

# Cuttlefish use visual cues to determine arm postures for camouflage

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To achieve effective visual camouflage, prey organisms must combine cryptic coloration with the appropriate posture and behaviour to render them difficult to be detected or recognized. Body patterning has been studied in various taxa, yet body postures and their implementation on different backgrounds have seldom been studied experimentally. Here, we provide the first experimental evidence that cuttlefish (*Sepia officinalis*), masters of rapid adaptive camouflage, use visual cues from adjacent visual stimuli to control arm postures. Cuttlefish were presented with a square wave stimulus (period = 0.47 cm; black and white stripes) that was angled 0°, 45° or 90° relative to the animals' horizontal body axis. Cuttlefish positioned their arms parallel, obliquely or transversely to their body axis according to the orientation of the stripes. These experimental results corroborate our field observations of cuttlefish camouflage behaviour in which flexible, precise arm posture is often tailored to match nearby objects. By relating the cuttlefishes' visual perception of backgrounds to their versatile postural behaviour, our results highlight yet another of the many flexible and adaptive anti-predator tactics adopted by cephalopods.

**Keywords:** cephalopod behaviour; anti-predator behaviour; visual ecology; postural camouflage; defence; *Sepia officinalis*

## 1. INTRODUCTION

Camouflage is common among animals [1–6] and provides valuable insight into the selective forces that drive their appearances and behaviours. This topic has found renewed scientific interest in recent years (e.g. [1,2]) following several pioneering studies on animal camouflage [3–6]. Animals make use of different camouflage tactics to evade visual detection or recognition. Some of these range from the animal's coloration to the use of morphological structures or material found in the environment [2,7]. In addition to skin patterning and coloration, an animal's posture can also aid in the avoidance of visual predation [6].

Postural camouflage is a common form of concealment in vertebrates as well as invertebrates [6,8,9]. Animals can move their body parts or appendages in particular ways or position their bodies in a particular microhabitat to implement effective postural camouflage. Orb-weaving spiders often move their legs into a stick-like posture, so the spider remains well camouflaged when hunting for prey [10,11]. Salamanders are also known to use their body, head, tail and legs in multiple postures that have anti-predator functions [12]. In other animals, somewhat fixed body shapes or appendages require that changes in posture are mostly changes in the overall orientation of the body. For example, shrimp [13], moths [14], frogs [15], fishes

[16,17] and birds [18–21] may adopt particular postures by behavioural alignment with substrate features to achieve the desired camouflage effect. There are few studies providing direct evidence that body orientations influence crypsis. An experiment conducted by Pietrewicz & Kamil [22] showed that blue jays (*Cyanocitta cristata*) were able to detect *Catocala* moth images and that this detection was affected by the background upon which the moth was placed as well as its body orientation. Recently, Webster *et al.* [14] found that moth orientation had a significant positive effect on crypsis. Using the human visual system as the 'predator', these authors found that the position of moths on trees, i.e. their orientation relative to the background, was important for avoiding detection. Körtner & Geiser [20] found that tawny frogmouths (*Podargus strigoides*) choose to roost on branches where they can position their bodies in an orientation that minimizes the risk of detection by predators. The least bittern (*Ixobrychus exilis*) is known for its postural camouflage behaviour; this bird positions its neck and bill to hide among reeds in its marsh habitat [21].

Cephalopods have a remarkably diverse array of chromatic, textural, locomotor and postural components of neurally controlled body patterns that enable them to camouflage against different backgrounds [23,24]. Postural camouflage in cuttlefish and squid is limited mostly to the arms because of internal body structures, such as the rigid cuttlebone or gladius. Octopuses lack any rigid internal structures and are far less limited for postures because they are extremely flexible and can change three-dimensional configuration of the whole body. Different postures are possible because the muscles of the arms of coleoid cephalopods (squid, cuttlefish and

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octopus) are organized as flexible muscular hydrostats that enable bending with multiple degrees of freedom [25–27].

Most of the recent research regarding cuttlefish camouflage (e.g. *Sepia officinalis*) has focused on understanding the control, mechanisms and functions of body patterning change [24,28–32]. Changes in body pattern for camouflage, including both chromatic and textural components (three-dimensional skin papillae), appear to be driven solely by visual cues [29,33,34]. Surprisingly, there have been no detailed studies of the cues that drive adaptive static postural camouflage in cephalopods. In this paper, we examine if and how the visual environment can influence the posture of the arms of the common European cuttlefish *S. officinalis* by presenting them with two-dimensional visual cues. We also discuss evidence of postural camouflage in other cephalopods.

## 2. MATERIAL AND METHODS

### (a) *Animals and experimental protocol*

Ten young cuttlefish *S. officinalis* (mantle lengths between 3.2 and 3.7 cm) were used for behavioural tests. Cuttlefish were reared and maintained at the Marine Resources Center of the Marine Biological Laboratory from eggs laid in nature in southern England. Each animal was placed inside a bisected teardrop-shaped arena (figure 1a) in an aquarium supplied with running sea water. The different experimental backgrounds (see below) were presented on the curved, teardrop-shaped wall; the opposite, straight wall was created by the glass of the aquarium that held the arena. The entire experimental set-up was enclosed by a black curtain that shielded the cuttlefish from external visual stimuli; a small opening in the curtain allowed the camera lens to view the cuttlefish through the glass aquarium wall. After each animal had acclimated to the experimental chamber for a minimum of 10 min, a digital photograph was taken from the side, perpendicular to the background and levelled with the animal using a Nikon Coolpix 5400 camera. An animal was considered acclimated when swimming and hovering movements had ceased and the animal was sitting in the corner of the arena (see drawing in figure 1a, for animal location).

### (b) *Experimental stimuli and analysis*

Knowing that cuttlefish respond to objects presented on the wall [35], we tested whether arm-raising behaviour can be evoked with visual cues and whether animals controlled the direction of arm posture according to the orientation of the square wave (stripes).

All 10 animals were presented with each of four walls in random order: (i) grey wall (control); (ii) a square wave (horizontal stripes) oriented parallel to the animals' main body axis; (iii) a square wave (45° stripes) oriented at a 45° angle; and (iv) a square wave oriented perpendicularly to the animals' main body axis (vertical stripes). A grey floor was used with each wall. The period of the each square wave was 0.47 cm, a size determined by the mean width of the animals' first arm base, 0.235 cm. For each animal on each substrate, the angle of the first arm closer to the stimulus wall relative to the horizontal was measured using IMAGEJ (National Institute of Health, available online). These data were then compared statistically using a repeated measures analysis of variance (ANOVA) followed by a pairwise

comparison of estimated marginal means using a Bonferroni correction.

## 3. RESULTS

Cuttlefish adjusted their arm position in accordance with the orientation of the background stimuli (figure 1b,c). The within-subjects repeated measures ANOVA using a Greenhouse–Geisser correction and type III sum of squares indicated there was a significant difference in the angle at which the animals held their arms in the presence of different square wave orientations ( $F_{2,329, 20.959} = 28.965$ ;  $p < 0.001$ ; partial  $\eta^2 = 0.763$ ;  $\epsilon = 0.776$ ). Comparisons of estimated marginal means with a Bonferroni correction revealed that the distributions of arm angles presented in response to the control (grey) wall or differently oriented square waves (stripes) were significantly different from each other with one exception: the arm angles presented in the presence of the 45° wall were not significantly different from those shown in the presence of the wall with the vertically oriented square wave (mean difference = 6.96°, 95% confidence interval for difference =  $-65.556^\circ \leq \mu_{45} - \mu_v \leq 51.636^\circ$ ; figure 1b).

When presented with the grey wall, no animal raised its arms (mean angle relative to the horizontal  $\pm$  standard error =  $-41.8^\circ \pm 1.4$ ; figure 1b,c). When presented with the horizontally oriented square wave (stripe) wall, the first pair of arms was stretched almost parallel to the animal's body (mean  $\pm$  s.e. =  $0.9^\circ \pm 8.2$ ). When presented with the square wave (stripe) oriented at 45°, all but one animal (an extreme outlier indicated by the asterisk under the boxplot of the 45° distribution) held their first pair of arms obliquely (mean  $\pm$  s.e. =  $59.8^\circ \pm 12.2$ ). Although 59.8° does not intuitively seem to be a good match to the square wave angled at 45°, examination of the images collected during this experiment showed the arm-raising behaviour was appropriate for the stimulus on the wall (figure 1c). When presented with the vertically oriented square wave, all but two animals held their first pair of arms vertically (mean  $\pm$  s.e. =  $66.8^\circ \pm 13.2$ ). Note this mean includes two outliers, one is a standard outlier (raised its arms to 34.6°, filled circle under boxplot for the vertically oriented square wave (stripe) stimulus; figure 1b) and the second is an extreme outlier (did not raise its arms, asterisk under boxplot for the vertically oriented square wave (stripe) stimulus; figure 1b). In this case, the median 84.9° (indicated by thick solid line in each boxplot) is a better estimate of the animals' response.

Changes in arm posture were often observed as soon as the animal was placed in the experimental chamber. Preliminary tests (data not reported) showed that the animals were able to hold their arms according to the orientation of the background structures for long periods (previous observations lasted 20 min). Field data collected on *S. officinalis* from northwest Spain revealed that these animals maintain arm postures for camouflage for 20 min or more (data not shown, but, for example, see photographs in figure 2).

In many animals, arm raising was also observed in the second pair of arms, but always at a lower angle relative to the horizontal than the first pair of arms (figures 1c and 2). In most cases, the remaining third and fourth pairs were held in a resting, arms-down position. In the

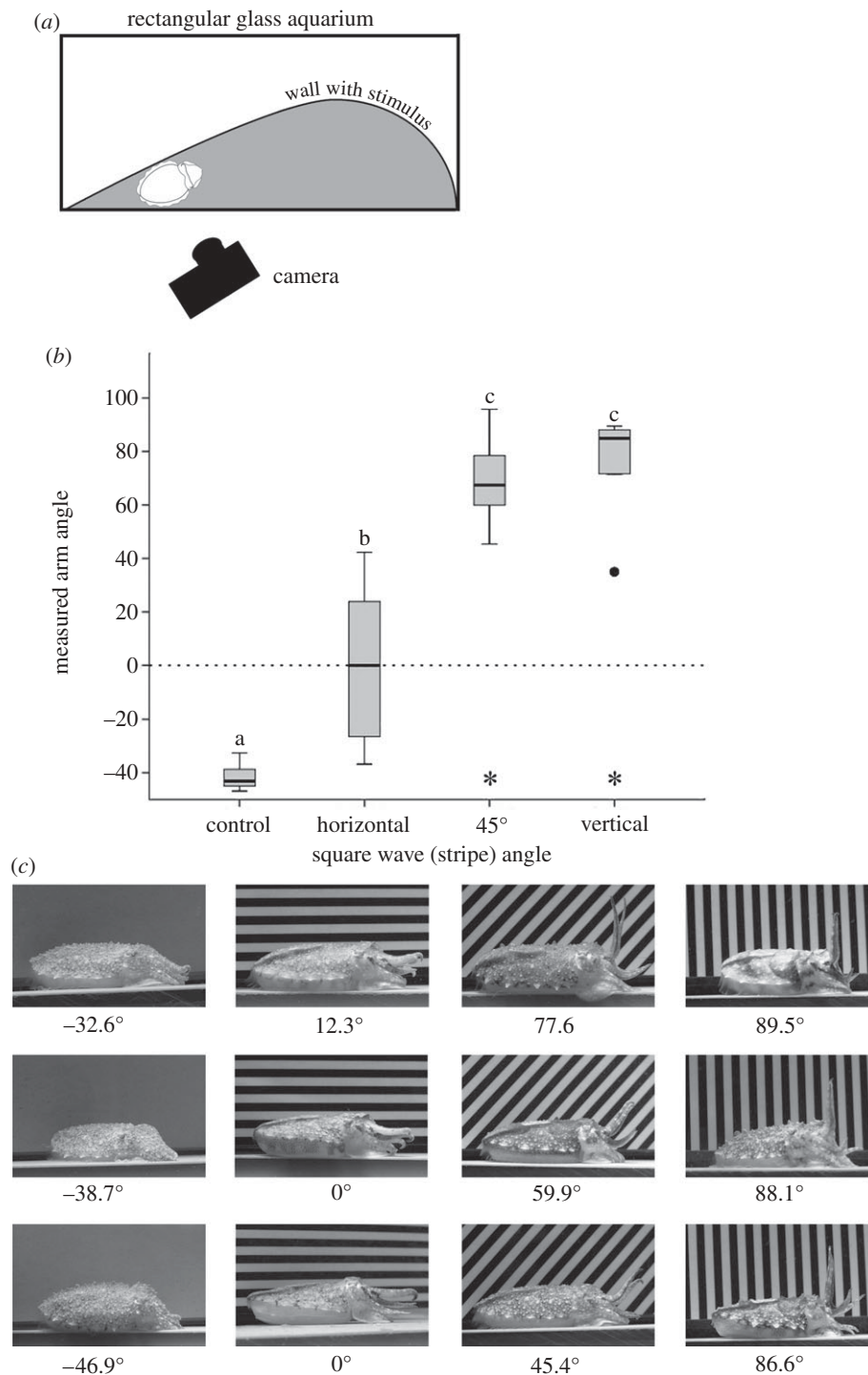


Figure 1. Postural arm camouflage in *S. officinalis* is affected by the orientation of visual stimuli in the background. (a) Top view drawing of experimental set-up showing rectangular aquarium, bisected teardrop-shaped arena and camera perpendicular to animal's long axis. (b) Boxplot showing the distribution of measured cuttlefish arm angles relative to the horizontal in the presence of the control (grey) wall and the different square wave (stripe) orientations. The bottom of each box represents the first quartile, the top represents the third quartile, the thick line represents the median and the whiskers represent the range. Filled circle is an outlier, asterisks are extreme outliers. (c) Representative images for cuttlefish holding their arms at angles above the median (top row), at the median (middle row) and below the median (bottom row) for each square wave (stripe) orientation. Cuttlefish positioned their arms in a resting, down posture when no stripes were presented. When presented with a horizontally striped wall, the first pair of arms was stretched parallel to the animal's body. Cuttlefish held their arms obliquely when presented with 45° stripes. When presented with vertical stripes, the cuttlefish arms were held upright. Different letters indicate significantly different distributions.

presence of the wall with the horizontally oriented square wave, the third pair was occasionally stretched out in the water column. In all conditions, the animals held their arms in the water column above or in front of their heads; they did not touch the wall.

#### 4. DISCUSSION

In the wild, cuttlefish are often seen near three-dimensional structures (i.e. corals, algae, rocks) and field observations have suggested that arm postures during camouflage are driven by visual stimuli. This robust



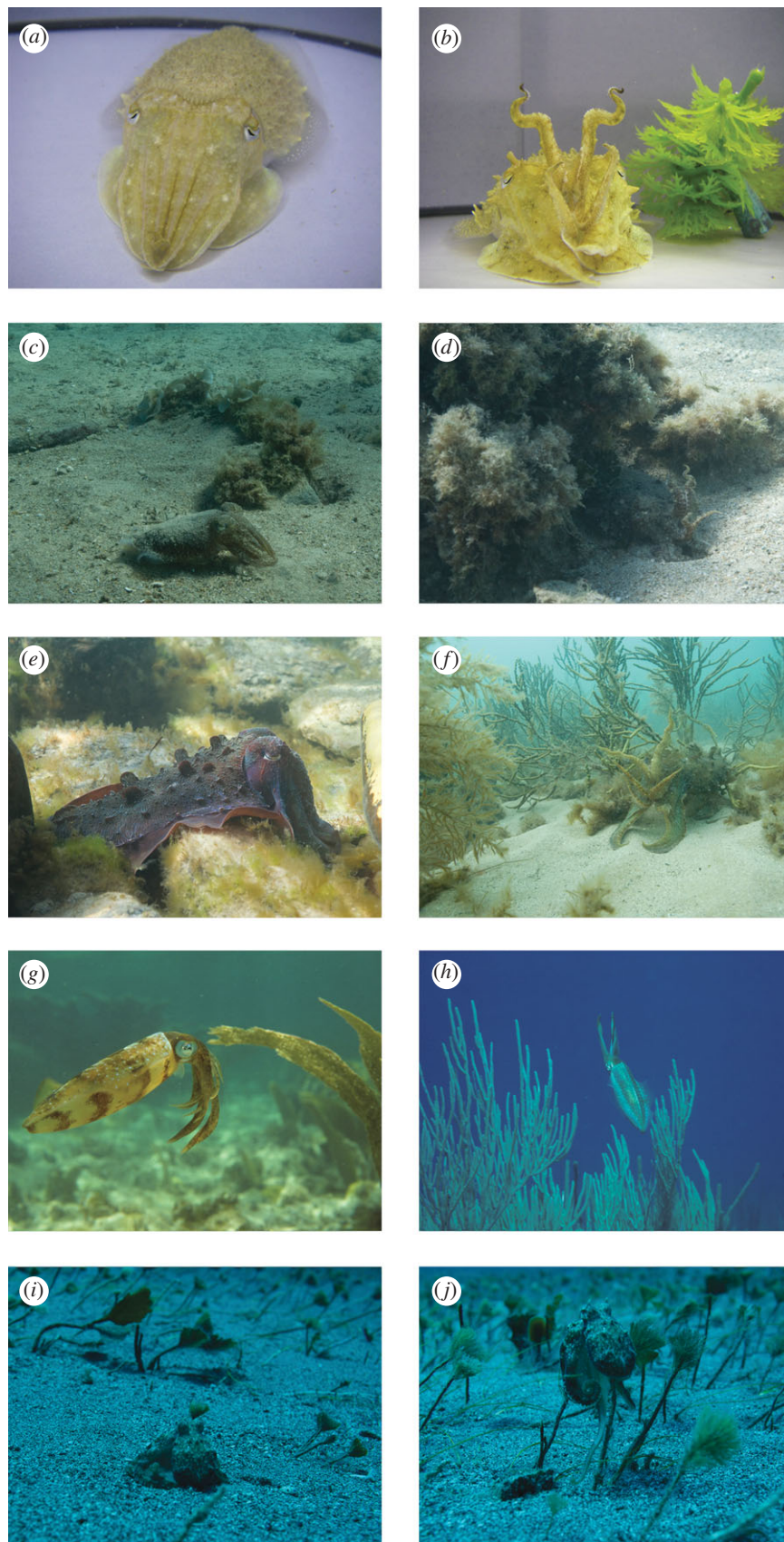


Figure 2. (a,b) Laboratory and (c–j) *in situ* images of cephalopods performing postural camouflage. Please note the variety of arm postures these animals use on diverse backgrounds. (a,b) Cuttlefish *S. officinalis* in the laboratory in the absence (a) and presence (b) of artificial algae. (c,d) Cuttlefish *S. officinalis* with arms down in sand (c) and the same animal sitting near algae with its arms raised (d). (e,f) Cuttlefish *S. apama* with arms down on rocks (e) and with arms raised near algae (f). (g,h) Squid *Sepioteuthis sepioidea* with arms down near sea fan (g) and with arms raised near soft coral (h). (i,j) Octopus *Octopus burryi* with arms under mantle on sand (i) and perched on algae with arms extended below mantle (j). Photo credit for (e): N. Justin Marshall.

behaviour can be evoked in the laboratory using artificial algae (figure 2*a,b*). Figure 2*c,d* illustrates variations in *S. officinalis* arm postures relative to nearby objects in several natural habitats; additional photographs of arm postures in the giant Australian cuttlefish *Sepia apama*, the Caribbean reef squid *Sepioteuthis sepioidea* and the octopus *Octopus burryi* are shown in figure 2*e–j*. Additional examples of this behaviour in cuttlefish and squid are provided in the electronic supplementary material, figure S1. Subsequent laboratory testing on *S. officinalis* reported herein supports the hypothesis that visual stimuli guide arm postures. The evidence is two-fold: (i) two-dimensional visual stimuli alone elicited arm raising (i.e. the animals did not receive any tactile or three-dimensional information from the wall) and (ii) the orientation of the visual stimuli strongly influenced the orientation of the raised arms (figure 1*b,c*).

Visual information determines much of cuttlefish camouflage behaviour, whether it is skin patterning and coloration (brief review in Hanlon [36] and Kelman *et al.* [37]), physical skin texture [29], body orientation [38] or, as shown here, arm posture. When approaching a new environment, visual sensing can commence from a distance. If an animal were to use tactile information to control posture, it would require them to make direct contact with several features of the environment from which they want to extract information. Not only would they have to be close to the background feature, tactile inspection might take more time and visually expose the animal to predators via inappropriate postures during inspection. Thus, gathering visual information from a surrounding environment may be faster; for a soft-bodied cephalopod with rapid adaptive camouflage, speed would seem to be an advantageous tactic. Moreover, decapod cephalopods (cuttlefish and squid) have reduced tactile brain centres compared with octopuses [23,39], which might be expected to use tactile information for some aspect of their camouflage patterning.

Aside from arm posture, the overall body orientation relative to the visual background to complement camouflage might be expected to occur in cephalopods. However, no proof of this facet of adaptable camouflage in cephalopods exists. Sohet *et al.* [38] investigated orientation sensitivity in the cuttlefish *S. pharaonis* on striped pebble patterns and showed that animals tended to orient themselves with their body axis across (not parallel to) the background stripes on the substrate. In this study, orientation sensitivity (as in moths [14]) was not tested, but the subject is worthy of future investigation with a variety of cephalopods.

Our study demonstrates that cuttlefish arm posture is adaptable and is correlated with the visual orientation of two-dimensional stimuli (designed to be approx. the width of the animals' arms) in the vertical field of view surrounding a cuttlefish. Many cephalopods change the shape and position of their arms in different directions according to the environment, either stationary or moving (figure 2) [39–44], presumably to be less conspicuous and prevent detection and/or recognition by predators and prey. More complex body patterns that include postures for camouflage may have evolved in relation to the level of complexity of the animal's habitat [39,45]. In contrast to this prediction, it has been suggested that the mesopelagic squid *Octopoteuthis*

*deletron* has variable body patterning and postures that may be used as a primary defence to cause search image impedance and avoid detection by a predator [46]. Because the open ocean is nearly a homogeneous visual environment, future research should assess if indeed evolution favoured a more varied repertoire of camouflage tactics for cephalopods living in complex environments (cuttlefish, octopus and near shore squids) than in those living in less complex environments (open water squids, mud flat octopuses, etc.) [23].

Cephalopods seem remarkable at exploiting the spatial and temporal components of visual scenes for camouflage (figure 2). A cuttlefish's coloration, texture and posture might prevent detection (e.g. perhaps via edge detection) or recognition by predators, particularly if postural and shape changes also enhance general background resemblance. Because a predator has to be familiar with a prey's specific three-dimensional shape to identify and detect it [47], an alteration in body shape (as in the case of an octopus) or arm posture (in cuttlefish and squids) might enhance camouflage by interfering with the predator's search image. Anecdotal evidence also suggests that cuttlefish and squid wave their arms and body, respectively, according to the movement of background elements [39,40] and by doing so render themselves less distinguishable [47].

Most coleoid cephalopods can adaptively and rapidly change their skin's colour, contrast and texture (octopus and cuttlefish), as well as their locomotion and posture, in response to visual cues. Therefore, this animal group is a suitable model for the study of camouflage and visual perception. While this paper focused on one detail of cuttlefish behaviour—arm postural camouflage—we have not exhausted this line of inquiry. For example, the role of body postures in reducing the probability of predator detection or how visual stimuli affect cuttlefish postural locomotion has never been experimentally tested. Ultimately, future studies could concentrate on behaviours of both cephalopods and their predators in the field to acquire a full understanding of the complex interactions between the visual environment and the mechanisms of camouflage.

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