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Light and the Optical Environment

You are about to take your dive in a submersible. Yesterday, the ship left port in a brackish lagoon on the Florida coast. There, the water was first brown and opaque, like chocolate milk, then green and clear like an aquarium that had not been cleaned in months. The weather was beautiful with a sun too bright to look at and a sky that was deep blue overhead and a paler blue near the horizon. Today, the water is an astonishing and pure shade of blue, with glints of white sunlight at the edges of the waves. The submersible dips below the surface, and the light becomes far more even. In fact, this is the most featureless environment that you have ever encountered. Ahead, the water is bright and blue. Overhead, the light is white, with some portions of the underside of the sea surface appearing mirrored. Underneath the submersible, the light is violet-blue, with shifting beams of brighter light that seem to radiate from a point directly below. As the submersible descends, the water slowly becomes dimmer and bluer, and the objects inside the passenger sphere slowly lose their colors. The first color to go is the red shirt of the pilot, which now looks black. Then the orange seat cushions go brown, and a yellow camera strap turns gray. Finally, the green lettuce on the sandwich you brought with you also turns grayish blue, and the only remaining nonblue objects are the red indicator LEDs inside the submersible. About 20 minutes after that, you notice that the submersible is descending into blackness, and the only light, which is now dim and gray, is directly overhead. Soon this vanishes, and you are surrounded by flashes of blue light, which appear to be made by objects impacting the sphere as it descends. Some flashes are small and brief, but others are large and frankly messy, much like a glowing pudding being smeared against the window. The submersible stops descending and all the flashing lights stop. The pilot turns off the indicator lights, leaving you in profound darkness.

After many hours of work at depth (with floodlights), the submersible resurfaces right before sunset. The sun at the horizon is a deep orange-red, and the sky is a riot of colors, ranging from blue to magenta to what can only be called a golden pink. About 20 minutes after the sun sets, the only color remaining in the sky is an extremely pure blue, bordering on purple. Twenty minutes after that, the sky is dark gray and filled with stars and the Milky Way. You cannot discern it but are told by a

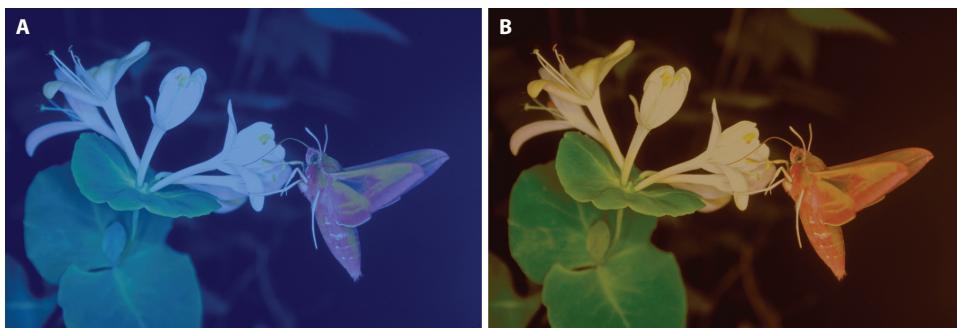


Figure 2.1 The elephant hawkmoth (*Deilephila elpenor*) as viewed during late twilight (A) and on a moonless night (B), showing the extreme chromatic changes that can occur within 30 minutes (images are set to have roughly the same average brightness). Note that the illumination on a moonless night is far warmer than that during late twilight due to the dominance of reddish stars rather than blue sky (see Johnsen et al., 2006, for details).

fellow crew member that the dim gray light between the stars is actually greenish, and the Milky Way is full of uncounted numbers of red dwarf stars. Later, the moon rises and everything takes on a much brighter silvery sheen. The moon is close to full, and there is enough light to do just about anything except read. The same know-it-all crew member mentions that the sky is now actually just as blue as the daytime sky, though a million times dimmer. The day ends with the arrival of a thunderstorm, which sends down bolt after bolt of purplish-white lightning into the dark sky.

Humans, and nearly all animals on Earth, witness astonishing variation in their optical environment. Brightness changes by many orders of magnitude each day, and colors also shift dramatically (figure 2.1). Those animals that enter forests and especially the water experience even larger changes. Given this, it is surprising that nearly all the natural light on Earth ultimately comes from two sources, the sun and bioluminescence. This chapter describes how these two sources (and a few minor players) light our world.

Light and Its Measurement

Before we can discuss the optical environment we first need to answer some questions and define some terms. The first obvious question is: What is light? To that question, the only honest answer is that we have no idea. No one does. Unfortunately, there is no intuitive reality to light as there is, for example, to a ham sandwich. As you are probably aware, light has been described as both a microscopically small packet of energy known as a photon and as a diaphanous electromagnetic wave that extends throughout space (figure 2.2). Although some physicists take the stand that light truly is one or the other (see Kidd et al., 1989), we suggest that it is best to take a practical approach and use whichever metaphor is most appropriate for the situation. For example, many people find it easier to think of light emission and absorption in photonic terms and polarization in wave terms. The metaphor you choose does not affect how you do your calculations and measurements. So, as long as you do those correctly, you can imagine light's true incarnate nature to be anything you

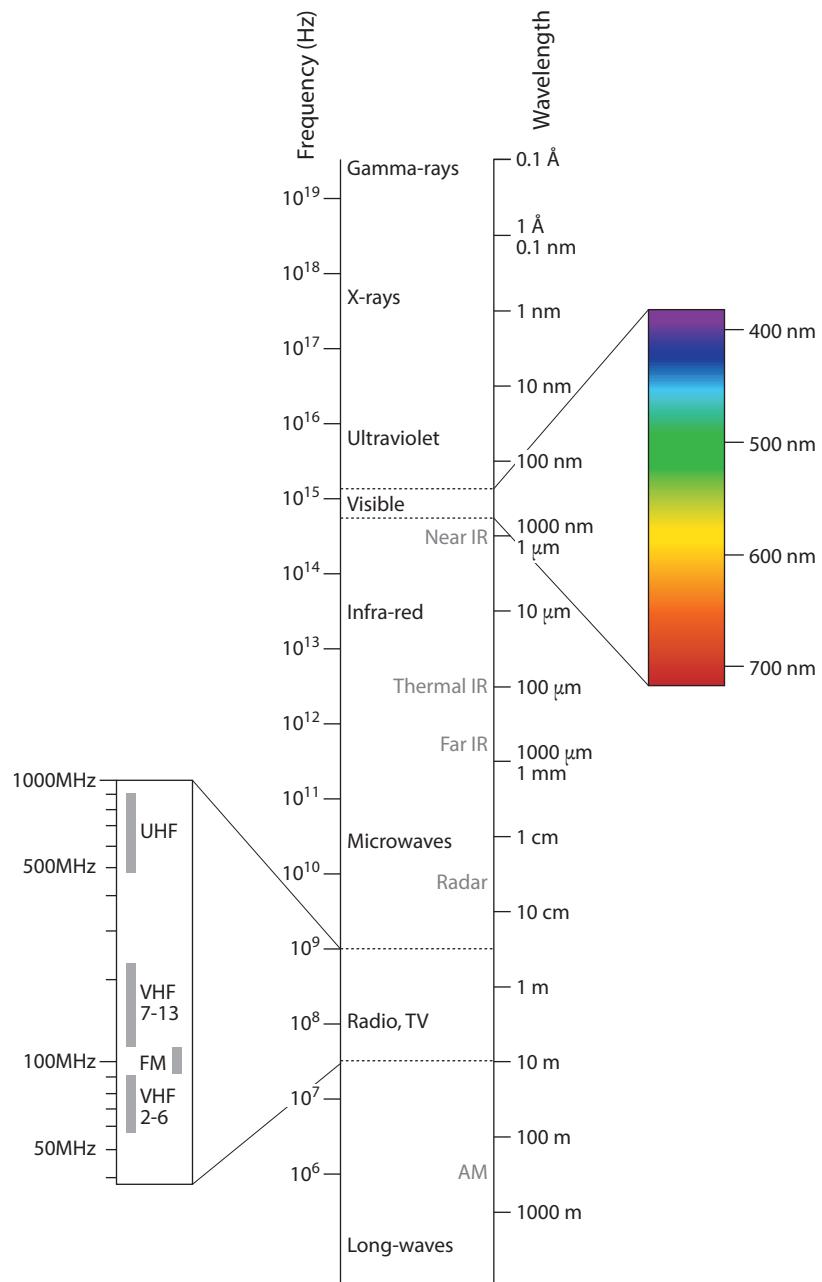


Figure 2.2 The electromagnetic spectrum.

like. We move freely between these two constructs throughout the book, starting with the next paragraph.

Regardless of how you think about it, a beam of monochromatic light has only three properties: (1) intensity, (2) wavelength/frequency, and (3) polarization. Intensity can be measured in two ways, in energy terms or in quantal terms. In other words,

one can either measure the amount of energy the beam imparts to a surface (usually in watts) or the number of photons that intersect that surface over a given period of time. In visual ecology it is generally better to measure light in photons because that is how photoreceptors work: they count photons rather than measure energy (see chapter 3). Unfortunately, most light detectors (which are built by and for physicists) measure light in energy units. However, it is simple to convert from one to the other if you know the wavelength of the light. Then the intensity of the light in photons per second per area is simply the intensity in watts per area multiplied by 5.05×10^{15} and the wavelength (in nanometers) of the light in air.

You must use the wavelength it would have in air (technically in a vacuum) because the wavelength of light changes in different media. For example, blue-green light transmits best in the ocean and has a wavelength 480 nm in air. Its wavelength in water, however, is 361 nm (480 divided by 1.33, the refractive index of water). Actually, the frequency of the light is more fundamental than the wavelength because it does not depend on the medium the light is going through. However, for historical reasons—and maybe because people like lengths more than frequencies—wavelength is far more popular with visual ecologists, and we use it throughout this book. Therefore, when we mention the wavelength of light, you should assume that it has been measured in air. The final property of light—polarization—is discussed in detail later (see chapter 8).

The intensity, wavelength, and polarization completely describe monochromatic light, which of course does not exist in nature. Instead, natural light is a collection of beams of different wavelengths, intensities, and polarizations. If we ignore polarization for now, the best way to describe natural light is via a spectrum that gives the intensity as a function of wavelength. In quantal terms, the units of each point in a spectrum are photons/s/cm²/nm. These units measure how many photons within a wavelength bin 1 nm wide impact a square-centimeter surface in a second.

Note that the term “bin” in the previous sentence implies that intensity spectra are histograms. As a result their shape depends on the nature of the bins. For example, it is just as correct to put a solar spectrum in equal-frequency bins as it is to put it in equal-wavelength bins. Unfortunately, equally sized wavelength bins will not have equal widths when moved into frequency space (see Johnsen, 2012). This matters because people often compare peaks of visual sensitivity curves to natural spectra to make statements about adaptation. For example, it has been said that the human photopic sensitivity curve is matched to daylight. Indeed, if one looks at a graph of this curve against a solar spectrum binned by wavelength, the fit seems good. However, if one bins by frequency units, the fit is terrible (figure 2.3). This is all described in detail elsewhere (see Soffer and Lynch, 1999; Govardovskii et al., 2000; Johnsen, 2012), but there are two take-home messages. First, one cannot compare the peaks of visual sensitivity curves with environmental spectra because the shape of the spectrum depends on how it is binned. Second, there is no such thing as spectrally flat, “white” light despite many researchers’ desires to use it as a control in experiments. A flat photon spectrum binned by wavelength will not look flat when binned by frequency, and neither the wavelength or frequency spectrum will look flat if energy units are used.

These caveats aside, we now come to what is actually measured. “Intensity” has an intuitive meaning but is not a useful term for visual ecology. Instead, we primarily deal with two properties, irradiance and radiance (figure 2.4). The first describes how much light is reaching a certain point from all directions, and the second describes

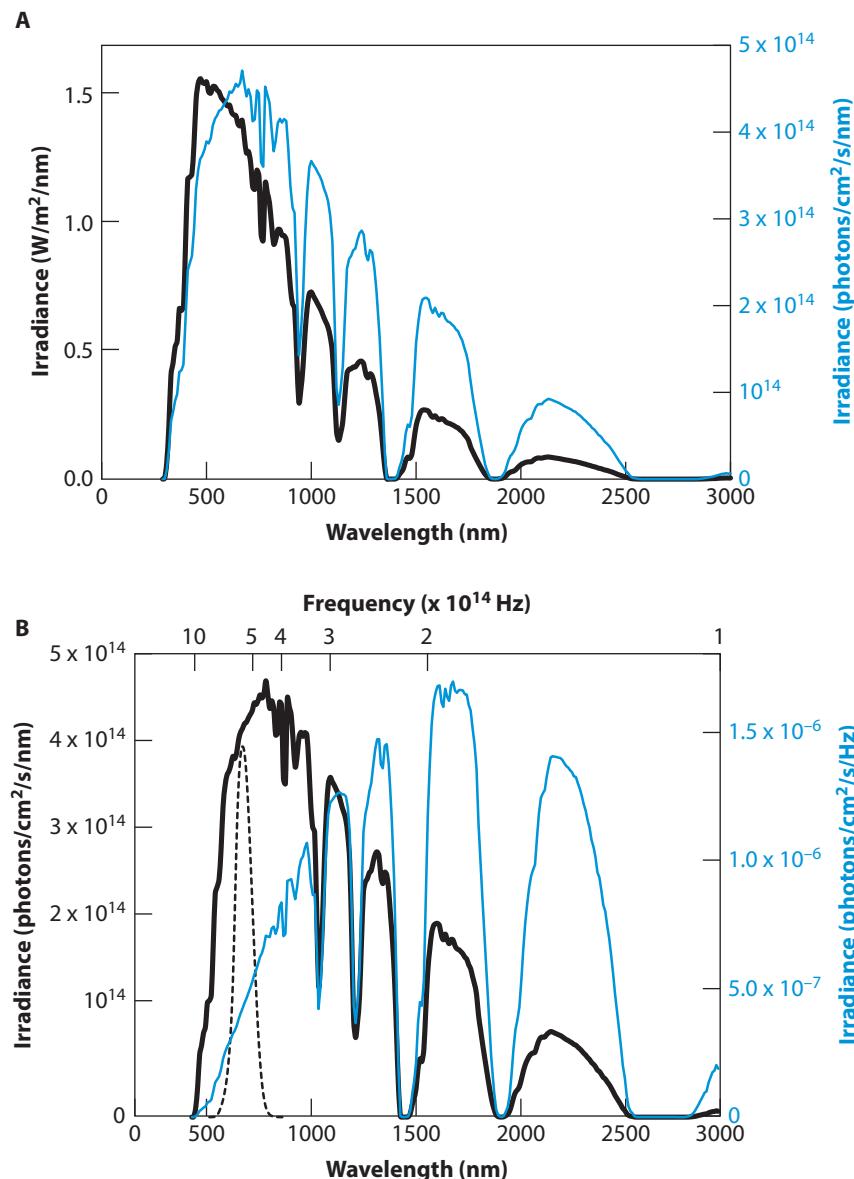


Figure 2.3 Daylight spectrum binned by equal wavelength intervals (A) and by equal frequency intervals (B). Human photopic (cone-based) sensitivity curve (in response per photon) is arbitrarily scaled and plotted as the dotted line.

how much light is coming from a certain direction. Taking irradiance first, most visual ecologists will measure one of two versions of it: vector or scalar. A vector irradiance sensor measures all the light that hits one side of a surface, weighted by the cosine of the angle of the light relative to the normal to the surface. In other words, light that strikes the surface perpendicularly is weighted the most, and light that strikes a glancing blow is weighted the least. Although this seems unnecessarily

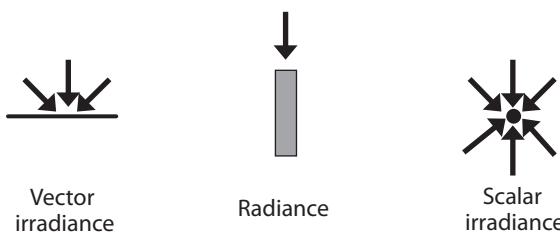


Figure 2.4 The three most common light measurements: vector irradiance, radiance, and scalar irradiance.

complex, many natural objects behave in this way. For example, the amount of rain that falls into a hole depends on the cosine of the angle of the rain relative to the hole, and how much the summer sun warms your forehead depends on the cosine of the angle between your forehead and the sun. Thus, this cosine-weighting function is the natural way to describe how much light strikes a flat surface.

Vector irradiance detectors are fitted with devices called cosine correctors that are usually flat disks of white plastic that scramble the incoming light direction, making the detector behave like the hole described above. These are compact, rugged, and relatively cheap, so at least 95% of irradiance measurements made by visual ecologists are of the vector variety. A potential disadvantage of these devices is that they are orientation dependent. So using them to measure environmental light levels can be ambiguous at best. For example, it is common but incorrect to use measurements of downwelling irradiance to determine the adapting illumination for an animal that is looking horizontally. Instead, one must measure horizontal irradiance (i.e., point the cosine corrector horizontally instead of up). Scalar irradiance sensors (which look like ping-pong balls on sticks) measure the light that comes from all directions, with all directions weighted equally. Thus, they give a single spectrum for an optical environment, which is potentially more valid and useful. Because vector irradiance is still the dominant form measured by biologists, we use it often throughout this book (particularly downwelling vector irradiance), but scalar irradiance measurements have many advantages and should be considered.

The other primary measurement of optical environments is radiance, which describes how much light comes from a certain direction. Thus, the measured light is divided by the solid angle (in steradians) of the field of view of the detector, giving units of photons/s/cm²/nm/sr. Radiance sensors typically have a narrow and circular field of view on the order of a degree or two across. Eyes are essentially radiance detectors because they provide information on how much light is coming from each small location in space. Many detectors, including bare fiber-optic cables, are not radiance sensors because their field of view is usually too broad.

Before we move on to the actual optical environment, we give a brief word of warning. The field of light measurement (known as radiometry) is subtle, with many pitfalls. Although any light detector or spectrometer will happily provide you with a number, it is easy to measure the wrong thing or the right thing in the wrong way. Intuition is also a poor guide because of both the logarithmic nature of visual adaptation and color constancy. Therefore, one can have an exceedingly wrong measurement and not know it. This brief introductory section is only meant to provide enough information to help the reader understand the optical measurements in the rest of this book. For a more complete understanding of light and how to measure it, see Johnsen (2012), Bohren (1987, 1991), or Bohren and Clothiaux (2006).

Daylight

Even in the densest urban center, outdoor light from 30 minutes before dawn to 30 minutes after sunset is completely dominated by direct and indirect sunlight. This sun, a fascinating celestial object, can for visual ecologists be summed up simply: it is an approximate blackbody radiator with a temperature of $\sim 5800^{\circ}\text{K}$ and an angular diameter of half a degree. A blackbody radiator is simply an object whose light emission spectrum can be predicted from its temperature and is maximal for that temperature (Planck, 1901). Most organisms are also blackbody radiators, but because they are at a much lower temperature, they radiate far less and mostly at nonvisible wavelengths. However, even at mammalian body temperature, the amount of emitted energy is considerable, about 1000 watts for an adult male human (which is 10–20 times our basal metabolic rate and, fortunately, counterbalanced by electromagnetic energy we absorb from the environment). At temperatures of 5800°K , the amount of radiated energy is impressive, even at visible wavelengths, as evidenced by the fact that even an object the size of your thumbnail at that temperature would keep you as warm as the sun when held at arm's length (and thus subtending an angle of half a degree). It would also slowly kill you because there would be no ozone layer between you and it to absorb the far-ultraviolet radiation it would be emitting. The ozone layer and other constituents of the atmosphere remove most of the ultraviolet radiation and large swaths of the infrared spectrum. This absorption makes direct sunlight at the Earth's surface not exactly blackbody radiation (figure 2.5), but it allows us to live on land without severe radiation damage.

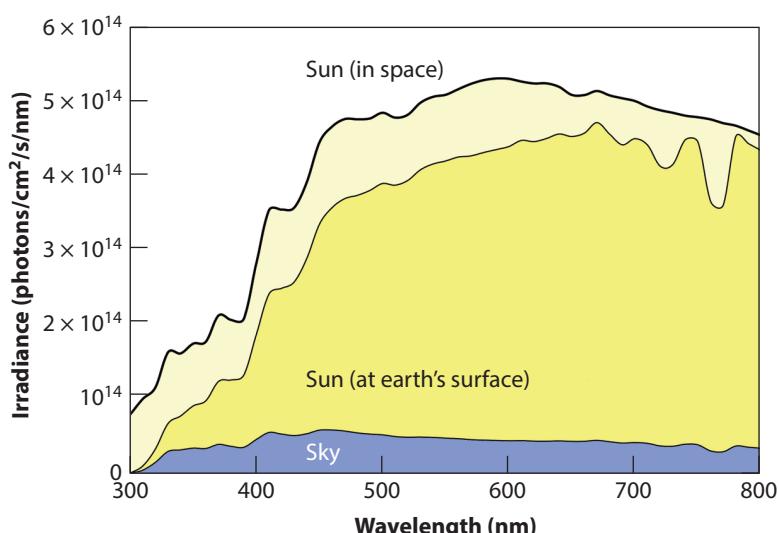


Figure 2.5 Solar irradiance outside the atmosphere (*light yellow*) and at the Earth's surface (*yellow*). The portion due to skylight is in blue. (Based on the standard reference spectra produced by the American Society for Testing and Materials)

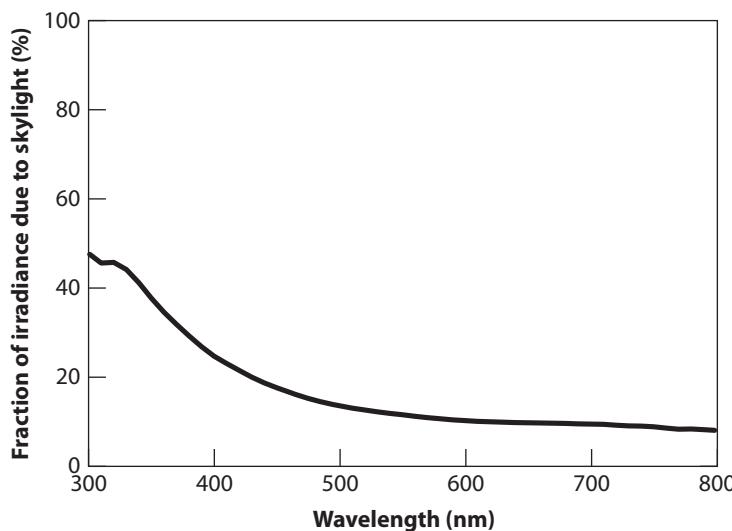


Figure 2.6 Fraction of irradiance (at Earth's surface near noon) due to skylight alone. (Based on the standard reference spectra produced by the American Society for Testing and Materials)

The direct light of the sun accounts for nearly all the infrared light that reaches the Earth and most of the longer visible wavelengths. However, as one moves into the shorter visible wavelengths and especially into the ultraviolet, the contribution of skylight (which is simply scattered sunlight) becomes more important (figure 2.6). Although the radiance of the sky is far less than that of the sun, the former is also far larger than the latter (~100,000 times larger). Skylight is also richer in shorter wavelengths as a result of Rayleigh scattering. Thus, in the blue region of the spectrum (400–500 nm), the sky contributes about 15–25% to the total downwelling irradiance. In the UVA (320–400 nm), it contributes 25–50%, and in the UVB (280–320 nm), it contributes 50% to nearly 100%. Thus, a person stepping under a small umbrella on the beach will immediately feel cooler (due to less infrared radiation) but may still get a sunburn (due to only moderately reduced UVB). Skylight is also special because parts of it can be highly polarized, which we discuss in chapter 8.

The Earth's rotation changes the apparent position of the sun in a manner that predictably depends on geographic location, season, and time of day (see appendix in Johnsen, 2012, for equation). Surprisingly, however, for most of the day, the elevation of the sun has only a minor effect on downwelling irradiance and even less on scalar irradiance. Once the sun is more than about 10° above the horizon, downwelling irradiance varies by at most 10-fold, and scalar irradiance only varies by about threefold (figure 2.7). This is roughly the same effect as moderate cloudiness and not visually significant due to the highly nonlinear nature of animal visual systems (see chapter 11). At higher latitudes the peak solar elevation is lower, and the total variation in irradiance is even less. Thus, the position of the sun during most of the day is unlikely to have a significant effect on light available for vision.

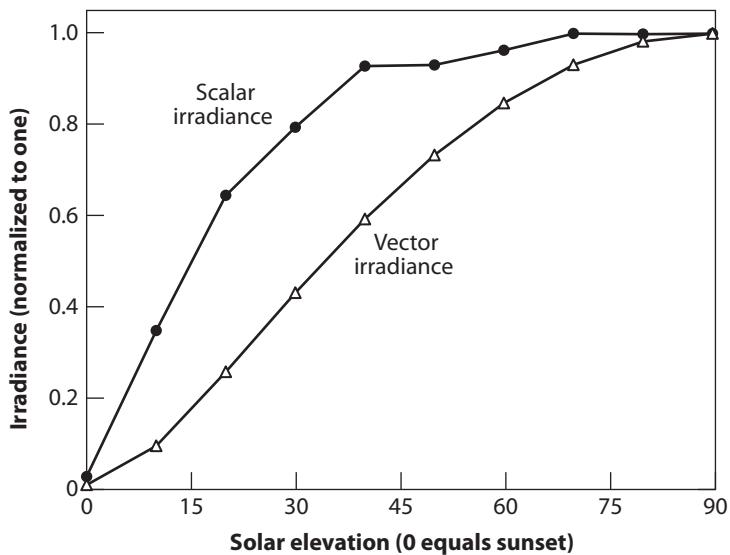


Figure 2.7 Downwelling vector irradiance and scalar irradiance (at 560 nm) as a function of solar elevation.

Twilight

The situation changes dramatically, however, once the sun approaches and crosses the horizon. Figure 2.8 shows this in detail. It uses illuminance (irradiance weighted by the photopic spectral sensitivity of humans; see chapter 3) instead of irradiance, but it is such a useful graph that it is worth showing. The illuminance decreases about 20-fold as the sun drops from 10° to the horizon, the roughly 30- to 40-minute period when people typically watch the sunset. In the next hour, the sun drops by about another 15°, and the illuminance decreases approximately a millionfold, which is about 10,000 times more than even the largest range of daytime illuminances. Our eyes adapt to darkness at about the rate that the light levels drop (probably not coincidentally), so we do not fully appreciate the magnitude of this drop until the sun is about 10° below the horizon. However, the drop is substantial and has many implications for vision, so twilight has been divided into three stages: civil, nautical, and astronomical. During civil twilight, when the sun is less than 6° below the horizon, the sky is still bright enough for normal daytime activities (Leibowitz and Owens, 1991), and only the brightest planets and stars are visible. During nautical twilight the sun is between 6° and 12° below the horizon, and the light levels drop extremely rapidly, and the sky goes from blue to black. The last stage of twilight is called astronomical and looks like night to most humans. Most relatively bright stars are visible at its beginning (when the sun is 12° below the horizon), and on a moonless and light-pollution-free night, galaxies and nebulae will be visible by the end, when the sun is 18° below the horizon.

In addition to the enormous drop in light levels, twilight is also distinguished by large changes in the color of the illumination. At sunset, the reddish sun is balanced by the blue sky and the various colors of the clouds (which are reflecting the reddish sunlight) to create an average illumination spectrum that can be highly variable but is generally

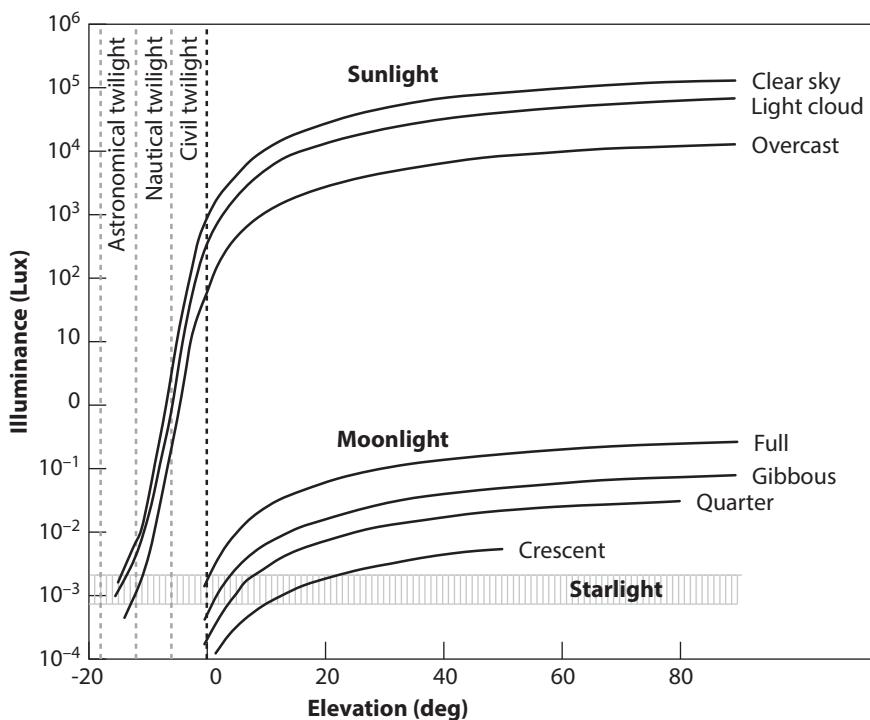


Figure 2.8 Illuminance due to moon and sun at various times of day. (From Bond and Henderson, 1963)

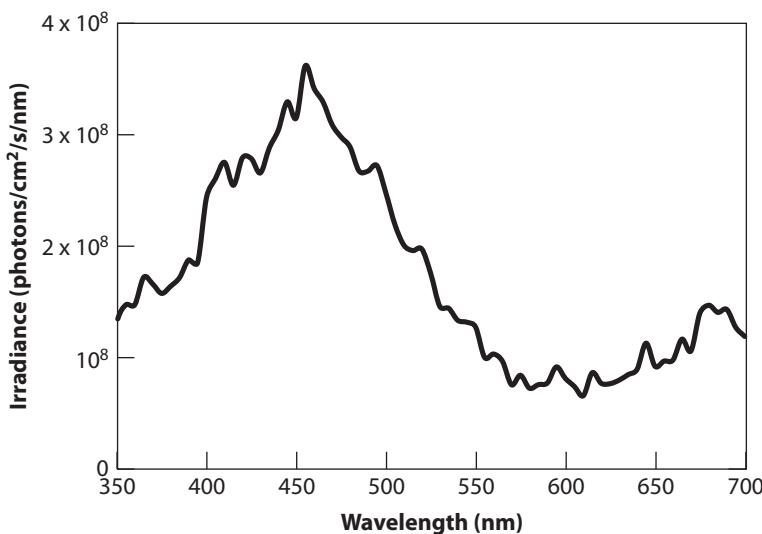


Figure 2.9 Irradiance on a North Carolina beach when sun was 10.6° below the horizon (late nautical twilight). (From Johnsen et al., 2006)

shifted toward longer wavelengths. However, once the sun is more than a few degrees below the horizon, the illumination becomes an intense blue. This may not seem unusual because the daytime sky is blue, but a spectrum of this twilight sky shows that it is different (figure 2.9). Instead of the blue being due to the scattering of sunlight (as it is during the day), it is due to sunlight that has traveled an exceptionally long distance

through the atmosphere (due to the low position of the sun) and had a portion of its visible spectrum filtered out by ozone. This absorption of visible light by ozone, known as the Chappuis band and centered at about 600 nm, is what makes the late twilight sky blue. Without ozone, it would actually be a pale yellow (Hulbert, 1953; Hoepppe, 2007). However, by astronomical twilight this effect fades, and the illumination is dominated by either moonlight or various features of the moonless sky that we now examine.

Moonlight

Moonlight is reflected sunlight, and, for animals that can see it (see Kelber et al., 2003), the colors of a moonlit sky and landscape are close to those under sunlight, although they are slightly shifted to longer wavelengths because the moon reflects twice as much long-wavelength light as short-wavelength light (figure 2.10). The moonlit sky is even polarized for the same reasons that the sunlit sky is (see chapter 11). On average, the moon is above the horizon for half of each night, but the amount of sunlight that it reflects to the Earth and how high it gets in the sky depend strongly on season and lunar phase. When the moon is full it provides a downwelling irradiance about 500,000 times weaker than that of the sun at the same elevation. Unexpectedly, the irradiance due to a half moon is not half that of a full moon but closer to 1/10 (figure 2.11). This means that a half moon is not only smaller than a full moon but has a lower radiance by about fivefold. This is primarily due to the longer shadows that lunar craters and mountains cast when the sun hits them at a lower angle. The irradiance from a crescent moon is only a few percent of that of a full moon and generally irrelevant because a crescent moon is always so close to the sun that the illumination is dominated by the latter.

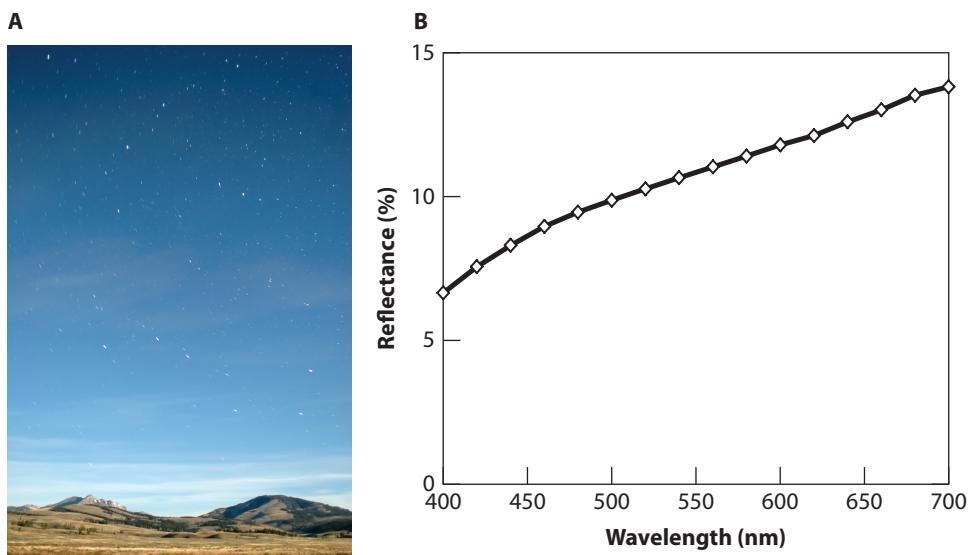


Figure 2.10 (A) Landscape photographed under full moonlight. Note that only the presence of stars distinguishes it from a daytime sky. (Courtesy of Joseph A. Shaw) (B) Spectral reflectance of the moon. (From Lawrence et al., 2003)

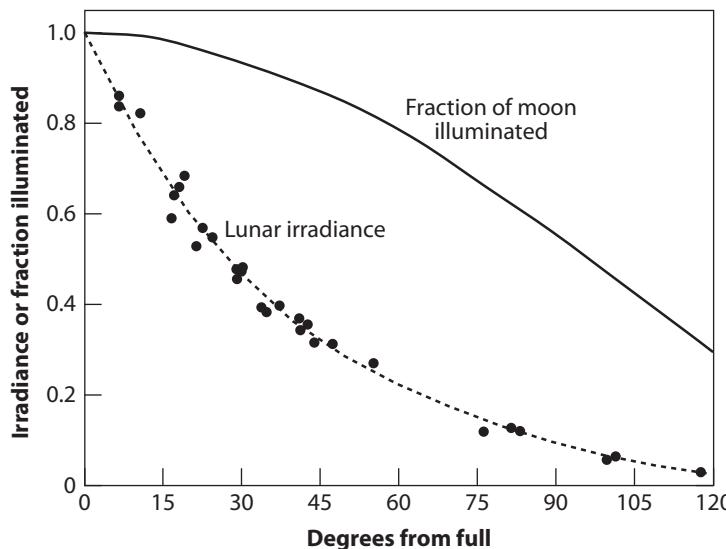


Figure 2.11 Lunar irradiance (normalized to 1 for a full moon) and fraction of moon illuminated as a function of degrees from full moon (0° is full moon; 180° is new moon). (Data taken from Lane and Irvine, 1973)

Season and latitude affect the height of the moon just as they affect the height of the sun, but in the opposite direction. During the summer solstice in the northern hemisphere, the sun has its highest maximum elevation, but the moon has its lowest. The situation is reversed for the winter solstice. Because irradiance is higher when the illuminating object is higher in the sky, the brightest northern hemisphere night sky occurs on the full moon that is closest to the winter solstice. At this time, the total illumination is roughly equivalent to early nautical twilight.

Another important aspect of lunar phase is that it affects how long the moon is above the horizon at night. A crescent moon is always close to the sun and thus only above the horizon for short periods after sunset or before dawn. It is, of course, also above the horizon for much of the day but not visible due to its proximity to the sun. A half moon is roughly at its zenith during dusk or dawn (depending on whether it is waxing or waning) and above the horizon for half the night. A full moon rises at sunset and is above the horizon all night. Thus, because a full moon is so much brighter and high in the sky for much of the night, the total amount of illumination it provides (irradiance \times time) is orders of magnitude greater than that of a crescent moon (5000 times greater if one ignores starlight). Thus, knowledge of the phase of the moon is critical for biologists studying nocturnal activities and rhythms (e.g., Korringa, 1947; Lohmann and Willows, 1987).

Moonless Night Skies

Although it may appear that the illumination from moonless night skies is primarily due to the stars that we can see, these actually only play a minor role. The major components are actually: (1) light from stars too dim to see, (2) zodiacal light, and

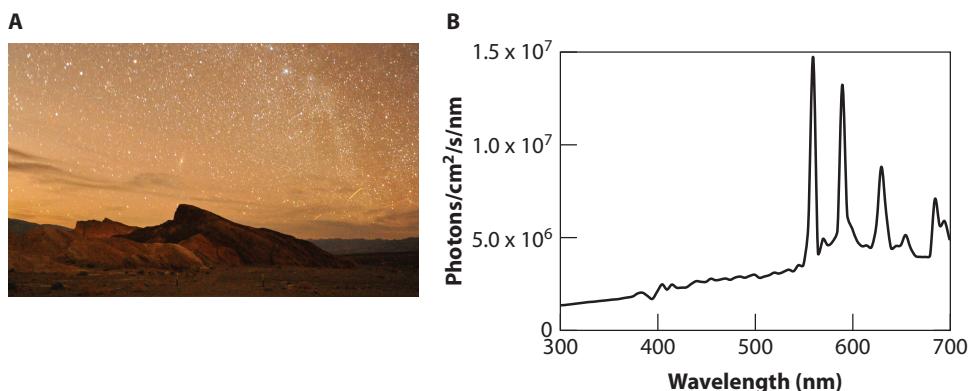


Figure 2.12 (A) Landscape under starlight (Zabriski Point in Death Valley, CA; color temperature preset to 5500K). (B) Reconstructed downwelling irradiance spectrum of moonless night sky. (From Johnsen et al., 2006)

(3) airglow (figure 2.12). The first component seems counterintuitive, but a careful tabulation of all the stars (Matilla, 1980) shows that those that are too dim for us to see (mostly red dwarfs with a stellar magnitude much dimmer than the human visible threshold of 6.5) have a total illumination equal to about 1000 first-magnitude (i.e., the brightest) stars. For comparison, only about eight first-magnitude stars are generally visible in the sky at any time. Because the dim stars are red dwarfs, they contribute a relatively large amount of long-wavelength light to the total irradiance. The second component, zodiacal light, is sunlight reflected from dust in the solar system and thus has a spectrum similar to that of the sun, which again is slightly long-shifted. Zodiacal light is most prominent after sunset and before dawn and is brightest directly above the location of the sun. The final major component, which is responsible for the narrow peaks in the spectrum, is airglow, which is light emitted when atmospheric oxygen, nitrogen, and water molecules that were split by sunlight during the day recombine at night (they also recombine during the day, but this cannot be seen). This light is what makes the spaces between visible stars at a rural site appear a dark gray rather than true black (although visual adaptation may also play a role). Airglow is dim but found everywhere in the sky, so it contributes a substantial fraction of the irradiance in moonless night skies.

Although there are other minor contributors to the irradiance of the night sky (e.g., Gegenschein and galactic light; see Lynch and Livingston, 1995), the only other major contributor (albeit limited to certain locations and seasons) is the aurora (figure 2.13). Like airglow, auroral spectra are due to light emission by excited atmospheric molecules, but in this case the excitation is due to high-speed charged particles from the sun (known as the solar wind) that manage to penetrate the Earth's magnetosphere near the poles. The total irradiance can approach that of full moonlight, particularly during solar sunspot maxima, and the red aurora is even polarized. However, they are relatively ephemeral phenomena, and it is not known if they have any visual significance to organisms at high latitudes. Because they form a ring around the magnetic poles rather than the geographic poles, and because the northern magnetic pole is in northern Canada, the aurora in the northern hemisphere is



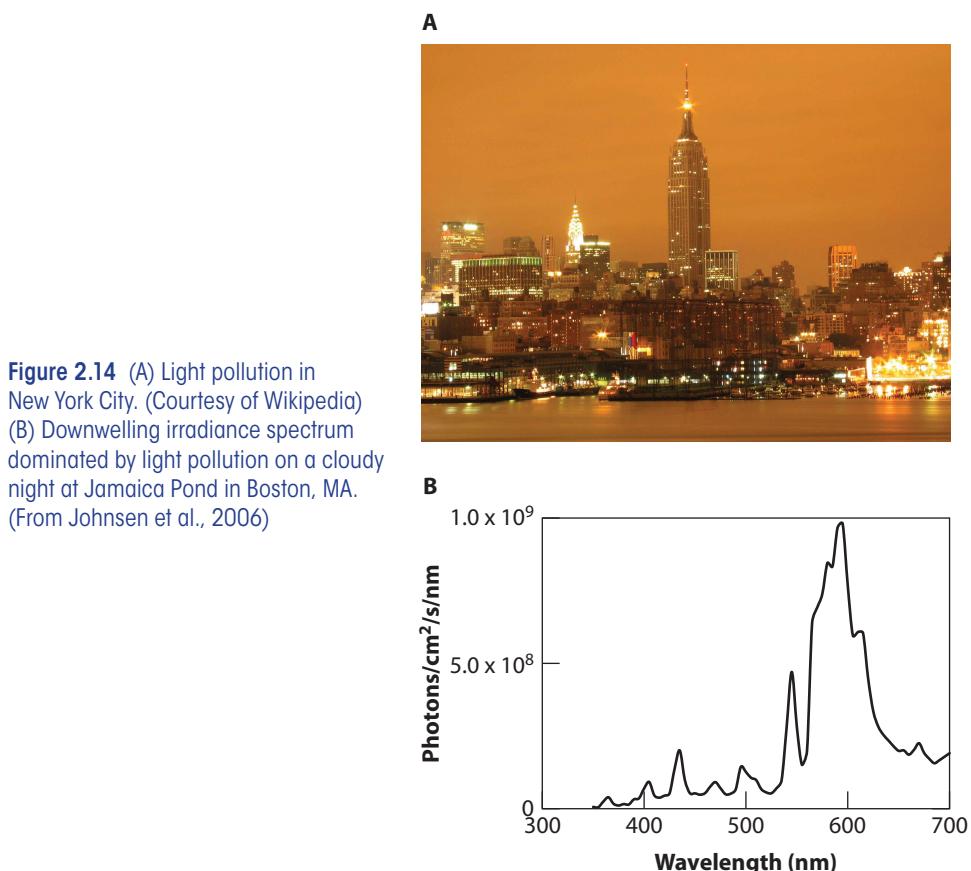
Figure 2.13 A green aurora combined with an unusually intense red aurora. Image taken at Hakoya island, just outside Tromsø, Norway, October 25, 2011. (Frank Olsen, Wikimedia commons)

more commonly observed in North America than in Europe and Asia. The southern aurora is less commonly seen due to the relatively smaller land mass at circumpolar latitudes below the equator. Whether the aurora affects animal behavior (for example, the daily vertical migrations of many oceanic animals) is unknown but would make an interesting study.

Light Pollution

Unfortunately, artificial lighting has a significant impact on the night sky in many locations (Garstang, 2004). Although the fraction of the Earth's surface that is affected by light pollution is still fairly low, this is the fraction where visual ecologists (and many of the animals they study) (figure 2.14) live. Because most universities tend to be in or near major urban centers, few visual ecologists see a true night sky on a regular basis, and their research often focuses on organisms that have been significantly impacted by artificial nocturnal illumination.

In addition to dramatically increasing the nocturnal irradiance, artificial lighting also significantly shifts its spectrum. By far the major portion of artificial illumination is not due to the incandescent and fluorescent lights found in homes but to commercial lighting, which primarily consists of mercury bulbs and high- and low-pressure sodium lamps. This results in a relatively monochromatic and substantially long-shifted spectrum (figure 2.14) whose effects on nocturnal vision and behavior are only just beginning to be explored (e.g., Moore et al., 2000; Longcore and Rich, 2004).



The Color Cycle of Terrestrial Irradiance

The various ways in which sunlight and starlight are manifested result in impressive color shifts whenever the sun or the moon rises or sets (Rozenberg, 1966; Meinel and Meinel, 1983; figure 2.15). As mentioned above, the irradiance goes from relatively spectrally neutral during the day, to long-shifted during sunset, followed quickly by a substantial shift to shorter wavelengths during twilight. This is then followed by a return to the somewhat long-wavelength-shifted spectra of either moonlight or a combined spectrum of starlight, airglow, and zodiacal light. The same process reverses itself during dawn. Thus, the periods surrounding the rising and setting of our two primary celestial bodies are times of significant change in the spectral composition of light in addition to enormous change in brightness. Much has been written about light adaptation, but the effects of these spectral shifts on vision and signal detection are poorly understood at best. Given the importance of crepuscular periods in the foraging and predatory behavior of many species of animals (e.g., Yahel et al., 2005; Rickel and Genin, 2005), this may be a fruitful avenue for future research.

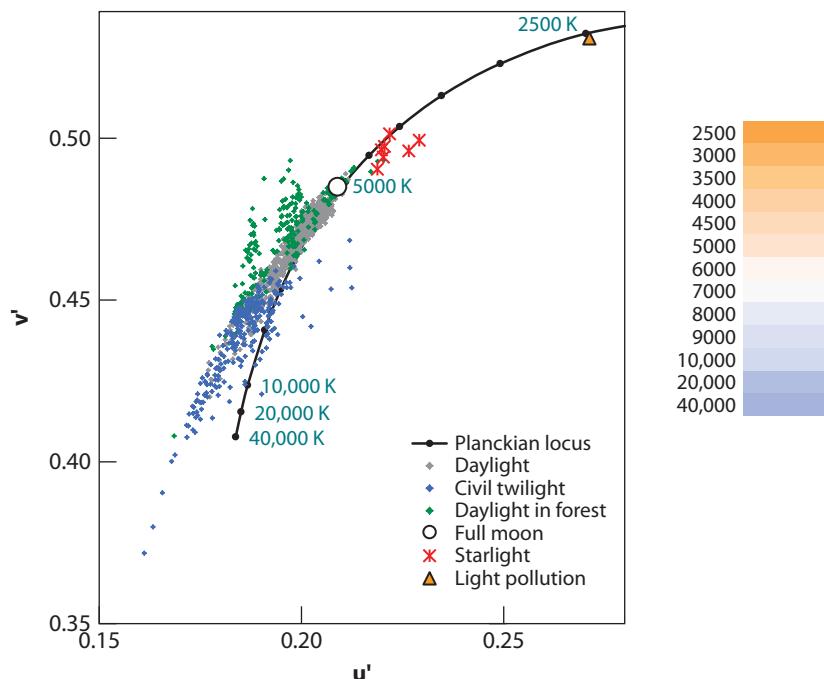


Figure 2.15 Human-based chromaticities (i.e., perceived color) of daylight, sunset, twilight, and nocturnal irradiances. The Planckian locus shows the chromaticities of blackbody radiators as a function of temperature. Data points for this locus are every 500K up to 5,000K, and every 1,000K up to 10,000K, after which each point is labeled. The color chart shows the sRGB appearance of each temperature. Note that twilight, starlight, and especially light pollution are far outside the range of daytime illumination, even when forest environments are also considered. (Modified from Johnsen et al., 2006) The CIE 1976 u' / v' coordinates are used instead of the more usual CIE 1931 xy chromaticity coordinates because the former are more perceptually uniform. Distances on the graph correspond to perceptual differences.

Light in Special Habitats: Forest

Terrestrial illumination during most of the daylight hours is roughly constant in spectral irradiance, but the situation is more complex within forests. The canopy can significantly reduce the intensity, particularly in dense tropical forests, and the wavelength-dependent absorption of light by chlorophyll and other pigments within leaves can affect the spectrum of the light that reaches the forest floor. Because leaves are numerous and small, and because they can be moved by the wind, these effects can vary over small spatial scales and short time periods, leading to diverse spectra (figure 2.16). Although it can be difficult to categorize forest illumination, it is fundamentally influenced by two factors. First, the spectrum is affected by whether the light that passes through gaps in the leaves is primarily due to the sky or the sun. Because the radiance of the sun is so much greater than that of the sky at all wavelengths, the penetration of direct sunlight through a gap in the canopy dominates the spectral irradiance at the forest floor. However, if direct sunlight is blocked by a large number

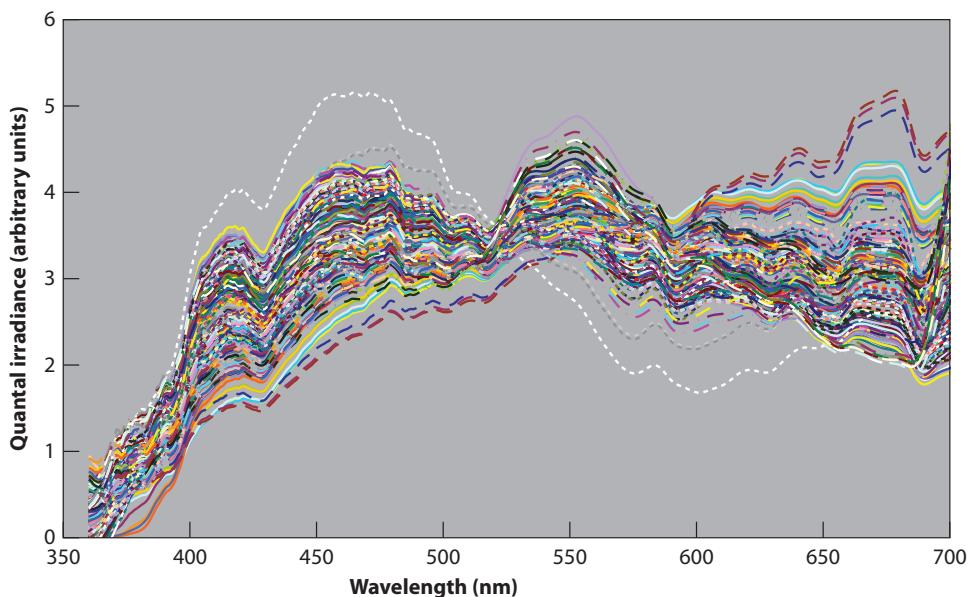


Figure 2.16 Superposition of 238 spectra of downwelling irradiance in a forest near Baltimore, MD. (From Chiao et al., 2000) The spectra are all normalized to have the same integrated irradiance (from 350 to 700 nm). Note that there are three peaks, representing (in order of increasing wavelength) the peak irradiance of a blue sky, the peak transmission wavelength of leaves, and the peak irradiance of the sun at visible wavelengths.

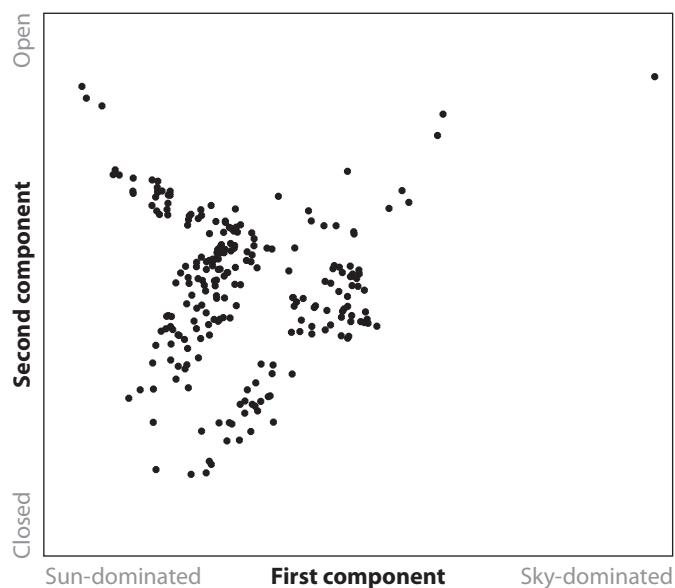


Figure 2.17 The first two principal components (statistical measures of major sources of variation) of the spectra shown in figure 2.16. The first component roughly represents whether the downwelling irradiance is dominated by sunlight or skylight, and the second component roughly represents how closed the canopy is. Note that although the data roughly fall into classes, there is strong variation, making the idea of a set of typical forest illuminants problematic.

of leaves or—more critically—a tree trunk or branch, then any gaps are dominated by skylight, which is significantly shifted to shorter wavelengths.

The second factor is how closed the canopy is. A completely closed canopy creates a downwelling irradiance that is heavily influenced by the absorption spectrum of leaves. This leads to the often-observed greenish light under dense canopies, particularly on sunny days. Because the closure of the canopy and degree to which direct sunlight reaches the forest floor are variable (in addition to the presence and degree of cloud cover), the spectra within forests form a continuum rather than falling into discrete groupings (figure 2.17). Thus, although it would certainly be convenient to use a “standard” spectrum for a forest, by far the better solution is to use a large number of measured spectra from the specific habitat in question to get a true sense of the local variation. Recent developments in low-cost and portable spectrometers have made this simpler than it was even a few years ago.

Light in Special Habitats: Water

The effect of leaves on illumination pales in comparison to the effect of water. Water covers approximately three-fourths of the Earth’s surface, and the oceans comprise over 99.5% of the Earth’s liveable space, so understanding light in this environment is critically important to much of visual ecology. In oceanic habitats the primary physical process that affects downwelling irradiance is the wavelength-dependent absorption of light by water (figure 2.18). The scattering of light by water is also wavelength-dependent, but its magnitude is far less than that of absorption and so plays a lesser role in attenuating light. In clear oceanic waters the absorption is least for 480-nm light, so light of this wavelength penetrates farthest. However, it is a common misconception that light of all other wavelengths attenuates far more quickly. In fact,

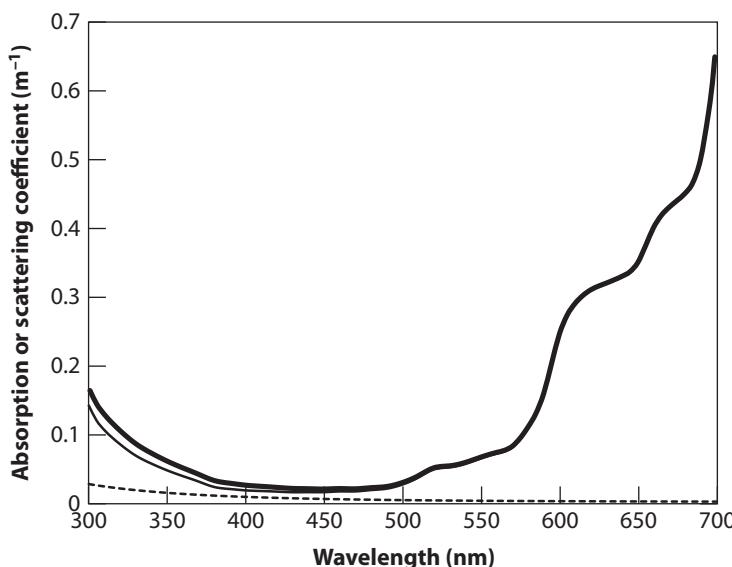


Figure 2.18 The absorption (solid line) and scattering (dashed line) coefficients of the clearest natural waters, along with their sum (heavy line). (From Smith and Baker, 1981) Note that light attenuation is dominated by absorption.

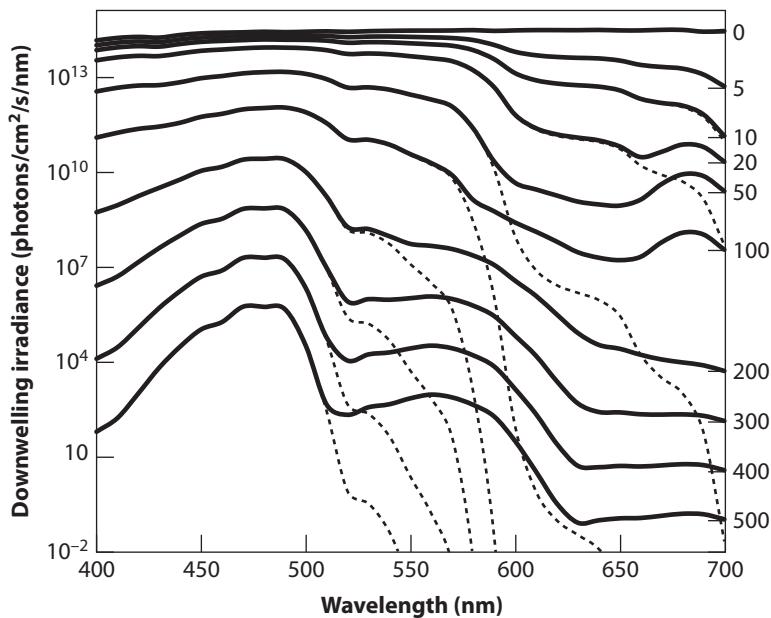


Figure 2.19 Downwelling irradiance in the equatorial Pacific modeled from vertical profiles of absorption, scattering, and chlorophyll concentration. The solid lines show the irradiance when Raman scattering and chlorophyll fluorescence are included. The dotted lines show the irradiance if they are excluded.

once a depth of about 200 m or so is reached, most of the visible light at wavelengths greater than 480 nm attenuates at approximately the same rate as 480-nm light (figure 2.19). This is because most of the long-wavelength photons at depth did not originate as long-wavelength photons from the surface. Instead these long-wavelength photons are primarily created via a fluorescence-like process known as Raman scattering, where a small fraction of the 480-nm photons are converted into photons of lower energies and thus longer wavelengths (Marshall and Smith, 1990). This means that there is far more long-wavelength light at depth than is generally appreciated, by nearly a hundred orders of magnitude for 700-nm light at 1000 m depth. This light is still at least four orders of magnitude dimmer than the main 480-nm peak but still bright enough (at depths less than 100 m or so) to be detected by visual systems of animals living there and potentially isolatable from the main peak via the filtering in the oil droplets found over the cones of certain aquatic birds and reptiles (see chapter 7).

An additional factor in the top 200 m is fluorescence from the chlorophyll in phytoplankton, which peaks at about 680 nm. Due to the presence of this fluorescence and Raman scattering, one cannot simply extrapolate light levels at depth from values measured near the surface as was done in many earlier works in ocean optics (e.g., Jerlov, 1976). Because few direct measurements of deep-sea irradiance exist, the best current method is to input vertical profiles of measured absorption and scattering coefficients (see chapter 9) along with chlorophyll concentration into optical modeling software designed for these sorts of calculations (e.g., Hydrolight, Sequoia Scientific Inc.; see Mobley, 1994).

Scattering plays a minor role in the downwelling irradiance of the open ocean, but it critically affects the radiance distribution. Without scattering, the open sea in all

directions except toward the sun and sky would be black. Together, absorption and scattering eventually create what is known as an asymptotic radiance distribution at depth, which is fairly well developed by about 200 m depth in clear water (figure 2.20). In this distribution the radiance is always greatest directly overhead and—for 480-nm light—is roughly 200 times brighter than the radiance directly below. This is true regardless of the position of the sun because the direct downward path through the ocean has the shortest path length and thus the least attenuation. This difference in path length has a small effect in the top 100 m but becomes increasingly important with depth.

Raman scattering and chlorophyll fluorescence, in addition to greatly increasing the amount of long-wavelength light at depth, also affect the radiance distribution of these wavelengths. This is because both processes are isotropic, meaning that they emit light in all directions roughly equally (figure 2.20, lower graph). Therefore, the radiance distribution of these wavelengths at asymptotic depths is nearly uniform, which may have significant implications for open-ocean camouflage (see chapter 13).

Although the blue ocean is by far the largest aquatic habitat, most biological studies occur in nonoceanic waters because of their easier accessibility. These can be either coastal marine habitats or fresh water. Even more so than with forests, these waters vary tremendously in their effects on light. Scattering and absorption coefficients can be far higher than are found in the open ocean and also have different wavelength dependencies that vary by season, tide, depth, proximity to substrate, current, and other factors. For this reason it is unwise in the extreme to make generalizations from one “standard” water type. Jerlov’s (1976) water classification scheme provides a rough guide, but it does not remotely capture the variation and is not useful for fresh water or marine waters within a few miles of the coast (where much biological research is performed). Although there is a general trend of water color shifting from blue to green to brown as interaction with land increases, this is only the loosest of guidelines and has many exceptions.

That said, as a very general rule, the absorption and scattering in nonoceanic waters are usually primarily affected by three substances (aside from the water itself): phytoplankton, suspended sediment, and dissolved organic matter. Waters in which the optics are dominated by water and phytoplankton are known as Case I waters and are relatively simple to analyze and categorize because the main parameter is the chlorophyll concentration. These range from open-ocean water (with low chlorophyll) to eutrophic waters that are intensely green. However, much coastal water and nearly all fresh water has significant amounts of suspended sediment and dissolved organic matter. These are known as Case II waters and are harder to categorize. Even Case I waters can be challenging because different species of phytoplankton have different absorption and scattering characteristics. Thus, as with forests, it is important for aquatic visual ecologists to characterize the water of their study habitat. As any scuba diver knows, even the tide and recent rainfall can profoundly affect the optics of coastal and inland waters, reducing visibility from several meters to only a few centimeters and decreasing light levels at even 10 m depth by orders of magnitude. Fortunately, the tools required to characterize a body of water have become less expensive and simpler to use in the last few decades, and large databases of optical measurements now exist.

Most discussions of aquatic optics begin with Snel’s window (yes, this is how his name is actually spelled: see Bohren and Clothiaux, 2006), but we end with it to emphasize that it is a relatively minor factor in most considerations of aquatic vision. As is true of every situation where a beam of light passes from a medium of one

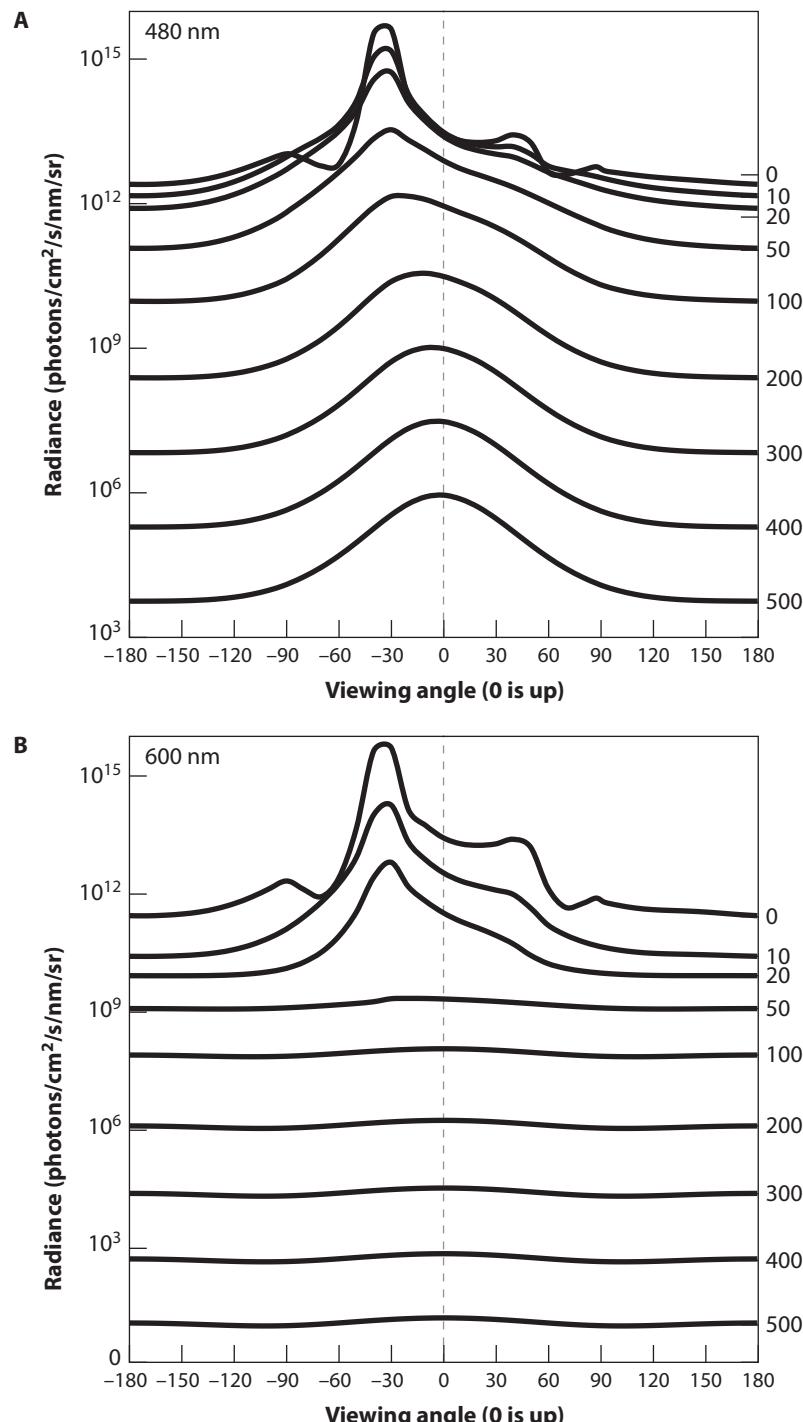


Figure 2.20 Radiance as a function of viewing angle and depth in equatorial Pacific waters, with the sun 45° above the horizon. (A) 480-nm blue-green light. (B) 600-nm red light. Note that the radiance is greatest in the sunward direction (corrected for refraction at the air–water interface) for shallow depth but moves to the zenith as depth increases. The 600-nm light is dominated by Raman-scattered light; thus, the radiance is nearly equal in all directions.

refractive index to a medium with a larger index, the beam appears to bend more toward the direction of the perpendicular to the plane of the interface. In the case of light going from air to water:

$$\theta_{\text{water}} = \sin^{-1}\left(\frac{3}{4}\sin\theta_{\text{air}}\right) \quad (2.1)$$

where θ is the angle of the beam relative to the zenith of the sky. Thus light from the horizon ($\theta = 90^\circ$) has an angle of about 48° in the water, and the entire hemisphere of the above-water world is compressed into an underwater circle 96° across. This circle is known as Snel's window, and if one is underwater looking up, one cannot see the outside world when looking outside this angle. Instead one sees a mirrored undersurface if shallow and scattered light if deeper. However, in reality Snel's window is seldom apparent. This is due to a few factors. First, with the exception of small sheltered lakes and ponds, the surface is seldom smooth but instead is broken up by waves of all sizes. These waves not only obscure the edges of Snel's window but also act as positive and negative lenses that create a highly dynamic light field with short bursts of intensity that can be a couple of orders of magnitude brighter than the average. Second, near the surface, the downwelling light is far brighter than the light in other directions, and it is difficult to look up without being dazzled. If one goes deep enough to escape the lensing and the intense radiance, scattered light obscures the window. Finally, in most aquatic habitats Snel's window contains only the sky, which does not look dramatically different from the water outside the window. Thus, an obvious presence of Snel's window is usually limited to small, still ponds within forests. For example, an archer fish would often have a splendid view of it.

Bioluminescence

Thus far, we have dealt with illumination that either directly or indirectly comes from stars, either our own or others. However, there are other sources of light in the biosphere. Many (e.g., lightning, lava, meteors) are unlikely to have biological relevance, and another (mechanoluminescence; see below) is only hypothetically relevant. Bioluminescence, however, is clearly important to many organisms. Although it is mostly confined to a few insects and fungi on land and nearly nonexistent in fresh water (for unknown reasons), bioluminescence is common in marine habitats, particularly in the mesopelagic realm of the ocean (200–1000 m depth). Although a reliable estimate is of course difficult to obtain (or even define), it appears that about 80% of mesopelagic fish and crustaceans are capable of emitting light (Herring, 1976; Herring and Morin, 1978; Hastings and Morin, 1991). Bioluminescence is also nearly ubiquitous in mesopelagic cephalopods and gelatinous zooplankton but less common in certain mesopelagic taxa (e.g., copepods, amphipods) and rare or absent in others (e.g., heteropods, pteropods, chaetognaths, salps, doliolids) (Herring, 1987; Hastings and Morin, 1991; Haddock and Case, 1999). In marine benthic habitats, bioluminescence is less common and found in only a few percent of species, typically ophiuroids, sea pens, fish, and certain polychaete worms and hydroids (Morin, 1983). However, those species can often be abundant, so the total number of bioluminescent organisms in certain benthic habitats can be large.

Unlike sunlight and starlight, which are due to thermal radiation, bioluminescence is a form of chemiluminescence in which light is produced via chemical reactions.

This is a far more efficient way to produce visible light and the only possibility for organisms because producing even dim levels of visible light via thermal radiation would require a body temperature of at least 650°K. In the case of bioluminescence, the process appears to have evolved independently tens of times and always involves an enzyme-mediated and ATP-dependent oxidation of a small organic molecule. Although the actual substrate varies (see Widder, 2010, for a review), it tends to have antioxidative properties and is always known as a luciferin. The enzyme is in turn always referred to as a luciferase.

The reaction itself occurs in one of three places. In many fish and a few cephalopods the light is produced by symbiotic bacteria that live in a pouch. The bacteria produce light continually, so the animal uses a shutter to control whether the light actually exits the body. The connections between the bacteria and the host are deep and have been explored in detail by Margaret McFall-Ngai (reviewed by Nyholm and McFall-Ngai, 2004). In many other cases the light is produced by the animal itself inside cells known as photocytes. These cells are often part of beautifully complex organs that contain filters, mirrors, lenses, and other apparatus for controlling the color and direction of the light. Finally, some marine species perform the chemical reaction outside of their bodies, essentially vomiting the necessary reactants into water. Certain shrimp and other crustaceans are masters of this, producing brilliant clouds of what is termed “spew bioluminescence.”

Although it is more efficient than thermal radiation at producing visible light, the process is nevertheless energetically expensive, and even the brightest bioluminescence is still just barely visible under room light. Thus, bioluminescence is limited to mesopelagic depths and/or night. The rate of photon emission varies over several orders of magnitude, even within the same individual, but appears to peak at roughly 10^{12} photons/s (integrated over all wavelengths and in all directions). The spectra themselves generally take two forms. In most cases they have a Gaussian shape that can be defined by a peak wavelength and a spectral width parameter known as the full-width half-max (FWHM), which is the wavelength range over which the spectrum is at least one half the peak value (figure 2.21). In oceanic species the light emission nearly always peaks in the blue and blue-green portions of the spectrum (440–530 nm). However, longer peak wavelengths occur in coastal and terrestrial species, with many green emissions and a handful of yellow and red ones.

The second form of bioluminescence spectrum is generally due to the addition of fluorescence. In this case the original emitted light is blue but is then converted to light of a longer wavelength via a co-occurring fluorophore such as green fluorescent protein (GFP). These spectra, because they are fluorescence emission spectra, tend to be narrower and often have a shoulder (note the peak and FWHM of the sea pens in figure 2.21).

The functions of bioluminescence appear to be varied but are often poorly understood. A central problem is that bioluminescence is best developed in mesopelagic species, a set of animals that are difficult to collect in good condition (or even in poor condition) and that are about the worst lab rats imaginable. Therefore, direct behavioral confirmation of many of the proposed functions is lacking, and most hypotheses are based on morphology alone. The primary proposed functions include luring, defense, camouflage, communication, and illumination (figure 2.22), and they have been extensively reviewed in Haddock et al. (2010) (also see chapter 13).

The temporal dynamics of bioluminescent emissions are highly varied and depend on function. In many organisms, such as dinoflagellates, mechanical disturbance

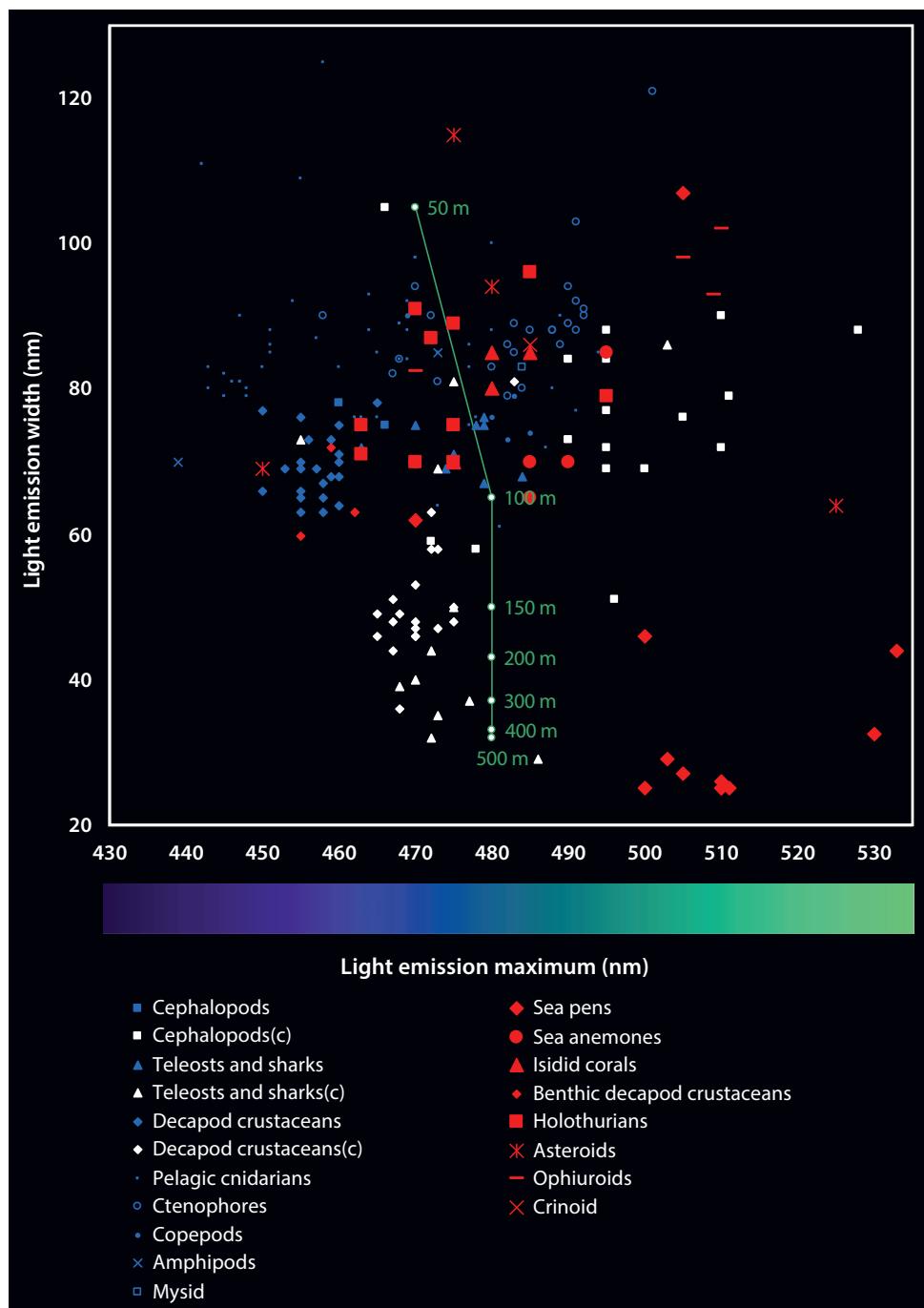


Figure 2.21 Peak wavelength versus emission width (full-width half-max) for the light emissions from deep-sea benthic and mesopelagic species. White symbols represent photophores used for counter-illumination (c). Blue symbols represent light emitted for other purposes in pelagic species. Red symbols represent light emitted by deep-sea benthic species. The green line gives the peak wavelength and spectral width of the downwelling irradiance in clear oceanic waters as a function of depth. All spectra are calibrated in energy units. (Modified from Johnsen et al., 2004, and Johnsen et al., 2012)

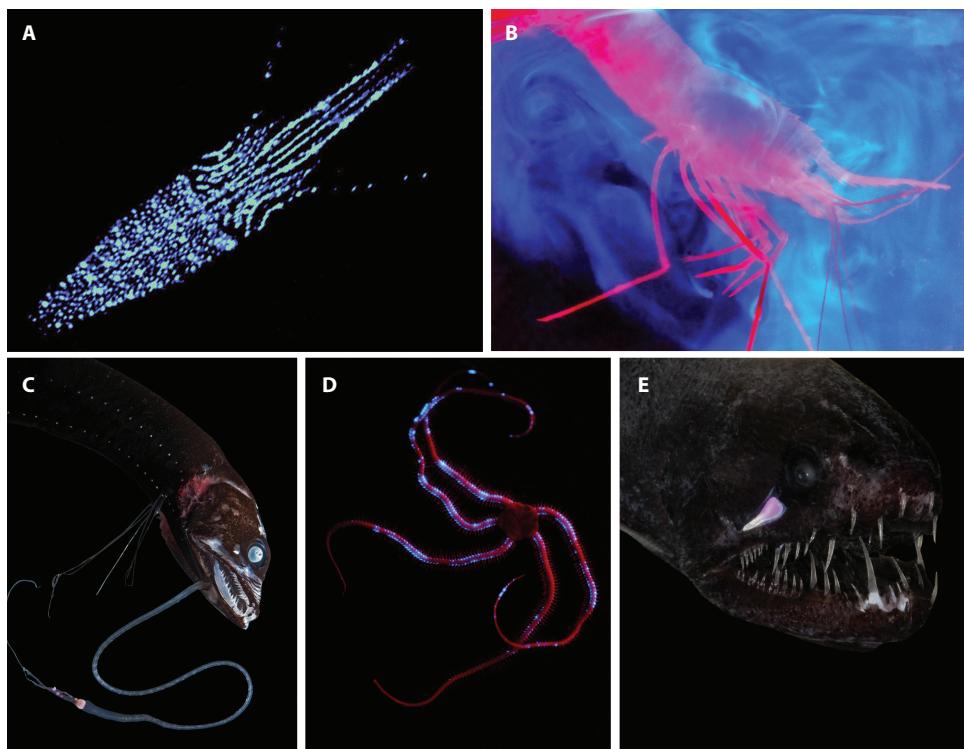


Figure 2.22. Examples of the various uses of bioluminescence. (A) Counterillumination of the ventral surfaces in the eye-flash squid *Abralia veranyi*. (B) Defensive spew bioluminescence in the shrimp *Parapandalus* sp. (C) The bioluminescent lure of the barbeled dragonfish *Eustomias pacificus*. (D) Possibly aposematic bioluminescence in the ophiuroid *Ophiochiton ternispinus*. (E) Bioluminescent searchlight under the eye of the threadfin dragonfish *Echiostoma barbatum*.

triggers a brief and presumably defensive flash of light. However, in some species (particularly gelatinous ones), repeated stimulation leads to more complex and longer-lasting patterns of emission including, for example, the rotating pinwheel emissions of the deep-sea coronate medusa *Atolla* that are thought to attract higher-order predators that—in theory at least—will attack whatever is preying on the medusa. In fact, a simulation of the bioluminescent emissions of *Atolla* (using blue LEDs) was recently used to attract the giant squid *Architeuthis* to a submersible. In animals that use bioluminescence for luring or counterillumination (using ventral photophores to obscure the silhouette), the light emission tends to be steady, although in the latter case it adjusts to match the changing intensity of the down-welling light. The emissions of animals that spew bioluminescence for defense or leave bioluminescent secretions that mark a predator tend to slowly fade over tens of seconds. In the case of light emitted for communication, there is a vast gulf between what is known for fireflies and what is known for nearly all the remaining bioluminescent species. The patterns of light emission for fireflies are species and gender specific and well known. Aggressive mimicry has even been established in certain species (Lloyd, 1965, 1975). However, with few exceptions (the mating displays of the Bermuda glow worms *Odontosyllis enopla*, the flash patterns of the ostracods *Oncea*

and *Vargula*, and the circumoral light organ of brooding females of the pelagic octopus *Japetella*), communication via bioluminescence has not even been established in other species. The complex photophores of mesopelagic fish and cephalopods and the species-specific patterns of their distribution suggest communication, but behavioral proof of this has not been obtained.

Mechanoluminescence

A final source of light that is potentially relevant to vision is mechanoluminescence. In this process, light is produced by mechanical processes, including deformation (piezoluminescence), fracturing (triboluminescence), and crystallization (crystalloluminescence) (see Walton, 1977, for a review and Sweeting, 1990, for an accessible discussion of the relevant principles). The latter two have been suggested as being at least partially responsible for ambient light at deep-sea vents. A highly sensitive multichannel imaging system showed that the light from deep-sea vents cannot entirely be explained by thermal radiation due to their high temperature (Van Dover et al., 1996) (figure 2.23). The emissions at the red end of the spectrum are approximately 19 times brighter than would be predicted from thermal radiation, and—more importantly—the emissions at shorter wavelengths are far higher. For example, one vent emitted 10,000 times more 500-nm light than would be predicted by thermal radiation (White et al., 2002). The actual source of this light has been heavily debated but appears not to be due to bioluminescence. Active deep-sea

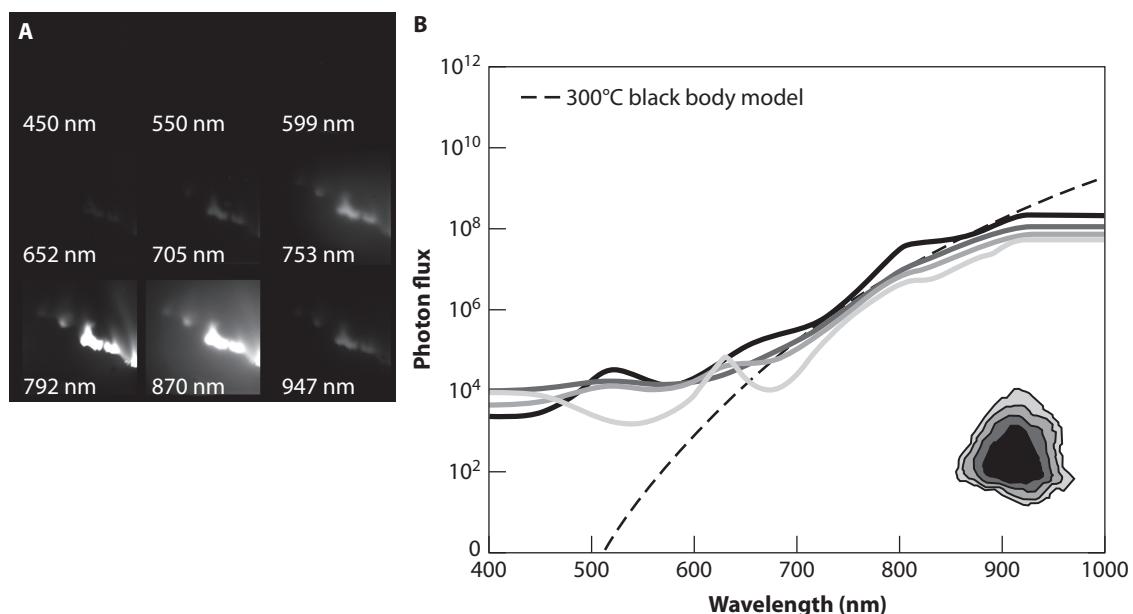


Figure 2.23 (A) Ambient light images of a deep-sea volcanic vent at nine visible and near-infrared wavelengths imaged by the ALISS camera system. (B) Spectrum of emitted light at four locations within vent (line colors match contour colors) compared to the spectrum of a blackbody radiator at the vent temperature. Note that there is far more short-wavelength light than predicted from thermal radiation. (From White et al., 2002)

vents are sites of powerful mechanical forces and intense crystallization when the magma is quickly cooled by the surrounding cold water; thus, mechanoluminescence is the primary candidate. Interestingly, one of the prominent species at deep-sea vents is the shrimp *Rimicaris exoculata*, which has nonimaging eyes with high sensitivity (Van Dover et al., 1989). Analyses of these unusual eyes show that they are most sensitive to blue-green light, suggesting that they are not specialized to detect the thermal emission from the vent but light produced via another process such as mechanoluminescence.