Strange enough, I became curious about the colors of fish not while diving in the crystal-clear waters of Australia’s Great Barrier Reef, surrounded by countless incredibly colorful fish. On the contrary: I was in the murky, turbid waters of Heron Island’s Coral Cay Lagoon, near the southeastern edge of the reef, close to Shark Bay.

Sitting slightly apprehensively at a depth of only two meters, I was trying to catch fish in a hand net. Suddenly I became dimly aware of hundreds of little black dots shooting past me almost at the limits of my vision in the silty water. Sucking air through my dive regulator and pondering this strange event, I was stunned to realize the black dots were the eyes of an enormous school of kyphosids swimming past on their way to the reef edge. The bodies of these fish, which are also known as drummers, are about 30 centimeters (nearly 12 inches) long and are a silver-blue color. When vertical in water, they merged perfectly with the dim, blue light pervading the lagoon.

Here was a wonderful example of camouflage underwater. I was humbled by my ineptitude as a predator—I allowed literally tons of fish to pass within a meter or two of me and my net before I even realized what they were. As a marine biologist interested in vision in the sea, however, I immediately thought of several questions. How is the skin of drummers so well adapted to merge with the sea? What is it about the visual capabilities of the fish that prey on drummers that enables them, presumably, to see the drummers while mine was so ineffective?

I noticed that many of the fish and other reef creatures that the school had by now joined were boldly colorful, their bright patterns making them pop out from the background—and also, it would seem, making them an obvious meal. I wondered how the environment of the coral reef could have given rise to the virtually invisible drummer and frogfish as well as the highly conspicuous angelfish and butterfly fish.

**Extreme Biodiversity**

It is such questions that occupy me on field trips to the University of Queensland’s research stations on Heron and Lizard islands. These two islands are at either end of the 2,300-kilometer expanse of the Great Barrier Reef (map), which is by far the largest reef system in the world and rightfully one of its seven natural wonders. The huge expanse is a living area of 200,000 square kilometers consisting of some 3,000 small reefs that include more than 400 species of hard and soft corals. For comparison, a typical Caribbean reef might be tens of kilometers long and have perhaps 40 kinds of hard and soft corals.

Like terrestrial rain forests, coral reefs are isolated enclaves that are important for their extreme biodiversity. In this respect, too, the Great Barrier Reef is superlative: it is home to around 1,500 species of fish. This huge variety is all the more surprising in light of the relatively young age of the reef. It began to form 12 to 18 million years...
ago and in some places is only two million years old; reefs of the western Atlantic and central Pacific formed 25 million years ago.

The diversity of colored fish and invertebrates on the Great Barrier Reef is truly awe-inspiring. Yet the color patterns exhibited by these inhabitants did not evolve for human eyes. The brilliant blue spots of the semicircle angelfish, or the contrasting yellow and blue fins of the yellowtail coris wrasse [see illustrations at top of pages 56 and 57], are a vital component of the survival strategies of these species on the reef.

To understand this role of color and appearance requires some understanding of survival on the reef and also of the optics of the undersea realm. At its most fundamental level, survival for any animal species demands three things: eating, not being eaten and reproducing. Unfortunately for sea creatures, the demands on appearance imposed by the first two of these survival requirements conflict with those of the third.

A good way to avoid being eaten, or, indeed, to lurk undetected while waiting for prey to swim by, is to be camouflaged to match the background (the scientific term is “cryptic”). Masters of camouflage include the frogfish [see illustration at bottom of page 57] and the school of kyphosids I saw in the Heron Island lagoon. But to attract a mate, chase rivals away or provide other warnings, bright colors that are easily seen underwater may be the order of the day. In the blue waters of the reef, the colors yellow and blue travel the farthest, so many reef animals have evolved bodily patterns of yellow and blue in striped or spotted combinations. Because yellow and blue are also widely separated in the spectrum, they offer strong contrast underwater.

Just what does a butterfly fish look like to another butterfly fish? How does a drummer appear to a shark? It is this goal to understand color vision and its evolution from the point of view of the animals themselves that my colleagues and I at the University of Queensland’s Vision, Touch and Hearing Research Center are striving toward at present. Our research has revolved around three critical questions: One, what are the animals’ visual capabilities? To explore this matter, we are carrying out experiments in which we are quantifying colors nonsubjectively, using the world’s first underwater spot-reflectance spectroradiometer. Two, what are the light and surroundings like in the habitat where these creatures live? Experienced divers know that seawater is so blue that all red light is absorbed within 20 meters of the surface; a bright-red fish at this depth therefore appears black. And three, under what circumstances, and to what other creatures, do fish show off their color patterns? Clearly, displaying bright colors to impress a potential mate would be unwise when visually guided predators are lurking nearby.

Such impressive visual capabilities might seem to be unnecessary on the reef, where so many creatures have evolved bold patterns that emit strong visual signals. Alternatively, it may seem incredible that these brightly colored fish manage to survive with markings so striking that they would seem to attract the attention of even weak-eyed predators.

Could it be that coral reefs are colorful, and therefore that colorful animals fit in and may even be camouflaged? Logical though it may seem, the notion does not hold up to scrutiny. A reef stripped of its fish and other mobile life-forms is actually relatively monochromatic. Most of the corals are brown or green, their colorful splendor coming out only at night when the polyps open or under the falsely bright illumination of the camera strobe or video light.

Another possible explanation revolves around disruptive coloration, a principle first described in detail in the 1940s and subsequently used for military camouflage. The central idea is the use of large, bold patterns of contrasting colors that make an object blend in when viewed against an equally variable, contrasting background.

Compared with some species of fish and other creatures, humans are relatively color-blind. People have three color receptors in their eyes: the blue-, green- and red-sensitive cones. Some reef fish (and indeed amphibians, reptiles, birds and insects) possess four or more. The record is currently held by the mantis shrimp (a stomatopod), a reef dweller whose eyes have 12 color receptors. With these additional receptors, the animals can see the region of the near ultraviolet, with wavelengths between about 350 and 400 nanometers (humans cannot see wavelengths shorter than about 380 nanometers). Also, they can see in greater detail some of the colors humans see.

Why Are Reef Fish So Colorful?
The light and dark branches, pockets and shafts of light on a reef provide just such a background.

Good examples of disruptive camouflage on land are the striking patterns of some snakes or the stripes of a zebra. These colorations, when viewed against the kinds of highly patterned backgrounds common in the animals' natural habitats, aid camouflage or at least make it difficult to see where the animal begins and ends. For example, zebras—like many boldly colored fish—group together for protection. In these groupings, the context against which predators see individual patterns and colors is not, typically, a natural background but rather the school or herd itself, enabling one animal to become lost in the swirling mass of its neighbors.

Complicating matters is the fact that most reef fish are capable of changing colors to some degree. Some, notably the triggerfish and goatfish, can do so at nearly the speed and complexity of chameleons. In other fish, color changes may take several seconds, may be associated with night and day, or may occur during maturation. Parrot fish change color in association with a sex change, a drab female in a harem changing into a gaudy dominant male if the resident male is lost. Changes are also known to occur with "mood"—for example, during conflicts or flight from a predator. Although one can guess at the causes behind these and other color changes, at present almost no convincing hypotheses explain their function.

Parts of fish may be disguised by a pattern, such as the dark stripes that run near the eyes of the Moorish idol [see illustration on page 54]. Similarly, colorations may make it difficult for a predator to determine which end is the head and which is the tail. Many species of butterfly fish, for example, have a black dot on either side of the body near the caudal fin; these dots are easily mistaken for eyes [see illustration on page 54]. In patterns on other fish species, blocks of blue match the blue of the ocean.

The effectiveness of highly contrasting body stripes, spots and blotches as a means of reef camouflage can be fully appreciated only under natural illumination. Yet few people get to see fish this way: often reef creatures are viewed in photographs, their colors set ablaze by the flash of a strobe and against a background that is nothing more than a featureless, dark field. Lit up in this manner, the fish are being seen as they are when they are "displaying." Fish sometimes position themselves in shafts of sunlight to reveal the full splendor of their colors to a rival or potential mate. At other times, even the multicolored harlequin tuskfish or iridescent blue angelfish disappear under the dim, highly textured illumination of the coral ledges where they spend much of their time.

Also, just as birds will puff out and spread their feathers in dramatic displays, some reef fish will erect highly colored fins or reveal bright patterns on frontal head areas or even inside the mouth. The positioning of the fish relative to the viewer is obviously critical here; frontal regions are obscured when the fish is seen from the side, whereas the erect-fin displays such as the butterfly fish will intentionally turn sideways to present a broadside of color to a rival or mate.

Bright colors can also warn of toxicity. Boxfish, blue-ringed octopuses [see illustration at right] and nudibranchs are all known for such aposematic displays, in which, again, yellow and blue are a common theme underwater. In contrast to the furtive behavior of animals that are disruptively camouflaged by their bright patterns, however, aposematic displays are generally accom-
panied by bold and indiscreet behavior. As an interesting side note, evolution has produced aposematic animals unable to see their own beautiful colors. This is the case for nudibranchs and for the blue-ringed octopus. Both these invertebrates lack the retinal features necessary to see colors, indicating that their bright patterns evolved solely in response to their predators' much more capable visual systems.

As noted, color vision in some reef fish and other animals may be based on four photoreceptor types rather than three, as in humans. Because the additional sensitivity afforded by the extra photoreceptor is often in the ultraviolet, we became interested in the possibility that the visual signals sent by a select number of reef fish encompass the ultraviolet as well as the colors visible to humans.

Using our spot-reflectance spectroradiometer, we found this indeed to be the case. The advantage of this device is that it can “see” colors we cannot, including both the near-ultraviolet and the near-infrared regions of the electromagnetic spectrum (with wavelengths of 300 to 400 nanometers and 700 to 800 nanometers, respectively). As a result, we can begin to understand how color patterns have evolved for animals that see these colors. Our work has involved trying to establish what the various reef fish can see. Our most recent results indicate that in adult life, a relatively small proportion of reef fish see the near ultraviolet. As with aposematic coloration, however, it is becoming clear that animal colors are not necessarily correlated with their own visual systems.

Although the exact function of this possibly “secret waveband” remains a mystery, ultraviolet is in theory a good color for local signaling. The fact that ultraviolet is highly scattered and attenuated by water means, for example, that the visual signals of a sexual display could be sent to a nearby potential mate—and that the signal would degrade to invisibility over the longer distances at which predators might lurk.

There are many related issues about which we know little. For instance, color vision changes substantially during the life spans of reef fish. For example, it appears that the eyes of reef fish larvae do not block ultraviolet, and yet most of the adults of these species cannot see this part of the spectrum. We know that the change is to accommodate the demands of a new mode of life—the emergence from the plankton, where all fish begin life. So far, however, the details of this vision change are known for only two of the 1,500 species on the Great Barrier Reef.

This is just one of the mysteries that leave vast gaps in our knowledge. We still have only fragmentary ideas about what the colors of a reef mean to its inhabitants, making each visit to this world of secret color communication an endeavor as tantalizing as it is beautiful.

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