In summary, larval settlement is a challenging proposition in the rocky intertidal. Given the highly energetic, unpredictable flows and intricate, convoluted surfaces, the odds are against larvae landing in hospitable adult habitat. But, because of behavioral interactions with local near-bed flow regimes, sometimes they do.

SEE ALSO THE FOLLOWING ARTICLES

Boundary Layers / Dispersal / Metamorphosis and Larval History / Recruitment / Surf–Zone Currents / Turbulence

FURTHER READING

Butman, C.A. 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanography and Marine Biology Annual Review* 25: 113–165.

LeFevre, J., and E. Bourget. 1992. Hydrodynamics and behaviour: transport processes in marine invertebrate larvae. *Trends in Ecology and Evolution* 7: 288–289.

Underwood, A.J., and M.J. Keough. 2001. Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms, in *Marine Community Ecology.* M.D. Bertness, S.D. Gaines, and M.E. Hays, eds. Sunderland, MA: Sinauer, 183–200.

LIGHT, EFFECTS OF

MOLLY CUMMINGS

Section of Integrative Biology,
University of Texas, Austin, Texas

SÖNKE JOHNSEN

Biology Department, Duke University,
Durham, North Carolina

Light is the portion of the electromagnetic spectrum that stimulates visual and photosynthetic pigments, comprising radiation with wavelengths in air between 300 and 700 nanometers (ultraviolet to red). The spectral distribution of light energy is important for both vision and photosynthesis, and can be affected by the medium in which the light travels, particularly by water. The absorption of light by water molecules is high and depends strongly on wavelength, with the least absorption occurring at 460 nanometers (blue light). Light underwater is also strongly attenuated by interactions with other constituents, such as absorption and scattering by phytoplankton, dissolved organic matter, and suspended solids. Because of this variation, the aquatic near-shore environment is a challenging world for organisms that see, as well as for organisms trying to communicate or hide.

THE INTERTIDAL LIGHT FIELD

Three primary factors alter the light field in the intertidal zone: (1) tides, (2) waves, and (3) dissolved and suspended substances. The tides modify the benthic intertidal light field by changing the path length that light travels in this strongly absorbing medium. At low tide, when the intertidal zone is exposed, organisms encounter spectral irradiances similar to terrestrial environments. As the tide moves in, however, the light passes through a medium that changes both its intensity and its spectral distribution. Because water molecules absorb light most strongly in the short (blue-violet) and long (red) wavelength regions of the spectrum, increases in tidal depth selectively attenuate these wavelengths. Figure 1A illustrates how increasing water depth alters the ambient light field. For example, in the near-shore water column of temperate California, light at 650 nm is present at 1 m and nearly absent at 10 m. In contrast, green light (λ = 500–550 nm) is most prevalent at depth.

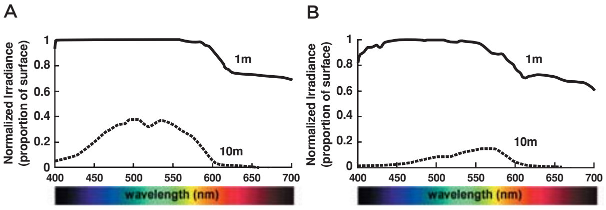

FIGURE 1 Downwelling irradiance measurements, $I_D(\lambda)$, normalized to surface spectral irradiance, at 1 (—) and 10 (···) m depths collected in Hopkins Marine Life Refuge, Pacific Grove, California, with a diver-operated spectroradiometer. Measurements were collected under sunny skies between 12 and 1 PM on two days that differed in phytoplankton concentrations: (A) minimal concentration, and (B) a dense phytoplankton bloom. In B, most of the blue and green light has been absorbed.

As tides rise in the intertidal zone, they generally are accompanied by waves. The effect of waves on the intertidal light field is difficult to estimate because waves complicate the underwater light field immensely. First, waves significantly change the depth of the water column and do so over short time scales. Whereas tidal cycles change in average depth over a matter of hours, waves can alter the water column depth in the intertidal in seconds. Even relatively modest waves substantially change both the intensity and the color of the light in the benthic environment.

A second effect of waves is that they act as lenses. Wave peaks act as positive lenses, creating bright regions at their foci. Wave troughs act as negative lenses, darkening the region below them. Given the almost limitless variety of shapes the ocean surface takes near the shore, the light field underneath has enormous temporal and spatial variability. The differences between this effect and that of the increased height of the waves are that it is spectrally neutral (affecting all wavelengths equally) and that it occurs over smaller spatial scales.

Last, wave breaking alters the intertidal light field. Turbulence, particularly in protein-laden seawater, creates large numbers of bubbles of all sizes. These scatter light, deflecting it from its original direction. Areas directly below the bubbles are darker; areas to the side of the bubbles can be much brighter. In addition to their effect on illumination levels, bubbles dramatically affect underwater image propagation. Even a relatively thin layer of bubbles can render any object behind it invisible. Similar to the effects of waves and light focusing, the formation and persistence of bubbles is unpredictable and highly variable on small spatial and temporal scales.

Light in the intertidal is affected not only by tides and waves but also by the filtering effects of particles within the water column. At low tide, organisms experience the full spectrum of daylight. However, as tides and waves roll in, they usually bring in particles that interact with light more intensely than do the water molecules themselves. Microscopic algae known as phytoplankton are a major group of light-interacting particles that can be present in near-shore and intertidal waters. Many marine algal species differ from terrestrial plants by having a range of accessory pigments that are able to absorb light more effectively in the middle wavelengths. These accessory pigments are important in the aquatic environment, because water differentially filters out the wavelengths that the typical terrestrial plant and green algae pigments (chlorophylls *a* and *b*) absorb (400–450 nm; 680 nm). A concentration of phytoplankton in the water column removes much of the short and middle wavelengths of light leaving only green-yellow wavelengths (e.g., 530–580 nm) for benthic organisms (Fig. 1B).

ADAPTATIONS TO THIS VARIABLE WORLD: ANIMAL VISION

In general, visual systems adjust to the average background light levels and respond only to changes in it. This process, known as adaptation, is useful in that it greatly increases the range of response of the receptor cells. In the terrestrial world, changes in illumination levels are often slow, and consequently visual systems usually adjust to these changes over a matter of several minutes. However, in intertidal habitats, the changes can be abrupt, making it difficult to adapt over the appropriate timescale. The bright flashes and shadows of a flickering surface make it difficult for visual species to focus on small objects or adjust to the diverse levels of background light. As anyone who has spent time directly below a wavy surface can attest, the variation of intensity in this region approaches and can surpass one's ability to adapt, particularly when looking up.

Although wave focusing and bubbles produce spectrally neutral challenges for intertidal organisms, the wavelength-dependent effects of tidal range, wave depth, and phytoplankton change the color of the ambient light, which creates new challenges. Both intertidal and shallow-dwelling organisms address these using visual systems characterized by broadened visual sensitivity (e.g., greater number of visual receptor cells known as photoreceptors sensitive to different parts of the spectrum) as well as visual sensitivity shifted to longer wavelengths relative to deeper or open-ocean environments.

Photoreceptors' properties differ by species according to the light found in their habitats. In general, receptors shift to be sensitive to shorter wavelengths as depth increases, because the longer wavelengths have been attenuated (Fig. 1B). This shifting is a common property of both invertebrate and vertebrate marine and aquatic organisms. Crustaceans such as the intertidal *Gonodactylus* (stomatopod) species have λ_{max} values (wavelength of peak sensitivity) that are long wavelength shifted relative to their deeper dwelling congeners. Vertebrate fish show a similar trend, as shown by the temperate marine surfperch and aquatic Lake Baikal cottoids, which have long wavelength–sensitive photoreceptors exhibiting a shift toward longer λ_{max} values at shallower depths. The intertidal peacock blenny, *Salaria pavo*, living in Mediterranean mudflat regions has a visual system that also exhibits a shift to long wavelengths in shallow, intertidal environments. The intertidal peacock blenny differs from most other shallow-water fishes in that it lacks a short wavelength–sensitive cone entirely. It is also unique among fish in containing a screening pigment in some of its photoreceptor outer segments, which shifts the absorption of the long wavelength–sensitive photoreceptor to even longer wavelengths.

ANIMAL SIGNALS IN THE INTERTIDAL

The challenge of communication in the intertidal zone arises from two different properties of the intertidal light field: (1) high tide conditions, which reduce the number of wavelengths available (the full spectrum is reduced to just middle wavelengths), particularly if the water contains phytoplankton; and (2) spectrally neutral effects of waves—such as lens effects and bubbles—that produce dynamic changes in brightness.

The optical variability and the inability to see well in the intertidal combine to make reliable signaling very difficult. Animals using color for sexual advertisement, warning coloration, or other purposes find it difficult to send a constant color signal, and the relevant viewers find it difficult to see anything at all, particularly in the surf zone. There is little that can be done about the latter problem, but the former can be mitigated by a judicious choice of colors. The constancy of the perceived color (or hue) of an animal's color signal is affected by whether its reflectance is saturated or unsaturated. Saturated colors are those that reflect light in a concentrated portion of the spectrum, so that only a narrow bandwidth of light is reflected from the animal. On the other hand, unsaturated colors, such as silver or white, have a high degree of reflectance across a wide range of wavelengths. The hue of an animal with a broad, or unsaturated, reflectance curve (with some reflectance at all wavelengths) is significantly changed by any changes in the spectral quality of the light striking it. But the hue of an animal with a narrow or saturated reflectance curve (with high reflectance only at a few select wavelengths) remains relatively constant.

Narrow reflectance curves are difficult to produce using pigments, however, because natural pigments generally have very broad reflectance curves. There are some solutions to this problem. One is to have a broad reflectance curve that appears narrow because most of it occurs outside the range of vision. For example, an animal using a pigment that reflects at very long or short wavelengths at the right concentration can produce an intense orange or red (at long wavelengths), or violet or blue (at short wavelengths). In both cases, the majority of the reflectance curve is found outside the visual realm, in the infrared for the red case, in the ultraviolet for the violet case. Consequently, the color will change little under varying illumination. Another solution is to use structural colors. These are not bound by the restrictions of natural pigment absorption curves and can produce narrow reflectance curves if they are constructed in a sophisticated layering system in which interference restricts the bandwidth of light reflected. Therefore, one would predict that intertidal animals sending visual signals would use either interference colors to produce nearly monochromatic signals or pigments concentrated on either end of the spectrum (violet, blue, orange, or red) so that only a small portion of the pigment's reflectance occurs within the animal's visual spectrum, producing visually saturated coloration.

An intertidal fish demonstrates how coloration may follow the general principles outlined above. The peacock blenny has sexually dimorphic coloration, with males that signal to females using orange-yellow crests and blue-ring eyespots against a dark brown body (Fig. 2A). The blues and oranges of the peacock blenny reflect approximately equal amounts of light under

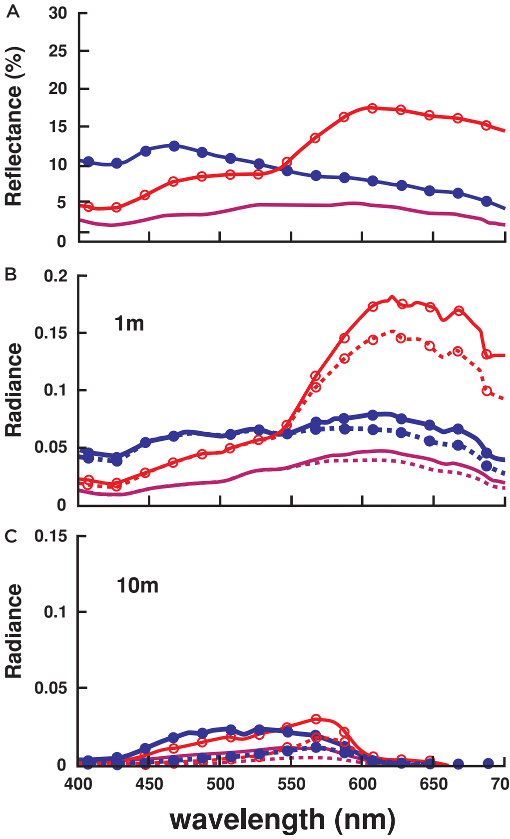

FIGURE 2 Measured spectral reflectance, *R(λ)*, and estimated radiance, $(I_D(\lambda)R(\lambda)/2\neq$, of a territorial male peacock blenny, *Salaria pavo* (photograph courtesy of D. Gonçalvez). (A) Mean spectral reflectance measurements of *S. pavo* dark flank (—), blue ring (●), and orange crest (○). (B) Estimated color pattern radiances of these three color elements at 1-m depth under clear optical conditions (—) and high plankton conditions (---) using spectral irradiance measurements from Fig. 1. These colors are easily distinguished from each other at this depth, regardless of phytoplankton density. (C) Estimated color pattern radiances at 10 m under clear optical conditions (—) and high plankton conditions (---). These colors are less distinguished from each other at this greater depth, where the bandwidth of available light is diminished.

full-spectrum conditions, and each color reflects wavelengths at opposite regions of the spectrum. Both the blue- and orange-colored spots exhibit greater saturation than the unsaturated brown background coloration. The brown body coloration reflects similar amounts of light across the visual spectrum, reflecting 33% of its total reflectance in the orange (>600 nm) end of the spectrum and 26% in the blue (<500 nm). Meanwhile, the orange and blue color elements have more concentrated reflectance, with the orange crest reflecting 48% of its total reflectance in the longwave portion of the visual spectrum (>600 nm) and the blue rings reflecting 42% of their total reflectance in the shortwave bandwidth (<500 nm). These saturated colors are likely to be less mutable across the dynamic changes in intertidal ambient light spectra. We can investigate how these colors change with light conditions by the estimated radiance (see Glossary) of these color patterns under different light fields. The estimated average radiance $L_{avg}(\lambda)$ from a diffusely reflective cylindrical target (e.g., fish) viewed horizontally in a light field dominated by direct downward light is given by

$$L_{avg}(\lambda) = \frac{I_D(\lambda)R(\lambda)}{2\pi}$$

where $I_D(\lambda)$ is the downwelling light spectrum representing the light falling upon the surface of the signaler, $R(\lambda)$ is the diffuse reflectance of that particular color element on the animal's body.

Calculating the estimated radiances for the intertidal peacock blenny shows that its richly saturated color patterns maintain a degree of color constancy (they retain their spectral shape) despite very different ambient light conditions (e.g., presence and absence of phytoplankton; Fig. 2B). The dynamically changing optical environment of the intertidal, therefore, may favor saturated and dark colors that are not greatly affected by rapid changes in the ambient spectrum. As species inhabit deeper waters in the near-shore environment where phytoplankton drastically reduces the spectral bandwidth, however, these dark colors become less distinguishable (Fig. 2C), suggesting that such dark and saturated colors would not be favored in deeper environments.

CRYPSIS IN THE INTERTIDAL

The optically dynamic intertidal environment also has special implications for crypsis. For a benthic animal, crypsis is achieved when its spectral reflectance matches that of the background (or of some random sample of the background). If the match is good at all wavelengths where vision occurs, then changing illumination does not affect crypsis. Note, for crypsis to occur, it need only match body and background wavelengths in the spectral region to which its predators can see. This means for animals whose predators have simple, single-photoreceptor vision (such as crabs), crypsis can be crude. However, for animals in the intertidal with bird predators that have multiple photoreceptor cell types, color crypsis must be a much better match, as these predators can see across a wide spectral range (300–700 nm).

Animals can be cryptic by matching the color of their background, as well as matching the brightness (total reflected light) of their background. The dynamic change in incident brightness over small spatial scales is likely to make brightness matching against a background very difficult in the intertidal zone. The lens effect of waves produces focal regions small enough that many animals more than a few centimeters in diameter have multiple regions of differing brightness. However, it may also provide a means to hide, as viewers cannot discern the entire form of an animal with multiple bright spots of illumination. The dark pigmentation found in intertidal animals, such as seen in the peacock blenny (Fig. 2), may make it difficult for highly pigmented animals to match a brightly flickering background. Dark pigmentation reflects back only a small fraction of the incident light. If the total reflectance of the animal coloration is much lower than the rock, sand, or algal background, then there will be a mismatch between animal and background brightness. Hence, as the light flickers on dark-pigmented animals (such as the blenny), these spots will differ from those of the possibly brighter background (granite rock, sand).

The spectral quality of the illuminating light in the intertidal zone is highly variable, for all the reasons described in previous sections. Therefore, animals must match their reflectance to that of the background for all wavelengths relevant to vision if they wish to be continuously cryptic. Given that the rock background is made of molecules quite different from those found in biological pigment, this may be a challenging task.

SEE ALSO THE FOLLOWING ARTICLES

Bioluminescence / Blennies / Camouflage / Photosynthesis / Tides / Vision

FURTHER READING

Johnsen, S. 2002. Cryptic and conspicuous coloration in the pelagic environment. *Proceedings of the Royal Society of London: Biological Sciences* 269: 243–256.

Lythgoe, J.N. 1975. Problems of seeing colours under water, in *Vision in fishes*. M. Ali, ed. New York: Plenum Press, 619–634.

Partridge, J.C., and M.E. Cummings. 1999. Adaptation of visual pigments to the aquatic environment, in *Adaptive mechanisms in the ecology of vision*. S.N. Archer, M.B.A. Djamgoz, E.R. Loew, J.C. Partridge, and S. Valerga, eds. Dordrecht: Kluwer Academic.

LIMPETS

GEORGE M. BRANCH

Zoology Department, University of Cape Town, Rondebosch, South Africa

Limpets are perhaps the best known animals on rocky shores. They are defined as gastropod molluscs with a conical cap-shaped shell, but this definition covers species from at least three radically different and only distantly related groups. The first and largest group is the Patellogastropoda, which includes what most people would regard as true limpets: the Lottiidae in the Americas and Pacific Ocean; the Patellidae in Africa, Europe, and the Indo-Pacific; and the Nacellidae in the sub-Antarctic. The second group is the keyhole limpets or Fissurellidae, which are characterized by shells with a hole at the apex, through which wastewater and feces are passed, thus avoiding fouling the gills. Third, the family Siphonariidae includes the so-called false limpets, which are related to land snails and have lost their original gills and acquired lungs, only to develop secondary false gills so that they can now breathe in air using their lungs and respire under water using their gills.

Despite being only distantly related in evolutionary terms, all three groups share features that result in their having a common lifestyle. All have a cap-shaped shell that covers and protects the body, all have a large foot that allows tenacious attachment, and all have a radula that allows them to rasp algae off the rock surface.

HANDLING PHYSICAL STRESSES

Compared with most other animals, limpets are superbly adapted to wave action. Their shells are low and flat, reducing drag to water movement, and they have disproportionately large feet, increasing their tenacity. Attachment is not by means of suction, as popularly believed. If they were attached by suction, they would not be able to exceed one atmosphere of pressure in terms of the forces they can resist. In reality, they use an adhesive-like mucus, which is thinly spread between the foot and the rock face, and the powers of attachment of some species exceed the equivalent of five atmospheres of pressure. Part of their effectiveness is due to the relative rigidity of the foot. The more rigid it is, the less easy it is to dislodge a limpet. Take a limpet by surprise, and it is easy to dislodge it with a quick tap; but give it warning and its foot tenses up, increasing rigidity and strength of attachment.

The shape and texture of the shell also influence the relative resistance of the shell to passing waves. Theoretically, there are two avenues open to limpets to reduce drag. First, the shell may be low rather than tall. Most limpets achieve this, although, as seen herein, there are good reasons why some have relatively tall shells. Second, the shell may be streamlined. This can be accomplished by having the apex of the shell about one-fourth of the distance from the front end of the shell. However, few species conform to this theoretically desirable shape. Perhaps this is not unexpected: Most limpets will face waves rushing up the shore one moment, only to be confronted soon after by the same waves in reverse flow down the shore. As limpets cannot alter their positions at the rate that waves march up and down the shore, a streamlined shell that would be perfect for water movement in one direction would achieve the opposite effect when water movement is reversed. There are a few species of limpet that do have a guaranteed direction of water flow, namely, those that live their entire lives attached to the fronds of kelp plants. *Lottia insessa* in North America and the kelp limpet *Cymbula compressa* in South Africa are two examples. Because kelp sways back and forth with the waves, these species always experience water flow from the base of the kelp plant toward to its tips. In these species, the shells are strongly streamlined, to capitalize on the predictable flow of water.

Limpets may have a wonderful design in terms of wave action; but they are not ideal in terms of other physical stresses. Heat stress and water loss are major issues, especially on tropical shores, where the rock face may reach 60 °C. Limpets gain heat from solar radiation, and the flatter they are, they greater the planar area exposed to the sun. They also potentially gain heat by conduction though the rock face via their feet. Flat shells and large feet may be brilliant for dealing with strong wave action, but they are a disaster for reducing heat uptake. Shell color and texture can help avoid overheating. Pale shells are reflective, and textured shells increase the area from which heat can be lost by reradiation. Water loss is also a problem for limpets. Having a flat shell that covers the body inevitably means a large circumference to the