CHAPTER 14:

Light, Colour, and Vision in the Ocean

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Introduction

The reflected surface colour of the ocean, whether seen from the deck of a ship or measured by an orbiting satellite, provides information about the contents, and processes, immediately below. Many of these near-surface processes, ranging from the absorption of red light by chlorophyll to the multihued visual signalling of reef fish, are dependent on colour. Interactions deep below the surface are also affected by colour; indeed, the colours of the animals caught in a research trawl give a good indication of the depth from which they have come. ‘Colour’ itself is a rather subjective concept; its perception is critically dependent upon both the light conditions of the environment and the visual systems of the observer. A more objective assessment requires knowledge of the spectral distributions of ambient, reflected, and absorbed light.

Like most research tasks, understanding the role of light and colour in the sea has not been straightforward. Ironically, many of the life activities of deep-sea animals have been assumed from the anatomy of dead specimens. This can make for some spectacular mistakes (such as earlier interpretations of light-emitting organs as eyes or ears), but in most cases the conclusions are probably reasonably close to the truth. However, it is salutary to remember that illustrations of the deep-sea fauna, portraying fish and other animals oriented horizontally, do so more by convention than by information. One of the great advances has been the recent use of remote vehicles, cameras, and manned submersibles to see what life in the deep sea really looks like (or, at least, looks like when floodlit). A surprising number of fish, for example, routinely stand on their heads or their tails. Swimming brittle stars, luminous swimming sea cucumbers, meter-long siphonophores coiled in huge spirals, squids that shed their tails; these are but a few of the many unexpected behaviours that have been observed.

Much more about the interactions of light and animals can be learned only by careful experiments in the laboratory on perfect specimens. The laboratory may be on a ship, with all the limitations and discomforts attendant on working in a cramped, noisy, and disconcertingly mobile space, but with the advantage of immediate access to captured animals. It may be on shore, if the technical difficulty of maintaining the particularly delicate deep-sea species can be overcome. Such studies have shown that the eyes of deep-sea animals are irreparably damaged by brief exposure to daylight (or a submersible’s floodlight) – so special cold and dark trawl buckets (or cod-ends) have had to be developed for experiments on the vision of these animals.

The brief account below draws on all these methods for its data, but previous experience indicates that our present interpretations will not do full justice to the extraordinary abilities of the deep-sea fauna.

Characteristics of Light in the Sea

Light in the sea derives from two sources, the Sun and the organisms. Sunlight (and reflected moonlight) illuminates at most only the upper kilometre of the ocean. Bioluminescence occurs at all depths. The intensity distribution of sunlight at the sea surface varies by only a factor of about two over the visible range of 400–700 nm (Figure 14.1). Moonlight and starlight intensities are, respectively, about 6 and 9 log units lower than sunlight, while the intensities of bioluminescent sources can approach that of moonlight.

Light below the surface differs from that above in both quality and quantity. A major change occurs at the air–sea interface; here, the combined consequences of reflection from the surface (at glancing angles of incidence), and refraction into it, reduce the angular distribution of light entering calm water to a narrow cone of solid angle $97^\circ$. A fish looking upward sees the world above the surface through this limited window (Snell’s window). All it sees outside this window is back-scattered light from deeper water (by total internal reflection at the air–sea interface). Any initial asymmetry in the radiance distribution within the window (due to the Sun’s angle, for example) is rapidly degraded with depth, through the effects of scattering by both water molecules and suspended particles. Ice cover acts as a spectrally neutral diffuser and reflec-
Figure 14.1 Light at depth differs markedly from that at the surface. (a) The narrow spectral distribution of light at a depth of about 500 m in clear ocean water (d), compared with that of sun- and sky-light above the surface (s). (b) The symmetrical angular distribution of light in the ocean about the vertical axis. The length of the arrows indicates the relative radiance (intensity per unit solid angle) from point O in the respective directions. The radiance is maximum vertically downward and halves at 35° to the vertical. The vertically downward:upward ratio (D:U) in oceanic waters is about 200:1 (after Denton).

To produce a uniform, but dimmer, light field at the surface. Even in open water the light field soon becomes symmetrical about the vertical axis, with a downward radiance some 200 times the back-scattered upward radiance (Figure 14.1). At increasing depths this angular distribution of radiance remains unchanged, but scattering and absorption reduce the light intensity in an exponential way. Both these processes are wavelength selective. Water absorption preferentially removes both long (red) and short (ultraviolet) wavelengths, rapidly resulting in near-monochromatic blue light, which even in the clearest oceanic waters is reduced by 90% for every 70 m of depth; this means that moonlight makes the same contribution to ambient light at 400 m as does sunlight at 800 m.

In coastal waters dissolved yellow material derived from plant decay (both marine and from river input) may absorb additional short wavelengths and result in a greener hue to both the downwelling and back-scattered light. Scattering by particles of very small size is inversely proportional to the fourth power of the wavelength of the light (1/λ^4); blue light at 470 nm is scattered five times more than red light at 700 nm. Larger particles scatter all wavelengths more evenly (1/λ). These characteristics determine the light conditions in the sea and the resulting adaptations of the organisms. The biological imperative for every marine animal is to survive and reproduce; this requires the ability to find food and (usually) a mate, and to avoid or deter predators. Sensory systems such as vision, and effector systems such as bioluminescence and colour, provide some of the means whereby this is achieved.

Colour

Shallow water

Life in the upper layers of the ocean is dominated by daylight. In the near surface layers the spectral consequences of absorption and scattering are relatively minor and the animals are exposed to a bright light containing all wavelengths. At the margins of the oceans this is associated with a structurally complex background of shore or reef within (or against which) individuals can hide. The bright colours of many reef fish are responses to this complex optical (and biological) environment. They allow their owners to display and signal to each other with the relative immunity of a safe haven of retreat. The body colours are effective only because the ambient light contains all wavelengths at sufficient intensity for different colours to be selectively reflected. They also presuppose that the observers have sufficient variety of visual pigments to allow them to discriminate the colours, or at least to recognise their contrasts.

Open ocean

In the open ocean the animals are faced with the same illumination, but with the radical difference that the background is uniform. There is no complexity of pattern or topography within which to hide. Bright colours could be used to send the same messages as in shallow waters, but, with nowhere to escape to, these beacons would become a dangerous liability. Disappearance is possible only by matching the background radiance. Animals living right at the air-sea interface, and vulnerable to predators from above, are frequently blue in colour, matching the
Figure 14.2 The 40 mm diameter coelenterate Porpita floats at the surface, where it is camouflaged by a blue carotenoprotein pigment.

Figure 14.3 This 10 mm long surface living shrimp, Hippolyte coerulescens, is camouflaged by a blue carotenoprotein pigment and white reflective dorsal chromatophores. (Courtesy of the Southampton Oceanography Centre, England.)

upward scattered radiance of clear ocean waters. The colour is achieved in different ways by different species. Blue carotenoprotein or biliprotein pigments are commonly used (Figures 14.2, 14.3). Blue structural colours (selective diffuse or specular reflection) are other means of achieving the same result (Figure 14.4). The deep blue colour with which many upper ocean fish camouflage their dorsal surfaces has a similar structural basis.

Transparency and silverying
For smaller organisms in the upper waters, camouflage can be achieved by transparency. Many planktonic species, particularly the gelatinous forms, rely on this for their protection (Figure 14.5). For larger animals the complexity of the body tissues renders transparency impracticable. However, in the particular light environment of open water (with the brightest light from vertically above and a symmetrical radiance distribution about this axis), a mirror stood vertically in the water becomes invisible from any angle of side view. Many animals have taken advantage of this to mimic transparency by turning themselves into the equivalent of vertical mirrors. This is best

Figure 14.4 Blue colour can be achieved without pigment. In the isopod Idotea metallica (12 mm long), tiny reflective particles in the upper structure reflect blue light much better than red. The transmitted red is then absorbed by a dark pigment beneath the reflective layer. (Courtesy of the Southampton Oceanography Centre, England.)
achieved by flattening the body, so that the flanks are vertical, and covering these with reflective material. Fish are consummate examples of this strategy, none more so than the hatchet fish (Figure 14.6). For their reflective material they use tiny crystals of guanine (an excretory product derived from nucleic acids), which are aligned parallel to the body surface. The crystals are arranged in multiple stacks, alternating crystal and cytoplasm (the watery matrix of the cell), whose spacing is such as to achieve constructive interference reflection. For a particular wavelength of light, \( \lambda \), viewed at right angles to the stack of crystals, ideal interference reflection occurs when the optical thickness of each layer is 0.25\( \lambda \). With such a system, almost 100% reflectance is achieved with only 5–10 crystals. Without such spacing, five crystals would have a reflectance of only 20%.

One potential drawback of the system is that the best-reflective wavelengths shift toward the blue end of the spectrum as the angle of viewing becomes more oblique.

Effective silveriness requires reflection of all wavelengths, at all angles of view. To achieve this, the spacing of the stacks is adjusted so that either different colours are reflected from different stacks (which may be adjacent or superimposed on one another), or the spacing within the stacks varies in a regular way. Vertical flanks are not compatible with a muscular stream-lined body, so most fish

Figure 14.6 In the radially symmetrical light distribution in the ocean (Figure 14.1), a vertical mirror is invisible from the side. These hatchet fish (*Argyropsopon*, 25–30 mm long) have turned themselves into mirrors by flattening their sides and silverying them, using stacks of guanine platelets as interference reflectors.
have a more elliptical cross-section. If the reflecting stacks in the skin or scales remain vertically orient-
ed, despite the curved body surface, the effect of a vertical mirror is retained.

Figure 14.7 Where some organs remain opaque they can still be camouflaged by silvering them separately, as is the case for the liver and eyes of the 40 mm long squid Cranchia scabra.

Even when much of the body is transparent, there may be particular tissues that remain opaque (e.g., eyes, red muscle, or digestive organs). These organs can still be silvered individually to achieve effective camouflage. Squid use the same strategy, but employ reflective platelets of protein rather than guanine crystals (Figure 14.7).

The concealment value of vertical reflective surfaces rapidly disappears as the surfaces are tilted. This property can be used to good effect to distract predators (e.g., the flashing of a twisting school of fleeing sardines or the eponymous silversides). Changes in body orientation can also be used to send optical signals to nearby members of the school.

The dramatic colour changes visible in some oceanic fish (e.g., the coruscating colours of a captured dolphin fish, Coryphaena) are brought about by very rapid changes in the spacing of the crystals in the reflecting cells. Each stack of crystals behaves like venetian blinds as contractile elements in the cells tilt the individual crystals, altering their distance apart and hence their reflected colour. Rapid colour changes, under similar control, take place in the reflective stripe of the freshwater neon tetra and in some damselfish.

Deep-water colours

If reflection is the saviour of animals in reasonably well-lit open water, it spells potential disaster for those in the dark of the ocean depths. Here, the reflection of a bioluminescent flash or glow could break the cover of an animal hitherto invisible.

Figure 14.8 The uniform scarlet colour of the 70 mm long deep-living shrimp Acanthephyra purpurea is due to a carotenoid pigment that absorbs any incident blue light. We see it as scarlet in the white light of the camera flash; it is invisible in the deep sea, where blue bioluminescence is the norm and most predators only have blue-sensitive eyes. (Courtesy of the Southampton Oceanography Centre, England.)

Figure 14.9 The black melanin pigment of this typical deep-sea fish (Gonostoma bathyphilum, 110 mm long) plays the same camouflage role as does the scarlet pigment of the shrimp. (Courtesy of the Southampton Oceanography Centre, England.)
against the black background. Thus, silvering is an anathema in deeper water, and is replaced by uniform matt colours of brown, purple, black, or scarlet (Figures 14.8, 14.9). This is a particularly clear example of the functional equivalence of subjectively very different colours. Dramatically different as these colours may appear to us in the sunlight on deck, they are all equally effective at preventing the reflection of any residual dim blue light filtering down from the surface, or of stray flashes of blue bioluminescent light. As the bioluminescence may come from any direction, the colouring is spread over the whole of the animal.

At intermediate depths, where daylight from the surface is dim but still significant, and day–night intensity changes are still important, a compromise is reached in which animals have some element of colour and some of silvering or transparency. This enables them to adjust their colouring quite markedly in response to changes in light intensity. Fish silvered in daylight have mobile dark pigment cells which disguise their silveriness at night. Shrimps have a ‘half-red’ appearance, in which the red pigment is present in large pigment cells, and are able to disperse or aggregate the colour as appropriate to the light conditions (Figure 14.10). In both cases, the pigment distribution is primarily dorsal, in response to the continued dominance of downwelling light.

As the bottom is reached, quite marked changes occur in the colours of the animals. Many animals are now grey, pale, or even white. There is no obvious rationale for this change, except that in any bioluminescent light the paler species present a less-er contrast when seen against the lighter sediment than do their heavily pigmented pelagic relatives only a few tens of metres above (Figure 14.11). Many of the animals on the bottom have large sensitive eyes, so vision clearly still plays an important role in this environment.

Many oceanic animals undertake substantial vertical migrations during their lifetimes. In general, the larvae and juveniles live at shallower depths than the adults, and thus experience gradual changes in the light conditions as they move deeper in the water column. Their appearance at any given stage of development reflects the depth at which they are living. Early shrimp larvae near the surface may be transparent, the juveniles at mid-depths half-red, and the adults at depth uniformly scarlet. Colour is clearly a key feature in the life of oceanic animals, but its appearance to the denizens of the deep is not always quite what it seems to the human eye in sunlight.

Figure 14.10 In midwater, where light from the surface is still important and day–night changes are substantial, the limited colouring of the 50 mm long shrimp Sergestes is mostly distributed in large dorsal chromatophores. This allows the animal to change its appearance according to the light environment.

Figure 14.11 Many bottom and near-bottom animals are very pale, like this 220 mm long rat-tail Nezumia, at a depth of 1100 m off southwest Ireland. In the light of the flash these animals are not easily distinguishable from the pale sediment on the bottom; this may also be the case in whatever dim bioluminescence exists on the sea floor. Also here (just above and to the left of the fish) is a shrimp with a reflective eye (see also Figure 14.18) and (above and to the right) two large pot-like glass sponges. (Courtesy of the Southampton Oceanography Centre, England.)
Vision

The light environment of the ocean is matched by the visual adaptations of its inhabitants. Vision depends on the absorption of photon energy by the visual pigments and its transduction into a neural signal. The spectral sensitivity of the eye is determined by the absorption characteristics of the visual pigments in the retinal receptors. In vertebrates these receptors are single cells (rods and cones); in invertebrates, they are units (rhabdoms) formed from several cells.

Visual pigments

In general, the absorption maximum of the main visual pigment is a good match to the spectral characteristics of the environment. Thus, deep-sea fish usually have rod visual pigments with absorption maxima in the blue wavelengths around 480 nm (Figure 14.12), while shallow coastal species have maxima at longer wavelengths. Near the surface the high intensity and broad spectral range of ambient light provide the opportunity for both colour vision and high acuity. The dominant visual task is to maximise the contrast present in the target area. When a dark object, or silhouette, is seen against the background of downwelling light, or horizontally against an infinite background of scattered light, the contrast is maximised by having a visual pigment which matches the spectral transmission of the water. When, on the other hand, a bright reflective object is viewed horizontally, maximum contrast can be achieved by exploiting the spectral differences between the reflected and background light, using a visual pigment whose absorption maximum is offset from that of the background.

Visual pigments are formed by linking a protein, one of the opsins, to a vitamin A₁ or A₂ derivative (forming a rhodopsin or a porphyropsin, respectively). Porphyropsins absorb at longer wavelengths than do their rhodopsin partners. Although a few marine fish do have this pair of pigments, many of them lack the porphyropsin, but have more than one rhodopsin (i.e., vitamin A₁ with different opsins) and thus retain the potential for colour vision. Additional visual pigments may also be present, usually in different types of cone cell, and coloured filters or oil droplets may further differentiate the spectral sensitivity of individual receptors. In the most extreme cases (some mantis shrimps) there may be up to eight kinds of receptors, each with different spectral sensitivities. Recent work has shown that the shrimp Systellaspis debilis has a visual pigment which is sensitive to near-ultraviolet light, as well as one sensitive to blue-green light (Figure 14.13).

Colour vision is also theoretically possible for fish with only one visual pigment, but with a retina containing multiple banks of rods. Each layer modifies the spectral nature of the light transmitted to
the next layer, giving them, in effect, different spectral sensitivities.

Major changes in the light environment of fish occur during the lifetime of those, like the eel, which have a marine and a freshwater phase or, like the pollock, migrate into deeper water as an adult. These changes are compensated by visual pigment changes, either between rhodopsin and porphyropsin pairs or by opsin shifts between different rhodopsins. In either case the new suite of pigments is more appropriate to the visual tasks of the new environment.

The upward view

Light in the deep-water environment is dimmer, bluer, and highly directional. Animals in the upper few hundred metres are likely to sight prey or detrital particles within an angle of 35° from the vertical; here, the downward radiance does not drop below 50% of its maximum value (Figure 14.1). This limited, but bright, cone of view (70°), dominates the visual environment. Many animals at these depths have responded by evolving upwardly pointing eyes. Every stage between fully lateral and fully upward eyes can be found in one or other species of mesopelagic fish, culminating in the extreme cases of Opisthobranchia, Benthobrotula (Figure 14.14), and the hatchet fish Argyropelecus. Visual acuity (resolution) needs to be maximised in this direction and both amphipods and euphausiids have a gradation of forms whose eyes range from round, with a uniform acuity over the whole visual

Figure 14.13 The shrimp Systellaspis debilis (60 mm long) has two visual pigments, one absorbing in the blue-green, the other in the near ultraviolet. Since these wavelengths have different transmission characteristics, their ratio could give the animal an indication of its depth. The dark spots on the thorax and abdomen are light-emitting organs.

Figure 14.14 The tubular eyes of the 100 mm long fish Benthobrotula provide a binocular overlap, allowing it to determine the range of prey as well as providing a large aperture for high sensitivity. (Courtesy of the Southampton Oceanography Centre, England.)
field (*Meganyctiphanes*), through double eyes with a narrow upper visual field of high acuity and a more extensive lower visual field of low acuity (*Phronima, Stylocheiron subniss*, Figure 14.15), to those with effectively only an upward eye of high resolution and narrow field (*Cystisoma*).

**Maximum sensitivity**

At greater depths (and, of course, at night nearer the surface) the light levels become marginal for vision and the adaptations of the eyes of the animals are largely dedicated to maximising their sensitivity. This is determined by two factors: first, the illuminance of the retina and, second, the probability of photon capture by the receptors.

**Image brightness**

The illuminance (or image brightness) is a function of the aperture (pupil) and focal length of the eye. The aperture determines how much light enters. In the compound eyes of crustaceans, the aperture can be greatly increased by changing from an apposition type of eye to a superposition one*. Apposition eyes have the individual units (ommatidia, each containing one rhabdom) optically isolated from each other (usually by pigment). The eye has good resolution, but the effective aperture is that of a single facet. In superposition eyes, the units (ommatidia) are not optically isolated and the light from a large number of ommatidia can be focused on a single receptor. The aperture is now the facet area of all these ommatidia, giving a huge increase in sensitivity (Figure 14.16). Deep-sea shrimps of all kinds have such superposition eyes; often, their larvae, at shallower depths, have apposition eyes, which change into the superposition form as the larvae descend into deeper and darker water during their development.

The aperture of the fish eye is filled by the spherical lens (see Figure 14.15). Only in near-surface species is there an iris diaphragm to stop down the aperture in bright light. A larger aperture requires a larger lens, but the construction of the fish (and cephalopod) lens is such that the focal length is a constant ratio of the lens radius (2.5:1,
Matthiessen’s ratio). This means that any increase in aperture necessitates an equivalent increase in focal length, i.e., a larger eye. Large eyes are a feature of many deep-sea fish – but there is a practical limit to how large an eye can be, yet still fit on the head. A tubular eye overcomes much of this problem. A very large aperture is possible because only a tubular portion of the equivalently sized normal eye is retained. Fish such as Dolichopteryx have huge lenses, each almost half the width of the head; this is achieved by having a narrow tubular eye with a very limited field of view (Figure 14.17). Many fish with tubular eyes (including Dolichopteryx) have evolved secondary methods of increasing their visual field. Light guides, lens pads, and accessory reflectors capture some light from below the main visual field and convey it to an accessory retina. It is not focused, so no image is formed, but it does offer additional information to that available solely through the lens.

**Photon capture**

The probability of photon capture by the receptors is a function of the visual pigment density, its absorption maximum, the length of the light path, and the diameter of the receptors. Maximum sensitivity requires that the visual pigment match the ambient light very closely. Only a single visual pigment is normally present in the rods of deep-water fish. Cones are usually absent. The density of the visual pigment varies little between species, but the length of the light path through the receptors can be increased by lengthening the rods or having multiple banks of short rods. A simple means of doubling the light path is to place a specular or diffuse reflector (or retinal tapetum) at the back of the eye.

**Figure 14.16** (a) A crustacean apposition eye, in which each unit (ommatidium) is optically isolated, with the receptor (rhabdom, rh) joined to the crystalline cone (cc). Only a very narrow beam of near-axial light reaches each receptor through its own cone; off-axis light is absorbed by the dark pigment (p). (b) A superposition eye, in which the receptors are separated from the cones by a clear zone (cz); the aperture is now formed by a large group of facets, greatly increasing the receptor illuminance. This kind of eye can be constructed using refractive cones, as in (b) (e.g., in euphausid shrimps), or by reflective mirrors (m), as in (c) (e.g., decapod shrimps). (From Herring and Roe)
Many seals, fish, and crustaceans have such layers, which give the animal an intense eyeshine in bright light (Figure 14.18). In sharks and their relatives, black pigment covers the tapetum during the day and withdraws at night. The tapetum may be formed of layers of crystals, arranged for constructive interference of the ambient blue wavelengths, or of uniform granules or lipid spheres which give a more diffuse reflectance. Receptor diameter is effectively increased by pooling the output from a group of rods or rhabdoms into a single ganglion cell. This increases sensitivity, but at the expense of acuity, unless the focal length (i.e., eye size) is also increased to retain the same angular separation of the enlarged receptor units.

**Eye reduction**

In the depths of the ocean, where the only light is bioluminescence, some animals retain large sensitive eyes, but others lose much of the optical complexity present in shallower species and/or reduce the eye size to almost rudimentary proportions. In shrimp such as *Hymenocora*, all the focusing elements are lost and the eye retains only very complex rhabdoms and reflective material. In the fish *Ipnops*, the lens is also lost and the eye is little more than a flattened sheet of rod receptors.

The deep-water shrimp *Acanthephyra curtirostris* has tiny reflective eyes, compared with the larger pigmented ones of shallower relatives, such as *A. purpurea* and *S. debilis* (Figure 14.19; see also Figures 14.8, 14.13). The deepest-living euphausiids have equally tiny eyes, as do abyssal rat-tail fish. One remarkable shrimp (*Alvinocaris*) has completely lost its compound eyes, but has developed what appears to be a lens-less accessory visual system in the thorax. The visual pigment present

**Bioluminescence**

The presence of functional eyes in many abyssal animals, well below the maximum possible penetration of daylight, testifies to the importance of biological light, or bioluminescence, in the ecology of the deep sea. Fireflies and glow-worms are the well-known terrestrial examples of this phenomenon, but there are few others on land and only one (a New Zealand limpet) in fresh water. In contrast, the sea contains an immense variety of luminous organisms spread across 16 different major groups, or phyla. The organisms range from bacteria and dinoflagellates to squid and fish, and their distribution extends from the surface waters to the greatest depths. This rich variety of organism is matched by the astonishing range of their bioluminescent capabilities and functions. The conclusion to be drawn from the variety of luminous groups, and the different chemistries involved, is that the ability to emit light has evolved independently in many different organisms.

**Mechanism**

Bioluminescence is the harnessing of a chemiluminescent reaction by a living organism, with a sufficient quantum (photon) yield for the light to be visible. The overall reaction involves the oxidation of a substrate (‘photon’) catalysed by an enzyme (‘luciferase’), so that some of the energy released by the reaction is emitted as light rather than heat. The energy can be transferred into a second, fluorescent, compound which then emits light at its own characteristic wavelength (always longer than that produced by the original reaction). There are
many different kinds of luciferin, some restricted to particular groups of organisms, others spread across several different phyla. Relatively few have yet been identified. Most organisms make their own luciferin (although some may acquire it in their diet), but some fish, squid, and tunicates use symbiotic luminous bacteria as their source of light.

The brightest bioluminescence can only match the intensity of moonlight, so bioluminescence makes no significant contribution to the light of near-surface oceanic waters during the day. In turbid coastal waters, however, it may be the only light visible as shallow as 30 m, even during the day. At all other times and depths it is a major, and often the only, source of light in the sea.

**Colours of bioluminescence**

If the eyes of marine animals have adapted primarily to the characteristics of submarine daylight, with its blue transmission maximum in clear waters, it is likely that bioluminescence has followed this visual lead. The colours of marine bioluminescence are, indeed, very largely confined to blue–green wavelengths. These, of course, are not only best perceived by other marine organisms, whether or not they are themselves bioluminescent, but also will be best transmitted through the water, both features maximising their effective signalling range. Some animals, particularly hydrozoan jellyfish, add a green fluorescent protein to the luminous cells and emit green light. It is not clear whether this is a response to a more coastal environment, with its greener water transmission, or a means of increasing the quantum efficiency (i.e., the light yield) of the reaction.

It may be more important (for maximising the effective range) to have a bright green light than a dimmer blue one, if there is little difference in an observer’s spectral sensitivity to the two wavelengths. There are a few other colours of bioluminescent light; the worm *Tomopteris* has a yellow luminescence and the fish *Malacosteus* (and a few others) has a deep red light, as well as a blue one. In the latter case, the red organ (under the eye) has a narrow bandwidth emission with a maximum at about 700 nm; this light is invisible to the dark-adapted human eye. A blue organ just behind it emits at 480 nm. The red light is probably produced by the same chemistry as the blue light, but with a combination of an additional red fluorescer in the light organ and a deep-red filter on its surface (*Figure 14.20*). The red organ cannot be very efficient; about 80% of the light it produces is absorbed by the filter in order to achieve the narrow bandwidth.
Figure 14.21 Malacosteus (175 mm long) has both blue- and red-sensitive visual pigments. The red sensitivity is further enhanced by a red reflector (tapetum) behind the retina, providing the red colour to the eye visible here in daylight. (Courtesy of Dr N.A. Locket, Adelaide University, Australia.)

Figure 14.22 (a) The hatchet fish Argyropelecus (Figure 14.6), seen from below, showing the photophores arranged along its ventral margin, each containing a magenta-coloured filter. This results in the emitted bioluminescence being a clear blue, exactly matching the colour of light in the sea (courtesy of P.M. David, Southampton, England). (b) A luminescing specimen by its own light.

The long wavelength light must be very important to the fish, but it would not normally be able to see it if it had only a typical blue-green sensitive visual pigment. Malacosteus turns out to have a red-sensitive visual pigment as well. It also has a scarlet tapetum (see earlier) to maximise its sensitivity to these long wavelengths (Figure 14.21). It thus has a ‘private’ wavelength, which could be used either as a secure communication with others of the same species or to break the camouflage of red shrimps, whose colour only works in blue illumination and whose blue-sensitive eyes would not detect the red illumination. Red light of these wavelengths is rapidly absorbed by sea water, so it can only be effective over short visual ranges.\(^3\)

A few other marine animals produce light of more than one colour. The stalked sea-pen Umbellula, for example, has green luminescence on its stalk, but blue emission from the polyps at the top. Some squid produce green and blue light from different light organs, and can also change the emission spectrum from a single light organ. Another coelenterate, a sea anemone-like zoanthid, has colonies in which some individuals have green light and some yellow.

Luminous camouflage

The ecological value of most of the exceptions noted above is not yet clear, but the value of precisely controlling the colour has been well-established in the hatchet fish. This fish lives at depths where daylight is still important and, as already described, has mirror-like camouflage and tubular eyes. Despite being very laterally flattened, it cannot altogether avoid being seen in silhouette from below. Like many other fish at mid-depths, it eliminates this silhouette by having rows of light organs along its ventral surface [Figure 14.22(a)]. All its light organs point downward, except one, which points into the eye. By adjusting the luminescence shining into the eye to match the downwelling daylight, it simultaneously matches all its ventral lights to the surrounding light—and vanishes. However, the broad bandwidth light produced within the light organ is not quite the
Figure 14.23  Mature females of the pelagic octopod Japetella (100 mm long) develop a yellow-coloured bio-luminescent oral ring which degenerates after they spawn. Males have no luminous organ, so it is assumed that this provides a sexual signal.

same colour as light in the sea. The aperture of each light organ contains a purple filter pigment which corrects this spectral mismatch. After passage through the filter the luminescence has a narrow bandwidth blue emission with a maximum at about 475 nm, corresponding exactly to the spectrum of light in the sea [Figure 14.22(b)]. To complete the camouflages, the design of the reflectors in the light organs ensures that the angular distribution of the luminescence also matches that of submarine daylight, as illustrated in Figure 14.1(b).

Other luminous defences
Camouflage is an example of a passive defensive function. The most common use of light in the sea is as an active defence, which can take the form of a single, short, bright flash (dinoflagellate), a volley of flashes (some fish), a wave of flashes moving over the body (sea-pens and medusae), or the discarding of sacrificial parts of the body which flash independently to distract a predator (scale worms and brittle stars). Another widely employed active defence is that of a squirted luminescence. Many shrimps, worms, a few squid and fish, and some medusae and ctenophores produce copious amounts of light in this form. Particularly among the ctenophores and medusae, it is not simply a cloud, but is composed of separately scintillating particles. Many of these gelatinous animals hang passively in the water fishing for prey; for any larger animal in the area, they collectively form a luminous minefield.

Sexual light signals
Small crustaceans, such as copepods and ostracods, have luminous glands whose secretions the animals kick away defensively as they swim. They can also be used for sexual displays. The pattern, timing, and trajectory of the luminous gobbets produced in the mating displays of males of the Vargula group of ostracods identify them to the waiting females, who swim up to join them. Syllid worms have analogous displays in many parts of the world (e.g., the Bermuda fireworm). Sexual differences in the size or position of the light organs of male and female lantern fish, stomiatoid fish, and some cephalopods also suggest that they have a sexual function (Figure 14.23). Female angler-fish have lures containing luminous bacterial symbionts, but the males do not. It is assumed that the lure attracts prey, but perhaps it also sends a specific signal to the males (Figure 14.24).
Luminous bacterial symbionts

Those animals utilising luminous bacteria have to constrain them in a particular gland or tissue, provide them with the right environment to thrive, dispose of dead ones, and ensure that the right bacteria are transferred to the next generation. Each host requires a particular species of bacterium, though many share the same species. Many hosts have light organs which are connected to the gut lumen and from which the symbionts can easily be cultured in the laboratory. As the natural (but largely accidental) bacterial flora of the gut contains some luminous species, acquisition of the right bacterium for the light organ is probably easy. The same bacterial species, and a few additional ones, are found ‘free-living’ on the surfaces of animals, on marine snow (see Chapter 7), and possibly free in the water. In the angler-fish and flashlight fish (Figure 14.25), there is no light organ connection to the gut and the bacteria are unculturable, so their origin is not known. Genetic data indicate that they are new species and very host-specific. Luminous bacteria glow continuously; the host has to develop a means of turning them off when necessary. Usually, this is achieved by pulling a shutter across the aperture of the organ, rotating the organ to face inward, or dispersing dark pigment over its surface, but control of the oxygen (blood) supply may sometimes be involved.

Photophore structure

The possible optical complexities of light organs fully match those of eyes. The light-emitting cells sit within a pigment cup which limits the aperture, while a specular interference reflector of guanine or protein platelets, or a diffuse granular reflector, greatly increases the output efficiency. A lens focuses the light, a lamellar ring collimates it, and interference or pigmeny filters change its spectrum. Light guides spread the output over a larger area and light pipes even allow the light to be emitted some distance from the light organ. Many hundred light organs are present on some fish and squid (Figure 14.26); individual species may have three or
four structurally quite different types at different sites on or in the body. We do not yet know what kind of light many of these organs produce, nor what functions they serve. If light, colour, and vision in the ocean are regarded as an interlocking jigsaw puzzle, these are some of the pieces which have not yet been fitted in.

General References

References