



A fish-eye view of cuttlefish camouflage using *in situ* spectrometry

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Cuttlefish are colour blind yet they appear to produce colour-coordinated patterns for camouflage. Under natural *in situ* lighting conditions in southern Australia, we took point-by-point spectrometry measurements of camouflaged cuttlefish, *Sepia apama*, and various natural objects in the immediate visual surrounds to quantify the degree of chromatic resemblance between cuttlefish and backgrounds to potential fish predators. Luminance contrast was also calculated to determine the effectiveness of cuttlefish camouflage to this information channel both for animals with or without colour vision. Uniform body patterns on a homogeneous background of algae showed close resemblance in colour and luminance; a Uniform pattern on a partially heterogeneous background showed mixed levels of resemblance to certain background features. A Mottle pattern with some disruptive components on a heterogeneous background showed general background resemblance to some benthic objects nearest the cuttlefish. A noteworthy observation for a Disruptive body pattern on a heterogeneous background was the wide range in spectral contrasts compared to Uniform and Mottle patterns. This suggests a shift in camouflage tactic from background resemblance (which hinders detection by the predator) to more specific object resemblance and disruptive camouflage (which retards recognition). © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 109, 535–551.

ADDITIONAL KEYWORDS: chromatic contrast – colour modelling – colour pattern – *Sepia apama* – spectral measurement.

INTRODUCTION

Many forms of camouflage operate by two basic mechanisms: to avoid ‘detection’ or to hinder ‘recognition’ by visual predators (Stevens & Merilaita, 2009a, 2011). The two are not mutually exclusive, yet before the relative roles of detection and recognition are understood, there is much to be learned about the degree to which visual systems of predators perceive camouflaged prey, rather than our own interpretation of the situation. The term background matching has been used recently to describe mechanisms that help prey to

avoid detection, although Cott (1940) used the term general background resemblance. Background matching is not an ideal term because it infers some manner of statistical ‘match’ between features of the prey’s camouflage relative to the visual background. There are at least three reasons why an absolute match in colour, brightness, contrast, pattern or texture need not be met to achieve camouflage. First, animal visual systems are of course determined by each animal’s specific visual capability and this final formula is determined by a number of often competing forces and selective pressures unique to that species (Marshall, 2000a; Endler *et al.*, 2005). Second, visual habitats in the natural world are too varied to allow an animal with a fixed or slowly changing camouflage pattern to match more than a subset of the background pattern

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features (and changing light fields can alter the appearance of animal versus background on time scales as short as seconds or minutes). Third, for animals such as cephalopods, which have the ability to move within greatly varied visual habitats (coral reefs, kelp forests, etc.) and produce adaptable camouflage throughout, it would be impossible, and indeed not necessary, to 'match' the hundreds of species of corals, sponges, algae, kelp, seagrass, and the array of rocks and sands that characterize such visually rich habitats. Thus, camouflage in animals is often a more general strategy based on specific predatory pressures and not an innate need to exactly match the background. Thus, we prefer Cott's (1940) term 'general background resemblance' because it provides a more reasonable experimental approach to linking an animal's camouflaged body pattern to the visual capabilities and limitations of its visual predators (Hanlon *et al.*, 2009, 2011).

Until relatively recently, sensory ecologists have been quite restricted in their ability to measure and test how a predator 'sees' a prey, or what features are used by the predator to detect or recognize it. This is partly because visual systems of few predators have been studied. It is also because of limitations in how light can be measured *in situ*. We and others (McFarland & Munz, 1975; Endler, 1993; Cuthill *et al.*, 1999; Marshall, 2000b; Marshall *et al.*, 2003a, b; Hochberg *et al.*, 2004; Stuart-Fox, Whiting & Moussalli, 2006; Mäthger *et al.*, 2008; Stuart-Fox, Moussalli & Whiting, 2008; Dalton *et al.*, 2010) have used the best-available spectrometers of various configurations in the field, and many investigators acknowledge the limitations of point-by-point sampling that hand-held spectrometry imposes; yet, these studies provide a useful way forward and await technology development (e.g. hyperspectral imaging) to improve such visual studies (Cronin, Chiao & Ruderman, 2000; Vora *et al.*, 2001; Wachtler, Lee & Sejnowski, 2001; Nascimento, Ferreira & Foster, 2002; Párraga, Troscianko & Tolhurst, 2002; Long & Purves, 2003; Volent, Johnsen & Sigernes, 2009).

In the present study, we use point-by-point spectrometry to investigate some details of cuttlefish camouflage. This is possible as a result of the unique annual breeding event for *Sepia apama*, the giant Australian cuttlefish, at Whyalla, South Australia. This aggregation (Hall & Hanlon, 2002) allows divers and scientists to approach the animals sufficiently closely to accurately measure small areas of skin in the wild. Previous laboratory studies (Marshall & Messenger, 1996; Mäthger *et al.*, 2008) showed that the reflectance spectra of *Sepia officinalis* skin patterns correlate closely with the reflectance spectra of a variety of natural substrates and it was argued that *S. officinalis* can produce colour matches on some

natural substrates despite lacking colour vision. Direct field measurements in *S. officinalis* have been lacking until a recent field study by Akkaynak *et al.* (2013) who used field techniques and instrumentation similar to that reported in the present study.

We found previously that cephalopods avoid detection primarily by deploying what we categorize as Uniform or Mottled camouflage patterns (Hanlon & Messenger, 1988; Hanlon, Forsythe & Joneschild, 1999; Hanlon *et al.*, 2009). Uniform body patterns are used on apparently uniform (or homogeneous) backgrounds and Mottled body patterns are used on heterogeneous backgrounds to achieve general background resemblance. To avoid (or at least hinder) recognition by a predator, there is also evidence that cuttlefish use Disruptive body patterns that break up the body into skin components of different size, shape, orientation, and contrast (Hanlon *et al.*, 2009). However, disruptive coloration in other animals, as well as cephalopods, is acknowledged to also help retard detection by providing some degree of general background resemblance; this is still a controversial and complex subject that is not directly relevant to the present study (Stevens & Merilaita, 2009a, 2011).

In the present study, we specifically quantify and compare colour and luminance aspects of general background resemblance, and ignore overall pattern analyses, when examining individual regions that may make up part of that pattern. Because different camouflage patterns and tactics rely upon distinct visual mechanisms for detection and recognition, it was not known whether Uniform, Mottle or Disruptive body pattern types achieve the same level of colour and luminance compared to their backgrounds. We address the following questions. In Uniform patterns, how well do colour and luminance compare to backgrounds on homogeneous or mildly heterogeneous substrates? In Mottle patterns, do the dark and light components of the cuttlefish body correspond closely to the light and dark background objects nearby? In Disruptive patterns, do the large-scale light or dark components compare in luminance and colour to the immediately adjacent light and dark background bits to effect coincident disruptive coloration? What do these patterns look like to potential predators with no colour vision, or with colour vision that may be di- or trichromatic?

MATERIAL AND METHODS

ANIMALS AND STUDY SITE

The giant Australian cuttlefish *S. apama* Gray migrates into shallow coastal waters to spawn during the austral winter months (May to August). The spawning aggregation of *S. apama* occurs over a

restricted area of rocky reef in northern Spencer Gulf, South Australia (Hall & Hanlon, 2002). This is the only known dense aggregation of spawning cuttlefish in the world and provides a unique opportunity for studying the mating system and sexual selection in a cuttlefish population under natural conditions (Naud *et al.*, 2004; Hanlon *et al.*, 2005). Although animals typically display rich sexual selection signals in this spawning ground, cuttlefish also frequently show dynamic camouflage body patterns in this habitat (Hanlon *et al.*, 2007; Zylinski *et al.*, 2011). To examine spectral properties of cuttlefish and their surrounding background features, three camouflage body patterns, namely Uniform, Mottle, and Disruptive (Hanlon & Messenger, 1988; Hanlon, 2007), were examined with *in situ* spectral radiance measurements.

All spectral measurements and underwater photography were conducted by SCUBA diving near Black Point (137°43.1'E, 32°59.5'S) in May/June of 2006 and 2007. The habitat is shallow water (3 m depth) and composed of algae, sea grass, open rocky bottoms, or open sand. The habitat is dominated by brown and red algae: tall stands of *Scabaria agardhii*, *Cystophora expansa*, and *Caulocystis* sp., with an understory of *Gigartitina brachiata* mats, *Asparagopsis taxiformis*, *Lobophora variegata*, and other species of *Dictyotales*.

SPECTRAL IRRADIANCE AND RADIANCE MEASUREMENTS

To characterize the light field of *S. apama*'s natural habitat, spectral irradiance (downwelling, upwelling, sidewelling) was measured at various depths from 1–3 m (Fig. 1). This was accomplished with a spectroradiometer (USB2000; Ocean Optics) connected to a palmtop computer (Compaq iPaQ; Hewlett-Packard) in a custom-made underwater housing (Marshall, 2000a). The probe head of the optic fibre was fitted with a cosine corrector for these measurements

(CC-3-UV; Ocean Optics; for details, see Marshall *et al.*, 2003b and Akkaynak *et al.*, 2013).

To measure the spectral radiance of cuttlefish and background, care was taken to avoid disturbing the cuttlefish at the same time as obtaining the light data so that the camouflage patterns were normal and authentic (Fig. 2A). This was achieved by allowing cuttlefish to adapt to the presence of divers before collecting the spectral data. The bare optic fibre of 400- μ m diameter, with a limited acceptance angle of approximately 20°, was pointed to the region of interest on animal skin or background object (e.g. algae, rocks, pebbles, and sand) at very close range (approximately 2 cm), to provide a sampling area of approximately 40 mm². Multiple radiance spectra measurements (two to ten) were taken using the same spectroradiometer. With previous experience and training using a back-illuminated fibre, and by choosing body regions with relatively large and apparently uniform colour patches, this method can be successfully used to sample discrete portions of animal or substrate. To derive the reflectance spectra from the radiance spectral data, a white reflectance standard (Spectralon; LabSphere) was measured at precisely the same location before and after the cuttlefish moved on. These measurements were averaged, both temporally and between similar body regions/colours, to obtain mean spectra for studied animals and substrates. Temporal averaging of each measurement of at least 10 integration cycles of the spectrometer is important to minimize the effect of surface flicker under such natural lighting situations. Most of the animal/substrate spectra were averaged from seven to ten repeated measurements with 3% mean error, except two regions where only two or three valid spectral measurements were available.

Because of the complexities of acquiring these data (e.g. multiple reading were taken on each sample, numerous blank measurements must be taken, clouds can alter the light field, which terminates a session,

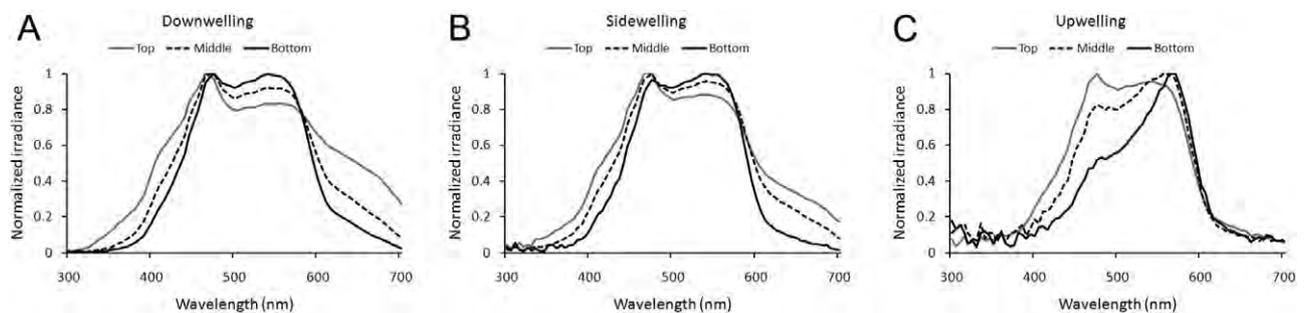


Figure 1. Characteristics of the light field in the habitat of *Sepia apama*. Normalized irradiance spectra of the study site measured *in situ* from downwelling (A), sidewelling (B), and upwelling (C) directions at various depths. Top, just below the water surface; middle, halfway in the water column; bottom, 30 cm above the bottom. Depth, approximately 3 m.

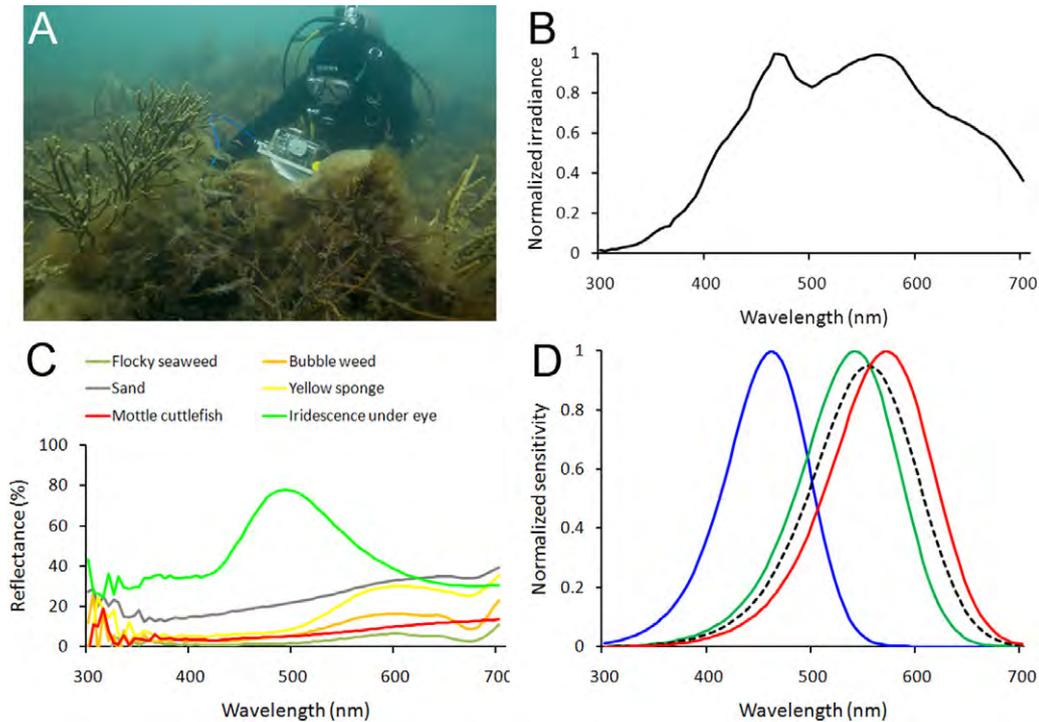


Figure 2. *In situ* spectral measurements of *Sepia apama* and their habitats, and spectral sensitivity functions of cones in hypothetical fish predators. A, one of the authors (NJM) taking spectral measurements of cuttlefish using the spectrometer underwater. B, downwelling irradiance spectrum of the habitat. C, reflectance spectra of the animals and their habitat objects (collected from multiple diving sites). D, spectral sensitivities of hypothetical fish cones. In the trichromatic system, λ_{\max} was 460, 540, and 570 nm (blue, green, and red curves, respectively). In the dichromatic system, λ_{\max} was 460 and 555 nm (blue and dashed curves, respectively).

animals can move, etc.), during the two seasons of field sampling, complete data sets were acquired for four different cuttlefish. Successful data sets required approximately 20 min each. The figures show exactly where the spectrometer data were acquired on various aspects of the cuttlefish body and the surrounding substrate.

The spectroradiometer as well as the fiber optic cables were calibrated for absolute irradiance/radiance using a NIST calibrated halogen light source (LS1-CAL; Ocean Optics). To coordinate these radiance measurements *in situ*, a simultaneous corresponding photograph of the recording site was taken by a SLR camera (Canon EOS 1-Ds Mark II) in a Subal housing equipped with a glass port and notes were taken regarding which objects in the frame were measured.

MODELLING CHROMATIC AND LUMINANCE CONTRASTS IN THE EYES OF FISH PREDATORS

Although the native predators of *S. apama* at the study site are uncertain, known predators in the vicinity of the spawning grounds include Indo-

Pacific bottlenose dolphins (*Tursiops aduncus*) and fur seals, and potential predators mullet (*Argyrosomus japonicus*, family Sciaenidae), large stingrays, snappers (*Pagrus auratus*, family Sparidae), yellowtail kingfish (*Seriola lalandi*, family Carangidae), and black bream (*Acanthopagrus sp.*) (Gales *et al.*, 1993; Finn, Tregenza & Norman, 2009). Although the cone sensitivity functions of these specific fish predators are not available, we chose one dichromatic fish and one trichromatic fish as their hypothetical predators to simulate their views of these camouflaged cuttlefish. In dichromatic fish, the double cone was assumed, and the λ_{\max} of S and M cones was 460 and 555 nm, respectively, which is similar to the spectral sensitivities of known dolphin species (Fasick *et al.*, 1998). In trichromatic fish, the λ_{\max} of S, M, and L cones were 460, 540, and 570 nm, respectively. The choices of the generic λ_{\max} of dichromatic and trichromatic visual systems were representative of those currently known (Lythgoe *et al.*, 1994; Shand *et al.*, 2002; Losey *et al.*, 2003). Furthermore, during modelling, we shifted the λ_{\max} of these cones up or down 10–20 nm with no

substantial effect on the overall results (data not shown).

To simulate what the fish predators see in these camouflaged cuttlefish, we followed the methods of Marshall & Vorobyev (2003) or Cheney *et al.* (2009), which are based on well-established models of Vorobyev & Osorio (Vorobyev & Osorio 1998; Vorobyev *et al.*, 2001a). Kelber, Vorobyev & Osorio (2003) provided a good summary of these methods and discussion of different colour vision types. This model assumes that the luminance information is disregarded, and colours are encoded by an opponent mechanism. It also assumes that the chromatic discrimination in this colour space is limited by noise originating in the receptors and determined by the relative proportion of this noise in each photoreceptor. This model calculates the 'distance' (ΔS), or the just noticeable difference (JND), between the colours in a di- or trichromatic visual space. Colours that appear similar within each visual system result in low ΔS values, whereas those that are chromatically contrasting are high in value. Examples of a dichromatic visual space and a trichromatic visual space (in this case, a Maxwell colour space, and not the noise limited space of Vorobyev & Osorio, 1998) are shown in Figure 3 where the example colours of cuttlefish and background from Figure 2 are plotted. Colours for which ΔS are large are more discriminable from each other than colours where the value is small. Note that the measurements in Figure 2 are for illustrative purposes only to show how data were computed. These measurements were collected from multiple sites and in different diving trips. Without morphological studies of the fish retina, the relative proportions of the different cone types in hypothetical fish predators were set for these calculations as 1 : 1 for dichromats and 1 : 1 : 1 for trichromats. We also modelled data with a ratio of 1 : 2 (S : M) for dichromats and 1 : 2 : 2 (S : M : L) for trichromats (Shand, Archer & Collin, 1999; Cheney & Marshall, 2009), although we found no significant differences in the overall results (data not shown).

How luminance versus colour vision is segregated is not known for any of the predators that we model here, and so we employ an often-used assumption: luminance contrast is modelled by using only the long-wavelength spectral sensitivity. Behavioural tests in humans (Wyszecki & Stiles, 1982), bees (Hempel de Ibarra, Giurfa & Vorobyev, 2002), and indeed fish (Neumeyer, Wietsma & Spekrijse, 1991) suggest that this is a reliable assumption. Monochromatic JNDs were calculated using the same receptor noise model as that used for calculating di- and trichromatic JNDs. This is achieved by computing the difference between responses of the long-wavelength cone for two loci and divided by the visual threshold.

RESULTS

CHARACTERISTICS OF THE LIGHT FIELD IN THE HABITAT OF *S. APAMA* DEPEND ON DIRECTION AND DEPTH

Cuttlefish are benthic animals, and their potential predators may view camouflaged cuttlefish from various angles. To assess the colour and luminance of these animals relative to their background substrates, it is necessary to characterize the light field of their habitats in different directions and depths. Figure 1 shows normalized irradiance spectra of the study site measured *in situ* from downwelling, sidewelling, and upwelling directions at various depths. Because of the shallow depth of the study site (approximately 3 m), the downwelling and sidewelling irradiance spectra at bottom only showed a slight reduction in spectral width, which would be typical at greater depths (Jerlov, 1976). However, the upwelling irradiance spectrum at bottom, which is equivalent to the mean habitat radiance spectrum (i.e. algae, sand, rocks), showed a significant reduction in the short wavelength range. These measurements demonstrate that characteristics of the light field in this habitat of *S. apama* depend on direction and depth. For example, note the similarity in the 600–700 nm range in Figure 1A (grey line for top of water column) and Figure 2B (measured at sea bottom).

LUMINANCE AND COLOUR COMPARISONS OF CAMOUFLAGED CUTTLEFISH DEPEND ON BODY PATTERN TYPES AND HABITAT

To test whether the three body pattern types (Uniform, Mottle, and Disruptive) achieve the same level of luminance and colour versus aspects of their backgrounds for camouflage, it is necessary to compare the luminance and chromatic contrasts of animal and background in the eyes of potential predators. By collecting radiance spectra of camouflaged cuttlefish with different body patterns and their surrounding objects *in situ*, and applying the receptor noise model (Vorobyev & Osorio, 1998) to compute the luminance and chromatic contrasts in the visual spaces of both di- and trichromatic fish predators, the level of luminance and colour matches for cuttlefish with different body patterns can be assessed.

Contrast cues available to animals can be divided into luminance only and colour only, although, clearly, the end behavioural result may be informed by both processes (Ottoson & Zeki, 1985). The colour vision models used in the present study negate luminance differences and look for chromatic contrast alone. Luminance contrast may be as salient a feature as colour for camouflage or communication and, indeed, several animals appear to choose this channel alone

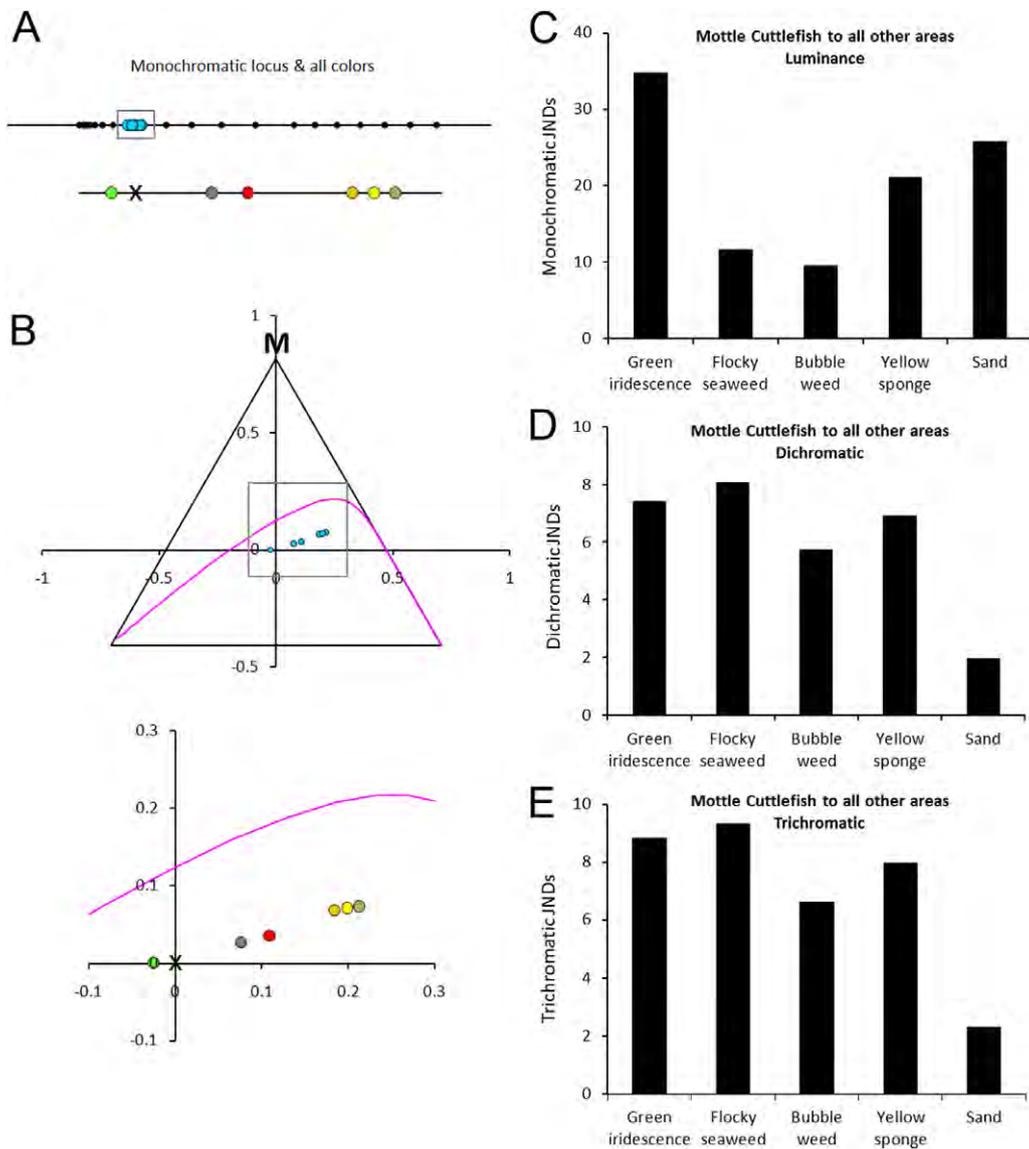


Figure 3. Modelling luminance and chromatic contrast in the eyes of di- and trichromatic fish predators. For estimating luminance signals, only the long wavelength photoreceptor was used in both di- and trichromatic systems. A, visualization of spectral loci of these measured colours in the dichromatic space (isoluminance, thus a straight line). Black dots are the loci of monochromatic lights (boundary condition), and blue dots indicate the loci of six spectral measurements in Fig. 2C. The grey box area was enlarged below to view these spectral loci clearly (the colour notation is the same as in Fig. 2C). The 'X' marks the achromatic point in the dichromatic space. B, similarly, these six spectral measurements (blue dots) were visualized in the trichromatic space (isoluminance, thus a Maxwell triangle). The magenta curve depicts the loci of monochromatic lights. The grey box area was enlarged below to show these spectral loci in higher magnification. The 'X' marks the achromatic point in the trichromatic space. C, the luminance contrast between mottle cuttlefish and other five measured areas. The monochromatic just noticeable difference 'JND' was calculated based on difference of longest cone responses using the receptor noise model (for details, see Material and Methods). D, the dichromatic contrast between mottle cuttlefish (red dot in A) and other five measured areas was calculated based on the JND of two loci in the dichromatic space. E, similarly, the trichromatic contrast between mottle cuttlefish (red dot in B) and other five measured areas was computed based on the JND of two loci in the trichromatic space.

or at least mainly this mode for camouflage (Cott, 1940; Cuthill *et al.*, 2005).

Homogeneous background and Uniform body pattern

In a habitat that appears mostly homogeneous as a result of the seasonal growth of a carpet of filamentous algae (Fig. 4A), cuttlefish show a Uniform body pattern. Radiometric measurements from animal and background paralleled each other closely with a peak at approximately 590 nm (Fig. 4B). For the algae at least, this is largely determined by the presence of chlorophyll; the reduction in long wavelength beyond 600 nm is the result of water absorbance (Jerlov, 1976). The luminance and chromatic contrasts calculated based on the visual systems of di- and trichromatic fish predators are shown in Figure 4B as a 'distance'.

The fact that these distances (known as ΔS or the just noticeable difference, JND, in other studies Vorobyev & Osorio, 1998; Kelber *et al.*, 2003) were considerably less than '1'; in all three cases (the

estimated discriminability threshold based on the receptor noise model Vorobyev & Osorio, 1998, and not standard Euclidian distances of a Maxwell triangle, for example) indicates that visual discrimination of both chromatic and achromatic (e.g. luminance) contrast between cuttlefish and algae is likely to be impossible or at least very hard for these potential fish predators. The choice of a ΔS of '1' as a threshold of detectability is discussed elsewhere (Vorobyev & Osorio, 1998). Although to some extent arbitrary and in all cases in need of behavioural proof to confirm, it is the threshold we have chosen here.

In comparison, when cuttlefish switched from camouflage mode to signalling mode, the body patterns changed drastically in the same habitat (Fig. 4C). The radiance spectra of animal and background were distinctly different (Fig. 4D). In addition, both luminance and chromatic contrasts calculated based on the visual systems of di- and trichromatic fish predators were significantly above 1 (i.e. 12–14), suggesting that the male's fourth arm, used as a signal in agonistic bouts, can be seen clearly by conspecifics.

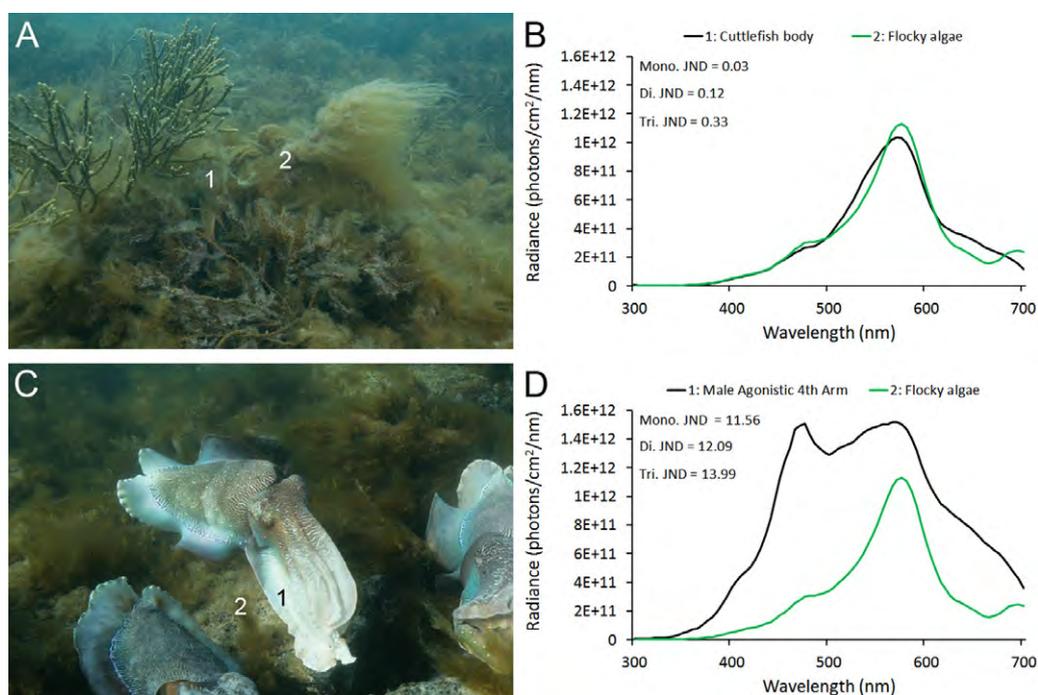


Figure 4. Luminance and colour comparisons between cuttlefish and surrounding algae in two distinct behavioural modes. A, a cuttlefish in camouflage mode. Underwater photograph showing cuttlefish in Uniform body pattern (1) and flocky algae (2) in the habitat, where the spectral measurements were taken *in situ*. B, spectral radiances of cuttlefish body (black) and flocky algae (green). Luminance and chromatic contrasts between cuttlefish and flocky algae as viewed by di- and trichromatic fish predators were computed based on the model shown in Fig. 3. C, a cuttlefish in display mode. Underwater photograph showing a male cuttlefish displaying agonistic fourth arm (1) and flocky algae (2) in the habitat, where the spectral measurements were taken *in situ*. D, spectral radiances of cuttlefish's agonistic fourth arm (black) and flocky algae (green). Luminance and chromatic contrasts between cuttlefish and flocky algae as viewed by di- and trichromatic fish predators were significantly different.

Mixed hetero/homogeneous background and Uniform body pattern

In some environments, there were patches of homogeneous sand with heterogeneous vertical branching algae. Some cuttlefish deployed a Uniform body pattern that appeared to provide quite good camouflage to a human observer or camera (Fig. 5A). The spectral characteristics of animal and background did not all match in absolute radiance (Fig. 5B, top), although the spectral shapes were relatively similar (Fig. 5B, bottom). Pairwise comparisons of luminance and chromatic contrasts between head/arm of cuttlefish and four sampled nearby objects (algae just above head, algae near head, arm of algae, and sand) showed that, although the head/arm did not resemble 'algae near head' in monochromatic luminance contrast (distance of up to 15 in Fig. 5C, top), the chromatic contrast was a good match (JNDs < 1) in the eyes of potential di- and trichromatic fish predators (Fig. 5C). By comparison, the anterior mantle of the cuttlefish showed good colour and luminance resemblance with most of the background features (Fig. 5D). Although not all calculated distances (JNDs) in Fig. 5C, D were below 1, it was mainly the sand or a particularly 'bright green' bit of algae near the head that were worst matches. In general for this situation, these results suggest that cuttlefish with Uniform body patterns achieve similar levels of luminance (or at least fall within the same upper and lower limits) and colour against their backgrounds for camouflage.

Heterogeneous background and mixed Mottle/Disruptive body pattern

On a benthic substrate with small rocks, close-cropped algae, and a few bits of homogenous sand, cuttlefish were in a mixture of a Mottle and Disruptive body patterns (Fig. 6A). The spectral characteristics of animal and some background features varied slightly in amplitude and shape (Fig. 6B, top). Most notably, the radiance spectrum of the distant red algae was visibly different from those of cuttlefish and other natural objects (Fig. 6B, bottom). Pairwise comparisons of luminance and chromatic contrasts between the white mantle bar of the cuttlefish and four sampled nearby objects showed that luminance and colour closely resembled little algae and white shell (both JNDs < 1), but not red algae (30 JNDs for luminance and five or six JNDs for colour) or the grey part of shell (20 JNDs for luminance and three or four JNDs for colour) (Fig. 6C). This latter mismatch is acceptable biologically because the White square is meant to break up the cuttlefish body pattern and to blend with some nearby objects (e.g. represent a random sample of other similarly sized, coloured, and brightness objects) but not others (Hanlon &

Messenger, 1988; Hanlon *et al.*, 2009). By comparison, although the luminance contrasts between dark bar posterior of cuttlefish and all objects were higher, the chromatic contrasts of dark bar posterior compared to little algae and white shell were much lower (Fig. 6D), rendering them indiscriminable in the eyes of potential di- and trichromatic fish predators.

Heterogeneous background and Disruptive body pattern

On a benthic substrate with scattered rocks and surrounding tall vertical algae, cuttlefish showed a Disruptive body pattern (Fig. 7A) with the first two pairs of arms raised vertically (for visual control of body postures, see Barbosa *et al.*, 2012). The most noteworthy result from this image is the wide range in both chromatic and luminance contrasts compared to the other patterns (Fig. 7B).

Pairwise comparisons of luminance contrast between white posterior triangle of cuttlefish and four sampled nearby objects showed that the mismatch in luminance was high for most objects (20–30 JNDs), except the adjacent sand; moreover, colour resemblance was very good for adjacent sand (Fig. 7C). This is a good example of the manner in which the white transverse mantle bar and the white posterior triangle show strong resemblance to the surrounding sand both in colour and luminance, thus rendering those parts of the cuttlefish mantle similar to a feature of the benthic substrate more than other parts of the animal; such a pattern arrangement can achieve what Cott (1940) called 'coincident disruptive coloration' because the light parts of the animal pattern seem contiguous with the substrate.

Conversely, both luminance and chromatic contrasts between anterior dark mantle bar and all objects were high; thus, they may hypothetically be easily discriminated by some potential di- and trichromatic fish predators (Fig. 7D).

DISCUSSION

The present study reports spectrophotometric measurements of camouflaged cuttlefish (*S. apama*) and their surrounding background objects in a field setting. The only other field study to date on *S. apama* signalling or camouflage is that of Zylinski *et al.* (2011), in which intensity differences between cuttlefish body patterns and backgrounds were compared using digital images; however, no spectrophotometric data were collected. In a previous laboratory study, Mäthger *et al.* (2008) investigated the European cuttlefish *S. officinalis* and showed that the reflectance spectra of their skin patterns correlated with the reflectance spectra of the natural substrates they camouflaged on. It was argued that this close

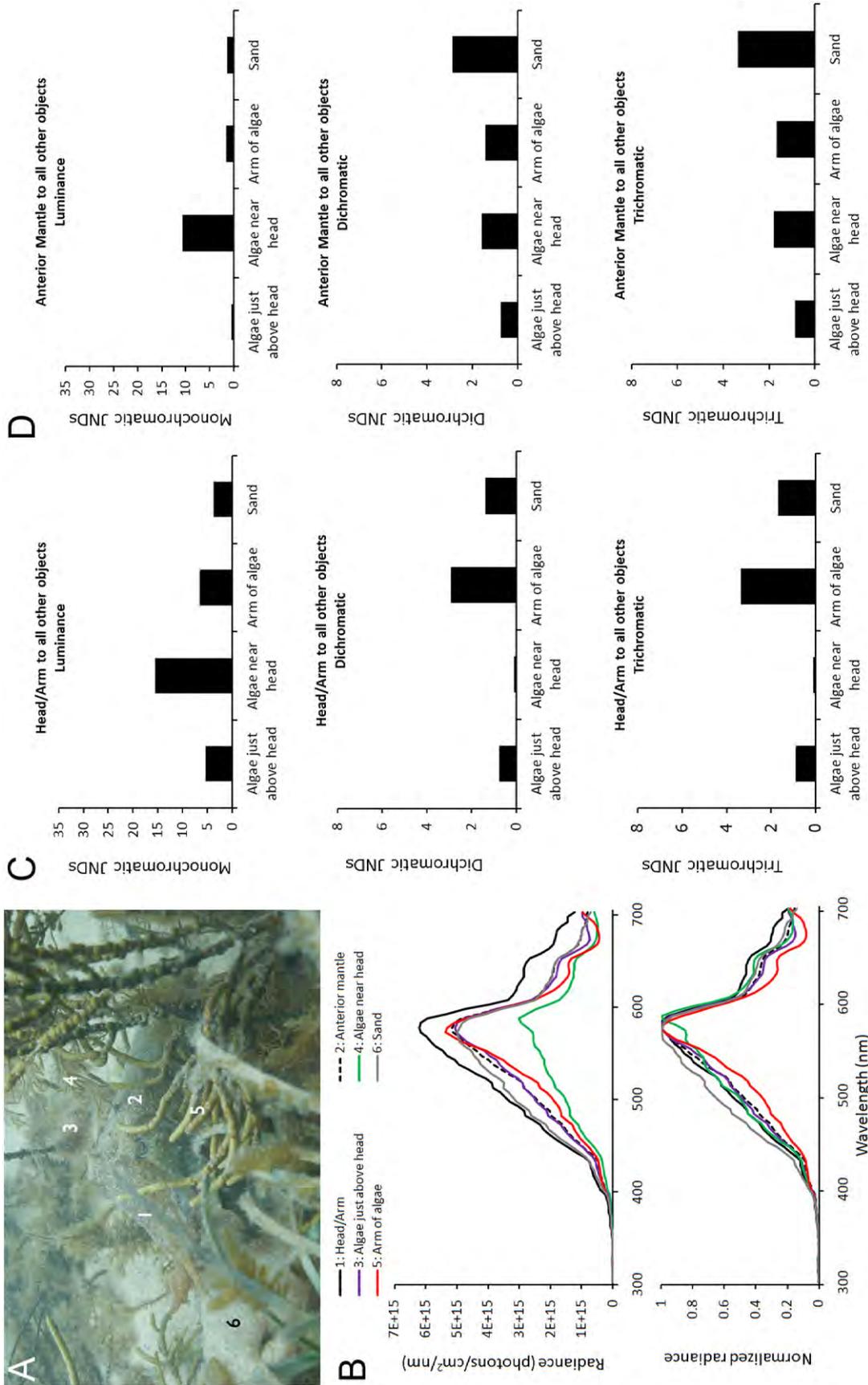


Figure 5. Luminance and colour comparisons in cuttlefish with Uniform body pattern and its surrounding. The corresponding spectral measurements of animal and background were labelled. B, radiance spectra of cuttlefish (black solid and dashed curves) and nearby objects (colour curves). Normalized radiance were also shown for comparison of spectral shapes. C, luminance, di-, and trichromatic contrasts between Head/Arm (#1 in A) and four other objects as viewed by di- and trichromatic fish predators. D, similarly, luminance, di-, and trichromatic contrasts between Anterior Mantle (#2 in A) and four other objects.

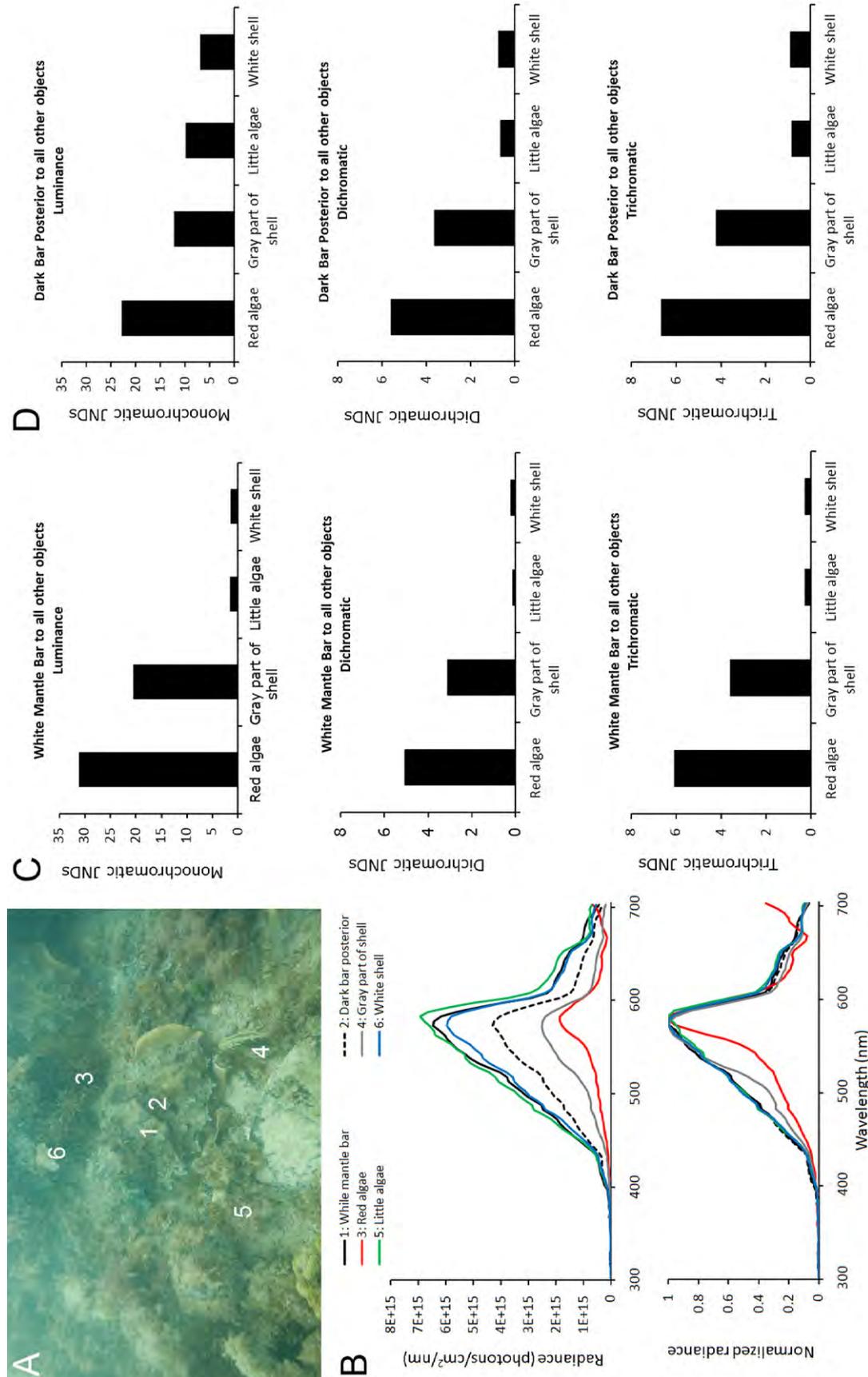


Figure 6. Luminance and colour comparisons in cuttlefish with mixed Mottle/Disruptive body. A, underwater photograph showing a cuttlefish in Mottle/Disruptive body pattern and its surrounding. The corresponding spectral measurements of animal and background were labelled. B, radiance spectra of cuttlefish (black solid and dashed curves) and nearby objects (colour curves). Normalized radiances were also shown for comparison of spectral shapes. C, luminance, di-, and trichromatic contrasts between White Mantle Bar (#1 in A) and four other objects as viewed by di- and trichromatic fish predators. D, similarly, luminance, di-, and trichromatic contrasts between Dark Bar Posterior (#2 in A) and four other objects.

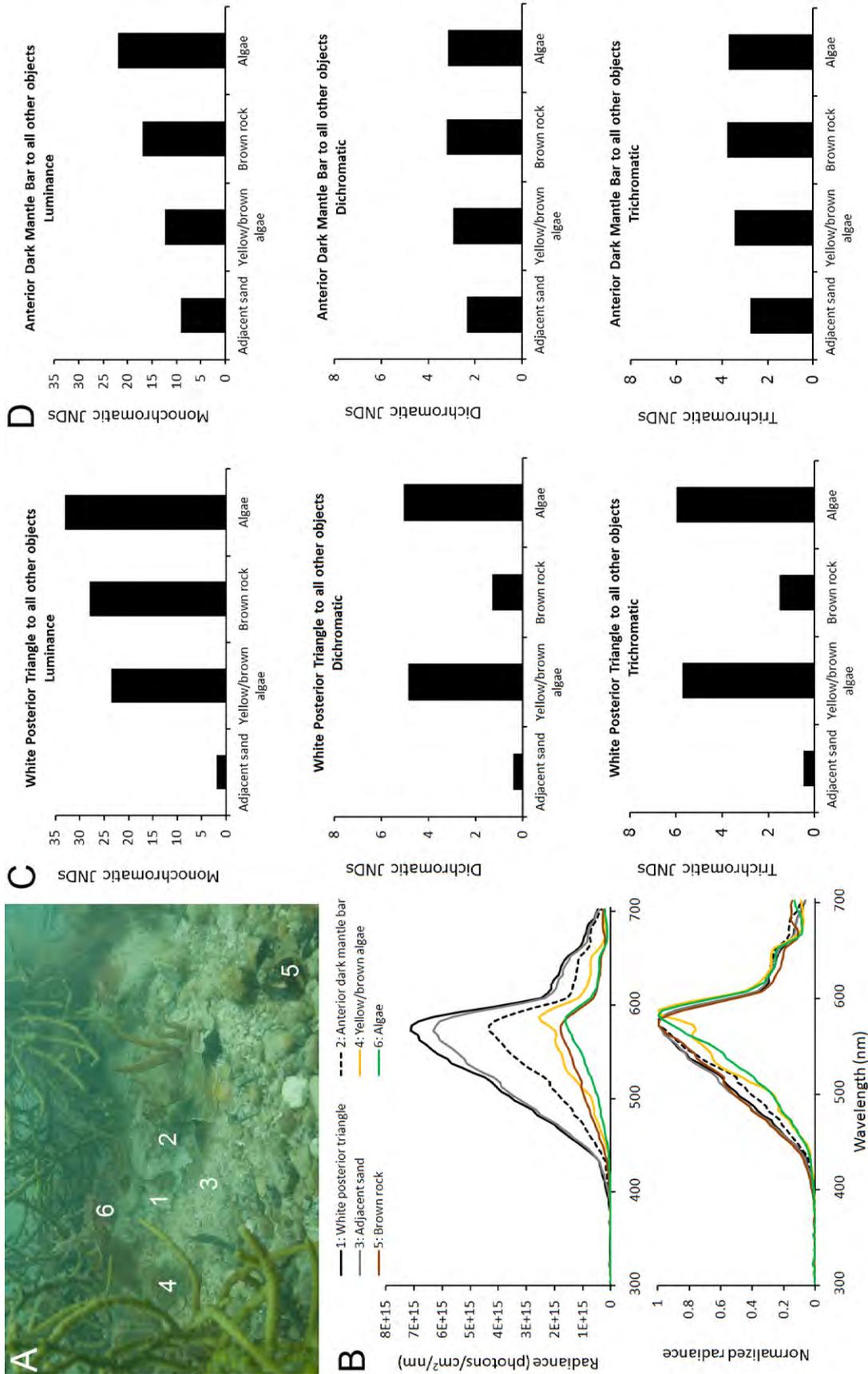


Figure 7. Luminance and colour matches in cuttlefish with Disruptive body pattern in Disruptive body pattern and its surrounding. The corresponding spectral measurements of animal and background were labelled. B, radiance spectra of cuttlefish (black solid and dashed curves) and nearby objects (colour curves). Normalized radiances were also shown for comparison of spectral shapes. C, luminance, di-, and trichromatic contrasts between White Posterior Triangle (#1 in A) and four other objects as viewed by di- and trichromatic fish predators. D, similarly, luminance, di-, and trichromatic contrasts between Anterior Dark Mantle Bar (#2 in A) and four other objects.

correlation may facilitate colour match on natural substrates in the absence of colour vision. In the present study, we expand on the previous studies of Marshall & Messenger (1996) and Mäthger *et al.* (2008) in two ways. First, the previous studies did not consider the predator's visual system in their analysis. Second, the present study was conducted in the animal's natural light field with a fuller array of natural backgrounds.

In the present study, four habitat/body pattern combinations were studied:

1. In a homogenous habitat, *S. apama* showed a Uniform body pattern. Spectral radiance measurements from animal and background were very similar, resulting in low JND values (< 1 ; Fig. 4; note that low JND values < 1 indicate that colours appear very similar to the visual system, high JND values > 1 indicate that colours may appear contrasting; Vorobyev & Osorio, 1998; Vorobyev *et al.*, 2001b), indicating that visual discrimination of chromatic and achromatic differences between cuttlefish and substrate is likely to be difficult or impossible for the potential fish predators chosen in the present study, at least for the components that were measured.
2. On mixed hetero/homogeneous backgrounds on which animals also showed a Uniform body pattern, the chromatic differences between animal and substrate were very low; however, absolute radiance, or luminance, differed more than in the homogenous habitat. This suggests that some parts of the cuttlefish may be discriminable by a monochromatic predator (or indeed another cuttlefish with monochromatic vision), discriminable to the luminance channel but indiscriminable when viewed through the chromatic contrast channel of di- and trichromatic fish predator models (Fig. 5). Without knowledge of how these fish may assign salience to different visual characteristics, we can only suggest that, if they were to look for cuttlefish using a colour-based search system, they would most likely not see them. Also, because the variance in luminance between cuttlefish and substrate was overlapping in this scene, any differences in luminance may be lost in the overall noise of the background. In other words, no part of the cuttlefish was remarkably lighter or darker than the background, thus rendering it well camouflaged.
3. On a heterogeneous background on which a mixed Mottle/Disruptive body pattern was shown, the spectral characteristics of *S. apama* and some background features differed very little, except for one background feature: a clump of red algae was notably different from the other spectra (Fig. 6). In

this habitat/body pattern combination, we found that some body areas closely resembled some background features (both chromatic and luminance contrasts were low) when viewed through the eyes of the predator models that we chose (JNDs < 1), although some body areas were markedly different, with JNDs as high as 7 (Fig. 6), suggesting that potential predators with visual systems similar to the ones modelled in the present study may be able to discriminate them from their backgrounds. It is interesting that the white mantle bar and the posterior dark mantle bar of the cuttlefish extend the full width of the cuttlefish (whose head is to the left) and tend to break up the continuity of the longitudinal axis of the body. Again, although our results suggest a higher degree of potential conspicuousness of some body parts (both in chromatic and luminance information in this scene), the variability in both colour and luminance of cuttlefish and background was similar (with the exception of the dark red algae; an unusually coloured object in this habitat). The end result appears as effective camouflage to a human observer.

4. On a heterogeneous background on which a Disruptive body pattern was shown, the most remarkable finding was the variation in luminance. Spectral differences were moderate but the mismatch in luminance was very high for most objects (except sand; Fig. 7), suggesting that some areas could easily be discriminated by potential di- and trichromatic fish predators. However, there are some components of the pattern that match nearby objects and some that do not, and this will present a disjunct arrangement that could hypothetically retard recognition by some predators.

Taken together, we found relatively small chromatic differences between animal and background (with some exceptions of infrequent objects such as bright red algae), or observed that the variation between these characteristics within the animal and within the scene was overlapping, indicating good overall colour resemblance (a result similar to the laboratory studies of Marshall & Messenger 1996 and Mäthger *et al.*, 2008; as well as the field study of Akkaynak *et al.*, 2013). As stated initially, we are deliberately avoiding any determination of which visual mechanism of camouflage we are describing but rather aim to quantify some of the variables.

Overall, it appears as though the camouflage of *S. apama* in its natural habitat is good insofar as we can measure it with currently available technology, and with simulations of potential fish predators. Although the 'degree of camouflage' of these cuttlefish is probably not better than many other camouflaged

animals, it is noteworthy that cuttlefish achieve this apparent effectiveness upon changing each time that they settle in a different microhabitat as they exercise their refined rapid neural polyphenism. The new technology of hyperspectral imaging is coming available to field researchers in the near future. Chiao *et al.* (2011), using a commercially available slow-exposure hyperspectral imaging under controlled laboratory conditions, showed that, in the eyes of hypothetical predators, *S. officinalis* had good colour match compared to their backgrounds. We and others will be able to advance the understanding of camouflage mechanisms when hyperspectral imaging field instruments are deployed in aquatic and terrestrial habitats, mainly because so many small or large objects in the background can be measured and compared pixel by pixel with components of the animal's pattern.

What is noticeable in the present field study is the increasing variation in luminance contrast between some body pattern components and their relative backgrounds for animals putting on increasingly Disruptive body patterns (i.e. the sequence shown in Figs 4, 5, 6, 7). This is an interesting finding because it suggests that disruptive patterns, which rely on distinct mechanisms for defeating detection and recognition by predators, may not need to achieve the same level of luminance similarities compared to their backgrounds as do colours used in Mottle or Uniform body pattern for general resemblance. Although at first this may appear counterintuitive, it has been shown that concealment may be enhanced by the involvement of otherwise conspicuous patterns (Schaefer & Stobbe, 2006; Stevens *et al.*, 2006; Stevens & Merilaita, 2009b; Dimitrova & Merilaita, 2010).

Although disruptive patterns in animal taxa may be most effective when all of the components match the background well, a combination of disruptive coloration and crypsis is more effective than either one on its own (Stevens *et al.*, 2006), which is a prediction already made by Thayer (1909) and Cott (1940). Disruptive patterning may enable an animal to remain cryptic on visually diverse backgrounds because disruption does not rely solely on obstructing detection (i.e. matching specific objects of any particular habitat) but is considered to interfere with recognition by the predator. Moreover, it may allow an animal to possess some conspicuous markings at the same time as remaining camouflaged. By placing such markings disjunctly and combining them with background-matching colours, the animal still maintains some level of crypsis (Stevens *et al.*, 2006), and the results reported in the present study and by Hanlon *et al.* (2009) suggest that the cuttlefish *Sepia* may be utilizing these dual mechanisms, although

this awaits experimental confirmation (as it also does in other animal taxa).

Schaefer & Stobbe (2006) suggest that, for disruptive patterns, chromatic contrast may be more important than achromatic contrast with respect to avoiding predation and that this may explain why many insects and reptiles have more chromatic than achromatic patterns. By contrast, Stevens *et al.* (2006) showed that bird predators rely on achromatic contrast more than chromatic contrast when detecting prey. This may differ from species to species.

We found evidence for higher achromatic than chromatic contrast in *S. apama* camouflage patterns (mainly Mottle and Disruptive); does this mean that cuttlefish camouflage takes advantage of a potential weakness in the visual capabilities of their predators? That is, this apparent 'relaxation' in luminance matching may also be the result of the way visual systems work once they evolve towards colour vision. Many animals with colour vision are less effective at learning or categorizing grey shades because it appears that the information required for such tasks is more reliable through colour channels (Kelber *et al.*, 2003). This means that a cuttlefish attempting to camouflage with both colour and luminance details may need to invest less energy with respect to an exact resemblance in the luminance domain than to the colour matches because their main predators are more sensitive to colour but less sensitive to contrast differences. We suggest that this is why cuttlefish camouflage is so successful, especially to our eyes, which are certainly biased towards colour (Zeki, 2000).

Maximov (2000) has gone so far as to suggest that colour vision (i.e. the use of at least two spectral channels) evolved in shallow-water habitats to account for variability and inconsistencies in this continually flickering light field. Waves produce the flicker and two spectrally offset channels can subtract this noise from a scene, leaving behind the main details and not the luminance variations. This also argues that it is spectral matches (and not luminance matches in a luminance-noisy background) that are more important.

One additional fact may explain the low chromatic contrast in cuttlefish camouflage. With increasing depth, underwater daylight becomes more and more confined to the blue-green parts of the spectrum (Tyler & Smith, 1970; Jerlov, 1976). In such a light field, using colour as a reliable information channel becomes harder, except for some subtle spectral differences within the available blue-green waveband. Because of this, many marine habitats are not very rich spectrally, with the exception of some shallow water habitats, where the white light field has not

undergone extensive spectral filtering (notably the coral reefs, McFarland & Munz, 1975; Chiao, Cronin & Osorio, 2000; Hochberg & Atkinson, 2000; Marshall, 2000b; Marshall *et al.*, 2003a; Hochberg *et al.*, 2004). At greater depths, intensity matching would be a more effective camouflage tactic (Cott, 1940; Denton & Nicol, 1966; Lythgoe, 1979; Johnsen, 2001). It also remains to be determined whether deeper-living cuttlefish or other cephalopods also become better at luminance matching with depth.

As we do not know the exact absorbance spectra of the predator's visual pigments, or indeed the array of predators for *S. apama*, the analysis reported in the present study is hypothetical and should be repeated once visual pigment data of specific predators become available. Furthermore, although shifting λ_{\max} of the hypothetical cone spectral absorbance by ± 10 – 20 nm did not affect the results (data not shown), we did not include a theoretical ultraviolet (UV) visual pigment in our calculations. Cheney *et al.* (2009) showed that predators with colour vision (but lacking UV vision) were unable to discriminate between the colours of the mimic fish and the models these mimic fish were resembling. However, fish with a UV-sensitive visual pigment were better at discriminating between the mimics and their models. It is not likely, however, that the necessarily relatively large predators of *S. apama* possess UV vision because this is generally an attribute in smaller fish species (Siebeck & Marshall, 2001).

Another variable worthy of investigation is the distance at which a prey animal is viewed. Intuitively, the farther away a stimulus, the less likely it is to be perceived, especially where a breakdown in resolution results in combination of features that might be distinct closer up (Collin & Pettigrew, 1989; Marshall 2000a, b). Defrize, They & Casas (2010) found that crypsis of crab spiders was excellent at a longer distance but, at a shorter distance, it was poor when modelled through the eyes of bird and insect predators. In another study (They, *et al.*, 2005), chromatic contrast (used for short-range detection) between a spider and the flower that it was camouflaging on was compared with the detection thresholds of the spider's insect prey and their bird predators. The same study also computed achromatic contrast, used for long-range detection. For both visual systems, each spider was efficiently matching the colour of the flower on which it was camouflaged, demonstrating the importance of considering distance in the interpretation of animal camouflage. Underwater, colour and contrast break down much faster than on land (Marshall & Johnsen, 2011) and one problem we experience as terrestrial visitors to the underwater realm is that we bring not only our colour vision type, but also our highly acute visual system for viewing long distances

in air. Underwater, it is rare that water clarity allows long distance vision and many animals living there have an at least ten-fold poorer spatial acuity than humans (Collin & Pettigrew, 1989) and this may mean that coloured parts of animals actually combine over visual distance (Marshall, 2000b; Marshall & Johnsen, 2011). Compounding these problems, the scattering and absorptive quality of water (Jerlov, 1976; Stramska *et al.*, 2000) again degrades the image quality both in terms of detail as well as colour and luminance contrast.

Cephalopods may be the most impressive colour-changing animals but they do not present the only example. Chameleons change colour for a variety of reasons, such as thermoregulation, camouflage, and communication. In the dwarf chameleon, the camouflage body patterns are even tailored to the visual system of the predator that they are aiming to avoid (Stuart-Fox *et al.*, 2006, 2008; Stuart-Fox & Moussalli, 2009). Thus far, we do not fully understand the specifics of cephalopod camouflage body patterns in response to different predators. In a recent study (Langridge, Broom & Osorio, 2007; but see also Hanlon & Messenger, 1988), it was reported that cuttlefish (*S. officinalis*) respond differently to different predators, although only signalling and flight responses were described, rather than camouflage body patterning. Camouflage patterns in cuttlefish (*S. officinalis*) show some subtle variations (Hanlon *et al.*, 2009): do these target the visual systems of the predators they are trying to deceive? More field observations are needed to answer this question. Furthermore, as more information on predator visual systems is gathered and new technologies become available (such as hyperspectral imaging), we can refine our modelling approaches and improve our understanding on the mechanisms of cephalopod adaptive camouflage body patterning.

One of the shortcomings of the present study (as indeed is the case for much work investigating detection and camouflage) is that we have simply taken snapshots, literally, of a moving world in which light is changing often. The visual systems of many animals, especially predators, are adapted exquisitely to movement detection and some camouflage patterns may perform better than others with respect to hiding their owners in this world of visual motion.

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