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REGULAR ARTICLE

Malleable skin coloration in cephalopods: selective reflectance, transmission and absorbance of light by chromatophores and iridophores

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Abstract Nature's best-known example of colorful, changeable, and diverse skin patterning is found in cephalopods. Color and pattern changes in squid skin are mediated by the action of thousands of pigmented chromatophore organs in combination with subjacent light-reflecting iridophore cells. Chromatophores (brown, red, yellow pigment) are innervated directly by the brain and can quickly expand and retract over underlying iridophore cells (red, orange, yellow, green, blue iridescence). Here, we present the first spectral account of the colors that are produced by the interaction between chromatophores and iridophores in squid (*Loligo pealeii*). Using a spectrometer, we have acquired highly focused reflectance measurements of chromatophores, iridophores, and the quality and quantity of light reflected when both interact. Results indicate that the light reflected from iridophores can be filtered by the chromatophores, enhancing their appearance. We have also measured polarization aspects of iridophores and chromatophores and show that, whereas structurally reflecting iridophores polarize light at certain angles, pigmentary chromatophores do not. We have further measured the reflectance change that iridophores undergo during physiological activity, from "off" to various degrees of "on", revealing specifically the way that colors shift from the longer end (infra-red and red) to the shorter (blue) end of the spectrum. By demonstrating that three color classes of pigments, combined with a single type of reflective cell, produce colors that envelop the whole of the visible spectrum, this study provides an insight into the optical mechanisms employed by the elaborate skin of cephalopods to give the extreme diversity that enables their dynamic camouflage and signaling.

Keywords Color change · Spectral reflectance · Polarization · Body pattern · Squid, *Loligo pealeii* (Mollusca Cephalopoda)

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Introduction

Cephalopods (squid, cuttlefish, octopus) show an extensive repertoire of body patterns for camouflage and signaling (Hanlon 1982; Hanlon and Messenger 1988, 1996; Moynihan 1985; Packard 1972; Packard and Hochberg 1977). These body patterns are mediated by the dual action of thousands of chromatophores, which are small pigmented organs (subjectively classified into two or three color classes per species: red, yellow/orange, and brown/black), and by light-reflecting cells (iridophores and leucophores; Cloney and Brocco 1983; Hanlon and Messenger 1996; Messenger 2001).

Chromatophores have attached to them dozens of radial muscles that are innervated directly by the brain, and by contracting and relaxing these muscles, the pigmented sac of a chromatophore increases or decreases in area (Florey 1969). The size of chromatophores varies among species. In squid, such as *Loligo plei*, an expanded chromatophore may have a diameter of up to 1.5 mm, whereas a retracted chromatophore may measure as little as 0.1 mm (Hanlon 1982; see also Fig. 1a). Expansion and retraction of distinct groups of chromatophores enables cephalopods to produce an array of body-patterning components, such as bands,

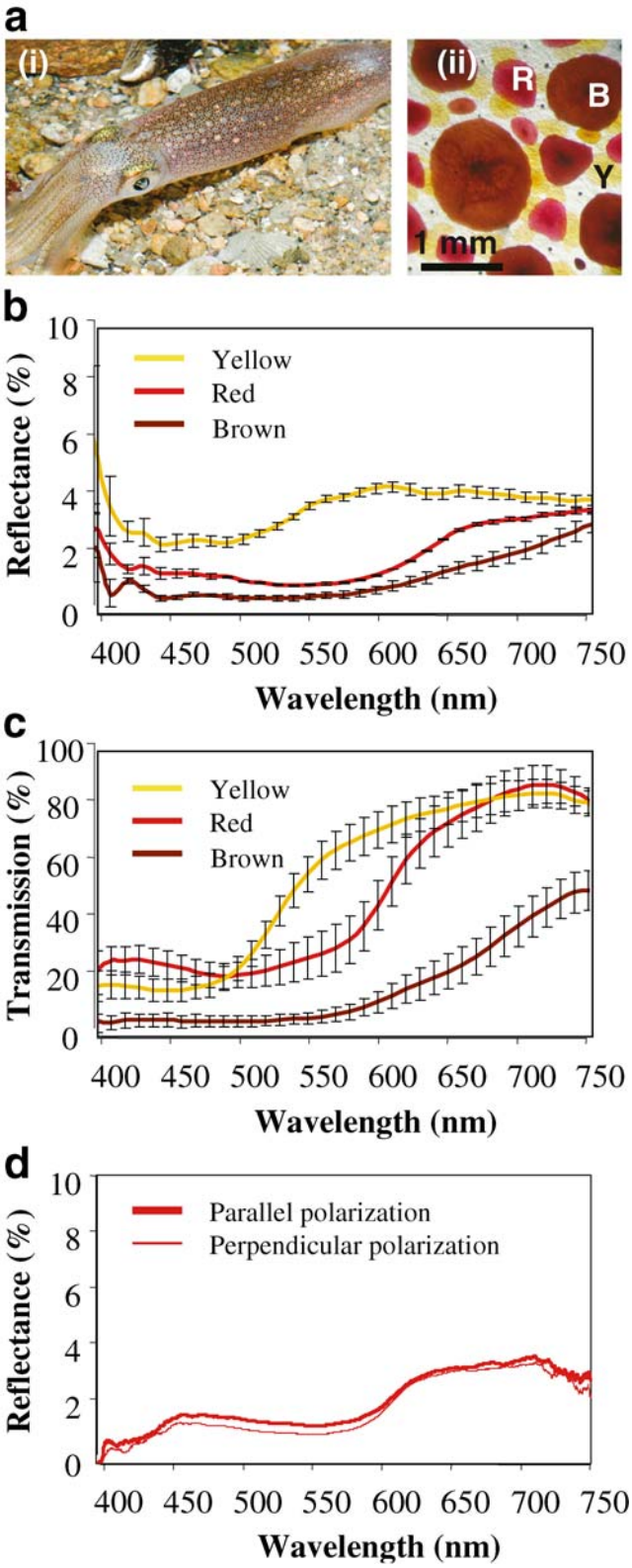
stripes and spots (see, for example, the repertoire of the subject of this study, *Loligo pealeii* (Hanlon et al. 1999); an image of the squid is shown in Fig. 1a).

Importantly, however, cephalopod skin has another system that interacts with light: the various types of structural reflectors that lie subjacent to the pigmented chromatophore organs (Cloney and Brocco 1983). Squid generally only have iridophores. These are colorless cells of variable sizes, generally smaller than 1 mm (Mirow 1972b). They are made up of stacks of thin plates that reflect light by thin-film interference (Denton and Land 1971; Land 1972; Mäthger et al. 2004; Mäthger and Denton 2001). The light reflected from a multilayer reflector of this kind is almost always colored. Two pre-requisites are that (1) there is a difference in refractive index between the plates and the spaces separating them, and (2) the plates and spaces have thicknesses comparable to the wavelength of light. The mechanism of reflectance is the same as that of colored soap bubbles (Boys 1959).

Light reflectance from iridophores can be changed by applications of acetylcholine (ACh) acting on muscarinic cholinergic receptors, and changeable reflectance has been observed in living squid (Cooper and Hanlon 1986; Cooper et al. 1990; Hanlon 1982; Hanlon et al. 1990; Mäthger et al. 2004). However, in contrast to chromatophores that can change within a fraction of a second, changes in iridophore reflectance take longer, e.g., several seconds to minutes. In the loliginid squid *Lolliguncula brevis*, Cooper and Hanlon (1986) have reported that the reflected wavelengths shift from the long (red) end of the visible spectrum to the shorter (blue/ultraviolet [UV]) end with increasing concentrations of ACh. To date, the way that this wavelength change is achieved remains unknown. Recent evidence has provided confirmation that the plates of squid iridophores are made up of proteins called reflectins (Crookes et al. 2004; see also Cooper et al. 1990). Cooper et al. (1990) have pointed out that a protein state change (affecting refractive index) combined with a change in the thickness of plates could explain the observed changes in reflectance.

Iridophores are located in a distinct layer beneath the chromatophores (Hanlon and Messenger 1996; Williams 1909). The appearance of the animal thus depends on which skin elements affect the light incident on the skin. Light may be reflected by either chromatophores or iridophores, or a combination of both, and the physiological changeability of chromatophores and iridophores thereby enables the skin to produce such impressive optical malleability.

We present the first quantified measurements of different wavelengths that can be recorded at the surface of squid skin. In previous publications, we, and others, have looked at some aspects of squid coloration caused by either iridophores or chromatophores, or otherwise on a grosser scale of observation (Cooper and Hanlon 1986; Cornwell et al. 1997; Hanlon 1982; Hanlon et al. 1990, 1999; Mäthger and Denton 2001; Mirow 1972a, b). However, to date, no



documentation exists regarding the detailed nature of the optical interactions between the pigmentary and structurally reflecting skin elements.

Materials and methods

Specimen preparation

Squid (*Loligo pealeii*), found in coastal waters around Cape Cod, were caught by trawls and held in an open sea water system at the Marine Resources Center (MBL, Woods Hole, USA). For skin measurements, squid were killed by decapitation. Small specimens of mantle tissue with intact skin were dissected and pinned onto the Sylgard covered dish of a goniometer, thereby allowing 3-dimensional positioning of the tissue.

Squid skin is highly elastic. Hence, if the mantle tissue is left attached to the skin, it ensures that the skin elements retain their natural orientations within the tissue.

Spectral measurements of skin components

Spectral reflectance and transmission measurements were obtained by using a fiber optic spectrometer (USB2000, Ocean Optics, USA; spectra recorded on PC, using OOIBase 32 software, which automatically plotted reflectance) connected, via a 1-mm-diameter fiber, to the c-mount of a dissecting microscope (Zeiss; angle of acceptance: 13°). At the highest magnification of the microscope, the area of the measured field was approximately 0.3 mm in diameter. Illumination was provided by a Schott fiber-optic microscope-light source. The spectral range of measurements was limited from 400 nm to 800 nm, mainly because the microscope optics absorbed wavebands outside this range. Measurements in the UV and infra-red (IR) part of the spectrum were taken without use of the microscope. Instead, optical fibers were held in place by micromanipulators. To take measurements in the UV part of the spectrum, we illuminated skin samples with a xenon light source (PX-1, Ocean Optics, range 200–750 nm). Illumination for IR measurements was provided by a tungsten halogen light source (LS-1, Ocean Optics, range 360–2000 nm). A diffuse reflection standard (WS-1, Ocean Optics) was used to standardize measurements.

For transmission measurements of chromatophores, chromatophore layers were dissected, pinned out to original size in a Petri-dish filled with Sylgard, and placed over a diffuse glass plate and into a beam of light reflected directly into the microscope by using a mirror. Brown and red chromatophores (approximately 1–1.5 mm diameter fully expanded) were larger than yellow chromatophores. Therefore, we could measure single brown or red chromatophores but were not always able to measure single yellow chromatophores. Instead, groups of 2–3 yellow chromatophores were measured. We ensured that only yellow chromatophores were expanded, and that the overlap between chromatophores was minimal (less than 10% of area), so that the effects on reflectance and transmission were negligible.

For polarization measurements, a linear polarizer (Jessop, UK) was placed under the microscope and turned to analyze polarization from the specimen.

Results

Chromatophore reflectance and transmission properties

In *Loligo pealeii*, as in most other loliginid squid, there are three long-wavelength classes of chromatophores (previously described as brown, red, and yellow; Fig. 1a,b). Spectral measurements of reflectance properties of expanded chromatophores are shown in Fig. 1b. In the long-wavelength band (above 550 nm), all three color classes of chromatophores reflect less than 5% of incoming light. In the shorter wavelengths (below 550 nm), light is heavily absorbed; reflectance is as low as 1% (Fig. 1b). Most of the light incident on chromatophores is transmitted through the pigment to the underlying iridophores. For yellow and red chromatophores, transmission between 550 nm to 700 nm may be as high as 70%–90%. Brown chromatophores transmit less light in comparison; between 700–750 nm, this may be as little as 20%–30% (Fig. 1c). The amount of light reflected or transmitted depends critically on the relative expansion of the chromatophore pigment sac. Light reflected from all three color classes of chromatophores is unpolarized, i.e., light is reflected equally well in both planes of polarization (Fig. 1d for red chromatophore; data for yellow and brown not shown).

Only chromatophores considered to be expanded have been measured in this study. When chromatophores are retracted, more unfiltered light is transmitted through the skin to the underlying iridophores. So far, we have been unable to take spectral measurements of chromatophores in a retracted state.

◀ **Fig. 1** **a** (*i*) Squid (*Loligo pealeii*) chromatophores and reflective iridophores. (*ii*) Brown (*B*), red (*R*), and yellow (*Y*) chromatophores in transmitted light. **b**, **c** Spectral reflectance (%) and transmission (%) measurements, respectively, of yellow, red, and brown chromatophores (n=8 for each color class). *Bars* indicate SE of the mean. **d** Spectral measurements of reflected light in both planes of polarization (90 degree angle to each other) for a red chromatophore, showing that reflected light is unpolarized, i.e., light is reflected equally well in both planes of polarization

Iridophore reflectance properties

One of the key features in squid skin coloration is the iridescence produced by light-reflecting iridophores. These are found in a distinct layer all over the body and may appear dimly or brightly iridescent red, green, or blue. All iridophores have similar optical properties. (1) With increasing angle of incidence, the wavelengths of the reflected light shift toward the shorter (blue/UV) end of the spectrum (Fig. 2a,b). (2) At oblique angles of incidence, the reflected light is linearly polarized. Polarization is maximal at 45–50° incidence (as predicted by Brewster's law; i.e., angle of maximal polarization; Fig. 2b).

The wavelengths reflected by iridophores vary widely. For example, in *L. pealeii*, "splotches" of reddish pink (viewed at normal incidence) occur on the dorsal mantle: however, spectrometer measurements reveal variations from deep red (above 700 nm) to orange and almost yellow (approximately 600 nm). As has been shown before, iridophore reflectance is physiologically active, with ACh acting on muscarinic cholinergic receptors (Hanlon et al. 1990; Mäthger et al. 2004). In Fig. 2c,e,f, we provide the first spectral measurements of this change. Images of this change are illustrated in Fig. 2d, in which a non-reflective iridophore patch (i) turns reflective after applications of 1 mM ACh: first red (ii), then orange (iii), and finally yellow (iv). Figure 2c shows an iridophore reflecting red light (approximately 640 nm), in the process of "turning off" of its own accord; this involves a shift in reflected wavelengths toward the longer (IR) end of the spectrum and a subsequent decrease in overall reflectance. The iridophores reflect wavelengths around 705 nm before turning off completely.

In the example shown in Fig. 2e, applications of 1 mM ACh cause a splotch of red-reflecting iridophores to undergo an approximately 60-nm shift toward the shorter end of the spectrum and a doubling of absolute reflectance. Iridophores of the collar region reflect weakly in the IR part of the spectrum when visually "turned off". Applications of ACh cause these iridophores to "turn on" with wavelengths shifting from approximately 800 nm to 670 nm (Fig. 2f).

Iridophores appear not to reflect in the UV part of the spectrum.

Chromatophore-iridophore interactions

Chromatophores have the ability to expand over underlying iridophores thereby changing the optical appearance of the skin. Following reflectance from an iridophore, light passing upward through a chromatophore is filtered (i.e., partially absorbed), thus altering the reflectance spectrum of the iridophore and adding to the light reflected from the chromatophore. This interaction makes the chromatophore appear brighter, in some instances giving rise to a color that neither chromatophore nor iridophore alone is capable of producing. As shown above, because of their structural nature, iridophores can reflect almost any waveband of the visible spectrum from deep red to near-UV. Three color classes of chromatophores cover the body of a squid, and thus a variety of iridophore-chromatophore combinations are possible, but only a few examples are given here.

Figure 3a illustrates one combination of a yellow chromatophore covering greenish-blue iridescent iridophores. Line 1 (peak 530 nm) shows the reflectance of the iridophores alone. Line 2 represents a yellow chromatophore alone (peak 575 nm). Line 3 demonstrates the interactive effects: the spectrum of the iridophore shifts toward that of the chromatophore (peak 595 nm), greatly enhancing its appearance. In Fig. 3b, a red chromatophore (line 2) covering an orange-reflecting iridophore (peak at 630 nm; line 1) is shown. Although not as pronounced as the previous example, the spectral change (peak at 670 nm; line 3) is nevertheless noticeable. In Fig. 3c, a yellow chromatophore (line 2) covers a red iridophore (peak at 680 nm; line 1). Here, the peak wavelength is not shifted as the chromatophore covers the iridophore, but the spectrum becomes broader, and the color appears as orange. Figure 3d shows an interesting color combination that is not possible to produce by iridophores or chromatophores alone. A red chromatophore covering a blue iridophore (red iridophore at 50° incidence, see Fig. 2a,b) results in the appearance of a purple color. The peak wavelength of the blue iridescence (line 1, 470 nm) is greatly reduced, whereas the long wavelength part of the reflectance (630 nm–750 nm) is retained.

Brown chromatophores transmit little to no light. Therefore, their function may be to block, rather than modify, reflectance from iridophores.

Discussion

The rapid color change found in cephalopods is unique in the animal kingdom. Most animals only have one available body pattern; this may undergo seasonal or ontogenetic changes but more often stays the same throughout the life of the animal (Cott 1940; Edmunds 1974; Booth 1990). Although most animal body patterns may not be changeable, some are highly reflective, such as those of many birds (Cuthill et al. 1999; Osorio and Ham 2002; Vorobyev et al. 1998) and reef fishes (Marshall 2000). In most animals with changeable body patterns, these changes generally take several seconds, hours, or even days (e.g., fish: Fujii 1993; Kasukawa et al. 1987; Lythgoe and Shand 1989; lizards: Hadley and Oldman 1969; Taylor and Hadley

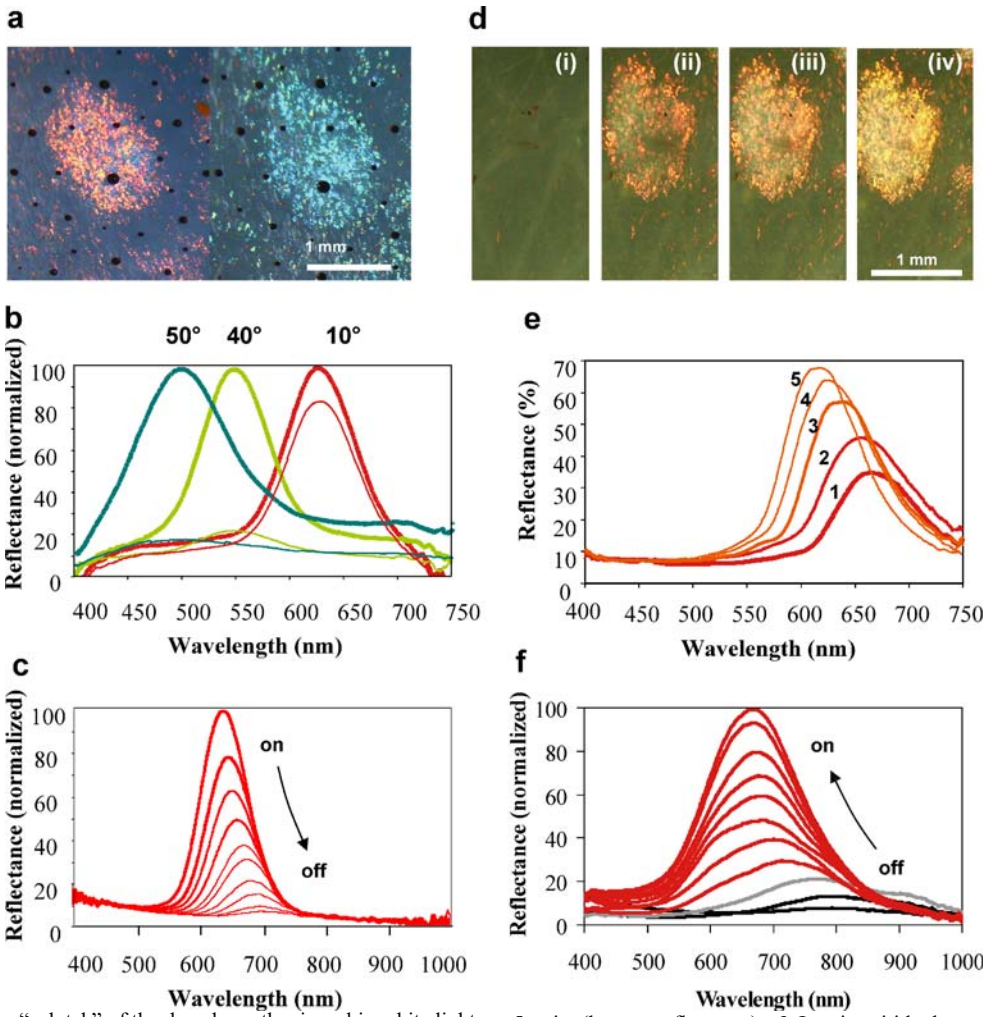


Fig. 2 **a** Iridophore "splotch" of the dorsal mantle viewed in white light at near-normal incidence (*left*, *red*) and at approximately 50° incidence (*right*, *blue*). **b** Reflective measurements for both planes of polarization of a dorsal iridophore splotch, reflecting red at near normal incidence (10°). At 40° incidence, the color is greenish-yellow at a peak wavelength of approximately 550 nm; at 50°, the color is blue-green at a peak wavelength of approximately 500 nm (*thick line* parallel plane, *thin line* perpendicular plane of polarization). At near normal incidence (10°), reflected light is almost unpolarized; at oblique angles, polarization is strong. **c** Spectral measurements of an iridophore patch in the act of "turning off". Peak wavelength at the beginning of the measurement is 640 nm. Measurements were taken at 0 min (highest reflectance), 30 s, 1 min, 1 min 30 s, 2 min, 2 min 30 s, 3 min, 3 min 30 s, 4 min, and 5 min (lowest reflectance). **d** In vitro iridophore color change after application of 1 mM acetylcholine (ACh). Images were taken at 20-s intervals. Iridophores change from non-reflective (*i*) to orange (*iv*) within 1 min. **e** Reflective changes resulting from ACh application. Measurements taken at 15-s intervals (*curve 1* before ACh, *curve 2* 15 s after ACh application, *curve 3* 30 s after ACh application, *curve 4* 45 s after ACh application, *curve 5* 1 min after ACh application; cf. **c**). **f** Reflective changes resulting from ACh application (1 mM). Before ACh application, iridophores are non-reflective (*black line* infra-red reflectance invisible to the human eye). Iridophores then move through the infra-red part of the spectrum (800–750 nm) before reflecting red light visible to the human eye. Measurements taken at 30-s intervals. Highest reflectance measured after 5 min: 670 nm

1970; tree frogs: Stegen et al. 2004). One known exception may be the paradise whiptail (*Pentapodus paradiseus*), a tropical fish whose reflective changes are fast (i.e., fractions of a second; Mäthger et al. 2003).

To our knowledge, this is the first study that examines, at a microscopic level, the interactions between pigments and structural reflectors of any animal. In fish, coloration and patterning are also produced by several structures in the skin (chromatophores, leucophores, iridophores); a descriptive account of these interactions can be found in Fujii (1993). However, no spectral measurements are given. Several authors have tackled the optical properties of cephalopod iridophores and chromatophores individually, but we stress that the dynamically changing interactions of pigmentary and structural color are the keys to understanding the optical malleability of cephalopod skin.

First, we have confirmed previous findings that squid iridophores act as multilayer reflectors, as described in Land (1972) and Mäthger and Denton (2001). Because of their structural nature, iridophores can reflect almost any waveband of the visible spectrum from deep red to near-UV. Moreover, the wavelengths of iridescence can be

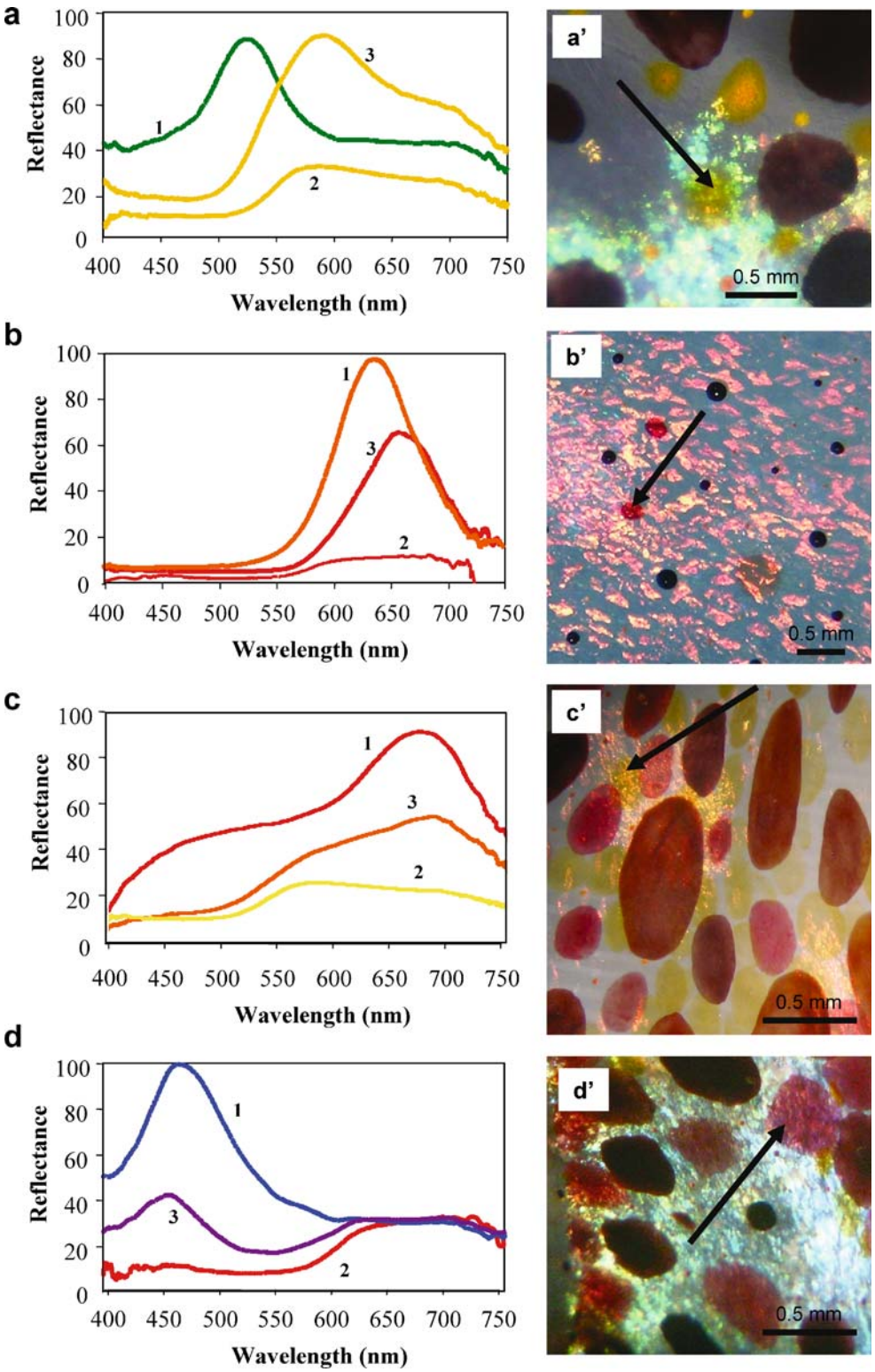


Fig. 3 Spectral measurements and corresponding images of chromatophores covering iridophores, showing the resultant spectral shift (*curve 1* reflective spectrum of iridophores only, *curve 2* chromatophore only, *curve 3* chromatophore over iridophores, *arrows* location of measurement). **a** Yellow chromatophore over green iridophores. **b** Red chromatophore over pink iridophores. **c** Yellow chromatophore over pink iridophores. **d** Red chromatophore over blue iridophores

changed swiftly under physiological control and can also be turned on and off; such delicate changes nevertheless greatly affect the gross appearance of the skin. Three color classes of chromatophores cover the body of *L. pealeii* (yellow, red, and brown). Thus, a variety of iridophore-chromatophore color combinations are possible, even though we have only given a few examples here. Generally, red and yellow chromatophores transmit much of the incoming light (Fig. 1b,c) and therefore play an important role in modulating iridescence. Brown chromatophores transmit less light in comparison, especially when only partially expanded, and their function may be (1) to block

iridescence and polarization and (2) to produce the darkest aspect of gross patterning in body coloration. From our results, we conclude that the combination of the three pigmentary colors (red, yellow, and brown), combined with multilayer reflectors, enables squid to reflect any wavelength of visible light. Reflectance in the IR part of the spectrum has only been found in the collar region of the mantle. The biological function that this may have is unknown, since squid eyes are not sensitive in the IR (Morris et al. 1993). Furthermore, IR light is absorbed heavily by water (Jerlov 1976) and may not be available for reflectance.

Interestingly, polarized light reflected from iridophores is not depolarized when it passes through the pigmented chromatophores, a recent finding (Mäthger and Hanlon 2006) suggesting that this may be a private communication channel that might reach an intended receiver while the animal is camouflaged by using pigmented chromatophores.

We have used squid as a model to study the interactions between chromatophores and iridophores, primarily for reasons of simplicity. *L. pealeii*, like other *Loligo* spp. (Hanlon 1982), have large chromatophores whose density in the skin is low; furthermore, the dermal layers of chromatophores and iridophores are easily separated by dissection. The skin of octopus and cuttlefish is similar, although more complicated in structure, because the density of chromatophores and various reflecting cells is much greater (Hanlon 1988; Packard and Hochberg 1977). The layers are not structured as clearly, and in addition, octopus and cuttlefish have light-scattering leucophores that produce whiteness in the skin (Cloney and Brocco 1983; Froesch and Messenger 1978; Hanlon and Messenger 1988). To date, no spectral data are available for the interaction between the skin components of cuttlefish and octopus, but the general principles that we report here for *L. pealeii* probably also apply to cuttlefish and octopus.

At shallow depths of water, where daylight penetrates without much loss of the red and UV ends of the spectrum, the natural environment can be colorful (Jerlov 1976; Marshall et al. 2003). Having the ability to modulate skin coloration to such a fine degree makes color matching for camouflage purposes necessary, since many predators of cephalopods (teleost fishes, for example) have color vision (Fritsches et al. 2000; Losey et al. 2003; Partridge 1990). However, no data are available to show whether squid, or any cephalopod, match background colors. Evidence thus far suggests that squid, cuttlefish, and octopus are colorblind (Brown and Brown 1958; Marshall and Messenger 1996; Mäthger et al. 2006; Messenger 1973; Morris et al. 1993). Therefore, the concept of color matching is especially intriguing considering that these animals have no color perception. At greater depths, the question of color matching becomes less important, since daylight is reduced to the blue and green parts of the spectrum (Jerlov 1976). At such depths, squid skin will lose its colorful appearance and instead will appear as more or less bright shades of the prevalent waveband. Here, squid skin may be adapted to intensity and contrast matching by controlling iridescence and modulating it using overlying pigmented chromatophores.

Further investigations into the nature of the optical interactions between chromatophores and iridophores in cephalopod skin should help us understand better the mechanisms of camouflage and signaling in these animals and to broaden our knowledge of animal visual ecology.

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References

Booth CL (1990) Evolutionary significance of ontogenetic colour change in animals. Biol J Linn Soc 40:125–163

Boys CV (1959) Soap bubbles - their colors and forces which mold them. Dover, New York

Brown PK, Brown PS (1958) Visual pigments of the octopus and cuttlefish. Nature 182:1288–1290

Cloney RA, Brocco SL (1983) Chromatophore organs, reflector cells, iridocytes and leucophores in cephalopods. Am Zool 23:581–592

Cooper KM, Hanlon RT (1986) Correlation of iridescence with changes in iridophore platelet ultrastructure in the squid *Lolliguncula brevis*. J Exp Biol 121:451–455

Cooper KM, Hanlon RT, Budelmann BU (1990) Physiological color-change in squid iridophores. II. Ultrastructural mechanisms in *Lolliguncula brevis*. Cell Tissue Res 259:15–24

Cornwell CJ, Messenger JB, Hanlon RT (1997) Chromatophores and body patterning in the squid *Alloteuthis subulata*. J Mar Biol Assoc UK 77:1243–1246

Cott HB (1940) Adaptive colouration in animals. Methuen, London

Crookes WJ, Ding L, Huang QL, Kimbell JR, Horwitz J, McFall-Ngai MJ (2004) Reflectins: the unusual proteins of squid reflective tissues. Science 303:235–238

Cuthill IC, Bennett ATD, Partridge JC, Maier EJ (1999) Plumage reflectance and the objective assessment of avian sexual dichromatism. Am Nat 160:183–200

Denton EJ, Land MF (1971) Mechanism of reflexion in silvery layers of fish and cephalopods. Proc R Soc Lond [A] 178:43–61

Edmunds M (1974) Defence in animals—a survey of anti-predator defences. Longman, Harlow, UK

Florey E (1969) Ultrastructure and function of cephalopod chromatophores. Am Zool 9:429–442

Fujii R (1993) Coloration and chromatophores. In: Evans DH (ed) The physiology of fishes. CRC Press, Boca Raton, pp 535–562

Fritsches KA, Partridge J, Pettigrew JD, Marshall NJ (2000) Colour vision in billfish. Philos Trans R Soc Lond Biol 355:1253–1256

Froesch D, Messenger JB (1978) On leucophores and the chromatic unit of *Octopus vulgaris*. J Zool (Lond) 186:163–173

Hadley ME, Oldman JMG (1969) Physiological color changes in reptiles. Am Zool 9:489–504

Hanlon RT (1982) The functional organization of chromatophores and iridescent cells in the body patterning of *Loligo plei* (Cephalopoda: Myopsida). Malacologia 23:89–119

Hanlon RT (1988) Behavioral and body patterning characters useful in taxonomy of field identification of cephalopods. Malacologia 29:247–264

Hanlon RT, Messenger JB (1988) Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. Philos Trans R Soc Lond Biol 320:437–487

Hanlon RT, Messenger JB (1996) Cephalopod behaviour. Cambridge University Press, Cambridge

Hanlon RT, Cooper KM, Budelmann BU, Pappas TC (1990) Physiological color-change in squid iridophores. I. Behavior, morphology and pharmacology in *Lolliguncula brevis*. Cell Tissue Res 259:3–14

Hanlon RT, Maxwell MR, Shashar N, Loew ER, Boyle KL (1999) An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Loligo pealei* off Cape Cod, Massachusetts. Biol Bull 197:49–62

Jerlov NG (1976) Marine optics. Elsevier, Amsterdam

Kasukawa H, Oshima N, Fujii R (1987) Mechanism of light reflection in blue damselfish motile iridophore. Zool Sci 4:243–257

Land MF (1972) The physics and biology of animal reflectors. Progr Biophys Mol Biol 24:75–106

Losey GS, McFarland WN, Loew ER, Zamzow JP, Nelson PA, Marshall NJ (2003) Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. Copeia 3:433–454

Lythgoe JN, Shand J (1989) The structural basis for iridescent colour changes in dermal and corneal iridophores in fish. J Exp Biol 141:313–325

Marshall NJ (2000) Communication and camouflage with the same "bright" colours in reef fishes. Philos Trans R Soc Lond Biol 355:1243–1248

Marshall NJ, Messenger JB (1996) Colour-blind camouflage. Nature 382:408–409

Marshall NJ, Jennings KJ, McFarland WN, Loew ER, Losey GS (2003) Visual biology of Hawaiian coral reef fishes. III. Environmental light and an integrated approach to the ecology of reef fish vision. Copeia 3:467–480

Mäthger LM, Denton EJ (2001) Reflective properties of iridophores and fluorescent "eyespots" in the loliginid squid *Alloteuthis subulata* and *Loligo vulgaris*. J Exp Biol 204:2103–2118

Mäthger LM, Hanlon RT (2006) Anatomical basis for camouflaged polarized light communication in squid. Biol Lett 2:494–496

Mäthger LM, Land MF, Siebeck UE, Marshall NJ (2003) Rapid colour changes in multilayer reflecting stripes in the paradise whiptail, *Pentapodus paradiseus*. J Exp Biol 206:3607–3613

Mäthger LM, Collins TFT, Lima PA (2004) The role of muscarinic receptors and intracellular Ca^{2+} in the spectral reflectivity changes of squid iridophores. J Exp Biol 207:1759–1769

Mäthger LM, Barbosa A, Miner S, Hanlon RT (2006) Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. Vision Res 46:1746–1753

Messenger JB (1973) Some evidence for colour-blindness in *Octopus*. J Exp Biol 59:77–94

Messenger JB (2001) Cephalopod chromatophores: neurobiology and natural history. Biol Rev 76:473–528

Mirow S (1972a) Skin color in the squids *Loligo pealii* and *Loligo opalescens*. I. Chromatophores. Z Zellforsch 125:143–175

Mirow S (1972b) Skin color in the squids *Loligo pealii* and *Loligo opalescens*. II. Iridophores. Z Zellforsch 125:176–190

Morris A, Bowmaker JK, Hunt DM (1993) The molecular basis of a spectral shift in the rhodopsins of two species of squid from different photic environments. Proc R Soc Lond [Biol] 254:233–240

Moynihan M (1985) Communication and noncomminucation by cephalopods. Indiana University Press, Bloomington

Osorio D, Ham AD (2002) Spectral reflectance and directional properties of structural coloration in bird plumage. J Exp Biol 205:2017–2027

Packard A (1972) Cephalopods and fish: the limits of convergence. Biol Rev 47:241–307

Packard A, Hochberg FG (1977) Skin patterning in *Octopus* and other genera. Symp Zool Soc Lond 38:191–231

Partridge JC (1990) The colour sensitivity and vision of fishes. In: Herring PJ, Campbell AK, Whitfield M, Maddock L (eds) Life and light in the sea. Cambridge University Press, Cambridge, pp 167–184

Stegen JC, Gienger CM, Sun L (2004) The control of color change in the Pacific tree frog, *Hyla regilla*. Can J Zool 82:889–896

Taylor JD, Hadley ME (1970) Chromatophores and color change in the lizard, *Anolis carolinensis*. Cell Tissue Res 104:282–294

Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC (1998) Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol [A] 183:621–633

Williams L (1909) The anatomy of the common squid, *Loligo pealii*. Brill, Leiden