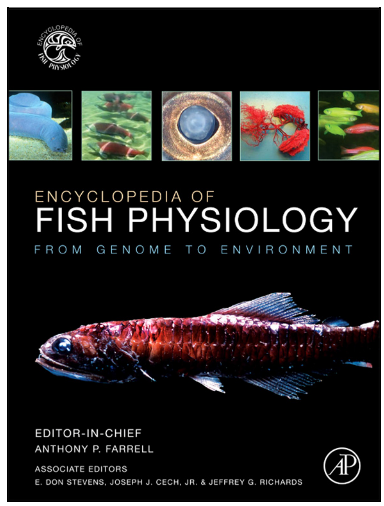

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Color Vision and Color Communication in Reef Fish

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Glossary

Aposematic Warning signal; aposematic coloration is often bright or conspicuous, warning potential predators that animal is toxic or in some other way unpalatable.

Color An object's color is determined by its spectral reflectance, the spectral sensitivity of the visual system viewing the object, and the way in which these signals are interpreted by the brain. This varies substantially among animals depending on the composition of photoreceptors and their connections.

Cone The sensory cell type in the eye (photoreceptor) involved in color vision and bright light conditions.

Irradiance The amount of light or electromagnetic radiation at a surface. Spectral irradiance is used here to describe the light incident on the reef available for vision.

Radiance A radiometry term to describe the amount of light, emitted from a particular area and from a defined solid angle or direction.

Rod A rod-shaped photoreceptor type in the eyes of vertebrates that functions in dim light conditions so may allow night vision. The photoreceptor molecule within rods generally absorbs light in the middle of the spectrum giving it a spectral sensitivity around 500 nm.

Spectral reflectance The wavelengths of light reflected, and therefore not absorbed or transmitted, through an object, as determined by the pigmentary or physical structure of the objects surface. For visual purposes this often expressed as a curve from ultraviolet to far red (300–700 nm).

Spectral sensitivity The specific spectral region, usually a bell-shaped curve, within which a photoreceptor absorbs light. This includes the absorptive effect of any photostable pigment, such as a yellow lens, on the absorbance of the visual pigment molecule within the photoreceptor.

Introduction

Anyone who has snorkelled or dived on a coral reef always surfaces exclaiming about the beauty of the fish. These jewelled inhabitants of this shallow tropical habitat have been a source of wonder and interest since the first reef was encountered. Both Darwin and Wallace, the grandfathers of the theory of evolution, were so worried by the diversity of what they saw on reefs that both questioned if their new idea could explain the myriad colors of the reef inhabitants. Today, the more we learn about the language of reef fish colors and the design of the eyes that decode their message, the more astonishing this aquatic world becomes.

It is important to realize that in fact there is no such thing as color out in the environment. Objects reflect the spectrum of light that reaches them differently, depending on the physical or pigmentary properties of their surface. Photoreceptors, usually cones for color vision, absorb this light according to the spectral absorption of the visual pigment molecule within them and convert this to an electrical message that is sent to the brain. These steps and the way in which the brain combines and interprets these messages is what gives us the sensation of colors and, as made clear later in this article, this varies substantially between animals.

Few of the color codes on the reef have been explained well, but the basic principles of evolution, natural selection, and sexual selection help us to understand some of the functions of reef color (Figure 1). New technology and spectrophotometric (light measuring) methods have also advanced our knowledge of the ways in which fish see and how they use color in the context of their marine environment for survival.

Coral reefs are the densest packed ecosystem on the planet for animal life per cubic meter and this gives one clue to the explanation behind the color diversity of the fish and other animals living there. As recognized by last

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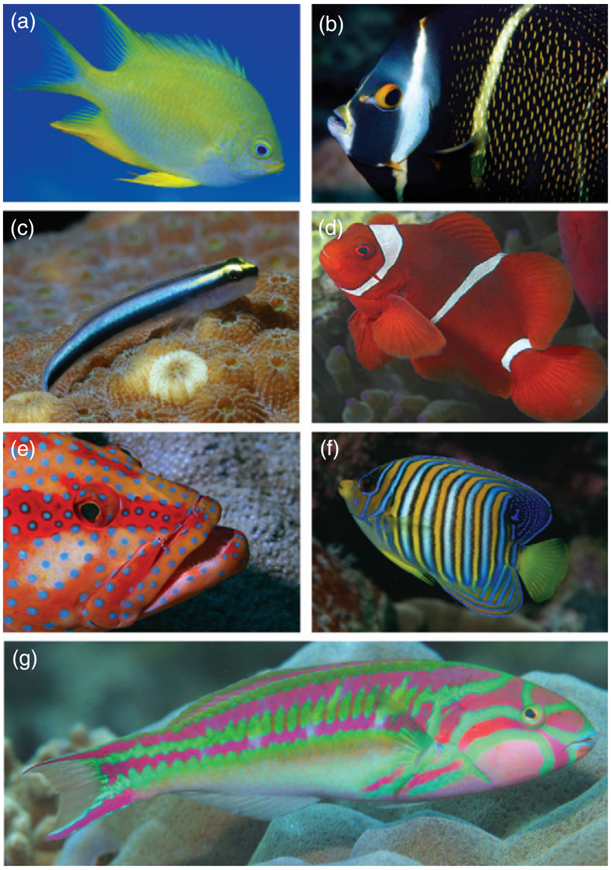


Figure 1 Reef fish and their color patterns. (a) The yellow color of the golden damselfish *Amblyglyphidodon aureus* is highly contrasting against a blue ocean background. (b) French angelfish *Pomacanthus paru* uses strongly contrasting colors to disrupt its body outline. (c) Cleaner goby *Elacatinus evelynae* combines yellow and blue to construct a cleaner fish guild flag. (d) Anemonefish *Premnas biaculeatus* uses strongly contrasting color patterns possibly for disruptive camouflage and for aposematic ('I am distasteful') communication in different circumstances. (e) Coral cod *Cephalopholis miniata* is covered in small spots of color that are highly contrasting at close range but mix additively with the background color of the rest of the fish at a distance for camouflage. (f) The angelfish *Pygoplites diacanthus* uses yellow and blue, contrast-enhanced with white and black stripes for communication and camouflage. (g) The unusual colors of five stripe wrasse *Thalassoma quinquevittatum* are strikingly complementary at close range and blend to match water color at a distance.

century's keen observers of the reef such as Longley, Thayer, Cott, and later on Lorenz, reef inhabitants are in constant communication or anti-communication with each other. Konrad Lorenz, who taught us many of the principles of how to observe animal behavior, said of reefs that "There is in all the world, no other biotope which has produced .. . . in so closely allied groups of animals, an equal number of extremely specialised forms." He was mostly talking about the fish and their variety of form and color, and this led him to the idea of poster coloration in reef fish, bright colors that enabled fish to sort themselves out into species types and a hierarchical social structure. That is, conspicuous colors and patterns encode species identity enabling close cohabitants to rapidly decide what to do when encountering each other as far as aggression, defense, and the desire to mate are concerned. However, this idea has yet to be explicitly tested.

Anti-communication, an attempt to conceal or camouflage, is intricately woven into the physical nature of light on coral reefs and the eyes that attempt to recognize camouflaged individuals for various reasons. The same close relationship exists between light and color used in deliberate communication and this article gives examples of both communication and camouflage.

Communication methods may be loud and very specific, as noted by Lorenz. Many reef fish are probably colored aposematically, meaning that they use bright coloration to advertise toxicity, or other spiny reasons that make them difficult to swallow. The importance of considering all these possible ways of hiding and conveying information through 'the eyes of the beholder' cannot be overstated and an understanding of the visual capabilities of reef fish, rather than using our own eyes for analyzing particular colors or patterns, is critical.

This article also provides a brief review of the visual ecology of the reef and examines some of the recent advances in our knowledge of the eyes and colors of reef fish. Visual ecology, an area of biology most elegantly explained by John Lythgoe, links the physics of light and color of an environment to the visual system and signaling systems that have evolved there, and lastly examines the visually driven behaviors a species exhibits (Figure 2). This must be done not only from the perspective of the visual system observing the color and pattern, but also from the scale of the species under consideration.

The fish we see when we go to a reef represent a small proportion of the biomass of fish that live there. Most fish on the reef are less than 3 cm long and many of them are cryptic (hiding) or shy. However, because we are relatively large animals, we tend to see relatively large fish, perhaps a velvet blue-yellow angelfish defending his territory of sponges and pink-purple parrot fish male with his drab harem of females in tow.

Another subjective problem is partial color blindness because some reef fish have a very different color vision than we do. Humans are primates and our color vision evolved for the tasks of survival in forests and other terrestrial environments looking to find ripe fruit or young red leaves. Put a primate in a mask and snorkel on the reef and the first things they often notice are all banana-colored objects (Figure 1(**a**)) at the long-wavelength end of the spectrum, which get our special attention.

In the relatively clear blue waters of the reef, one thing any diver knows is that by the time he gets to 20 m or so, a red snorkel has become greenish-black and blood looks dark green. The reason for this is that the absorption (or more accurately the total attenuation which includes scatter) of water at 20 m has removed red light (Figure 2). This would make the red-belly signaling system of a stickleback male ineffective here. Reef fish have evolved communication colors and visual systems set by the physical envelope of light wavelengths that their water transmits best. Their world is very ultraviolet (UV)/blue/ green dominated (Figure 2). Because their reef visual systems are adapted to see well in this spectral range, yellow, orange, and red may be less conspicuous and indeed match the general reef background.

Camouflage may be achieved by directly matching the color, intensity, and sometimes the texture of the reef substrate (Figure 1). As superbly detailed by Cott in his 1940s book *Adaptive Coloration in Animals*, it also pays to have highly contrasting even seemingly ridiculous bold body patterns where the background is bold and highly contrasting (Figure 3). The tropical sun coming through the waves, coral branches, coral plates and other reef structures creates a very high contrast environment, and reef fish colors and patterns must be considered in this context. The coffee-table-book flash photography does not achieve this. The colors of the background are deliberately masked or de-focused and the bold colors of the fish picked out with full spectrum light to show them off as best as possible. This topic of color contrast and visual adaptation deserves attention, as many reef inhabitants clearly use this principle of disruptive camouflage, but it is not detailed any further here.

Camouflage and Communication on the Reef

Yellow and Blue, Reef and Water

The underwater visual scene at around 10 m is quite different to land. Directly up to an angle of 43° (Brewster's angle beyond which total internal reflection starts), there is the bright shimmering surface, through which the sky may be more or less visible depending on the waves. Below this is a relatively uniform and dimmer blue, diffuse background body of water into which vision cannot penetrate more than a few tens of meters. The coral and other reef structures appear at a various heights, depending on the ruggedness of the reef and the observer's own size. In shallow water habitats over light reflective sand, looking down may also be very bright, a terrestrial condition experienced only when light reflects off the surface of snow.

The aquatic world is also more three dimensional. Observers and signalers are more dispersed and this is important when considering what angle to view others at and when trying to be camouflaged from all angles. Many reef animals also tend to 'hug the ground' or hide in the reef structure for protection and camouflage. Nonetheless, reef fish may take off into the water column at some stage or indeed some species do spend most of their life there, and this can be dangerous but a good way to advertise your presence. Ultimately, the intrinsic

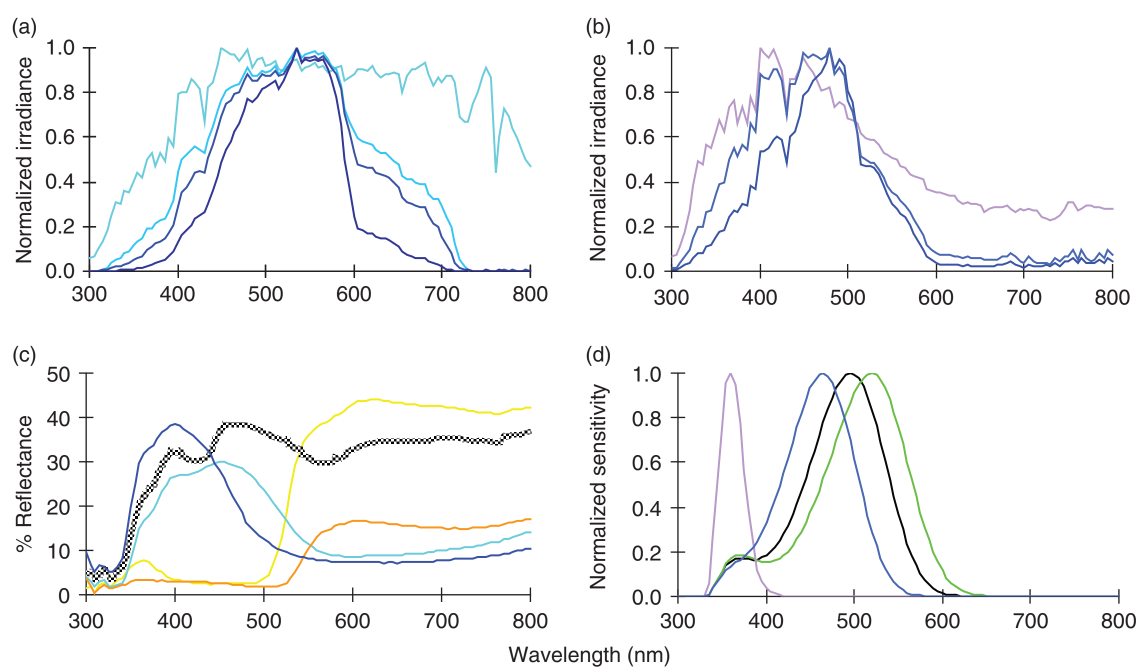


Figure 2 (Continued)

(e)

(f)

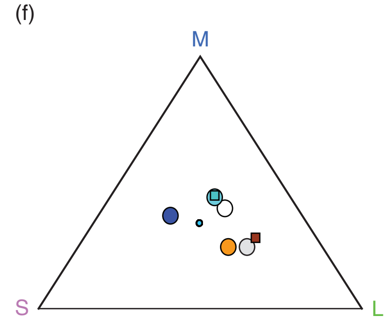


Figure 2 Extended caption – visual ecology. In order to understand and quantify the way in which other animals see the colors of their world, four bits of information are required. (1) The environmental light envelope may be quite different meaning that some parts of the spectrum are not available and therefore not worth investing visual sensitivity in. This is especially so in different water environments. On the coral reef, wavelengths from near UV (350 nm) to yellow (600 nm) are most useful. (2) The colors produced must be measured as their spectral shape can reveal much about how the color is used and combined. Complex colors, that have two or more areas of reflection, may make use of both regions of chromatic reflection or one area may be irrelevant. This seems to be the case for many reef fish colors that contain a long-wavelength component (**Figure 5**). (3) Visual systems on the reef are very different to those on land and indeed than those in freshwater environments. Color vision can be constructed by two or more cones and reef fish show a diversity of color vision types ranging from apparent dichromacy to apparent tetrachromacy. One new observation that has not been explained is the astonishing diversity of spectral sensitivity mechanisms in reef fish. (4) A good understanding of the behavior of the species is essential to appreciate how their visual system and color communication or camouflage systems have evolved. This includes basic observations such as depth range and habitat (does the fish spend its time under a coral ledge, in mid-water, or hidden in holes in the reef) as well as the more complex inter- and intraspecific interactions for predation, defense, and reproduction. The above components and observations can then be used to make predictions and model ideas of how reef fish colors can be used. This sort of calculation is often plotted in a visual space and an example of that is shown here for the colors of angelfish *P. diacanthus* and its possible background colors. (a) Downwelling irradiance or spectral distribution of light on the reef at different depths (0, 3, 5, and 10 m – light blue to dark blue lines). With increasing depth, the filtering and scattering effect of water filters out wavelengths at either end of the spectrum, resulting in a narrowed spectral envelope or light habitat, depending on depth and water type. (b) Radiance or light that might directly reflect from a fish from different angles at a depth of 1 m (purple, from above; light blue, from the side; and dark blue, from below). This directional difference in light background demonstrates the variability of light on reefs, even at a single depth. (c) The spectral reflectance or colors of *P. diacanthus* (**Figure 1**(**f**)). Reef fish colors can be measured with a reflectance spectrophotometer and the resulting peaks and steps and complex colors enable us to nonsubjectively quantify how colors are used. Line colors are color coded to match approximately the colors of the fish in life (**Figure 1**(**f**)). (d) The spectral sensitivities of rods (black line) and cones (purple, blue, and green lines) of reef fish must be known before a good understanding of their visual ecology can be built up. This may be achieved through a variety of methods and defines the species color vision range and complexity. (e) Behavioral observation of how colors are used and the context of their use are essential. Here damselfish alerted to the photographer, sort themselves against different backgrounds that provide more effective camouflage for their respective basic body colors. (f) The measurements (a)–(c) above can be combined in visual models to estimate how different colors are used or are effective in the visual world of different species. The Vorobiev/Osorio model is often used and essentially combines light, spectral sensitivity, and spectral reflection in a weighted scatter-plot as seen here. Each data point represents how the fish with visual system in (d) sees the colors of the angelfish colors in (c). The small black circle in the center is the white point and achromatic colors fall close to this point. Note how the white of the fish (gray line in (c)) does not fall near the white point in this visual space as the fish visualizing these colors has UV sensitivity (d). The distance between the data points on this plot is related to how easy each color is to distinguish. Where color vision is potentially trichromatic, with three photoreceptor types or cones, the plot falls into a triangle with each corner representing one of the three spectral sensitivities and labeled here S, M, and L for short, medium, and long wavelength, respectively, and color coded as in (d). The plot shown here is called a Maxwell triangle. The round symbols are the fish colors in (c) and are color coded the same as the colors they represent. This is also their approximate color in life (**Figure 1**(**f**)). The square symbols are background reef colors shown in **Figure 4**, water background (blue square) and an average of 255 coral and algae found on the reef (brown square). Note how closely the fish yellow matches coral color and how closely one of the fish blues matches water color. This is also demonstrated in **Figure 4**.

turbidity and absorbance of water over a reef precludes the need for long-distance vision and also breaks down fine color patterns at relatively small distances.

Thus, the horizontally divided, distance-truncated three-dimensional habitat of the reef has resulted in a number of specific visual and signaling adaptations. Reef fish lack the high visual acuity of many land animals (most reef fish have resolving power around 10 times worse than humans) and some have evolved relatively simple color vision with only two cone types or color channels. These dichromatic fish are much like many mammals on land and are in some ways similar to a red–green color blind human. These two-channel color vision systems can extract enough information from the world for survival on just one color axis. In behavioral tests for humans, this is called the blue-yellow axis, and for all dichromatic

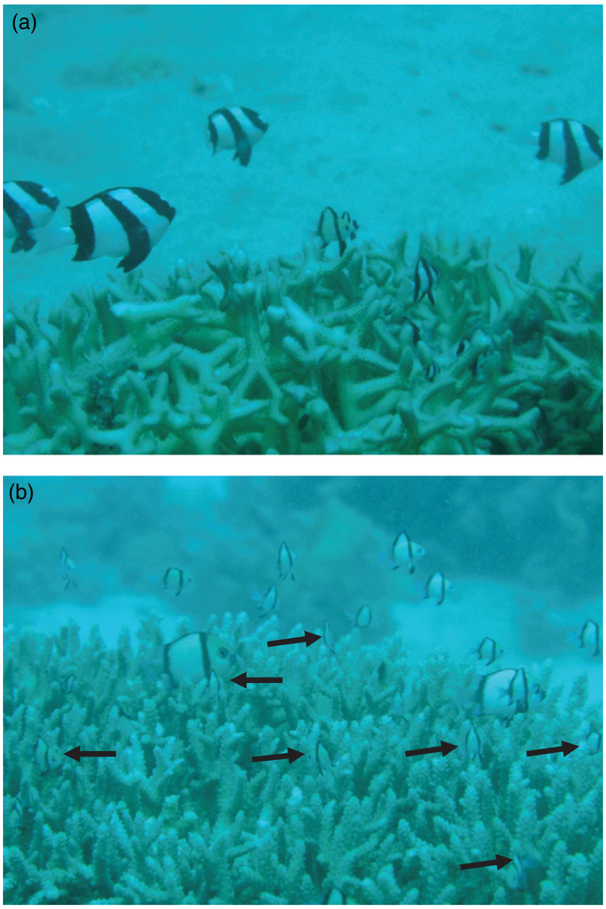


Figure 3 Apparently conspicuous fish in natural surroundings with natural illumination are well camouflaged. Black and white provides the strongest contrast and potential for conspicuousness. (a) Humbugs (*Dascyllus aruanus*) above the coral head in which they live are maximally conspicuous and this may help communication within the school. (b) The damselfish *Dascyllus reticulatus* also inhabits coral heads and when these or *D. aruanus* drop down into the coral branches, they merge with the background through disruptive camouflage. This is especially effective in juvenile *D. reticulatus*, which also mimic the coral fingers. Arrows indicate individual fish.

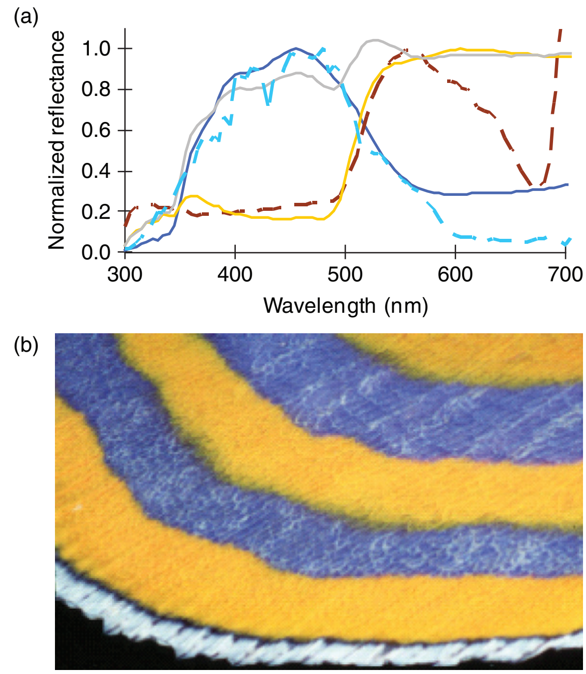
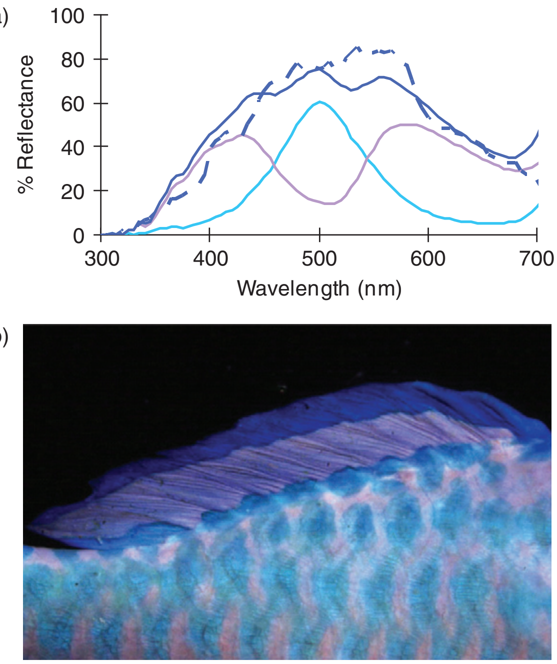


Figure 4 Yellow and blue colors within reef fish body patterns may combine in an additive mixture to reflect gray. This only works when the pattern is constructed of fine stripes or spots which blend at a distance as the resolving power of the eye fails. (a) Reflectance spectra of the yellow/orange and blue anal fin of angelfish *P. diacanthus* (Figure 1(f)) shown in (b). Yellow/orange and blue solid lines are color coded to match the body colors in (b). Gray solid line is the additive mix of these two colors. This would appear gray to both fish and humans lacking UV spectral sensitivity as it reflects fairly evenly from 400 to 700 nm. Dotted blue line is side-welling radiance of reef water (Figure 2(b)); dotted brown line is average coral and algae reflectance (255 samples). Note the spectrally close match between these colors and the fish colors (Figure 2(f)). (b) The anal fin of *P. diacanthus* (Figure 1(f)).

species it is constructed from a photoreceptor sensitive to the short wavelength or blue part of the spectrum and one sensitive to longer wavelength around yellow. Color detection or discrimination that requires information from the red–green axis has resulted in the addition of a third color channel or cone mechanism in some primates, allowing, for example, better determination of ripening fruit and other tasks. Some reef fish become trichromatic, and others possess four color channels. At depth, the whole color world is more restricted to wavelengths shorter than yellow (see Figure 2 and extended caption for further explanation). However, a fish living very close to the reef top will experience close to full spectrum daylight, like that on land. As a result, if their lifestyle demands it, coral reef fishes clearly take advantage of the colors available and increase their color sampling range.

The color code adopted for effective camouflage and communication in this habitat is biased toward yellow and blue (Figure 4). Several small reef fish species, notably in the damselfish (Pomacentridae), are colored mostly blue, blue-green, or yellow all over. Other larger fish, such as the angelfish (Pomacanthidae) or surgeonfish (Acanthuridae), use stripes or large blocks of yellow and blue colors (Figure 1). These complementary colors are clearly being used to communicate. Complementary colors are ones that contrast strongly with each other, the result of them reflecting in opposing parts of the spectrum (Figures 4 and 5). To almost any color vision system, these yellow and blue colors, seen side by side, stand out and it is not just fish such as *P. diacanthus* (Figures 1 and 4) that parade this combination in agonistic and sexual displays. Smaller reef fish that are blue all over can get the same effect by positioning themselves against the

(a)



(b)

Figure 5 The unusual colors of parrotfish and wrasse can combine to give broadband blue, a good match to background water color. These colors are often intense green and purple/pink (see also Figure 1(g)) and are complementary as they reflect in different regions of the spectrum. This makes them highly conspicuous at close range. (a) Reflectance spectra of green and purple/pink scales of parrotfish *Chlororus sordidus*. Green, purple/pink solid lines are color coded to match the body colors in (b). Blue solid line is the additive mix of these two colors. Dotted blue line is reef-top water color (radiance) where these fish are often found. Note the spectrally close match between this additive color and the background allowing such fish to be well camouflaged at distance.

yellow-brown of coral and yellow fish can do the same against the blue water background (Figure 1).

Lythgoe, Loew, McFarland, and other investigators have also pointed out that yellow and blue colors transmit information a long distance in marine waters, mainly because their regions of largest spectral change fall within the marine environment lighting envelope. The frequently used colors on the reef are also those that can transmit information over a long distance while also remaining good for camouflage in certain circumstances.

Reef fish containing yellow and blue within their body patterns are not doomed to be constant beacons of communication and open to predation. Little fish become instantly well camouflaged, blue-green against blue-green water and yellow against yellow-brown coral. Larger reef fish can take advantage of one of the important scaling factors previously discussed. In an enlarged close-up, many striking patterns are quite finely detailed with spots or stripes (Figure 1) that are ideal for close encounters with the opposite sex, or in aggressive displays over mates, food, and territory ownership. From further away, however, this fine detail becomes blurred. Here the complementary nature of the colors is of benefit, as their spectra combine (additive color mixing), and the resulting color is gray and dull because it now reflects over the whole spectrum (Figure 4). The relatively poor resolving power of potential predators means that at only a few meters away brilliantly colored angelfish becomes a shadow.

Pointillism in Parrotfish and Other Reef Fish

There is another, more subtle, color mix story found in the parrotfish (Scaridae) and wrasse (Labridae). These fish often possess rather spectrally complex colors with many peaks and troughs (Figures 2 and 5) that appear striking pink and green to our eyes. These are also complementary colors and may function differently to yellow and blue. These colors combined do not just render the fish dull and gray, but make it an astonishingly good match to background water color (Figure 5). This is again additive color mixing, resulting in a good match to the blue-green water background, which may be a more effective camouflage against the distant eyes of predators and more in line with the lifestyle of these species. Whereas angelfish often lurk in the overhangs and shadows of the reef and may want to appear like a shadow, parrotfish and wrasse patrol over the top of the reef, in the case of the former looking for coral and algae to graze, and, for the latter, looking for crustaceans and other food. As a result, the social function colors of wrasse and parrotfish are unknown, but one function in the parrotfish seems to be to keep the drab female harem together and to signal competitively to other males.

It is worth pointing out that the impressionist painters, particularly the pointillists, secondarily discovered the usefulness of adding small dots and stripes of color to appear one way when observed in close proximity, and another way when observed further away. Seurat and Signac were disappointed with the dullness of the result, as they were searching for ways to make colors more vibrant. Instead, they ended up with dull blues and grays, which eventually they learned were useful to represent the blue-gray cast of shadow, just like an angelfish or a parrotfish at a distance.

Communication and Deception

Cleaner Blue (and Yellow)

Reef fish can be divided into guilds, or color clubs that, according to either behavior or habitat, could explain some of the color diversity. Eibl-Eibesfeldt, Losey, and others have suggested that there is a blue cleaner fish guild. Cleaner fish, often wrasse or gobies, are relatively small and offer a skin, teeth, and gill cleaning services to

clients. Fish cannot easily preen themselves of the many invertebrate parasites, such as worms and crustaceans. Cleaner fish exploit the protein banquet by picking off these itchy hitch-hikers and cleaning dead skin and scales from wounds from generally larger reef, or clients. This mutualistic relationship is a delicate one, as the small fish must enter the mouths of predators to pick off parasites and damaged skin. If the predators swallowed the cleaner, or if the cleaner ripped off more than just the required bit, the relationship would never have evolved.

Cleaners may set up a cleaner station on the reef and clients learn where to come to be cleaned. Part of this service involves advertising by the cleaners and there are stereotyped movements and dances cleaner fish perform over their station to show off what they offer. Many cleaner fish from diverse families are yellow and blue, normally in longitudinal stripes and often with black to increase contrast (**Figures 1**(**c**) and **6**). The idea of a cleaner blue guild that arose was untested until recently. Not surprisingly from what we know of yellow and blue on the reef, through a combination of behavioral tests and visual system models, the cleaner fish colors, including blue, were indeed shown to be an effective advertisement color combination, and likely instrumental in setting up the mutualism required. Thus, the cleaner blue guild has given way to a cleaner yellow-blue guild, in many cases emphasized with black.

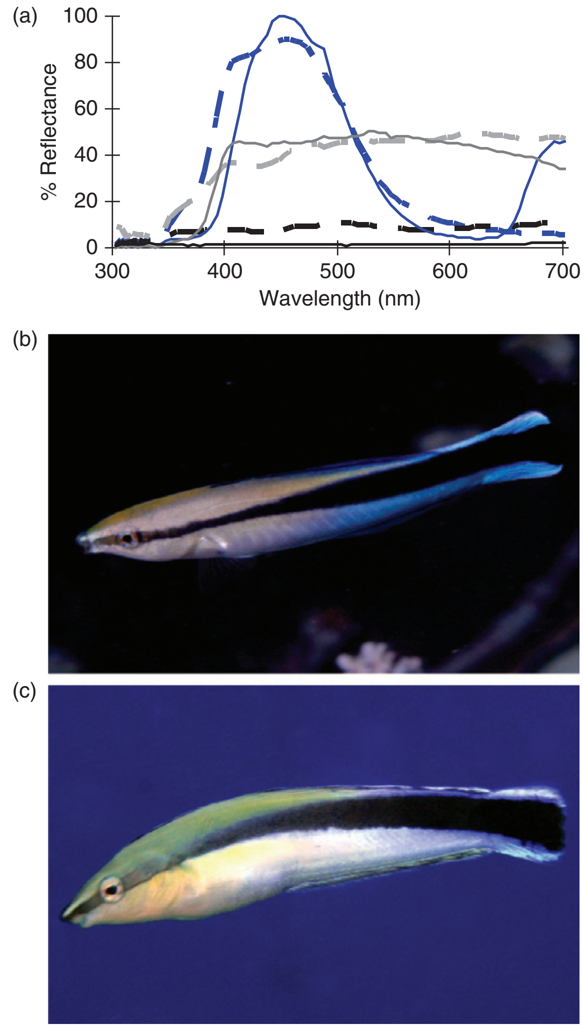


Figure 6 Mimic fangblenny *Aspidontus taeniatus* takes on the color pattern of a cleaner fish *Labroides dimidiatus* to fool clients and cleaner fish allowing them close enough to rip off scales and eat eggs. (a) Reflectance spectra of cleaner fish and fangblenny. Solid lines, cleaner fish colors; dotted lines, fangblenny. Lines are color coded to match the fish colors. (b) Cleaner wrasse *L. dimidiatus*. (c) Fangblenny *A. taeniatus*.

Deception and the Use of Your Neighbors Color Message

Any relationship, even the cleaner–client mutualism, is open to exploitation. For example, some fangblennies imitate the colors and patterns of cleaner fish. *A. taeniatus* is a remarkable blenny mimic of the cleaner wrasse, *L. dimidiatus*, borrowing the blue-yellow-black stripe uniform of the cleaner (**Figure 6**). This sabre-toothed fish visually deceives unsuspecting clients, biting off chunks of skin as well as feeding on cleaner fish eggs.

Another fangblenny, *Plagiotremus rhinorhynchos*, also closely resembles juvenile *L. dimidiatus* and can rapidly change its body coloration through the neural control of melanophores and possibly other skin cells that produce color. By putting on different colors to prevent detection, the fangblenny effectively camouflages itself against the cleaner fish or within the school, and then darts out to bite unsuspecting victims. This matching and adaptable color change may also help them avoid retaliatory predation.

The UV Communication Channel and the Diversity of Reef Fish Vision

Around half the reef fish species that have the potential to see UV, unlike humans. This ability is often enabled with a cone having a spectral sensitivity between 300 and 400 nm. What is the advantage of UV vision, given the potential disadvantages of UV photodamage to the retina and poor UV transmission in water (**Figure 2**)? Small reef fish may benefit from short-range partially private or covert communication. The extra contrast and patterns are evident in the UV image of a damselfish *Pomacentrus ambionensis* (range 340–400 nm, **Figure 7**) would only be available to other fish with UV sensitivity. Large reef fish, often the predators, lack UV transmitting ocular media (lens and cornea) and cannot see the UV patterns of smaller fish.

UV facial patterns have recently been shown to be important in sexual selection of the UV-detecting

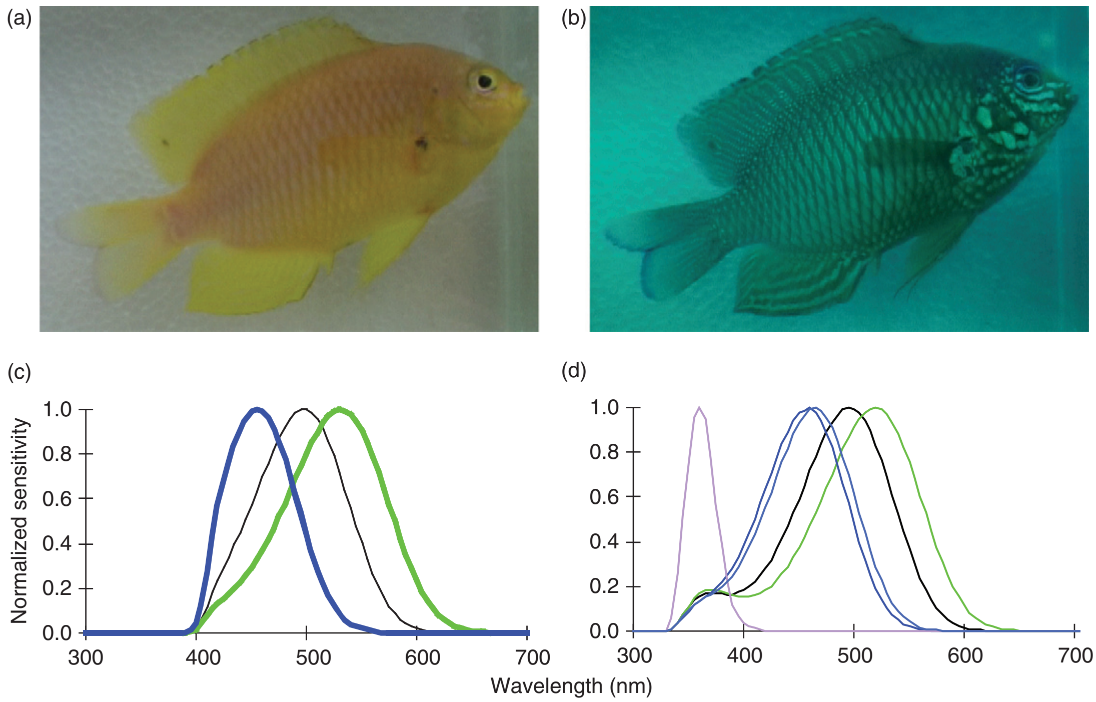


Figure 7 UV colors on damselfish are made visible with a UV camera sensitive to light from 350 to 400 nm. (a) Ambon damselfish *P. ambionensis* as non-UV sensitive humans or fish might see them. (b) Same fish viewed with UV sensitive camera reveals a pattern of high-contrast UV-reflective colors that are available for this and other damselfish species with UV sensitivity. The fish would not appear this way as this frame shows only contrast in the UV. (c) Spectral sensitivity of the barracuda *Sphyraena helleri* which, like humans, lacks UV sensitivity and would not be able to see these UV colors. (d) Spectral sensitivities of damselfish, which includes a dedicated UV cone. This sensitivity would enable these fish to see and communicate in this waveband.

damselfish *P. ambionensis.* UV patterns are effective over the short communication distances of males defending territories from other males. Such signals are therefore an effective close-up signal for little fish whose displays could attract unwanted attention from far away.

Conclusion

Both the number and spectral sensitivity of cone mechanisms are very diverse on the reef and so far we have no clear understanding of what drives this variability. Ideas of basic visual ecology can only explain some of the general trends such as the UV, blue, green bias of reef fish visual systems that broadly matches water transmission characteristics. Phylogenetic trends are very general and are also populated with general loose observations such as 'damselfish often have UV vision'.

The idea of co-evolution of colors and color vision has been proposed for a number of animals. Some correlation does exist between the spectral positioning of reef fish colors and cone sensitivity placement as noted by Marshall, McFarland, Losey, Loew, and others; however, this has many exceptions. There are no cases of fish possessing a color vision system that is designed specifically for its colors, and as reef fish colors are so diverse and there being many tasks that require color vision, this is perhaps no surprise.

We are still left with the mystery of why reef fish possess such apparently diverse color vision types. Aside from those fish in the deeper regions, or those species that are crepuscular or nocturnally active, the general light environment is the same for all species. As a result, to find the answer, we must further study the individual species on the reef and learn more about their specific ways of living.

See also: **Sensory Systems, Perception, and Learning**: Communication Behavior: Visual Signals. **The Skin**: Coloration and Chromatophores in Fishes. **Vision**: Adaptations of Photoreceptors and Visual Pigments; Behavioral Assessment of the Visual Capabilities of Fish; Photoreceptors and Visual Pigments.

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