

Communication Behavior: Visual Signals

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Astaxanthin A naturally occurring red carotenoid pigment.

Collimating Aligning in parallel.

Cue A stimulus that may provide information to a receiver, but has not evolved in the context of communication.

Eavesdropper An individual, such as a predator or rival, other than the intended receiver, such as a potential mate, that modifies its behavior in response to a signal.

Monochromatic Having only one color.

Opsin A protein found in photoreceptor cells, covalently bound to a chromophore that changes conformation when it absorbs a photon of light.

Receiver In animal communication, an individual that modifies its behavior based on its perception, processing, or evaluation of a signal or a cue.

Signal In animal communication, a stimulus that has evolved in response to selection for a communicative function.

Signaler An individual producing a signal.

Tunaxanthin A naturally occurring red carotenoid pigment.

Introduction

Visual communication accounts for much of the popular fascination with fish. The profusion of pattern, color, and form in coral reef fish skin patterns is one of the most striking phenomena in the natural world; and many a kitchen table is graced with a male Siamese fighting fish, directing aggressive displays at passers-by. For researchers, visual signals in fishes present a powerful model for asking basic questions about the evolution of communication and about environmental effects on signaling. This is due to both the sheer diversity of communication systems, coupled with the fact that fish occupy the full gamut of possible visual environments: from lightless ocean depths and caves, to tea-stained lakes and streams, to sunny shallow reefs (**see also Vision: Color Vision and Color Communication in Reef Fish and Deep-Sea Fishes**).

At its most basic, communication is a two-way interaction between a signaler, who produces a sensory stimulus or signal, and a receiver, who perceives the signal and makes a behavioral decision. Signalers and receivers often exchange roles, and eavesdroppers, such as predators locating prey, often exploit communication interactions.

A basic challenge in animal communication is distinguishing between a signal – a stimulus that has evolved in an explicitly communicative context – and a cue – a

stimulus whose communicative function is incidental. Signals are easy to identify if they involve postural changes, motor patterns, or skin-pattern changes performed only in the presence of an appropriate receiver, such as a ritualized courtship or aggressive display. Many of the most important visual signals in fish, however, are morphological structures such as fin extensions or constitutively expressed skin patterns that are always on. The situation is further complicated by the fact that some communication signals may have evolved in order to enhance transmission of a cue to a receiver. For example, close-range courtship motor displays may waft nonsignaling olfactory cues (e.g., metabolized steroid hormones) to the receiver (**see also Hormones in Communication: Hormonal Pheromones**).

Once a signal has been produced, it must be transmitted to the receiver, who then must detect it against background, evaluate it, and respond. An effective signal must therefore be both detectable in the environment in which it is produced and distinct from signals that would elicit a different response from the receiver.

From the receiver's point of view, a visual signal can be decomposed into spectral, spatial, and temporal components. The image that is projected onto each of a fish's two retinas consists of light varying in intensity and wavelength over space and time. Detection of visual signals is

largely determined by the degree of spectral and spatio-temporal contrast between the signaler and the visual background, or among different elements of the signal.

Generating a visual signal involves multiple approaches. In rare cases, fish will directly generate light through bioluminescence (see also **The Skin: Bioluminescence in Fishes**). The vast majority of visual signals, however, involve modifying the spectral, spatial, and temporal distribution of light generated by the sun after it has been filtered through the atmosphere and the water column. This typically involves specializations in pigment cell distributions, posture, and motor patterns (see also **The Skin: Coloration and Chromatophores in Fishes**).

With the exception of a growing body of quantitative studies on the color component of communication, most work on visual communication in fishes (and in general) does not take a quantitative approach to characterizing the color, spatial, or temporal properties of stimuli, backgrounds, or ambient light conditions, whether characterizing signals themselves or evaluating receiver response. Nevertheless, the fact that visual stimuli can be readily characterized, as well as experimentally manipulated through dummies, models, videos, and computer animations, has given us substantial insight into this mode of communication in fishes.

Although relatively few studies have explicitly isolated visual components of communication signals, fishes use visual communication extensively in the context of mate choice and aggressive displays, as well as recognition of conspecifics, shoalmates, and individuals. While visual signaling has mostly been studied between conspecifics, it can play an important role in interspecific interactions. For example, the characid *Hemigrammus erythrozonus* has a visual antipredator display. Deep-sea anglerfishes use bioluminescent lures to snare prey and the monacanthid *Paraluteres prionurus* uses shape and color patterns to mimic a toxic pufferfish. Many fishes, notably the color-changing flatfishes (Pleuronectidae) use skin patterning and morphological structures for camouflage. Cooperative interactions between cleaner wrasses and their hosts involve the production of stereotypic postural and color signals by both parties.

Bioluminescent Signaling

Many marine fishes produce their own light energy, either endogenously or more commonly, by concentrating bacterial symbionts inside specialized light organs. Bioluminescence (see also **The Skin: Bioluminescence in Fishes**) is particularly useful at night and in the deep sea, where exogenous light is scarce. Bioluminescence has evolved independently many times in teleosts, exclusively in marine taxa. Bioluminescence serves a variety

of functions, including prey capture and camouflage, and can play a role in shoaling and courtship.

Bioluminescence involves an enzymatic reaction whereby an oxygenase, luciferase, oxidizes a luciferin, producing oxyluciferin and emitting light. This is typically produced by symbiotic bacteria in specialized light organs, although in a few cases – midshipmen (Batrachoidae: *Porichthys* spp.), lanternfishes, and some apogonids – the luciferin–luciferase system is produced endogenously, with bioluminescence under neural control. Fishes have evolved a variety of structures to control the spectral, spatial, and temporal properties of emitted light. Both bacterial light organs and photophores can contain reflectors, filters, lenses, and light guides. Species with bacterial light organs use shutters controlled by specialized musculature to create flashes of light. Lampeyes (Anomalopidae) can use both musculature derived from the levator maxilla to draw a black pigmented curtain over the surface of the organ, or rotate the entire organ into a suborbital pocket. The fishes can cycle these movements up to 100 times per minute, creating a blinking effect that is used both for prey detection and intraspecific signaling. In the trachichthyid genus *Paratrachichthys*, bacterial organs are located around the anus, opening onto the rectum. The light is distributed anteriorly and posteriorly by translucent, collimating muscles piping light to various areas of the body in a manner analogous to fiber optics.

Three deep-sea genera of dragonfishes or loosejaws (Malacosteidae: *Malacosteus*, *Pachystomias*, and *Aristostomias*) couple a luciferin–luciferase system, emitting typical blue-green light, to red fluorescent protein and a series of filters to produce far-red light (maximum emission >700 nm) from suborbital photophores; in *Malacosteus*, the light is further modified using a superficial brown filter. Dragonfish detect these wavelengths not using a long-wavelength sensitive opsin, but with a novel, long-wavelength photosensitizer, derived from dietary chlorophyll. Accordingly, this light is invisible to most other deep-sea fishes, providing dragonfishes with a private channel with which to locate prey and signal to conspecifics. In all three of these genera, there is also an additional postorbital photophore that emits blue light, suggesting that these fish may be capable of sophisticated multicomponent signaling.

The difficulty of observing behavior in deep-sea fishes means that most inferences about bioluminescent signaling must be made from morphology. A rare exception is the leiognathids or ponyfishes, which occur in circumtropical shallow coastal waters of the Indo-Pacific. In some leiognathids, multiple shutters on the wall of the light organ mechanically control the duration and intensity of light emission. *Leiognathus elongatus* appears to be sexually dimorphic, with females lacking a light organ.

While bioluminescence allows the signaler to control the temporal characteristics of the signal, it has several

limitations. Most bioluminescent signals are spatially simple and monochromatic; more important, they are fairly ineffective in brightly lit environments where vision plays a dominant role. Most visual signals, therefore, involve forms, patterns, colors, and movement that reflect available light.

Signaling with Reflected Light

Reflected-light signals are characterized by spectral reflectance as a function of space and time. Reflectance is defined as the light reflected back from a target illuminated by a uniform white light source, as a function of wavelength. Reflectance can change as a function of the angle of illumination, spatial position, and time. Many fishes express complex color patterns; over the course of a courtship or aggressive display, they vary the color and intensity of these patterns and engage in changes in position, orientation, and posture. The amount of information that can be conveyed in a display is thus considerable.

The color sensitivity of fishes ranges from around 340 nm (the near ultraviolet) to 750 nm (the near infrared), with considerable variation in visual sensitivity among species. Fishes produce colors across this spectrum. Spectral variation in signals is produced either by pigments, which absorb portions of the light visible to receivers, or by morphological structures that selectively scatter light as a function of wavelength. Pigments are typically used to generate long-wavelength colors (yellows, oranges, and reds), while morphological structures are used for shorter-wavelength colors (blues, indigos, violets, and ultraviolet) (see also **Vision: Photoreceptors and Visual Pigments**).

Pigment-Based Colors

The chemical nature of a pigment determines the wavelengths of light it can absorb (see also **The Skin: Coloration and Chromatophores in Fishes**). Many pigments in fishes are organic compounds containing long chains of conjugated double bonds, such as carotenoids and pterins. In general, small molecules absorb only high-energy (short) wavelengths, while larger molecules additionally absorb longer wavelengths of light. Carotenoids and pterins typically absorb shorter wavelengths, thereby reflecting yellows, oranges, and reds. Carotenoids bound to proteins can absorb middle wavelengths while reflecting both red and blue to produce purple. Many carotenoid-based color patches also exhibit a secondary peak in the ultraviolet, within the range of sensitivity of many fishes. Melanins are large proteins that absorb most visible and ultraviolet light to produce black. Pigments are housed in chromatophores, within small packets called chromatosomes.

Fishes cannot synthesize carotenoids; they must be obtained from dietary sources. In freshwater systems, notably threespine sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*), males vary in carotenoid expression. Female sticklebacks and female guppies prefer more intense, purer carotenoid colors. The intensity of red color is determined by the concentration of astaxanthin carotenoids in the skin, while the chroma (color purity) of red is determined by the ratio of astaxanthins to tunaxanthin. Variation in astaxanthin deposition also appears to underlie the variation in the intensity and quality of orange coloration in guppies. The area of long-wavelength patches in guppies is highly heritable, while the intensity of color patches depends on carotenoid uptake from the diet and on parasite load. Intriguingly, while long-wavelength colors in freshwater fishes often appear to be limited by the availability of dietary carotenoids, this does not appear to be the case in marine fishes.

Structural Colors

Short-wavelength (green to ultraviolet) colors are often produced structurally, using small (<300 nm) particles embedded into a transparent layer backed by melanin pigment. Short wavelengths are scattered and reflected back to the receiver, while longer wavelengths are absorbed by the melanin. Adding filters to the transparent layer can further restrict the range of wavelengths being reflected.

Interference coloration is likely to account for the shimmering iridescent colors found in many freshwater fishes, notably poeciliids, cyprinodonts, and cichlids. This process involves a thin layer of transparent material, with a high index of refraction, coating the skin. Light hitting the surface at an angle is partially reflected to produce a primary reflection; much of the remaining light is refracted, reflected by the boundary at the bottom of the transparent material, then refracted again to produce a secondary reflection. The wavelengths for which these primary and secondary reflections are in phase depend on the viewing angle, the width of the transparent layer, and its refractive index. The apparent color can thus change substantially with viewing angle. Ultraviolet (UV) coloration in birds is produced by coupling multi-layer interference with a scattering mechanism. Many fishes produce signals that reflect primarily in the UV (**Figure 1**).

White coloration often is produced by guanine forming microcrystalline platelets that reflect all wavelengths. If guanine platelets are packed in a dense array, they produce the specular (mirror-like) reflectance characteristic of silvery scales. These dense arrays can be concentrated in iridosomes, which intensify pigment

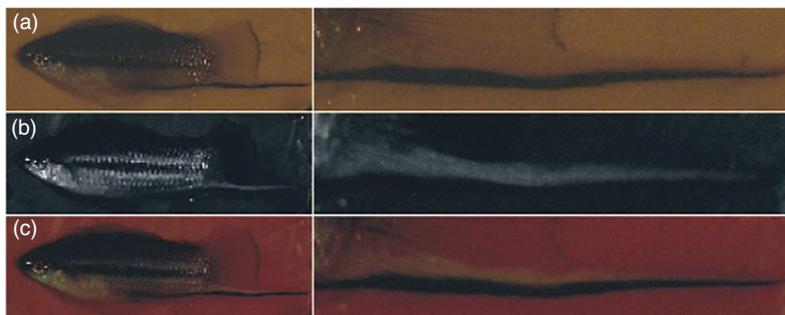


Figure 1 UV and visible spectrum imaging of male pygmy swordtail *Xiphophorus nigrensis* (Poeciliidae). (a) Color photograph in human visible (400–700 nm) range. Enlarged sword sexual ornament is shown for detail. (b) Photograph taken with UV bandpass filter (300–400 nm). (c) Composite of the above two photographs showing black/UV contrast. From Cummings ME, Rosenthal GG, and Ryan MJ (2003) A private ultraviolet channel in visual communication. *Proceedings of the Royal Society B: Biological Sciences* 270: 897–904.

colors by reflecting wavelengths transmitted by chromatosomes.

The spectral curves produced by fish colors can be characterized as simple (reflecting strongly in one region of the spectrum) or complex (with separate reflectance peaks in distinct portions of the spectrum). Simple colors are either step-shaped, with high reflectance of all visible wavelengths above or below a cutoff point, or peak-shaped, reflecting within a particular range of wavelengths. Long-wavelength colors tend to be step-shaped, short-wavelength colors peak-shaped. Complex spectral curves contain multiple peaks and/or steps. The purple expressed by labroids, particularly tropical wrasses and parrotfishes, is one of the most complex animal colors, with distinct peaks around 400 and 580 nm and a step around 730 nm (Figure 2). These color spectra might be produced by combining several interference colors together.

Spatial Patterns

A reflectance spectrum only describes a single point in space and time. Visual perception, however, depends on processing of contrast relationships among elements of a visual scene. In teleosts, notably coral reef fishes, these patterns can be intricate and highly specified. The Picasso triggerfish, *Rhinecanthus aculeatus*, for example, exhibits a black-and-white polka-dot pattern just anterior to the caudal fin; four white stripes running diagonally from the insertion of the anal fin to the midline of the body; brown and gray bands on the dorsum; a filigree of electric blue lines originating parallel at the eye and curving to meet on the gill cover; and a blue mustache above the mouth contrasting with a broad russet band that slopes down to meet the white belly.

The specification of such complex patterns has been a focus of research in evolutionary developmental biology. A diversity of repeating patterns, or textures, can be produced by subtle changes to a relatively simple

molecular mechanism. The noted mathematician Alan Turing proposed the reaction–diffusion system, whereby spot and stripe patterns arise as a result of instabilities in the diffusion of two or more morphogenetic chemicals (morphogens) in the skin during early development. Differences in boundary and initial conditions, and in the number of morphogens and diffusion properties of each morphogen, can interact to produce an array of stripe and spot patterns. Such a reaction–diffusion system is consistent with the development of the body pattern of juvenile angelfishes (*Pomacanthus* spp.), in which the body pattern is not fixed on the skin over ontogeny; rather, the size of the black melanophore coloration between yellow stripes is maintained constant, by continuous rearrangement of spatial patterns.

The developmental genetics of stripe formation have been extensively studied in *Danio* spp. (Cyprinidae). In the zebrafish, *D. rerio*, blue stripes consist of a mixture of xanthophores and melanophores, and white stripes consist of xanthophores and iridophores. While there is a fairly detailed picture of the mechanisms whereby pigment cells are recruited and aggregated, the forces underlying the spatial arrangement of stripes remain unclear. The lateral line system might be involved in recruiting stripes, as it is in salamander larvae; the zebrafish mutant puma exhibits defects in both lateral line and stripe development. The zebrafish leopard gene may be acting as a component of a reaction–diffusion system. Small changes in gene structure or regulation could thus induce qualitative changes in pattern elements (Figure 3(a)), producing dramatic differences in signal structure. Such a process could account for the striking differences in pattern sometimes seen among closely related species (Figure 3(b)).

In many cases, modifications of fin rays and axial vertebrae also appear to serve primarily in a signaling context. In many freshwater fishes, caudal and/or dorsalfins are prominently enlarged in adult males. In the Montezuma swordtail (Poeciliidae: *Xiphophorus montezumae*), the lower rays of the caudal fin are longer than the standard length in

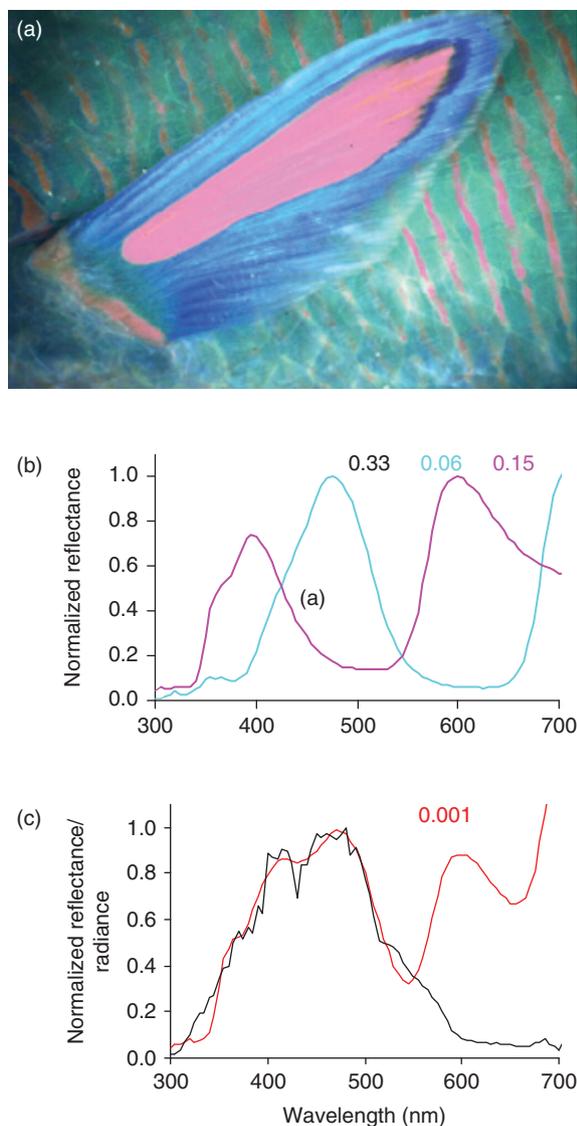


Figure 2 Communication and camouflage in an Indo-Pacific coral reef fish: (a) the purple-pink and blue pectoral fin of the wrasse *Thalassoma lunare* (Labridae) and (b) the colors of *T. lunare*'s pectoral fin. The black number 0.33 is the color distance between the two body colors. The blue number 0.06 is the color distance between blue color and background space light. The pink number 0.15 represents the color distance between purple-pink color and background space light. (c) The black curve shows background space light. The red curve indicates the purple-pink and blue reflectances of *T. lunare* added together. The red number 0.001 represents the color distance between the combined reflectances and background space light. Colors are highly conspicuous when viewed at close range, but smear into the background when viewed at a distance. Modified from Marshall NJ (2000) Communication and camouflage with the same 'bright' colors in reef fishes. *Philosophical Transactions of the Royal Society B* 355: 1243–1248.

some males. Females in several species prefer to mate with males bearing longer swords. By contrast, the highly dimorphic dorsal fin in the closely related sheephead

swordtail, *Xiphophorus birchmanni*, is unattractive to females but serves to deter rival males; accordingly, males modulate the elevation of the dorsal fin during courtship depending on whether rival males are nearby.

Temporal Properties of Visual Signals

In a signaling context, skin patterns and morphological structures are often coupled with stereotypical behaviors that maximize conspicuousness. Many fishes can change color patterns over a range of timescales, ranging from short-term flashes to ontogenetic changes over a lifetime. Male *Badis badis* (Badidae), for example, express nine distinct color patterns according to social context and dominance status. Simultaneously, hermaphroditic *Serranus subligarius* (Serranidae) alternate from a banded black and white male pattern to a solid black female pattern during a sex-changing courtship interaction. Males in several species of swordtails express conspicuous vertical bars on the flank, which they intensify over the course of courtship and agonistic interactions. Color change can operate over longer timescales as well. Male *Astatotilapia* (*Haplochromis*) *burtoni*, for example, express a drab, female-like pattern when subdominant and reproductively inactive, and a colorful, high-contrast sexually dimorphic pattern when dominant and reproductive. These shorter-term, reversible color changes are regulated via neural control of chromatophore cells, by aggregating or dispersing pigment granules within the cells.

Short-term temporal changes in reflected visual signals can also be effected by raising or lowering the fins, as in many poeciliids, or by postural changes which change the appearance of interference colors. Many signal interactions – courtship displays, aggressive displays, and cleaning solicitation displays – involve characteristic motor patterns which may also be providing information in nonvisual modalities, including olfaction and lateral-line detection of near-field vibration (See also **Social and Reproductive Behaviors: Sexual Behavior in Fish**). In some cases, fishes have evolved specialized motor control systems dedicated to communication. Male Siamese fighting fish *Betta splendens* (Osphronemidae) perform a dramatic frontal display to females and to other males, which involves a pronounced flaring of the gill covers. Both the musculoskeletal apparatus and motor control neurons appear to have been modified for this display. Female green swordtails *Xiphophorus helleri* attend specifically to the spatiotemporal visual characteristics of the male courtship display, and sticklebacks attend to variation in courtship tempo.

Color patterns also change over ontogeny (See also **Social and Reproductive Behaviors: Socially Controlled Sex Change in Fishes**). Ontogenetic color changes are also quite common. Many sex-changing reef fishes have strikingly different color patterns according to

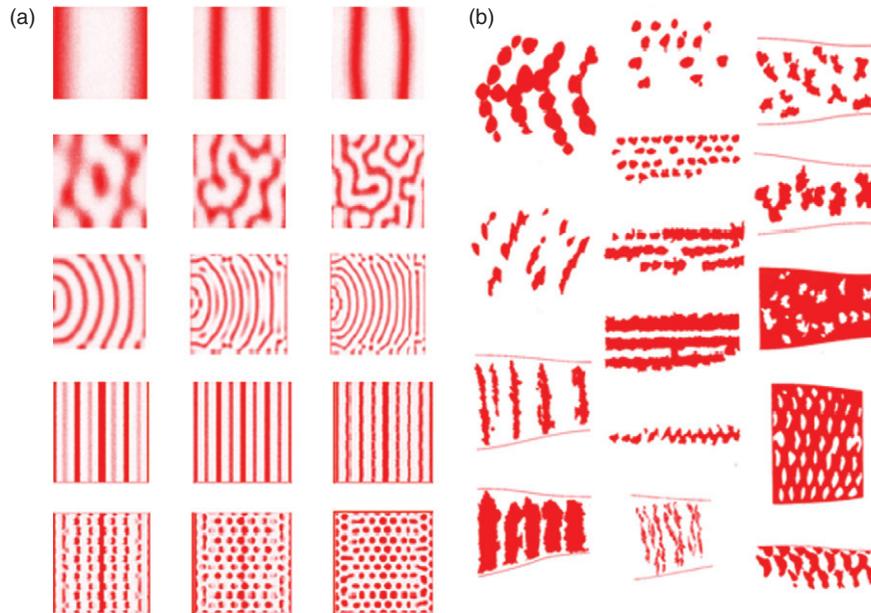


Figure 3 (a) Diversity of patterns generated by theoretical reaction–diffusion models of pattern formation. Small changes in gene structure or regulation can induce qualitative changes in pattern elements, producing dramatic differences in signal structure. (b) Such a process could account for the striking differences in pattern sometimes seen among closely related species. Distribution of red body pigmentation of 15 species of Cameroonian *Aphyosemion* killifish (Aplocheilidae). From Rosenthal GG (2007) Spatiotemporal aspects of visual signals in animal communication. *Annual Review of Ecology, Evolution, and Systematics* 38: 155–178.

sex and social status. In the bluehead wrasse *Thalassoma bifasciatum* (Labridae), both females and initial-phase males have yellow and black horizontal stripes; terminal males, which are derived from either females or initial-phase males, have completely different colors and spatial patterns: a blue head, black and white vertical bars, and a green posterior. Many pomacentrids and pomacanthids also have conspicuous juvenile color patterns strikingly different from the adult phase.

Evolution of Visual Signals

Visual signals in fishes are distinctive in the extent to which they depend on the underwater light environment. In aquatic environments, light quality and quantity varies with depth, water chemistry, and biotic factors such as plankton density. If a fish cannot make its own light, it must work with the available light environment to produce communication signals. Strong associations between transmission characteristics of the environment, visual sensitivity, and body color have been demonstrated in a variety of fish systems. Further, as on land, signal diversity is correlated with ecological complexity. The greatest profusion of fish visual signals is, accordingly, found in shallow waters on tropical coral reefs, where dozens of species coexist in a sensory environment that permits discrimination of fine spatial features and a broad range of colors (See also Vision: Color Vision and Color

Communication in Reef Fish). In deeper or murkier water, fish tend to be drabber and spatially simpler.

Microhabitat differences can drive sensory systems and thereby speciation. Female sensitivity to red in sticklebacks correlates with the abundance of red light in the environment, and with female mating preference for red versus black males, producing divergent selection for red and black males in divergent environments. Human-induced disturbance can produce the reverse effect: in haplochromine cichlids, eutrophication of clear lake water masks the apparent color differences between two recently diverged species, promoting hybridization.

Sexual selection – both in the context of conspicuous advertisements to potential mates, and in the context of aggressive signals among sexual rivals – is a primary driver of visual exuberance in fishes. In swordtails, genus *Xiphophorus*, females exhibit an ancestral preference for the conspicuous sword elongation of the caudal fin. The preference appears to be a special case of a more general preference for large apparent size. Conspicuous signals are, however, open to exploitation by eavesdroppers. The Mexican tetra (*Astyanax mexicanus*, Characidae), a swordtail predator, shares the same broad visual biases as female swordtails, preferentially targeting males with swords. The visual spectrum is not universally shared among receivers, however. The UV (320–400 nm) is the primary area where visual sensitivity varies substantially across fish taxa, providing the opportunity for a degree of signal privacy. Only about 30% of reef-dwelling fish

species are sensitive in the UV. Swordtails are sensitive to UV wavelengths, while *A. mexicanus* are not. Male swordtails in highly predated populations exhibit bright UV stripes, which females attend to in mate choice, but which are relatively inconspicuous to predators (Figure 1). Similarly, male guppies court at times of day and in microhabitats that minimize visual conspicuousness to long-wavelength (red) insensitive invertebrate predators, while retaining conspicuousness to females.

Sexual selection is insufficient to explain the flamboyant signals of many reef fishes, which are often highly stereotyped within a species, often identical in males and females, and in some cases, like beaugregory damselfish (*Stegastes leucostictus*) appear more conspicuous to us in juveniles than in adults. Konrad Lorenz, one of the founders of early ethology, proposed that reef-fish signals had evolved under pressure in a diverse, crowded community. By iconically encoding species identity, a distinctive pattern would minimize the incidence of aggression among heterospecifics not competing for resources. While Lorenz's idea of poster coloration remains to be thoroughly tested, some reef-fish signals are certainly targeting a broad array of receivers. For example, territorial males in many pomacentrid species express a distinct black-on-white pattern to warn off all intruders, and various species of cleaner fish have converged on a conspicuous blue-and-yellow cleaning pattern that serves to attract hosts to cleaning stations.

Spatial patterning may allow such patterns to be salient to receivers close by, while affording some degree of camouflage from larger midwater predators. High spatial frequency patterns (fine lines and small spots) provide high contrast at close range. When viewed at a distance, however, they smear together and blend into the background (Figure 2).

Fishes inhabit almost every conceivable visual environment, and the underwater environment poses considerable challenges for visual communication. Nevertheless, fishes have evolved a remarkable range of solutions to environmental constraints on signaling, and visual signals encode information that is critical to many

fishes' social relationships, cooperative interactions, and reproductive biology. Recent advances in technology, including UV-sensitive cameras and hyperspectral imaging, will be instrumental in understanding how these sophisticated signals are detected and perceived in complex natural environments.

See also: **Deep-Sea Fishes. Hormones in Communication:** Hormonal Pheromones. **Social and Reproductive Behaviors:** Sexual Behavior in Fish; Socially Controlled Sex Change in Fishes. **The Skin:** Bioluminescence in Fishes; Coloration and Chromatophores in Fishes. **Vision:** Color Vision and Color Communication in Reef Fish; Photoreceptors and Visual Pigments.

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