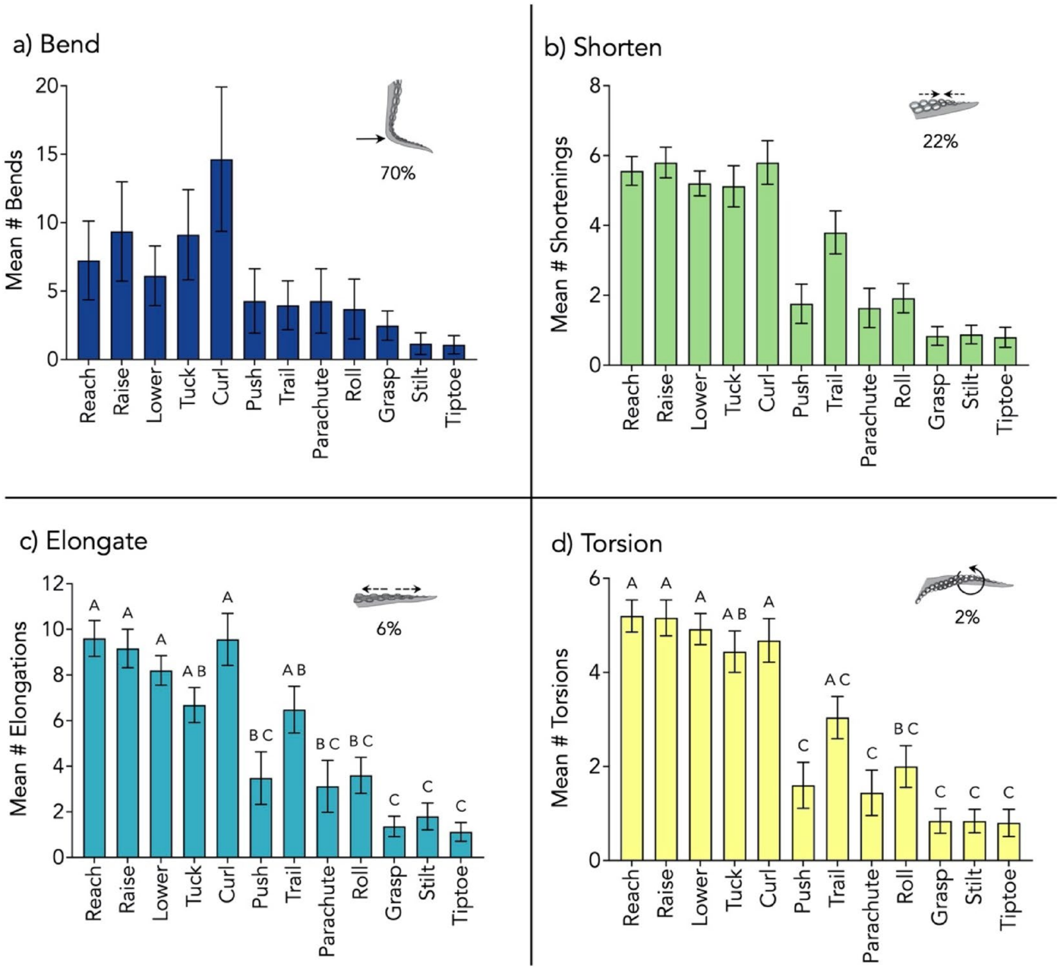

Fig. 5. Frequency of arm deformations used for each arm action in naturally behaving octopuses. Overall, bend was the most frequently used (70%) followed by elongate (22%), shorten (6%) and torsion (2%). (**a**) Mean number of bends used for each action; bends were used with equal frequency for all arm actions (Kruskal-Wallis one-way ANOVA, $H_{11} = 9.895$, $P = 0.540$). (**b**) Mean number of shortenings for each arm action; the shorten deformation was used more frequently for some arm actions than others (Kruskal-Wallis one-way ANOVA, $H_{11} = 147.1$, $P < 0.001$). Dunn's multiple comparison tests (two-sided) indicated that reach, raise, lower, tuck, and curl used shorten more often than push, parachute, roll, grasp, stilt, and tiptoe ($P < 0.05$, see Table S1 for specific Z-scores and P-values). (**c**) Mean number of elongations for each arm action; the elongate deformation was used more frequently for some arm actions than others (Kruskal-Wallis one-way ANOVA, $H_{11} = 129.7$, $P < 0.001$). Dunn's multiple comparison tests (two-sided) indicated that reach, raise, lower, and curl used elongate more often than push, parachute, roll, grasp, stilt, and tiptoe ($P < 0.05$, see Table S2 for specific Z scores and P values). (**d**) Mean number of torsions for each arm action; some actions used torsion more often than others (Kruskal-Wallis one-way ANOVA, $H_{11} = 142.0$, $P < 0.001$). Dunn's multiple comparison tests (two-sided) indicated that the arm actions reach, raise, lower, and curl used torsion more often than push, parachute, roll, grasp, stilt, and tiptoe ($P < 0.05$, see Table S3 for specific Z-scores and P-values). Error bars indicate standard error of the mean. Different letters indicate statistically significant differences between arm actions (n = 25 octopuses).

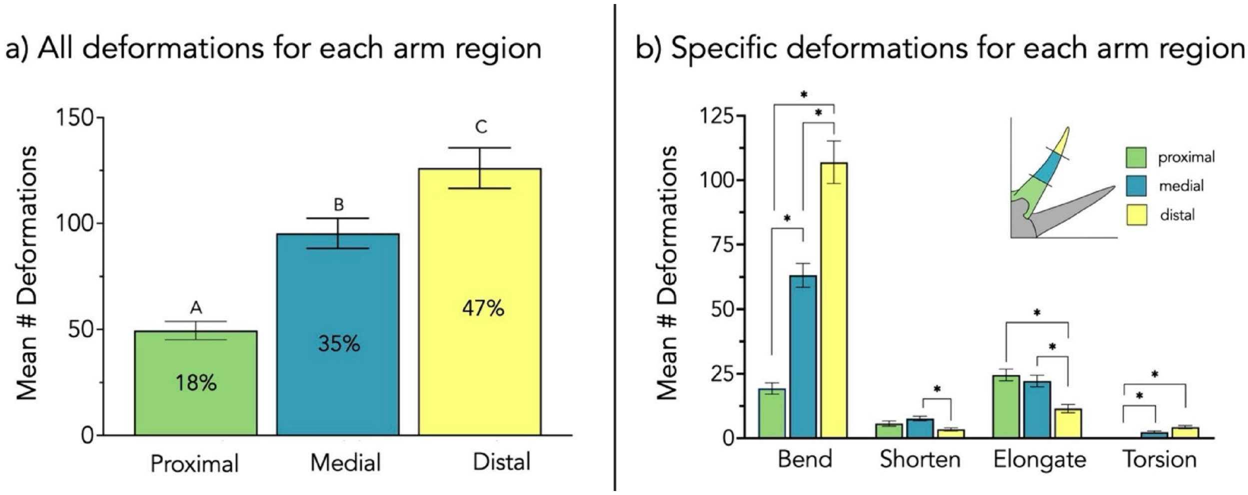

Fig. 6. Frequency of arm deformations for each arm region (proximal, medial, distal). (**a**) The mean number of deformations were unequally distributed within each part of the arm: distal (47%), medial (35%), and proximal (18%) (One-way ANOVA, $F_2 = 27.79$, $P < 0.001$). Tukey's post hoc tests showed that the distal part of the arms performed a greater number of arm actions (M = 126.1) than the proximal (M = 49.48, adjusted $P < 0.001$) and medial parts of the arms (M = 95.28, adjusted $P = 0.011$) and the medial part of the arms performed a greater number of arm actions than the proximal part of the arm (adjusted $P < 0.001$). (**b**) Bending was unequally distributed within each part of the arm (Kruskal-Wallis one-way ANOVA, $H_2 = 50.88$, $P < 0.001$). Dunn's multiple comparison tests (two-sided) indicated that bends occurred most frequently in the distal part of the arm (M = 107.0), followed by the medial (M = 63.20, distal vs medial adjusted $P = 0.027$) and then the proximal (M = 19.28, distal vs proximal adjusted $P < 0.001$; medial vs proximal adjusted $P < 0.001$) parts of the arm. Shortening occurred more often in the medial part of the arm (M = 7.60) than in the distal part of the arm (M = 3.4, adjusted $P = 0.025$); elongate occurred more frequently in the proximal (M = 24.52) and medial (M = 22.16) parts of the arm as compared to the distal (M = 11.48) part of the arm (proximal vs distal adjusted $P < 0.001$; medial vs distal adjusted $P = 0.003$); torsion was not observed in the proximal part of the arm and occurred significantly more often in the distal (M = 4.28, adjusted $P < 0.001$) and medial parts of the arm (M = 2.32, adjusted $P < 0.001$). Different letters indicate statistically significant differences between arm regions (n = 25 octopuses). Asterisks depict statistically significant differences.

(Fig. 6b). Bend occurred most frequently in the distal arm region, followed by the medial, then proximal arm regions (Kruskal-Wallis one-way ANOVA, $H_2 = 50.88$, $P < 0.001$; Dunn's multiple comparison tests: distal vs medial adjusted $P = 0.027$, distal vs proximal adjusted $P < 0.001$; medial vs proximal adjusted $P < 0.001$). Shorten occurred more often in the medial arm region than in the distal arm region (Kruskal-Wallis one-way ANOVA; Dunn's multiple comparison tests: adjusted $P = 0.025$). Elongate occurred more frequently in the proximal and medial arm regions compared to the distal arm region (Kruskal-Wallis one-way ANOVA; Dunn's multiple comparison tests: proximal vs distal adjusted $P < 0.001$; medial vs distal adjusted $P = 0.003$). Torsion was not observed in the proximal arm region and occurred significantly more often in the medial and distal arm regions (Kruskal-Wallis one-way ANOVA; Dunn's multiple comparison tests: proximal vs medial adjusted $P < 0.001$; proximal vs distal adjusted $P < 0.001$).

Laboratory versus field comparison

These field results can be compared with those of our previous laboratory study of *O. bimaculoides*[17]. That study did not create a specific behavioral ethogram; however, aquarium environments were created to elicit a reasonable diversity of behavioral responses to record a range of deformations for each arm and arm region. More deformations were scored in the laboratory setting, yet the results of both laboratory and field studies showed similar trends for the majority of arm deformation comparisons. Each study exhibited all 4 deformations used in all 8 arms and in all 3 arm regions with the single exception of torsion in this field study. Both studies reported bend being the most frequently used deformation followed by elongate, shorten, and torsion (respectively) and deformations occurring more frequently in anterior arms versus posterior arms. The most visible differences were for bend and elongate (Supplementary Information Fig. 2a,b).

For left versus right arms, the laboratory study indicated that all deformations occurred more frequently for the right arms with the exception of right arm 3 (R3). Although our field results showed deformations occurring slightly more often for right arms than left arms (including R3), we found no significant differences for left versus right arms when arm actions were compared. For anterior vs posterior arms, the laboratory study found that arm pair 1 had a larger number of deformation occurrences than the other 3 arm pairs, whereas this field study (for arm actions) illustrated differences for both anterior arm pairs 1 and 2 as compared to arm pair 4. Similar trends were observed for our deformations for arm pairs (1–4) (Supplementary Information Fig. 2c,d).

For specific arm regions, both studies reported similar results with bends occurring most frequently in the distal and medial arm regions. Elongate and shorten shared the same trends with both occurring most often in proximal region and least often in the distal arm region. For the laboratory study, torsion occurred across all 3 regions with no significant difference whereas in the field, torsion occurred significantly more often in both the distal and medial arm regions than the proximal arm region where it was not reported (Supplementary Information Fig. 2e,f).

Discussion

This study used a hierarchical approach to analyze 10,688 individual arm actions and deformations from naturally behaving wild octopuses across varied natural habitat types. A central question was addressed: how do diverse combinations of arm actions contribute to such a large repertoire of specific behaviors with only 4 arm deformations? We discuss the findings with respect to arm flexibility, behavioral ecology, and bioinspiration for soft robotics.

Arm flexibility

Octopus arms are recognized as one of the most flexible appendages in the animal kingdom, a characteristic that is supported by our observations of freely-moving octopuses in the wild. Analysis of 12 distinct arm actions illustrated the flexibility to produce 15 behaviors ranging in complexity from those composed of a limited number (2–3) of arm actions to those made up of many (8–11) arm actions. Another indication of arm flexibility was the ability of a single arm to perform multiple actions simultaneously, and the occurrence of distinct actions across multiple arms concurrently, illustrating complex arm coordination[31].

Although each of an octopus's 8 arms is anatomically and neurologically similar and capable of performing all arm actions and deformations, we observed multi-level arm partitioning. Limb specialization has been well studied among vertebrates (primates, rodents, and fish); however, evidence for limb specialization in cephalopods is limited. We found that octopus arm actions were not equally distributed across all 8 arms, but were instead partitioned (anterior vs posterior) for specific actions. Previous research has demonstrated this partial task division with anterior arms designated for reaching/exploring tasks and posterior arms designated for standing and locomotion[2,19,32]. Byrne et al. 2006 also made note of a lateralized bias of arm use for some individual octopuses in their laboratory study[32]. Our results did not indicate a lateralized preference for specific arms; instead, the arms appeared to function in coordinated left and right pairs. Recently discovered intramuscular nerve cords that connect each arm to another arm 2 arms away may provide an alternative path for inter-arm signaling, potentially regulating this anterior and posterior arm partitioning[33].

Deformations can span the entire length of the arm or be localized to specific regions[5]. While certain arm actions and behaviors (i.e., reaching[16] and fetch[34], referred to as "arm movements") have previously been described as involving only a single deformation (bends or bend propagation), our findings, along with other studies, illustrate that these arm actions—and others—are composed of multiple deformations used simultaneously[11]. We also discovered that certain deformations were more frequently localized to specific arm regions, demonstrating functional partitioning at the deformation level. While the muscular hydrostatic nature of the arm is continuous throughout its length, the size and composition of muscle groups vary depending on the arm region. For example, longitudinal muscles are larger in the aboral medial and distal arm regions and are important for bending, while transverse muscles are largest in the proximal and medial arm regions and are important for elongation[35]. The biomechanics and anatomical features of these muscle groups corroborate our analysis, which indicated that bending occurred predominately in the distal and medial arm regions, while elongation occurred more frequently in the proximal arm region.

Laboratory versus field comparison

Our previous laboratory study and this field study confirm the extreme arm flexibility of octopus arms, with all 8 arms and all 3 arm regions capable of each of the 4 deformations. There were a few minor differences between the two studies. For example, in the field, we observed more frequent use of arm pairs 1 and 2, but no differences between left and right arm pairs. Laboratory artifacts could have been the cause of these observed differences in arm preference. While our field data did not capture torsion in all arm regions, laboratory observations documented this phenomenon, illustrating the importance of integrating field and laboratory studies for a more comprehensive understanding of arm flexibility[17].

Behavioral ecology

Octopuses inhabit shallow-water environments that vary in structure and complexity (e.g., sand plains vs coral reefs), making it necessary for them to have a large behavioral repertoire to exploit so many specific environments. The majority of prey that octopuses seek (crustaceans and shelled molluscs) are hidden; thus arm dexterity among all arms is vital to their daily existence. We observed various combinations of arm actions used to produce (1) single-arm behaviors such as fetching, and retrieval of food towards the mouth; multi-arm behaviors such as (2) crawl bottom searching and (3) parachute, important for prey capture. Although octopuses are generalist hunters and all 8 arms can perform the same task, partial task division among the octopus's 8 arms has been suggested, with octopuses preferentially using anterior arm pairs for exploring and posterior arm pairs for locomotion[19,31]. In this field study, frequently used actions in anterior arms played a role in exploratory behaviors (e.g., speculative bottom searching) while actions observed in posterior arms played a role in locomotion (e.g., walking). Multi-arm behaviors observed for locomotion—for example moving rock and moving seaweed—are important for remaining camouflaged from visual predators (i.e., motion camouflage) while moving across substrates[3]. Aside from foraging and locomotion, arm strength and flexibility are also necessary for den construction, defense from predators, and male-male agonistic fights for sexual selection behaviors[1–3]. These attributes allow octopuses to efficiently investigate every facet of their environments, allowing behavioral exploitation of multiple habitats.

Bioinspiration for soft robotics

Octopus arms serve as an inspirational model for soft robotics due to their unparalleled flexibility, adaptability, and ability to accomplish both simple and complex tasks. Imitating the principles of control, coordination, and biomechanical features of octopus arms has the potential to inspire innovative robotic systems for diverse applications (defense, medicine, rescue)[15,36,37]. Our hierarchical analysis of arm flexibility offers additional insights into the combinations of deformations and arm actions required to execute particular behaviors. These findings could provide a basis for more detailed experiments leading to refinement of current models of octopus-inspired robotics and open avenues for exploring additional applications in soft robotics and engineering.

Concluding thoughts

This detailed field study with a hierarchical analysis supports and expands laboratory studies demonstrating the impressive flexibility and utility of the octopus arm. A wider range of arm actions and their relationship to behaviors has been analyzed, and these have been organized from the top down: whole animal behavior—specific arm action—tailored deformations that enable each action. All 3 tiers of analysis have been incorporated into a quite comprehensive ethogram. All 8 arms seem capable of nearly all actions and deformations, indicating adaptability and redundancy among the arms. Even with this redundancy, evidence of arm partitioning for specific tasks is noteworthy. The diversity of shallow-water habitats analyzed in this study offers further insight into arm flexibility; however, future work is necessary to examine any correlations between habitats and arm actions and deformations. Additionally, other octopus species have different proportions of arm size and length, and it would be informative to compare their degrees of deformation (i.e., arrangement of musculature) as it relates to different arm actions that drive behavioral capabilities. Appropriate examples might include the clade of octopuses with very long slender arms, such as the mimic octopuses *Macrotritopus defilippi* in the Caribbean[38] and *Thaumoctopus mimicus* in the Indo-Pacific[39]. Eventually it will be useful to learn the muscular arrangements and neural controls that drive these arm deformations.

Data availability

The datasets are available from the corresponding authors on reasonable request.

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Author contributions
C.O.B., K.C.B., R.T.H., and J.H.G. designed the study. Video collection was done by R.T.H and C.O.B. C.O.B., K.C.B., J.H.G., and T.D.M. conducted data collection and video analyses. K.C.B., C.O.B., J.H.G., and T.D.M. analyzed the data. C.O.B., K.C.B., and R.T.H. prepared the manuscript. All authors reviewed the final manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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