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Communication and camouflage with the same 'bright' colours in reef fishes

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Reef fishes present the observer with the most diverse and stunning assemblage of animal colours anywhere on earth. The functions of some of these colours and their combinations are examined using new non-subjective spectrophotometric measurements of the colours of fishes and their habitat. Conclusions reached are as follows: (i) the spectra of colours in high spatial frequency patterns are often well designed to be very conspicuous to a colour vision system at close range but well camouflaged at a distance; (ii) blue and yellow, the most frequently used colours in reef fishes, may be good for camouflage or communication depending on the background they are viewed against; and (iii) reef fishes use a combination of colour and behaviour to regulate their conspicuousness and crypsis.

Keywords: fish; vision; colour; reef; social communication; camouflage

1. INTRODUCTION

'Zoologists have long been uncertain how to interpret the vivid colouration of some animals. Many consider the advantage it confers measured by its conspicuousness. Others deny its utility; ascribe its appearance to the vagaries of metabolism; regard it as an expression of tendencies determined by racial constitution, or refer it largely to the action of external factors. To only a few, the conspicuousness of animals of high colour seems too lightly assumed, and they maintain that belief in its existence rests chiefly upon failure to appreciate the obliterative effect of bright or strongly contrasted hues when they are displayed under natural conditions. Thus it is that confusion prevails, and that new methods are required to rehabilitate a subject of investigation that has fallen somewhat into disrepute.' (Longley 1917, p. 533)

This opening paragraph to W. H. Longley's paper is unfortunately still true almost a century later; confusion still prevails. Longley identified five possibilities to explain 'high' colours—display, metabolic by-product, phylogeny, external factors, and camouflage—and went on to champion the last of these somewhat at the expense of others. The misconception that only one evolutionary pressure is responsible for the stunning and varied colours of reef fishes has appeared a number of times since (e.g. Lorenz 1962) and is surely short-sighted. The diversity of lifestyles and habitats on the reef make it probable that most colour patterns are a compromise between different functions, communication and crypsis, for example, and that the same colours may be used for different jobs under different circumstances (for examples in freshwater see Endler (1991)). The 'new methods' Longley referred to were chiefly observational ones as diving became possible. Today, we are fortunately capable of truly innovative non-subjective observations using field spectrophotometry to measure colour and light. As fishes live in microhabitats

underwater, measurements must be made at this level (Levine *et al.* 1980).

This paper uses new colour and light data from the reef (Marshall 1999) to re-examine and quantify some old ideas, which fall under the same general theme held dear by Longley (and see Cott 1940), that 'bright colours' may be used for camouflage (see Endler (1990) for an excellent review of the correct terminology for colour). Spectrophotometric measurements of the colours and environment, and some knowledge of retinal anatomy and sensitivity of the fishes allow further suggestions to be made as to the use of colour on the reef. The ideas examined are (i) What do fine-grain high colour contrast patterns look like at a distance? (ii) Are blue fishes or fishes containing blue body marks well camouflaged in a blue sea? (iii) Why is blue and yellow such a frequent combination in reef fishes?

A vital missing component in our attempts to answer such questions is knowledge of the colour vision system of the fishes themselves (see Marshall (1999) for references, especially those of McFarland and Lythgoe). The colours of two Great Barrier Reef (GBR) inhabitants *Pygoplites diacanthus* and *Thalassoma lunare*, are investigated in detail. Although unfortunately nothing is known of their colour vision capability, spectral sensitivities have been measured with microspectrophotometric (MSP) techniques in one co-habitant of the GBR, *Lutjanus bohar* (Lythgoe *et al.* (1994) referenced in Marshall (1999)). These results are used to construct a hypothetical dichromatic model visual system to examine discrimination of fish patterns and the colours of the patterns against a variety of natural backgrounds. From results gathered so far, there is good reason to believe that a number of reef fishes may be dichromats (with spectral sensitivities close to those of *L. bohar*; see Marshall (1999) for a review of known data; B. McFarland and E. Loew, personal communication) and this model is therefore as close to reality as we can

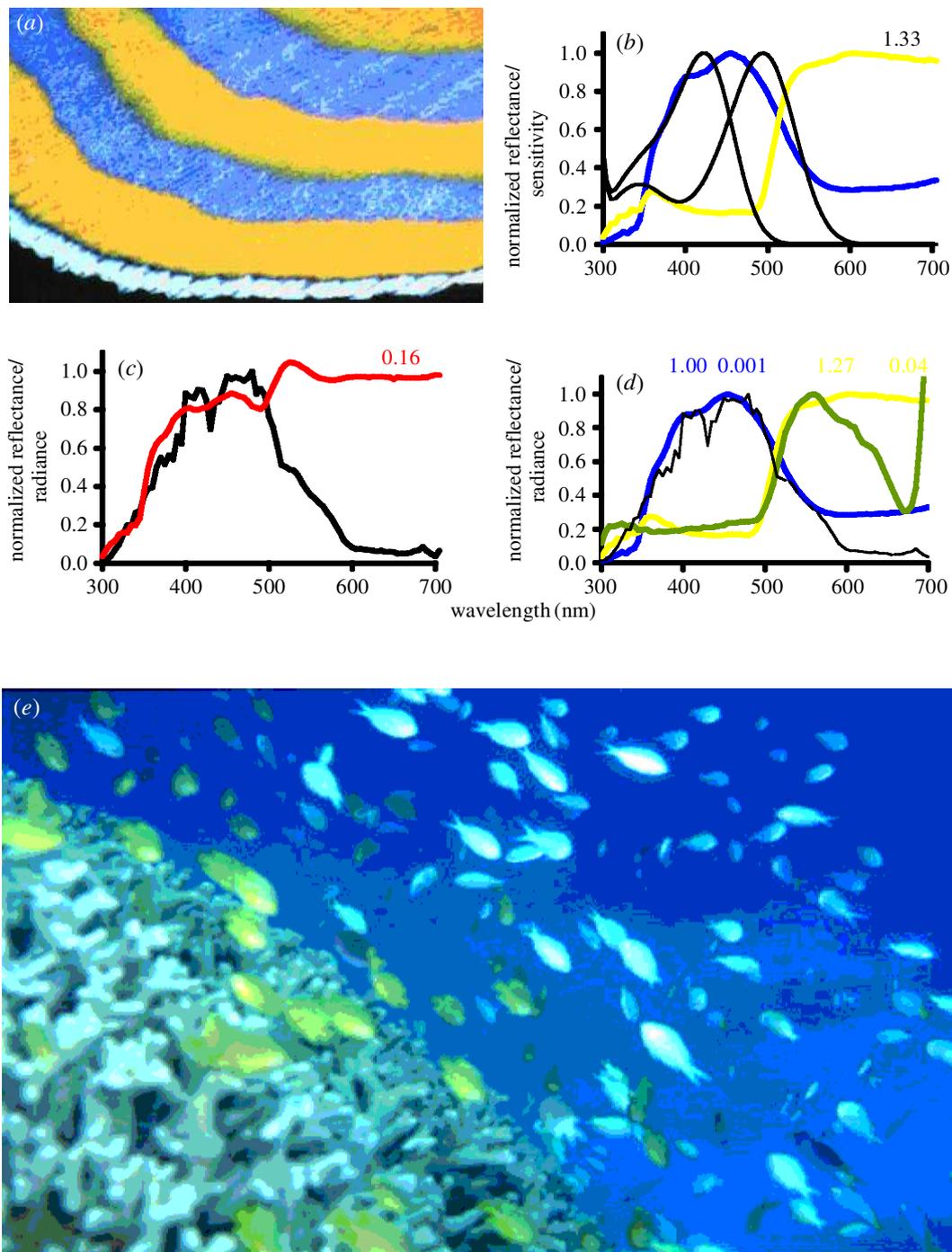


Figure 1. The use of yellow and blue. (a) The anal fin of the angelfish *P. diacanthus*. Each yellow or blue stripe is around 3 mm in width. (b) Reflectance of yellow and blue in *P. diacanthus*. Both colours normalized to the peak of blue. The two colours are complementary, that is, where one reflects strongly, the other one does not and vice versa. In the top right-hand corner the black 1.33 refers to the colour distance between yellow and blue, a measure of the contrast of the two colours, for the dichromatic system described in § 2. The thin black curves represent the spectral sensitivity of the visual pigments of this dichromatic system with absorbance (λ_{\max}) peaks at 424 nm and 494 nm. (c) The black curve indicates background space-light radiance (relative photons cm^{-2} steradians $^{-1}$ nm $^{-1}$ measured with the probe held horizontally pointing away from the reef at a depth of 1–2 m). This was presumed to be representative of a fish's eye view. The red curve represents the blue and yellow reflectances of *P. diacanthus* (as in b) added together. The red number 0.16 refers to the colour distance between the combined reflectances and background space-light. (d) The black curve indicates background space-light (as in c), the blue and yellow curves show the colours of *P. diacanthus* (as in b), and the green curve shows an 'average reef' reflectance, seven species of algae and five species of coral averaged and normalized to the peak at 550 nm. This is essentially chlorophyll reflectance from the algae in and around the coral. The blue number 1.00 refers to the colour distance between *P. diacanthus* blue and the 'average reef' colour. The yellow number 0.04 indicates the colour distance between the yellow colours of *P. diacanthus* and the 'average reef' reflectance. The second blue number 0.001 is the colour distance between *P. diacanthus*' blue and background space-light. The yellow number 1.27 indicates the colour distance between *P. diacanthus*' yellow and background space-light. (e) Clouds of damselfish, *Pomacentrus moluccensis* (yellow) and *Chromis viridis* (blue-green) in 'semi-threatened' stratified formation.

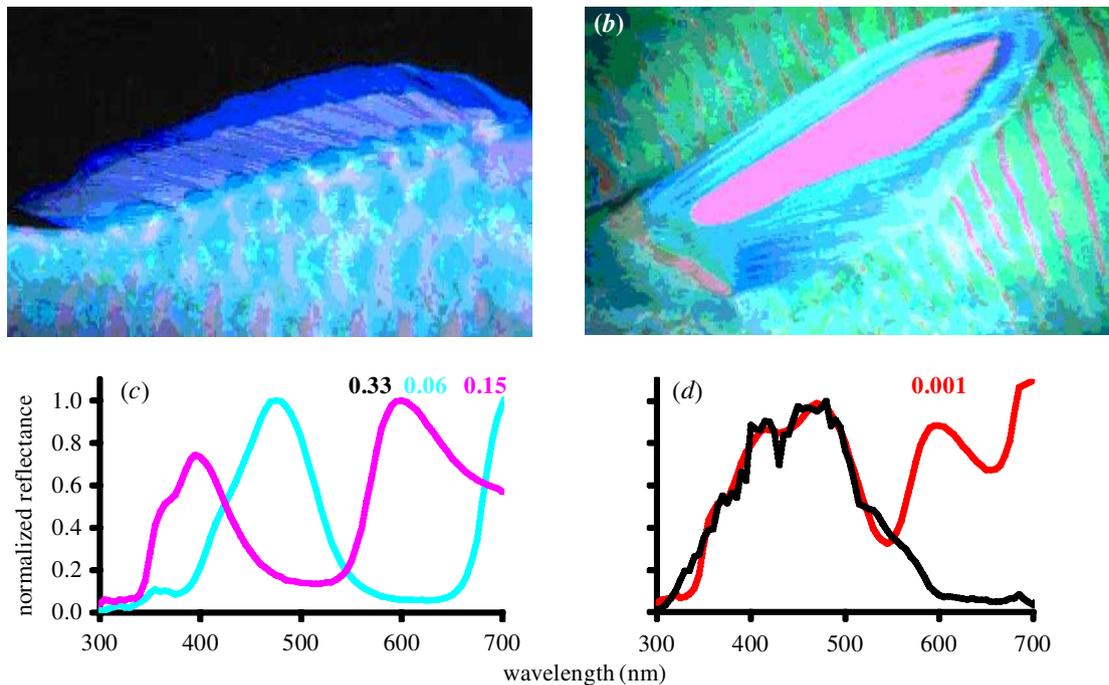


Figure 2 ‘Complex colour’ combinations in labriforms. (a) The dorsal fin of *Scarus spinus*, which is purple-pink and blue. (b) The pectoral fin of *Thalassoma lunare* which is purple-pink and blue. (c) The colours of *T. lunare*'s pectoral fin. The black number 0.33 is the colour distance between the two body colours. The blue number 0.06 is the colour distance between blue colour and background space-light. The pink number 0.15 represents the colour distance between purple-pink colour and background space-light. (d) The black curve shows background space-light (same as figure 1c). The red curve indicates the purple-pink and blue reflectances of *T. lunare* added together. The red number 0.001 represents the colour distance between the combined reflectances and background space-light.

get at present. The values calculated by the model estimate the position of different colours in the colour space of the fishes and then allow distances between colours in this space, and therefore their discriminability, to be judged. It is described in detail by Vorobyev *et al.* (1998). As well as the assumptions made by Vorobyev and colleagues, I also presume that the fish patterns are viewed in perfectly clear water and this is never the case, especially in the often turbid waters around a coral reef. However, as we will see, the resolving power of reef fishes is relatively poor so the visual interactions envisaged here are supposed to occur within a 5 m radius. On clear days intervening water over this range will have a negligible effect.

2. MATERIAL, METHODS, CALCULATIONS AND ESTIMATES

Fish were caught by divers using barrier nets and hand-nets at the following sites: Heron Island (GBR, Australia), Lizard Island (GBR), The Aquarius Habitat (Key Largo, Florida, USA) and Coconut Island (Hawaii, USA). Radiometric light levels and colours of all body regions and pattern elements were made on living or freshly dead fishes (University of Queensland Ethics Approval: Phys/Ph/317/99/VTHRC) using ‘Sub-Spec’ (Andor Technology/Oriel, Belfast, N. Ireland, UK) and Ocean Optics (Ft Lauderdale, Florida, USA) S2000 portable spectrophotometers (Marshall 1999; Siebeck & Marshall (this issue) for methods; see Endler (1990) for nomenclature and methods).

The appearance of striped or spotted colour patterns to a fish is approximated with available data and requires two

components: the acuity of the fish and the spatial frequency of the patterns on fish skin. Acuity estimates from Collin & Pettigrew (1989) indicate a range of 7–27 cycles deg^{-1} for known reef fishes with most being close to 10 cycles deg^{-1} . This is based on ganglion cell receptive fields rather than cone density in the retina. The sizes of coloured spots and stripes in 25 species of fishes was measured from photographs in Randall *et al.* (1997) and, where necessary, adjusted up or down in size for a fish 75% of the maximum length. The average figure from these measurements is 4 mm and this is doubled to give a full ‘grating cycle’ required for the calculations.

Armed with these two estimates we can now ask at what distance coloured fish patterns, become spatially blurred resulting in an additive mixture of the two colours of which the pattern is composed. A value of 10 cycles deg^{-1} means the angle subtended by two times the size of the ganglion cell field (the minimum separable angle to distinguish stripes in a grating) is 0.1° . If one cycle of the grating is 8 mm, this then becomes un-resolvable at a distance of $8/\tan 0.1 = 4585$ mm or 4.6 m. For a smaller fish with a smaller eye such as the blenny *Dasson variabilis* (10 cm body length; Collin & Pettigrew 1989), this distance drops to 1 m. Thus one can estimate that the fine coloured patterns of most reef fishes become unresolved at between 1 and 5 m. This is not true for bolder stripe markings.

To estimate the conspicuousness of fish colours, I have used a simplified version of a well-established discriminability model (Vorobyev *et al.* (1998) and references therein) to calculate the ‘distance’ (D) between colours, in a dichromatic visual space. Colours which appear similar to the dichromatic model are close and result in low values, while colours which are

chromatically contrasting are far apart and result in relatively high values in model calculations. This model assumes the luminosity signal is disregarded and that colour is encoded by an opponent mechanism based on two of the known cone sensitivities of *L. bohar*. The difference between calculations here and those of Vorobyev *et al.* (1998, equation 6) is that I have used a different estimate of the signal-to-noise ratio, or Weber fraction (ω) as the number of each photoreceptor type is not known and bright light conditions are assumed. For further explanation, see Vorobyev *et al.* (1998, p. 625). The estimate used here is

$$\omega_i = \sqrt{1/Q_i}, \quad (1)$$

where $i = 1$ or 2 denoting photoreceptor and Q is the quantum catch of the photoreceptor (Vorobyev *et al.* 1998; equation (1)). The photoreceptors are presumed to be adapted to three backgrounds: coral and/or algae on the reef, background space-light and colours of the fishes themselves. In the last case, part of the fishes' body pattern is treated as the background and part as the colour 'target' being examined. Three questions regarding colour discrimination can now be asked. (i) What is the contrast between the coloured elements of a pattern at a short distance? (ii) What is the contrast between these individual elements and a variety of natural backgrounds? (iii) At the distance where the fishes spatial resolution breaks down and the colour elements of the pattern become additive, what is the contrast of this combination against the same backgrounds?

The raw materials used to calculate Q are spectral sensitivities of *L. bohar* (peak sensitivity or λ_{\max} at 424 and 494 nm) taken from visual pigment nomograms (Vorobyev *et al.* 1998) adjusted for equal output and filtering by ocular media (Siebeck & Marshall, this issue), the reflectance of the colours, radiance or reflectance of the backgrounds (Marshall 1999) and the light illuminating the scene. For simplicity, I have assumed that the interactions generally occur in the top 5 m in relatively clear water and that the illumination is equal at all wavelengths. The spectral position of the photoreceptors used in the model lie close to the maximal transmission of most reef waters (Marshall 1999) so in fact the illumination will have relatively little effect on the calculations at greater depths.

3. RESULTS AND DISCUSSION

Yellow and blue body colours are frequent in reef fishes (Longley 1917; Lythgoe 1968; Marshall 1999). As pointed out by Lythgoe and others (Longley 1917; Lorenz 1962; Lythgoe 1968), yellow is very conspicuous in blue oceanic water and both yellow and 'dark' blue retain their colour well over long distances and at depth (Lythgoe 1968). The reason given for this is that both these colours contain a sharp reflectance change within the blue-weighted spectral envelope of light available in the sea. This makes yellow and dark blue very apparent to any colour vision system containing two or more spectral sensitivities sampling within this range. They are complementary colours, as one reflects much of the visible spectrum that the other does not, and for suitably positioned colour photoreceptors, this provides a strong colour contrast. On land, the human colour vision system is very good at distinguishing yellow and blue and registers high contrast between them. Our 'blue'-sensitive short wavelength (S cone, with a peak sensitivity at 420 nm) is well stimulated by blue and our longer-wavelength-sensitive medium (M, 530 nm) and long (L, 560 nm) cones are strongly excited

by yellow. As a result these two colours are often used in combination in a variety of signals and signs. It is for this reason that yellow and blue fishes, such as many of the angelfish, appear so attractive to us (figure 1; see Randall *et al.* 1997).

Although Lythgoe's observations remain sound, as he recognized himself, the human visual system is quite different to that of fishes and extreme caution is needed in interpreting the colours of animals with our own eyes (Bennett *et al.* 1994). There now exists enough non-subjective data to begin to predict the way reef fishes appear to each other (Marshall 1999) and by combining known spectral sensitivities of fishes with measured colours and illuminant spectra, this, to our knowledge, is attempted here for the first time. The goal is to quantify the way fishes appear in their natural microhabitat (Levine *et al.* 1980). Here I use two examples of differently coloured fishes—yellow and blue, in the angelfish *Pygoplites diacanthus* and the 'complex' colours (see Marshall (1999) for colour nomenclature of reef fishes) of the moon wrasse *Thalassoma lunare*. These colours are examined as targets for a dichromatic visual system against two natural backgrounds, the colour of the reef and the background space-light. Space-light is defined here as the colour seen when looking into open water from the reef. The skin colours of reef fishes are often arranged in complex patterns and the interaction of these colours is also examined. Finally, known estimates of reef fishes' spatial resolution are used to ask how these two fish colour patterns might appear at different distances.

(a) *Yellow and blue of P. diacanthus: contrast of colours in the skin and to background*

P. diacanthus is often found actively swimming in and around coral heads on the reef. As with many angelfish (Randall *et al.* 1997) its predominant colours are yellow and blue and these are arranged in alternating stripes or spots (figure 1a). A colour distance, D , of 1.33 between yellow and blue when 'viewed' by the dichromatic model (figure 1b) is high, (compared with subsequent calculations) suggesting that at least at close quarters, the colour combination of *P. diacanthus* is a conspicuous signal for its neighbour *L. bohar* (as it is for humans) and by assumption (see §2) to other reef fishes also. They are complementary colours, each one reflecting in the region of the spectrum where the other does not.

Human observers often remark on the apparently good match between the blue of a number of reef fishes and the blue water surrounding a reef (Longley 1917; Cott 1940). There is indeed a remarkably close match between the colour of background space-light and the blue of *P. diacanthus* (figure 1d). This yields a colour distance of only 0.001 (figure 1d), indicating that if *P. diacanthus* was composed of this colour alone, it would be well camouflaged against a pure sea-blue background. A number of other reef fishes are also wholly or partially coloured with this type of blue (Marshall 1999). This idea is quite contrary to the blue for the conspicuousness argument of Lythgoe (1968), however, as the blues he described as 'dark blues' are quite different to the colour of *P. diacanthus*. Human observers find blues hard to distinguish, whereas evidence here suggests differences in this

area of the spectrum are probably important for reef fishes (Lythgoe 1968; Marshall 1999).

P. diacanthus stands out against blue space-light due to the yellow component of its body pattern, which generates a colour distance value of 1.27 (figure 1d). The yellow of *P. diacanthus* and that of many other reef fishes also appears particularly conspicuous to our eyes, not only against blue water but also against the colours of the reef ('reef colour' is estimated in figure 1d). However, *P. diacanthus*' yellow (and indeed other reef fishes' yellows; Marshall 1999) is an extraordinarily good match to average 'reef colour' up to 570 nm and the dichromatic model generates a colour distance of only 0.04 between these colours (figure 1d). This may be a good example of how our colour vision system differs from that of reef fishes and this is most likely due to our relatively high spectral discrimination of colours close to yellow (Mollon 1982). It may be the differences beyond 570 nm that make this colour so apparent to us. However, to the hypothetically dichromatic reef fishes with its two relatively short wavelength spectral sensitivities, the yellow of *P. diacanthus* is a close match to coral and algae. Surprisingly then, what looks like a 'bright' yellow fish to us will be well camouflaged against the reef as fishes lack relatively long wavelength photoreceptors. The need for long wavelength, 'red', photoreceptors for good discrimination between green and yellow has been commented on in other animals (Lythgoe 1979; for a recent review, see Kelber 1999). Conversely, *P. diacanthus*' blue is therefore conspicuous against 'reef colour' (colour distance 1.00; figure 1d).

P. diacanthus' colours are strongly contrasting to each other and each one is very conspicuous against one of the backgrounds it is likely to be seen against (figure 1d). Therefore, it may seem that *P. diacanthus* is trying to be highly conspicuous in all situations and indeed it has been suggested that this species and other angelfish may be aposematic (see references in Marshall (1999)). Alternatively, this colour combination would also allow the fish to 'flag' its territory very efficiently (Lorenz 1962). However, as pointed out by Cott (1940) and others, bright colour combinations in bold patterns that break up body lines may also be useful for disruptive camouflage, especially when one of the colours matches part of the background. When approached closely, *P. diacanthus* tends to hide in branched coral which, when viewed from the side, casts a variegated backdrop of reef colour and blue space-light, both of which match one of the colours of the fish. In these circumstances, yellow and blue may be a perfect disruptive combination for *P. diacanthus* and indeed other yellow and blue fishes. This is perhaps particularly surprising to us due to the conspicuousness of this colour combination to our colour vision system.

Other yellow and blue fishes, may be well camouflaged against a disrupted coral and space-light background and may also be conspicuous over long distances if displaying against any one pure background. Clearly, behavioural choice of background and indeed depth at which displaying occurs, due to the accompanying spectral shifts with depth, are critical here.

A good example of behavioural choice of background is notable in two species of damselfish *Chromis viridis* and *Pomacentrus moluccensis*, which are often found living in and around the same head of branching coral (figure 1e).

Both species feed on particles in the water near the coral head. When approached rapidly, both hide within the branches of the coral. However, when confronted with a lesser threat, for example by a slowly approaching diver, they rapidly stratify with the yellow *P. moluccensis* just above the coral and the blue-green *C. viridis* in a cloud above them (figure 1e). Any predator approaching such a formation over the reef would see yellow fishes against the coral and blue-green fishes against the space-light background, colours against which may make it harder to locate each species with accuracy.

(b) Use of fine colour patterns for communication and camouflage

The moon wrasse *Thalassoma lunare*, other wrasse and many parrotfish (collectively the labriforms) also exhibit complementary colours (figure 2a,b; Marshall 1999). These colours are more complex than the simple monophasic blue and yellow (Marshall 1999), often possessing two or even three peaks in the spectrum. What is notable however, is that adjacent colours are generally complementary somewhere in the blue-green region of the spectrum, with a 'gap' left by a twin-peaked colour being filled by a single peak of another colour. In *T. lunare*, these colours appear a purple-pink and blue to us (figure 2b). Between 350 and 550 nm the colours are clearly complementary in *T. lunare* and result in a relatively high colour distance value for the dichromatic model of 0.33 (figure 2c). *T. lunare*'s purple-pink is of middle to low contrast to space-light ($D = 0.15$) and blue on its own is a fairly good match to space-light ($D = 0.06$; figure 2c).

Many labriform fishes are colourful at close quarters to humans but rapidly lose that 'colourfulness' with increasing distance and this seems to be due to the fine patterns of the skin becoming blurred at a distance, along with any degradation of the image by intervening water (Longley 1917). Using the reef fishes acuity data of Collin & Pettigrew (1989) and measurements of reef fishes' pattern size (taken from Randall *et al.* (1997)) an estimate can be made of the distances for reef fishes for which similar blurring and loss of spatial detail will occur. The result, around 1–5 m for fish ranging from 10–30 cm (details described in §2) for their best 'foveal' vision means that beyond this rather short range the details of these highly contrasting colour patterns are lost and the colours blur or add together. In *T. lunare*, this additive colour is an astonishingly close match to background space-light up to 550 nm (0.001; figure 2d). In other words, somewhere between 1–5 m the conspicuous colour signals between skin colours and between the fish and space-light become almost perfectly camouflaged against the blue ocean, changing D by a factor of 450. The additive colour of *T. lunare* is therefore easily visible against 'reef colour' (colour distance 0.90), so as with *P. diacanthus* this wrasse has a number of strategies open to it. It may be confident, however, that while displaying in the blue water above a reef, a behaviour observable in a number of wrasse, it will be both conspicuous to near neighbours that it may want to excite and relatively invisible to the eavesdropping eyes of more distantly placed predators.

The finely striped patterns of *P. diacanthus* will also be subject to spatial blurring at a distance resulting in an additive mixture of yellow and blue. This result is a

colour that is a good match to background space-light well up to 500 nm, due to the contribution from blue, but then flattens out to 700 nm (figure 1c). To almost any visual system, except one with a strong ultraviolet bias, this is likely to appear grey. Its colour distance from background space-light to the model system here is not high ($D = 0.16$; figure 1c), indicating that *P. diacanthus* may be better protected by simply appearing dull when viewed from a distance. What is certain is that to the poor spatial vision of reef fishes, at any distance beyond 5 m *P. diacanthus* goes from being one of the most strikingly conspicuous fish to an unremarkable one adding yet another possible adaptation for camouflage in this 'brightly coloured' fish.

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