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Hide and Seek in the Open Sea: Pelagic Camouflage and Visual Countermeasures

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Abstract

Camouflage is exceptionally challenging in pelagic environments because of their featureless nature. Thus, it is perhaps no surprise that pelagic species have evolved highly sophisticated cryptic strategies, three of which—transparency, mirrors, and counterillumination—are rare or absent in other habitats. Pelagic visual systems are equally complex, and several visual capabilities, including UV and polarization sensitivity and intraocular filters, are thought to facilitate detection of camouflaged animals. This article reviews the optical nature of the pelagic realm and both the camouflage and camouflage-breaking strategies of its inhabitants, focusing primarily on underlying principles and what remains to be discovered. A theme throughout is that far more is known about the structures of the optical and visual systems involved than about their function, an imbalance that is due primarily to the rarity of observations of undisturbed behavior.

INTRODUCTION

The pelagic realm of the ocean is by far the largest habitat on Earth, with an average depth of ~3,700 m and a volume of 1.33×10^9 km^3 (Charette & Smith 2010). Even if one generously assumes that the planet's entire land mass is inhabited over an average vertical range of 1 km, the water column of the ocean still constitutes more than 90% of the biosphere by volume. Although the diversity and biomass of this habitat are incompletely documented, it is generally accepted that pelagic species diversity is high (though low relative to volume) and that total biomass is substantial. Despite this, our knowledge of the physiology, behavior, and evolutionary relationships of all but a few pelagic species is poor, especially for those that live below 200 m (Webb et al. 2010).

Although historical factors have played a role in this lack of knowledge, the primary issue is accessibility. Simply getting the correct equipment offshore is challenging, often requiring expensive ship time that must be scheduled a year in advance. Using this equipment to then probe the physiology and behavior of animals at depth, ideally without disturbing them, is often impossible. Even submersible-based observations are tainted by their invasiveness, most likely recording stark terror and the blinding effects of floodlights rather than natural behavior. Thus, many biologists studying pelagic species operate as archaeologists, combining measurements and models of the oceanic environment with primarily morphological, electrophysiological, and biochemical insights from moribund or dead animals brought to the surface via nets and submersibles. This is unfortunate, because the pelagic realm is not only the primary planetary biome but also a fascinatingly alien environment compared with terrestrial, shallow-water, and even deep-sea benthic habitats. In addition to its great depth, it is nearly devoid of features and surfaces, leading to the convergent evolution of a suite of adaptations for buoyancy, light emission, and camouflage, the last of which is the concern of this review.

In the pelagic realm, there is literally no place to hide except in plain sight. Thus, camouflage is considerably more demanding than it is in other habitats, and three mechanisms have evolved that are rare or nonexistent elsewhere: transparency, mirrors, and counterillumination (**Figure 1**). Co-occurring with these are a number of visual adaptations—including ocular filters, polarization sensitivity, and UV vision—that have the potential to break all of these specialized forms of crypsis, suggesting a coevolutionary arms race between viewers and camouflagers.

Although the study of pelagic species presents many difficulties, the simplicity of the underwater light field and our ability to collect visual and morphological information from pelagic taxa make the archaeological approach feasible for studies of oceanic camouflage. Indeed there is a long history of research on the optical properties of pelagic animals (reviewed in Denton 1970, 1971; McFall-Ngai 1990; Johnsen 2001), their visual systems (reviewed in Warrant & Locket 2004), and the structure of the oceanic light field (reviewed in Jerlov 1976, Mobley 1994), along with well-developed theories of underwater visibility (Duntley 1952, 1963; Mertens 1970). Previous attempts to link these disparate fields (e.g., Aksnes & Giske 1993, Johnsen 2002, Johnsen & Sosik 2003) have shown that, although open-ocean camouflage is a tractable problem, it is also subtle and rife with counterintuitive conclusions, making it an excellent case study in organismal biophysics.

Two excellent reviews of pelagic camouflage have been published (McFall-Ngai 1990; Herring 2001, chap. 9), and comprehensive reviews are available for most of the mechanisms (see Johnsen 2001 for transparency, Denton 1971 for mirrors, Johnsen 2002 for pigmentation, and Haddock et al. 2010 for bioluminescence). Therefore, this article serves a different purpose. After providing introductions to the underwater light field and the theory of visibility, it explores the four major mechanisms of pelagic camouflage, focusing primarily on what remains to be discovered, in the hope that this will inspire further research.

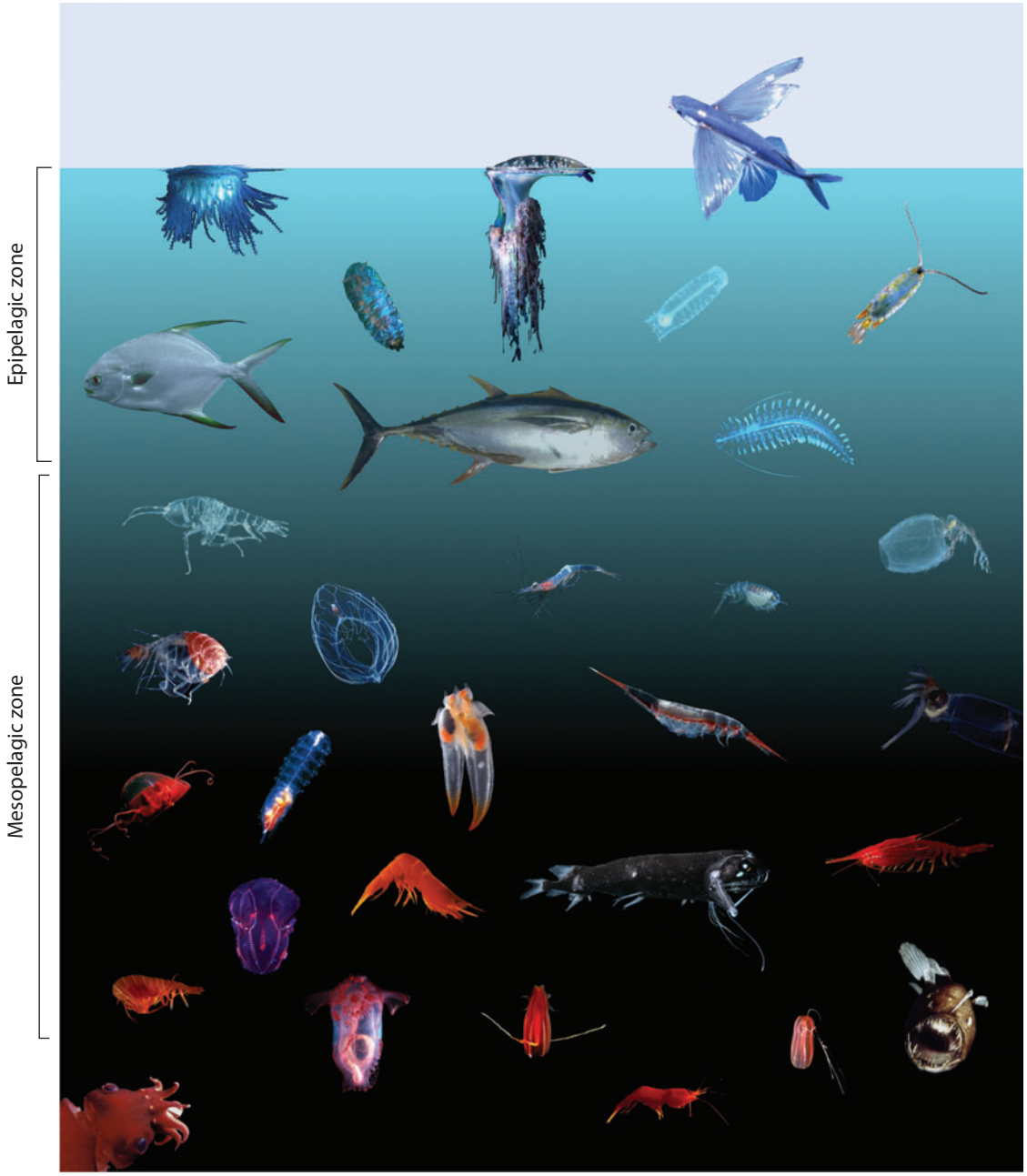


Figure 1

Three camouflage strategies (transparency, mirrors, and pigmentation; counterillumination not shown) as a function of depth in oceanic waters. The figure is not to scale; in clear waters, the epipelagic zone includes depths up to 200 m, and the mesopelagic zone includes depths from 200 to 1,000 m. The epipelagic zone corresponds roughly to the region where photosynthesis is possible, and the lower bound of the mesopelagic zone is where even the most visually sensitive animals can no longer see light from the surface. Adapted from Johnsen (2007).

THE UNDERWATER LIGHT FIELD

All natural waters absorb and scatter light to a far greater extent than air does. Whereas terrestrial mountains are often visible more than 50 km away, underwater mountains of the same size are visible only up to 125 m away, even in the clearest of waters (Duntley 1963, Mobley 1994). The optical properties of natural waters are also highly variable, and in certain turbid coastal and fresh waters, the same mountains would not be discernible from more than a few centimeters away. Fortunately for those studying oceanic camouflage and vision, the optical properties of offshore marine waters are relatively constant, with the primary variation attributable to phytoplankton density in the top 100 m (Jerlov 1976, Mobley 1994). Therefore, although extensive databases of depth profiles of optical properties (e.g., the Worldwide Ocean Optics Database at Johns Hopkins University; **http://wood.jhuapl.edu**) now allow one to consider the specific characteristics of nearly any natural water, by far the largest fraction of the hydrosphere has fairly universal properties.

The Effects of Wavelength and Depth

In oceanic waters, absorption plays a larger role than scattering for light with wavelengths greater than ~500 nm (i.e., green, yellow, orange, and red light) (Mobley 1994) (**Figure 2*a***). Except during algal blooms (and then only near the surface), this absorption is due primarily to the water itself. For wavelengths less than ~500 nm (blue, violet, and UV light), scattering (primarily by phytoplankton and particulates) is roughly equal to absorption, the latter of which is due to both water and chlorophyll. The total amount of scattering in oceanic waters is relatively low (Mobley 1994). Thus, except during blooms of highly scattering algae (e.g., coccolithophores; see Tyrrell et al. 1999), oceanic water is clear. Nevertheless, scattering and absorption, and their dependence on wavelength, dramatically affect both the intensity and the spectrum of the illumination with increasing depth.

Light with wavelengths greater than ~580 nm (yellow, orange, and red) is absorbed rapidly, reaching less than 1% of its surface value at depths of only ~10 m (**Figure 2*b***). Violet and green light attenuate at intermediate levels, reaching 1% of their surface values at depths of roughly 50 m. Blue-green light with a wavelength of 480 nm is attenuated the least, reaching 1% of its surface value at approximately 100 m and then dropping by roughly 40–50-fold for each additional 100 m. Thus, even clear waters rapidly become dark and monochromatic with depth. Even at noon in oligotrophic tropical seas, the illumination at 300 m is equivalent only to that of a moonlit sky. At 850 m, there is no longer enough light for humans to see by, and at 1,000 m, the same is true for even the most sensitive of animal eyes (Warrant & Locket 2004).

A complication in what is otherwise a relatively straightforward relationship between depth and illumination is that there is far more long-wavelength light at depth than might be expected from its initial attenuation at the surface (**Figure 2*b***). For example, there are 10^{44} times as many 600-nm photons at 500-m depth than would be expected by the attenuation of 600-nm light in water. Nearly all of these long-wavelength photons at depth did not enter the ocean as such, but instead entered as photons with wavelengths near 480 nm and were converted to longer-wavelength photons at depth via a process known as Raman scattering (Stavn & Wiedemann 1988). Raman scattering is highly inefficient, but it nevertheless has a significant effect on the underwater light field, especially as depth increases (Marshall & Smith 1990). Whether Raman-scattered light is visually relevant, however, is an open question. At depths of 50 m, the Raman light (at ~620 nm) is approximately 1/8,000th as bright as the main peak at 480 nm (**Figure 2*b***). Thus, although this light is bright enough to see, even a visual pigment optimized to detect it will absorb mostly photons from the main peak. However, certain aquatic reptiles

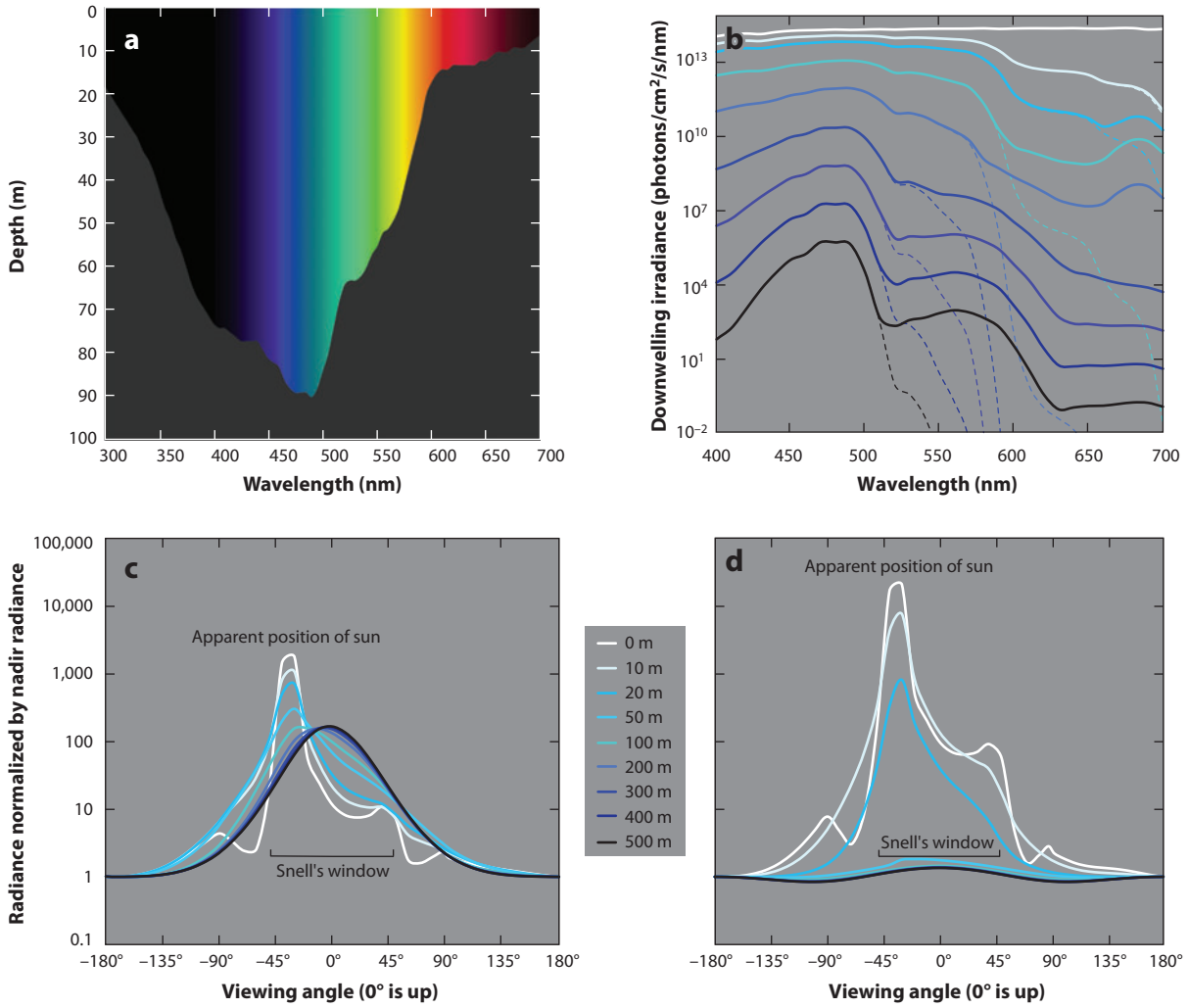


Figure 2

The structure of the pelagic light field in an oligotrophic tropical ocean. (*a*) The depth at which downwelling light is reduced to 1% of its original surface value, as a function of wavelength. (*b*) Downwelling irradiance as a function of depth, both including (*solid lines*) and not including (*dashed lines*) Raman scattering. (*c*) The radiance distribution of 480-nm (blue) light as a function of depth. The solar elevation is 45°. (*d*) The radiance distribution of 600-nm (red) light. Note that at depth, the 600-nm light field is far more uniform than the 480-nm light field, whereas at the surface, it is the 480-nm light field that is more uniform.

have strongly absorbing oil droplets specific to different cone classes that give them very narrow absorption spectra (e.g., Levenson et al. 2004), which may allow them to see Raman light at shallower depths, but whether this is ecologically relevant is unknown. Aquatic birds have similar oil droplets, but whether any forage deep enough that Raman light is significant is also unknown.

Another issue regarding wavelength and depth is that the attenuation of UV radiation (UVR; 280 nm $< \lambda <$ 400 nm) in oceanic waters is less than is often appreciated, especially at subtropical and tropical latitudes. Although most coastal and fresh waters strongly attenuate UVR, often

within the first 50 cm, this is due not to the water itself but rather to chlorophyll and dissolved organic compounds that preferentially absorb short-wavelength light. In the open ocean, where these compounds are found in lower concentrations, UVR penetrates relatively deeply. This is particularly relevant in horizontal and downward viewing directions, where scattering plays a larger role in shaping the spectrum of the underwater light field. In these directions, approximately 40% of near-surface photons are in the UV range (Losey et al. 1999).

The Angular Distribution of Underwater Light

The attenuation of light by water affects not only the total illumination but also the light's angular distribution. Except in the direction of the sun, the radiance in terrestrial ecosystems usually varies by less than two orders of magnitude. However, the downward radiance in the ocean can be several orders of magnitude brighter than the upward radiance, especially at longer wavelengths near the surface (Johnsen 2002) (**Figure 2*c***). Even at depths greater than 200 m, where the light field is more diffuse, the ratio of downward to upward radiance at 480 nm is still over 200. This has significant implications for camouflaging the ventral surfaces of animals (discussed in the Counterillumination section, below). The case is different, however, for Raman-scattered light at depth (**Figure 2*d***). Because this light is "created" at depth via an isotropic process, it is distributed nearly equally in all directions, which—if animals can detect it—can strongly influence camouflage success (Johnsen 2002, Johnsen & Sosik 2003).

The Polarization of Underwater Light

Whereas the light in most coastal and fresh waters is poorly polarized owing to multiple scattering (Horváth & Varjú 2004), light in the open ocean can have high degrees of linear polarization. The polarization pattern is complex and depends on wavelength, depth, and solar elevation (Ivanoff & Waterman 1958, Cronin & Shashar 2001), but it is usually strongest in horizontal viewing directions and weakest when looking upward or downward. In the horizontal viewing direction, the angle of polarization is roughly horizontal, and it becomes more so with increasing depth as the light field becomes more symmetric about the vertical axis (Cronin & Shashar 2001). A number of pelagic species, particularly crustaceans and cephalopods, can detect the polarization of light (Shashar et al. 1998), and many transparent and silvered tissues alter the polarization of transmitted and reflected light, respectively, which has implications for camouflage based on mirrors or transparency.

PRINCIPLES OF UNDERWATER VISIBILITY

Contrast

The key principle of underwater vision is that, even in the clearest ocean waters, the visibility of all but the smallest animals is determined more by their contrast than by their apparent size. In other words, as an aquatic animal becomes more distant, it usually fades from view before it becomes too small to see. Although it is often stated that this loss of contrast is due entirely to the scattering of light into the path between the animal and the viewer, it is in fact also due to the attenuation of the light reflected by the animal by both scattering and absorption. Because the ocean absorbs light at least as strongly as it scatters it, absorption plays a larger role in visibility than is commonly appreciated.

Although the visibility of objects against complex backgrounds is a difficult problem that intersects with perceptual psychology, a quantitative and predictive theory of visibility in the pelagic

realm is relatively straightforward. First, there are two forms of contrast to consider. For small targets on large, uniform backgrounds (e.g., pelagic fish), Weber contrast is typically used. This contrast is defined as the difference between the radiances of the target (L_t) and the background (L_b) divided by the radiance of the background, i.e.,

$$C^W = \frac{L_t - L_b}{L_b}. \quad (1)$$

Thus, Weber contrast runs from -1 for a black object to ∞ for a luminous object on a black background (the contrast for a black object on a black background is defined as 0). For patterns within a target (e.g., stripes on a pelagic fish with radiances L_1 and L_2), Michelson contrast is usually used. The only difference between it and Weber contrast is that the denominator is the sum of the two radiances:

$$C^M = \frac{L_1 - L_2}{L_1 + L_2}. \quad (2)$$

Michelson contrast runs from -1 for a black object to $+1$ for a luminous object on a black background.

It is important to realize that the common usages of the two forms of contrast are not sacrosanct. One can use Weber contrast for stripes and Michelson contrast for small objects on large backgrounds. The contrast values obtained will be different, but the actual measurable parameters, such as sighting distance (discussed below), are unaffected.

Another important consideration is that because radiance depends on wavelength, contrast does as well. In addition, photoreceptors absorb photons over a wide range of wavelengths. Therefore, the precise definition of contrast vis-à-vis a given visual system is (for the Weber definition)

$$C^W = \frac{Q_t - Q_b}{Q_b}, \quad (3)$$

where $Q = \int L(\lambda)S(\lambda)d\lambda$, and $S(\lambda)$ is the spectral sensitivity of a particular visual channel (e.g., cone class for vertebrates). Fortunately for pelagic visual ecologists, the underwater light field is nearly monochromatic, so the contrast derived using the radiances at the peak wavelength of illumination (~480 nm) closely matches that obtained using Equation 3 as long as the visual sensitivity function of the viewer also peaks near this wavelength, which it often does (Partridge & Cummings 1999, Douglas 2001). However, if one is interested in the contrast seen by a red-sensitive cone, which has a peak sensitivity that is far from the peak wavelength of the underwater light field, then one must use Equation 3 or its Michelson equivalent. However, for simplicity, the rest of this article uses contrasts at the peak wavelength (i.e., Equations 1 and 2).

Sighting Distance

A convenient aspect of contrast is that it decreases with viewing distance in a relatively simple manner. For Weber contrast, its value as a function of viewing distance d is

$$C^W = C_0^W e^{-(c - K\cos\theta)d}, \quad (4)$$

where C_0^W is the contrast at zero viewing distance, also known as the inherent contrast. The terms c and K are the beam and diffuse attenuation coefficients, respectively, and characterize the clarity of the water. The beam attenuation coefficient c describes how quickly a beam of light attenuates as it travels through the water. The diffuse attenuation coefficient K describes how quickly the entire underwater light field darkens with depth. The term θ is the angle between the viewer and the target; it equals 0° when the viewer is looking directly up at the target, 90° when the viewer is looking horizontally at the target, and 180° when the viewer is looking down at the target. The

equivalent equation for the attenuation of Michelson contrast is similar, though more complex:

$$C^{\mathrm{M}} = C_0^{\mathrm{M}} \left(1 + \frac{L_{\mathrm{b}}}{L_{\mathrm{avg}}} \left(e^{(c - K\cos\theta)d} - 1\right)\right)^{-1}, \tag{5}$$

which also includes L_{avg}, the average radiance of the pattern [i.e., $(L_1 + L_2)/2$].

In general, one is most interested in the maximum viewing distance at which an animal can still be detected. This occurs when the absolute value of the contrast decreases to the point where it equals the minimum contrast threshold of the viewer, C_{min}:

$$C_{\mathrm{min}}^{\mathrm{W}} = \left|C_0^{\mathrm{W}}\right| e^{-(c - K\cos\theta)d}, \text{ and } C_{\mathrm{min}}^{\mathrm{M}} = \left|C_0^{\mathrm{M}}\right| \left(1 + \frac{L_{\mathrm{b}}}{L_{\mathrm{avg}}} \left(e^{(c - K\cos\theta)d} - 1\right)\right)^{-1}. \tag{6}$$

Both of these equations can be solved for the sighting distance d_{sight}. The sighting distance for a small target on a large background is

$$d_{\mathrm{sight}} = \frac{\ln\left(\frac{|C_0^{\mathrm{W}}|}{C_{\mathrm{min}}^{\mathrm{W}}}\right)}{c - K\cos\theta}, \tag{7}$$

and the sighting distance for a pattern within a target is

$$d_{\mathrm{sight}} = \frac{\ln\left(\frac{L_{\mathrm{avg}}}{L_{\mathrm{b}}} \left(\frac{|C_0^{\mathrm{M}}|}{C_{\mathrm{min}}^{\mathrm{M}}} - 1\right) + 1\right)}{c - K\cos\theta}. \tag{8}$$

A final issue to consider before discussing the biological implications of Equations 7 and 8 is how to calculate the minimum contrast threshold. For bright conditions (e.g., daytime at scuba depth in oceanic waters), the Weber and Michelson contrast thresholds for fish are approximately 0.01 and 0.005, respectively (Douglas & Hawryshyn 1990). At light levels below a certain threshold, they are inversely proportional to the square root of the number of photons N_0 absorbed per photoreceptor (or group of photoreceptors, if they function as a single unit) per integration time of the receptor (Warrant 1999, Land & Nilsson 2012):

$$C_{\mathrm{min}}^{\mathrm{W}} = \frac{2\sqrt{2}}{\sqrt{N_0}}, \text{ and } C_{\mathrm{min}}^{\mathrm{M}} = \frac{\sqrt{2}}{\sqrt{N_0}}. \tag{9}$$

The number of absorbed photons depends on the background radiance and the visual sensitivity of the viewer and can be calculated using well-established techniques, provided that the basic parameters are known or can be estimated (for details, see Johnsen 2012). As a rule of thumb, the Weber contrast threshold is either 0.01 or Equation 9, whichever is higher, with the transition from a constant contrast threshold (0.01) to one that inversely depends on the square root of photon catch (Equation 9) occurring when the number of photons absorbed per unit integration time per photoreceptive unit is approximately 80,000. For a human blue cone, this occurs in bright terrestrial daylight. For the myctophid *Lampanyctus*, however, this transition point is likely reached at a depth of approximately 200 m (assuming a 0.25-cm pupil and a 1.5-s integration time). As discussed above, light levels in the open ocean drop by roughly 40–50-fold for each 100 m of depth, so below the transition point of 80,000 photons, the contrast threshold increases by approximately 6–7-fold over the same depth interval.

The implications of the sighting-distance equations for small targets are similar to those for patterns within targets, so I confine the discussion to the former because of its simpler form. Equation 7 can be considered the product of two factors: (*a*) the natural logarithm of the ratio of the inherent contrast to the contrast threshold, $\ln(C_0/C_{\mathrm{min}})$, and (*b*) a factor combining the clarity of the water and the viewing angle, $1/(c - K\cos\theta)$. The first thing to note is that the former

factor changes in a nonlinear fashion. For example, suppose that a camouflaging animal somehow decreases its inherent contrast from 0.5 to 0.1 and the viewer has a contrast threshold of 0.01. This 5-fold reduction in contrast results in only a 1.7-fold reduction in sighting distance. However a similar 5-fold reduction in contrast from 0.1 to 0.02 results in a 3.3-fold reduction in sighting distance, and a 5-fold reduction from 0.05 to 0.01 renders the animal visually undetectable.

Thus, a more useful form of the first factor is not the logarithm of a ratio but the difference of logarithms—i.e., $\ln C_0 - \ln C_{\min}$. It is this difference that camouflaging animals need to minimize. This can be done not only by lowering the inherent contrast via the camouflage mechanisms described below, but also by raising the contrast threshold of the viewer by moving to a deeper and thus darker depth. As mentioned above, once the viewer is below the transition point of 80,000 photons per receptor, every 100-m increase in depth increases the contrast threshold by 6–7-fold, which decreases $\ln C_0 - \ln C_{\min}$ by 1.8–1.95. Because $\ln C_0 - \ln C_{\min}$ equals only 4.6 for a black object silhouetted conspicuously against the daylight sky [ln(1) − ln(0.01)], lowering it by nearly 2 for each 100-m increase in depth significantly affects sighting distance. This by itself explains at least one selective advantage of diel vertical migration, because the dimmer light at depth increases the contrast threshold of viewers and thus lowers the sighting distance. It also helps explain the presence of luminous signals at depth. The absolute Weber contrasts of nonluminous signals are typically less than ∼3 (Johnsen 2002), which implies that $\ln C_0 - \ln C_{\min}$ is usually less than ∼6. A 300-m increase in depth below the viewer's transition point thus makes nonluminous signals difficult if not impossible to detect. Luminous signals against dark backgrounds, however, have much higher contrasts and so can still be seen at depth. Finally, the effect of increasing depth on sighting distances explains the presence of visual processes that increase photon capture, specifically increase in pupil area and—more important—spatial summation, where multiple adjacent receptors operate as one unit (Warrant & Locket 2004). Both occur in terrestrial species as well, but they appear to be more heavily developed in deep-sea species. These methods can substantially increase photon capture but come with costs: Increasing pupil diameter requires a larger eye or restrictions on the eye's field of view, and spatial summation reduces visual acuity.

Compared with the first term that affects sighting distance ($\ln C_0 - \ln C_{\min}$), the second term $[1/(c - K\cos\theta)]$ is more straightforward. The two attenuation coefficients describe different optical properties of the water but tend to change in proportion to each other. Thus, if the water is twice as clear, the sighting distance doubles. Although animals cannot directly alter the clarity of the water around them, those that inhabit murkier waters are harder to see. Because surface waters tend to be more turbid than those at depth, moving toward the surface can make an animal harder to detect. However, this must be weighed against the increased contrast sensitivity of the viewer in brighter conditions. A natural solution to this is to enter shallow water only at night, which again points to the value of diel vertical migration as a counterpredation strategy. Vertically migrating animals can remain in deep waters during the day, which raises the contrast thresholds of predators, and then at night rise to shallow waters, which remain dark but are also murkier.

Another property of the second term is that it depends on viewing angle. If a predator is looking up at an animal, this term equals $1/(c - K)$; if a predator is looking down, it equals $1/(c + K)$. The former is greater than the latter, often considerably so in clear ocean waters, where c and K are nearly equal at certain wavelengths (Jerlov 1976). For example, a predator at 200-m depth can see prey with a given inherent contrast seven times farther away when looking up at them instead of looking down. A factor that mitigates this difference is that the inherent contrast of animals viewed from above can be higher than that of those viewed from below. Many animals viewed from below are essentially silhouettes and have contrasts of −1. Those viewed from above are illuminated by relatively bright downwelling light and are viewed against the relatively dark background of the upwelling light, so their inherent contrast can be higher (Johnsen 2002, Johnsen

& Sosik 2003). In general, however, animals are visible from greater distances when seen from below than when seen from other angles, which has important implications for counterillumination (discussed below). Finally, although $1/(c+K)$ peaks at the wavelength at which the water is clearest (~480 nm), $1/(c-K)$ peaks at longer wavelengths (~515 nm), which may affect the evolution of spectral sensitivity in upward-looking predators.

Thus, underwater visibility depends on multiple factors, some of which camouflaging animals can affect directly and others of which they can affect only indirectly, primarily via behavior and habitat choice. However, surprisingly little work has been done on how animals manipulate their own detectability. For example, although it is accepted that reducing visual predation is one reason for diel vertical migration (Lampert 1993), few experiments or models have directly addressed this question.

I now turn to the four major direct methods for pelagic camouflage: transparency, mirrors, pigmentation, and counterillumination. The following sections focus in particular on unanswered questions and visual countermeasures possibly employed by viewing animals.

TRANSPARENCY

Transparency is both the simplest and most complex form of pelagic camouflage—simple because the underlying principle is intuitive (i.e., invisibility), and complex because the morphological and physiological mechanisms underlying it are poorly understood. It is also one of the most common strategies, particularly among invertebrates in the top 500 m of the ocean, where it is found in nearly all phyla with representatives larger than 1 cm (reviewed in Johnsen 2001). Although a formal phylogenetic analysis has not been performed, even casual study reveals that transparency has evolved multiple times and is tightly coupled to a pelagic existence (Johnsen 2001). In contrast, whole-body transparency is rare and relatively poorly developed in benthic species [with the spectacular exception of certain species of anemone shrimp (*Periclimenes*)] and nearly nonexistent in terrestrial species (with the exception of insect wings).

The main unanswered questions about organismal transparency concern its physical basis. How often transparency has evolved as a camouflage strategy and how often it is simply an epiphenomenon of other adaptations, such as the proliferation of gelatinous tissues for buoyancy, are also unknown. Finally, the ability of various visual systems to break transparency camouflage remains to be fully explored.

Physical Requirements

Unlike camouflage strategies that only require alterations to an animal's surface, transparency involves an animal's entire volume. This presents unique challenges, because the tissues must absorb and scatter as little light as possible. Absorption is relatively simple to minimize, because only a few necessary and abundantly expressed biological molecules (notably hemoglobin and myoglobin) absorb significant amounts of visible light. Scattering is far more difficult to minimize. Observable scattering is caused by changes in refractive index, which in biological tissues is roughly proportional to density; because tissues generally vary in density over many spatial scales, animals larger than a certain size tend to be opaque.

How transparent animals minimize light scattering is poorly understood. Certain species (e.g., hydromedusae and ctenophores) are able to minimize scattering because they are composed primarily of a highly hydrated extracellular matrix (e.g., mesoglea). Other animals, such as the phyllosoma and leptocephalus larvae of lobsters and eels, respectively, are laterally flattened, thus reducing scattering by minimizing the optical path length through their tissues. However, many

transparent taxa, such as crustaceans, pelagic mollusks, and larval fish, have relatively complex tissues in which the adaptations for transparency remain unclear.

Three main hypotheses have been put forward. The first, suggested by Johnsen & Widder (1999), is that more complex transparent animals adjust the size, shape, and packing of their organelles and extracellular components to minimize light scattering per unit tissue volume. This is possible because scattering per unit volume depends critically on these parameters. Size is particularly important, and repackaging a given volume of material into components that—for example—have 1/10th the diameter of the previous configuration can change the total amount of scattering by 100-fold (Johnsen & Widder 1999). Whether the scattering increases or decreases depends on the original diameters of the components, with the maximum scattering per unit volume being for components with diameters equal to approximately half the wavelength of the incident light. Interestingly, certain siphonophores (e.g., *Hippopodius hippopus*) use this property to change their transparency at will, precipitating and redissolving proteins in their mesoglea to effect this change (Mackie 1996). In contrast, other highly reflective tissues, such as the white wings of certain pierid butterflies, use large numbers of spheres with diameters that maximize scattering per unit volume (Stavenga et al. 2004). The shapes of tissue and cellular components also affect scattering per unit volume, but to a lesser extent—by only approximately an order of magnitude (Johnsen & Widder 1999).

Although Johnsen & Widder's (1999) predictions show that it is possible to increase transparency by changing tissue ultrastructure, whether any transparent species do so is unknown. The best evidence so far comes from as-yet-unpublished work on the Asian glass catfish (*Kryptopterus vitreolus*, formerly *Kryptopterus minor*) (S. Johnsen & W.M. Kier, unpublished observations). A comparative ultrastructural analysis of this species and several opaque congeners showed that the axial muscles of the former are composed of myofibrils with diameters larger than those of the latter, resulting in fewer myofibrils for a given path length through the muscle. This difference is optically significant because the high-index myofibrils are each surrounded by a low-index sarcoplasmic reticulum that scatters light. Reducing the number of these interfaces reduces scattering, but the larger diameter of each myofibril may increase muscle activation time because the calcium signal released from the sarcoplasmic reticulum must diffuse over a larger distance. Glass catfish are in fact less active than the more opaque congeners, following a general pattern of lower activity levels in transparent compared with opaque species that may be due to the sacrifice of internal complexity for transparency (reviewed in Johnsen 2001). However, Childress et al. (1990) have suggested that transparent animals are less active because their crypsis affords them this luxury.

The second major hypothesis for achieving transparency involves clearing agents—high-index soluble components that raise the index of the extracellular fluid and/or the cytoplasm so that it more closely matches that of other tissue and cellular components, thus reducing scattering. Technological versions of these have been used for decades by vertebrate embryologists and more recently by those desiring more transparent tissues for microscopy (Hama et al. 2011). Whether they exist in transparent species is unknown, though anecdotal evidence (A.M. Sweeney, unpublished observations) suggests that certain transparent amphipods may be filled with a high-index fluid.

A final hypothesis is that there are no special modifications for transparency and that the tissues of transparent animals are simply less complex. As mentioned above, transparent animals thus sacrifice various functions (e.g., rapid locomotion) for increased tissue clarity. Indeed, certain transparent species appear to have internal constructions that are simpler than those of related opaque taxa. For example, leptocephalus eel larvae have an extensive proliferation of gelatinous tissue relative to other larval fish, and the hyperiid amphipod *Cystisoma* is aptly named because it has a cyst-like construction with a liquid interior. As mentioned in the introduction, buoyancy

is also an important adaptation for pelagic species, and it is often mediated by large extracellular tissues that tend to be transparent (Clarke et al. 1979). In addition, a larger body has locomotory advantages for aquatic species (Vogel 1996), and gelatinous tissue can provide this increased size at relatively low metabolic cost. Thus, the extensive use of gelatinous extracellular matrices in many transparent species may primarily serve purposes other than crypsis.

Visual Countermeasures

Despite its possible costs, transparency is a highly effective form of camouflage, dramatically lowering the inherent contrast of the organism. Also, because it simply transmits the background light, it is also robust, functioning equally well at different depths, angles of view, and times of day. However, there are two possible visual countermeasures: UV vision and polarization vision.

As mentioned above, the upper pelagic zone is rich in UV radiation, so much so that radiation damage has been documented at depths of up to 20 m (reviewed in El-Sayed et al. 1996). Johnsen & Widder (2001) measured the UV absorption of the extracellular tissues of near-surface (~10-m depth) and deep (~300-m depth) transparent species and found that it is significantly greater in the former. Models assuming that this absorption has a protective function showed that the near-surface species could live approximately 5–15 m higher in the water column than they could if the absorption was not present. However, this possible protection comes at a potential visual cost because it may render otherwise cryptic animals vulnerable to detection by UV-sensitive visual systems. Although no systematic surveys of the visual systems of pelagic species have been performed, other studies have shown that approximately 50% of aquatic species in UV-rich environments (e.g., coral reefs) have UV vision (reviewed in Losey et al. 1999). Thus, it is possible that UV vision can break transparency camouflage in near-surface species that absorb UV radiation. Johnsen & Widder (2001) modeled this possibility using known UV visual systems and measured UV absorption spectra from transparent animals, and found that this potential conflict between photoprotection and crypsis is mitigated to some extent by the fact that many of these species absorb significant amounts of radiation only in the UVB portion of the spectrum (280–320 nm). Because most UV vision occurs in the UVA portion of the spectrum (320–400 nm), crypsis is not greatly affected.

The other potential visual countermeasure relies on the fact that the oceanic light field is polarized. In addition, certain transparent tissues (e.g., muscle and connective tissue) are often birefringent, meaning that their refractive index depends on the polarization of light. Birefringent materials can change the polarization of transmitted light and thus be visible to viewers with polarization sensitivity. Again, no systematic surveys of polarization sensitivity in pelagic species have been performed, but it is known to be relatively common among cephalopods and crustaceans (reviewed in Horváth & Varjú 2004), the former of which have been shown to strike at transparent but birefringent targets (Shashar et al. 1998). Johnsen et al. (2011) examined the potential for polarization sensitivity to break transparency camouflage using both laboratory-based and in situ polarization imaging of plankton and found that, although many transparent species are strikingly birefringent when viewed between crossed polarizers under transmitted light (**Figure 3**), the birefringence is not visible in situ. Instead, the primary component of the polarization image is due to unpolarized downward light being scattered horizontally by more complex tissues, such as the comb rows of ctenophores. Because the downward radiance near the surface can be thousands of times brighter than the horizontal background radiance, this scattering dominates the visibility of the organism. Thus, although polarization vision may increase underwater sighting distance for other reasons (see Schechner et al. 2003, Schechner & Karpel 2005), it does not appear to be useful for breaking transparency camouflage.

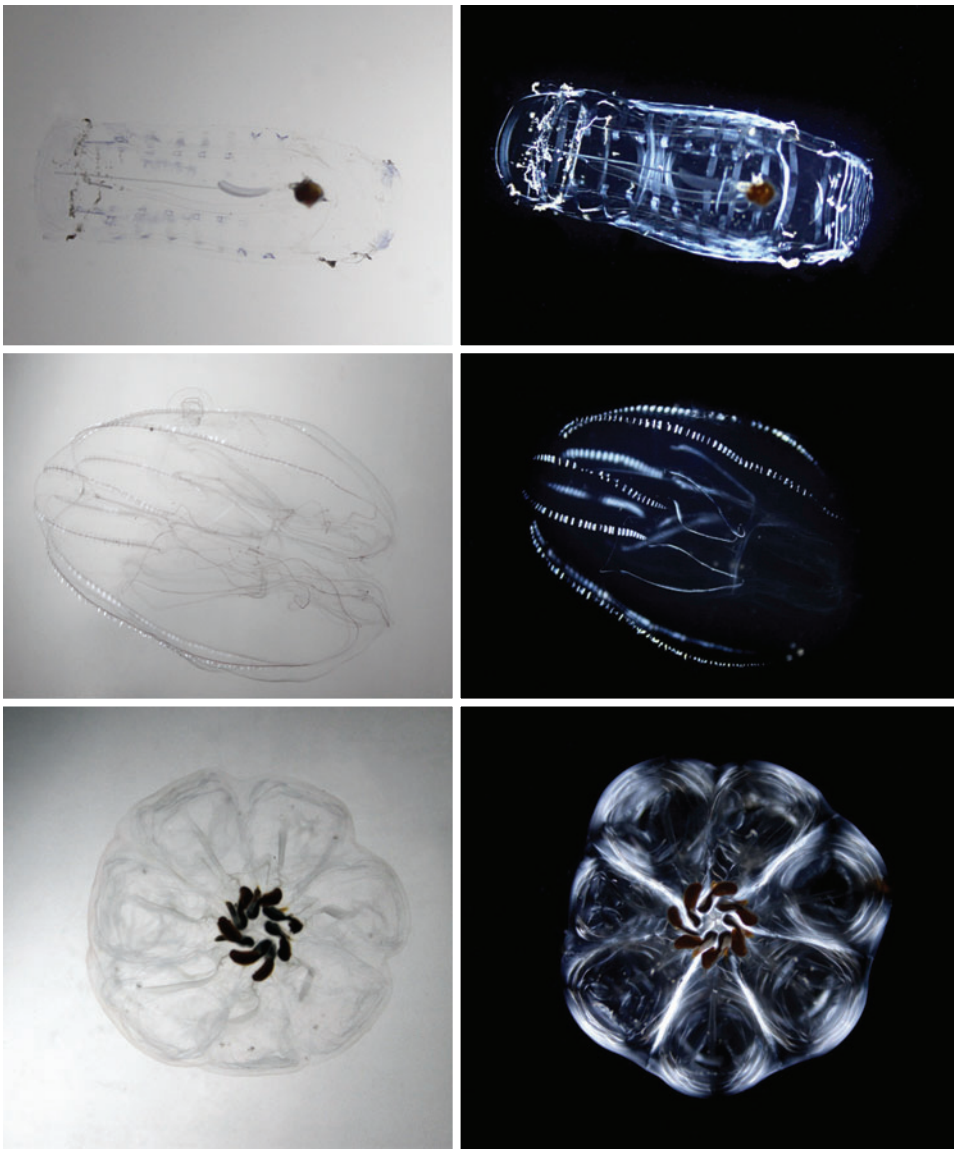


Figure 3

Transparent organisms viewed between parallel polarizing filters (*left panels*) and crossed polarizers (*right panels*), the latter of which reveal the presence of birefringent tissues. (*Top*) The salp *Salpa cylindrica* (solitary form). (*Middle*) The lobate ctenophore *Bolinopsis* sp. (*Bottom*) A chain of the salp *Cyclosalpa floridana*. Images courtesy of Edith Widder.

MIRRORS

Unlike transparency, mirrors are a nonintuitive camouflage mechanism, and many who look at the silvered sides of herrings and sardines are surprised to learn of their cryptic function. Their success relies on the fact that the underwater light field is roughly symmetrical about the vertical axis. An animal viewing a vertical mirror in this environment thus sees light reflected from a

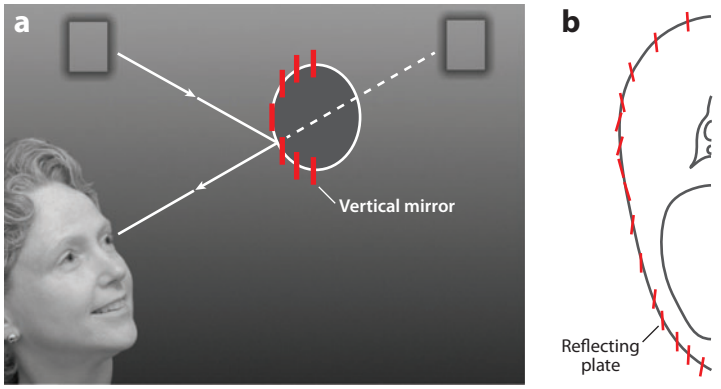


Figure 4

(*a*) Light reflected from vertical mirrors underwater. The radiance can match the radiance directly behind the animal because the underwater light field is roughly symmetrical about the vertical axis. (*b*) Cross section of the bleak (*Alburnus alburnus*), showing the orientations of the reflecting plates within the scales. Modeled after Denton (1970).

region of the underwater light field that approximates the region directly behind the mirror (**Figure 4*a***). The structure and optics of the silvered sides of fish were first investigated in detail by Denton (reviewed in Denton 1970, 1971), who showed that even fish with curved sides orient the guanine-based reflective structures within their scales so that the mirrors remain vertical, strongly suggesting that they have evolved to function as camouflage (**Figure 4*b***). In addition, he found that certain reflectors with less than 100% reflectance are slightly tilted, which compensates for the lower reflectance by reflecting light from a higher and thus brighter portion of the light field. He also divined the underlying mechanism of the reflection and showed that fish mix pigments with reflectors to allow the same portion of the animal to be cryptic from multiple viewing angles. More recently, McKenzie et al. (1995), Levy-Lior et al. (2010), and Jordan et al. (2012) further investigated the underlying physics of the reflectors themselves.

Several major questions remain unanswered. The first is why broadband silvery reflectors are limited to fish and a few pelagic mollusks, given that colored structural reflectors are found in diverse taxa. The second is how mirrored animals compensate (if they do at all) for the fact that the underwater light field is not as symmetric as is often assumed, particularly in the top 100 m. Finally, there are the questions of whether polarization vision can break mirror camouflage and whether certain species have evolved mirrors that remain cryptic even to those with polarization sensitivity.

Physical Requirements

All biological mirrors (and indeed all structural colors) are based on alternating regions of high- and low-refractive-index materials with spacings on the order of a quarter wavelength of the reflected light. The physics has been described in detail elsewhere (Denton 1971); briefly, these structures allow certain wavelengths of light to constructively interfere with one another upon reflection. If the spacings of the regions are uniform, then the reflected light is colored, as is seen in the iridescent wings of butterflies. However, the spacings of the regions in silvered surfaces tend to not be uniform, thus leading to constructive interference for a broad range of wavelengths (McKenzie et al. 1995, Holt et al. 2011). In fish, the alternating regions are made of low-index

cytoplasm ($n = \sim 1.35$) and high-index guanine crystals ($n = \sim 1.83$). In mollusks, the low-index regions are again cytoplasm, but the high-index regions are made of proteins known as reflectins ($n = \sim 1.6$) (Crookes et al. 2004).

Oddly, although structural colors are nearly ubiquitous, broadband reflection (i.e., silveriness) is confined to fish, certain cephalopod eyes and guts, the mirror eyes of scallops and the brownsnout spookfish (*Dolichopteryx longipes*), and the guts of pterotracheid heteropods (reviewed in Denton 1970, 1971; Seapy & Young 1986; Wagner et al. 2009). The mechanism is common only in fish, and it is especially prominent in the Carangidae, Characidae, Clupeidae, Megalopidae, Myctophidae, and Sternoptychidae families. One reason for this may be that fish use guanine, the exceptionally high index of which increases the spectral width of the reflectance (Dobrowolski 1995). More important, however, is that fish are among the few laterally flattened pelagic species (likely for efficient locomotion) and also among the few that tend to maintain a constant orientation in the water column. Underwater mirrors function as camouflage only when they are vertical; in other orientations, they become conspicuous, especially near the surface. Interestingly, the only other cases of mirror camouflage occur in structures that are actively kept vertical regardless of the animal's orientation (e.g., the guts of certain cephalopods and heteropods) (Seapy & Young 1986).

The Asymmetry of the Underwater Light Field

Because mirror camouflage works only in a symmetrical light field, it is important to know how symmetrical the underwater light field actually is. The light field is symmetrical when the sun is at its zenith and also at depths greater than 200 m, where the highest radiance is always directly overhead regardless of the elevation of the sun above the horizon. However, the sun is directly overhead only in the tropics and even then only at certain times, and many silvered fish are found primarily at daytime depths of less than 200 m. So symmetry is not guaranteed.

Figure 5 shows the results of a radiative transfer model that calculates the underwater light distribution from measured beam and scattering coefficients of the water (for details, see Mobley 1994). In oceanic waters, models of this sort are reliable, particularly for ratios of radiances (which are used here) rather than absolute radiances. In this case, they show that the Weber contrast of a vertical mirror is higher than might be expected. Even at depths of 100 m, the inherent contrast is well above the detection threshold (assuming clear water and bright sunlight). In addition, although the contrast near the surface is highest when the sun is close to the horizon, at greater depths it is highest when the sun is 45° above the horizon. Thus, the time of day when mirrors fail depends on depth. This model has recently been validated by measurements in the equatorial Pacific (S. Johnsen, E. Sawicka, R. Reynolds & D. Stramski, unpublished data).

Cephalopods can actively control the reflectance of their structural colors (Cooper et al. 1990), but silvered fish appear to lack this ability. However, many fish, including some with silvery reflectance, can change the pigmentation of their skin. It is therefore possible that, at least in some cases, silvered fish could lower their reflectance to give them a contrast that matches the background when the light field is asymmetric. In certain cases, however, the correction for asymmetric light requires a reflectance greater than 100%. This cannot be accomplished with pigments, but—as mentioned above—it is possible if the reflectors can be tilted upward to reflect a brighter portion of the light field. Whether any silvered fish employ either of these tactics is unknown. Another solution is for fish to orient themselves so that their long axes are parallel to the azimuth of the sun, making the light falling on each lateral side equal (barring the effects of clouds). Although some fish are known to use the sun for navigation (e.g., Levin et al. 1992), whether any fish species line up with the sun for camouflage purposes is unknown.

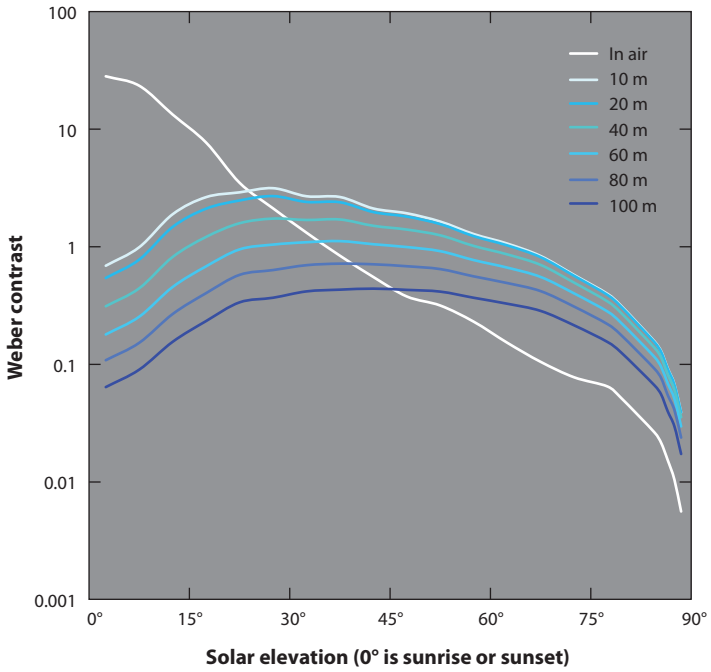


Figure 5

The Weber contrast of a 100% reflective vertical mirror in an oligotrophic tropical ocean as a function of depth and solar elevation. Note that for most of the day, the contrast is well above the typical minimum contrast threshold of 0.01, and that the peak contrast at depth occurs not at sunrise and sunset but at intermediate solar elevations. This is because direct sunlight contributes less to the total underwater illumination when the solar elevation is low, and thus the position of the sun matters less.

Visual Countermeasures

Although it is possible that certain mirrored animals reflect less light at UV wavelengths and thus could be detected by predators with UV vision, most research on visual countermeasures against mirror camouflage has focused on polarization vision. As mentioned above, the underwater light field is polarized. However, even if it were not, unpolarized light reflected from a smooth nonmetallic surface can become polarized. Therefore, the light reflected from the silvered sides of fish may be detectable to animals with polarization vision in both clear and turbid waters. Shashar et al. (2000) showed that cuttlefish can use polarization information to improve their predation on silvered fish; more recently, in situ polarization imagery of silvered fish (S. Johnsen, N.J. Marshall & T.W. Cronin, unpublished) showed that light reflected from their lateral surfaces is depolarized relative to the background polarization, rendering them visible to animals with polarization sensitivity. Although this study examined only 16 silvered species, it suggests the potential for polarization vision to break mirror camouflage.

This raises the question of whether any silvered fish have developed countermeasures to this visual countermeasure—that is, whether any of these animals have evolved a mirror that cannot be detected by its effects on polarization. Because the polarization of the underwater light field is roughly symmetric about the vertical axis, a mirror that is cryptic to animals with polarization vision must leave polarization unaltered. Unpolarized incident light must remain unpolarized upon reflection, and polarized incident light must leave the animal's surface with its angle and degree of polarization unaltered. Polarization-preserving reflectors of this sort have been devised

(Perilloux & Fischer 1988, Huang et al. 1996), but they all involve either coated metals or complex three-dimensional architectures that so far have not been observed in nature. Optical models using transfer matrix theory (S. Johnsen, N.J. Marshall & T.W. Cronin, unpublished) have shown that, although it is possible to create a polarization-preserving reflector over a narrow range of wavelengths and angles of incidence using guanine platelets, it is difficult and perhaps impossible to create a reflector that preserves polarization over a significant wavelength and angular range. However, there have been unpublished reports that the highly reflective lookdown (*Selene vomer*) may be able to minimize its polarization signature (Brady et al. 2013), so this intriguing possibility remains viable.

PIGMENTATION

Outside the pelagic realm, nearly all animal camouflage is mediated by pigments—molecules that absorb some or all of the visible spectrum (reviewed in Cott 1940, Ruxton et al. 2004). Pigment-based camouflage in the pelagic realm operates on the same principles and using many of the same pigments as in other habitats; for the sake of space, this section discusses only a few important differences and visual countermeasures.

Unlike pigmentation in other habitats, oceanic pelagic pigmentation follows a universal depth-mediated pattern (**Figure 1**). At the surface, animals tend to be entirely blue (Herring 1967). In near-surface waters, pigmented animals are often countershaded, with dark-blue dorsal surfaces and white ventral surfaces. As depth increases, red pigmentation becomes more prominent in invertebrates, beginning with opaque tissues and at greater depths extending to the entire organism (Herring 1973, Herring & Roe 1988). Red coloration is less common in deep-sea vertebrates, who are more commonly black owing to high concentrations of melanin.

The coloration found near the surface is well-suited for crypsis in the ambient light field (Johnsen 2002, Johnsen & Sosik 2003). The intense red and black pigmentation at depth appears to be primarily a defense against the bioluminescent searchlights of certain fish and other predators (Johnsen 2005). In this second viewing situation, any reflected light can render an animal detectable, and thus pigment concentration is high to absorb all the light emitted from a searchlight. Because deep-sea bioluminescence is primarily blue (Haddock et al. 2010), red and black pigmentation work equally well. Indeed, the deeper relatives of certain transparent taxa are often covered with blue-absorbing pigments, and certain deep-sea cephalopods can rapidly switch between transparency and pigmentation depending on the form of the light stimulus (Zylinski & Johnsen 2011).

Visual Countermeasures

Because the downward radiance is so much greater than the upward radiance, one obvious countermeasure is to view pigmented animals from below. Even a 100% reflective white ventral surface still appears black when viewed from underneath (Johnsen 2002). As discussed above, this viewing direction also preserves contrast for the greatest distance and is the brightest, thus lowering the contrast threshold of the viewer. Pigmented animals are therefore highly vulnerable to detection from below.

Another proposed countermeasure is the use of the intraocular filters described above. Because both the background radiance and the light scattered into the path between an underwater target and a viewer are primarily blue, Lythgoe (1979) suggested that short-wavelength absorbing intraocular filters function to increase contrast. However, although these filters do dramatically

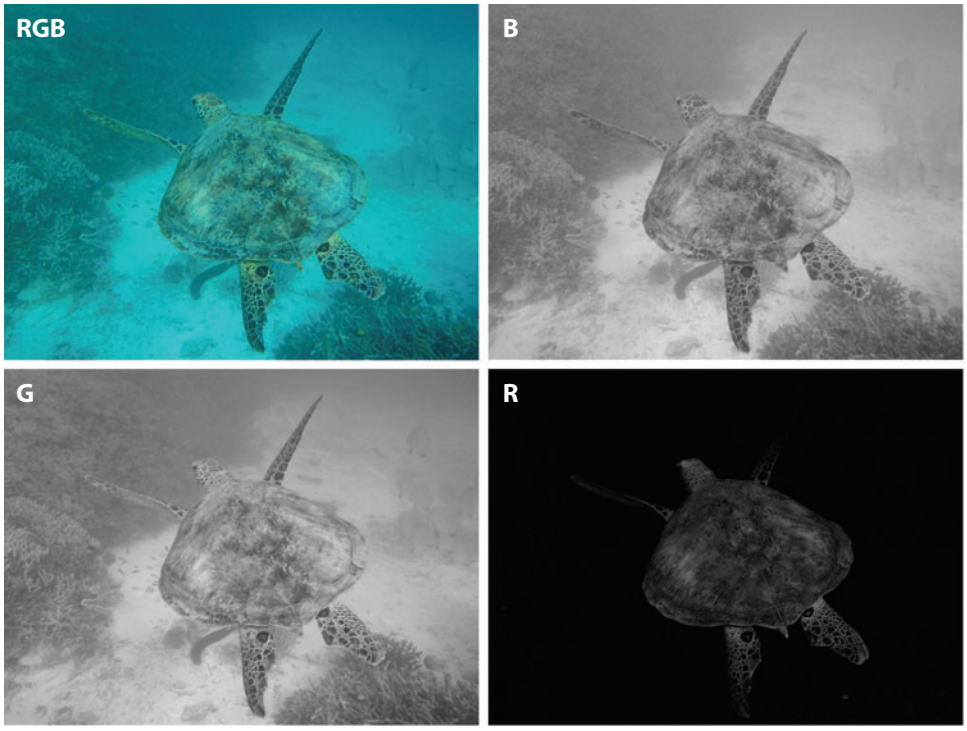


Figure 6

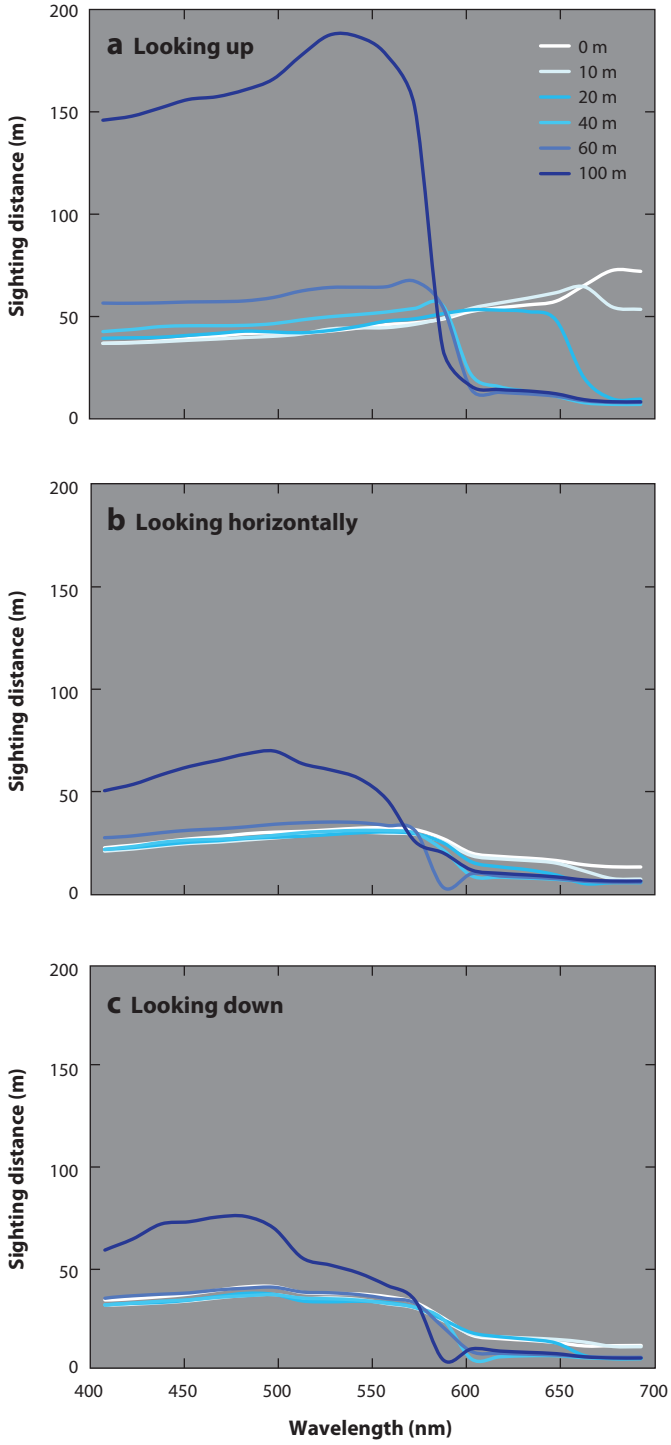
Green turtle photographed at a depth of ~10 m in the blue-green waters of the Great Barrier Reef viewed in RGB (red, green, blue) and in each of the three individual color channels, showing the effect of wavelength on the contrast of nearby objects. Note that the contrast of the turtle against the background is far higher in the red channel, primarily because the background illumination contains little red light. The turtle itself, lit from above by relatively broadband downwelling light, still reflects long-wavelength light.

increase contrast at short range (**Figure 6**), they do not actually increase sighting range (**Figure 7**), because the increased contrast is at longer wavelengths and thus attenuates rapidly.

One visual countermeasure that avoids this issue involves polarization vision. Schechner & Karpel (2005) showed that if the underwater light is even moderately polarized, a polarization-sensitive viewer can increase its sighting distance by examining the polarization characteristics of the scene. This is based on the assumptions that light reflected from the target is unpolarized and that the path radiance is polarized. Because these assumptions are typically both true, one can use polarization information to remove the path radiance from

Figure 7

Sighting distances for a very large 50% reflective gray object as a function of depth, wavelength, and viewing angle: (*a*) looking up at the object, (*b*) looking horizontally at the object, and (*c*) looking down at the object. The viewer is assumed to have a constant minimum contrast threshold of 2%. Note that even though inherent contrast is higher at longer wavelengths (see **Figure 6**), the greatest sighting distances are still in the blue and green portions of the spectrum. If one accounts for the fact that the decreased light levels at longer wavelengths lead to higher contrast thresholds, sighting distances at long wavelengths would be even lower than those presented here.



the image and increase sighting range (for details, see Schechner et al. 1998). Again, although a neural mechanism of this sort is plausible for polarization-sensitive animals, there is currently no evidence that any animals use their sensitivity in this fashion.

COUNTERILLUMINATION

The final camouflage strategy considered here is counterillumination—the use of bioluminescence to obscure one's ventral silhouette, which, as discussed above, is especially vulnerable to detection. Counterillumination occurs in a diverse array of taxa and is particularly common and well developed in mesopelagic squid, fish, and crustaceans (Herring 1976, 1985; Young & Roper 1976; Widder 1999). As with transparency, counterillumination is straightforward in principle. However, little is known about how it is accomplished, and in particular how it is regulated. A few visual countermeasures have been suggested, but none have been proven.

Physical Requirements

Because counterillumination is the only camouflage strategy that relies on light emission, it is limited in its depth distribution. Young & Roper (1977) estimated that counterillumination during the day by the squid *Histioteuthis heteropsis* at a depth of 400 m in clear oceanic water accounts for 0.3–0.9% of the animal's resting metabolic rate. Because the downward radiance that must be matched goes up by a factor of approximately 50 for every 100 m decrease in depth, they concluded that daytime counterillumination is limited to animals deeper than 350–400 m.

By definition, counterilluminators must match the ever-changing downwelling light field. The visual feedback mechanism by which this is accomplished is unknown but is likely complex, because the eyes of most counterilluminators cannot see their own ventral photophores. In addition, the emitted light must match the background light from a number of viewing directions, not just from directly below. This last ability has been tested only in the deep-sea hatchetfish (*Argyropelecus affinis*) and the viperfish (*Chauliodus sloani*), both of which use an ingenious combination of mirrors within the photophores to approximate the angular structure of the deep-sea light field (Denton 1971, Denton et al. 1972). Whether either animal can change this distribution to match different distributions of light (e.g., at shallower depths) is unknown. However, even matching only the direct downward radiance is nontrivial, because both its spectrum and its intensity change with depth. Although intensity changes can theoretically be mediated by a (currently unknown) visual feedback system, spectral changes are more problematic for a group of animals that nearly always have monochromatic visual systems. This has been studied in only two cephalopod genera (*Abraliopsis* and *Abralia*), which were found to use water temperature as a depth gauge (Young & Mencher 1980). When tested in cold water, these squid emitted relatively monochromatic blue light that approximated that found in the deep sea. When tested in warmer water, however, they emitted light with a broader spectrum, better matching that found near the surface (see also Herring et al. 1992).

Visual Countermeasures

Because it is difficult to match all aspects of the downwelling light field, there are multiple ways that a viewer can break this form of camouflage. First, with the exception of a few species (mostly squid), the ventral surfaces of counterilluminators are not evenly lit but instead contain a small number of discrete light organs. Because oceanic water is clear, the light from these separate organs is not blurred together, even at large distances (Johnsen et al. 2004). Therefore, viewers with acute vision can break the camouflage, particularly at close range. Acute vision is rare in the nocturnal

and deep waters where counterillumination occurs, owing to the spatial summation required to increase contrast sensitivity in low light (Warrant 1999, Warrant & Locket 2004), but it may nevertheless occur at moderate depths (350–500 m) and be used to break counterillumination.

The second countermeasure relies on the counterilluminator's limited ability to match the downwelling spectrum. First, bioluminescent emissions result from a small set of chemical reactions and do not have unlimited potential for spectral variation (Haddock et al. 2010). Second, the visual systems of most counterilluminators are monochromatic and thus cannot determine the spectrum of either the downwelling light or their own emissions. Instead, they can only match their emissions to their perception of the intensity of the downwelling light. Because visual systems vary, even in the deep sea, the counterilluminator's perception of a match may not be a match for a system with different spectral sensitivity. Also, the yellow lenses of some deep-sea species can potentially enhance the difference between the downwelling light and the counterillumination. The spectrum of counterillumination is often broader than that of the downwelling light, and Muntz (1976) showed that the filters in the eyes of certain mesopelagic fish are well suited to maximize this difference, though whether they actually function in this context remains to be determined.

Polarization and UV vision likely play little role in breaking counterillumination. Downwelling light at counterillumination depths is nearly unpolarized (Jerlov 1976), and UV light at these depths is too dim to detect.

WHAT WE DO AND DO NOT KNOW

It should be obvious from even this brief review that the field of pelagic visual ecology is full of unanswered questions. Although we have substantial information on the optical properties and visual capabilities of this environment's inhabitants, our understanding of even the most basic behaviors is extremely limited, leaving us with fascinating optical and visual structures that we have yet to see function in any natural context. Although mathematical models have allowed us to surmise what happens at depth, they are not a replacement for in situ observations, which can overturn even the most attractive of functional hypotheses (e.g., Johnsen et al. 2011). Therefore, what the field of pelagic camouflage, and the field of pelagic visual ecology in general, requires most is not more analyses of eyes and tissues but rather the development of noninvasive methods for studying the behaviors and life histories of the denizens of this largest of habitats.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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LITERATURE CITED

Aksnes DL, Giske J. 1993. A theoretical model of aquatic visual feeding. *Ecol. Model.* 67:233–50

Brady PC, Travis KA, Maginnis T, Cummings ME. 2013. Polaro-cryptic mirror of the lookdown as a biological model for open ocean camouflage. *Proc. Natl. Acad. Sci. USA* 110:9764–69

Charette M, Smith WHF. 2010. The volume of Earth's ocean. *Oceanography* 23(2):112–14
Childress JJ, Cowles DL, Avuzzi JAF, Mickel TJ. 1990. Metabolic rates of benthic deep-sea decapod crustaceans decline with increasing depth primarily due to the decline in temperature. *Deep-Sea Res.* 37:929–49
Clarke MR, Denton EJ, Gilpin-Brown JB. 1979. On the use of ammonium for buoyancy in squids. *J. Mar. Biol. Assoc. UK* 59:259–76
Cooper KM, Hanlon RT, Budelmann BU. 1990. Physiological color change in squid iridophores. II. Ultrastructural mechanisms in *Lolliguncula brevis*. *Cell Tissue Res.* 259:15–24
Cott HB. 1940. *Adaptive Coloration in Animals.* London: Methuen & Co.
Cronin TW, Shashar N. 2001. The linearly polarized light field in clear, tropical marine waters: spatial and temporal variation of light intensity, degree of polarization and e-vector angle. *J. Exp. Biol.* 204:2461–67
Crookes WJ, Ding L, Huan QL, Kimbell JR, Horwitz J, McFall-Ngai MJ. 2004. Reflectins: the unusual proteins of squid reflective tissues. *Science* 303:235–38
Denton EJ. 1970. On the organization of reflecting surfaces in some marine animals. *Philos. Trans. R. Soc. Lond. B* 258:285–313
Denton EJ. 1971. Reflectors in fishes. *Sci. Am.* 224:65–72
Denton EJ, Gilpin-Brown JB, Wright PG. 1972. The angular distribution of the light produced by some mesopelagic fish in relation to their camouflage. *Proc. R. Soc. Lond. B* 182:145–58
Dobrowolski JA. 1995. Optical properties of films and coatings. In *Handbook of Optics*, Vol. 1, *Fundamentals, Techniques, and Design*, ed. M Bass, pp. 42:1–130. New York: McGraw-Hill. 2nd ed.
Douglas RH. 2001. The ecology of teleost fish visual pigments: a good example of sensory adaptation to the environment? In *Ecology of Sensing*, ed. FG Barth, A Schmid, pp. 215–35. Berlin: Springer-Verlag
Douglas RH, Hawryshyn CW. 1990. Behavioral studies of fish vision: an analysis of visual capabilities. In *The Visual System of Fish*, ed. RH Douglas, MBA Djamgoz, pp. 373–418. New York: Chapman and Hall
Duntley SQ. 1952. *The visibility of submerged objects*. Final Rep. to Off. Nav. Res., Visibility Lab., Mass. Inst. Technol., Cambridge
Duntley SQ. 1963. Light in the sea. *J. Opt. Soc. Am.* 53:214–33
El-Sayed SZ, van Dijken GL, Gonzalez-Rodas G. 1996. Effects of ultraviolet radiation on marine ecosystems. *Intern. J. Environ. Stud.* 51:199–216
Haddock SHD, Moline MA, Case JF. 2010. Bioluminescence in the sea. *Annu. Rev. Mar. Sci.* 2:443–93
Hama H, Kurokawa H, Kawano H, Ando R, Shimogori T, et al. 2011. Sca*l*e: a chemical approach for fluorescence imaging and reconstruction of transparent mouse brain. *Nat. Neurosci.* 14:1481–88
Herring PJ. 1967. The pigments of plankton at the sea surface. *Symp. Zool. Soc. Lond.* 19:215–35
Herring PJ. 1973. Depth distribution of the carotenoid pigments and lipids of some oceanic animals. 2. Decapod crustaceans. *J. Mar. Biol. Assoc. UK* 53:539–62
Herring PJ. 1976. Bioluminescence in decapod crustacea. *J. Mar. Biol. Assoc. UK* 56:1029–47
Herring PJ. 1985. Bioluminescence in the crustacea. *J. Crustac. Biol.* 5:557–73
Herring PJ. 2001. *The Biology of the Deep Ocean*. Oxford, UK: Oxford Univ. Press
Herring PJ, Roe HSJ. 1988. The photoecology of pelagic oceanic decapods. *Symp. Zool. Soc. Lond.* 59:263–90
Herring PJ, Widder EA, Haddock SHD. 1992. Correlation of bioluminescence emissions with ventral photophores in the mesopelagic squid *Abralia veranyi*. *Mar. Biol.* 112:293–98
Holt A, Sweeney AM, Johnsen S, Morse DE. 2011. A highly distributed Bragg stack with unique geometry provides effective camouflage for Loliginid squid eyes. *J. R. Soc. Interface* 8:1386–99
Horváth G, Varjú D. 2004. *Polarized Light in Animal Vision*. Berlin: Springer-Verlag
Huang WP, Guo Q, Wu C. 1996. A polarization-independent distributed Bragg reflector based on phase-shifted grating structures. *J. Lightwave Technol.* 14:469–73
Ivanoff A, Waterman TH. 1958. Elliptical polarization of submarine illumination. *J. Mar. Res.* 16:255–82
Jerlov NG. 1976. *Marine Optics*. New York: Elsevier
Johnsen S. 2001. Hidden in plain sight: the ecology and physiology of organismal transparency. *Biol. Bull.* 201:301–18
Johnsen S. 2002. Cryptic and conspicuous coloration in the pelagic environment. *Proc. R. Soc. Lond. B* 269:243–56
Johnsen S. 2005. The red and the black: bioluminescence and the color of animals in the deep sea. *Integr. Comp. Biol.* 45:234–46

Johnsen S. 2007. Does new technology inspire new directions? Examples drawn from pelagic visual ecology. *Integr. Comp. Biol.* 47:799–807

Johnsen S. 2012. *The Optics of Life: A Biologist's Guide to Light in Nature*. Princeton, NJ: Princeton Univ. Press

Johnsen S, Marshall NJ, Widder EA. 2011. Polarization sensitivity as a contrast enhancer in pelagic predators: lessons from in situ polarization imaging of transparent zooplankton. *Philos. Trans. R. Soc. Lond. B* 366:655–70

Johnsen S, Sosik HM. 2003. Cryptic coloration and mirrored sides as camouflage strategies in near-surface pelagic habitats: implications for foraging and predator avoidance. *Limnol. Oceanogr.* 48:1277–88

Johnsen S, Widder EA. 1999. The physical basis of transparency in biological tissue: ultrastructure and the minimization of light scattering. *J. Theor. Biol.* 199:181–98

Johnsen S, Widder EA. 2001. Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. *Mar. Biol.* 138:717–30

Johnsen S, Widder EA, Mobley CD. 2004. Propagation and perception of bioluminescence: factors affecting the success of counterillumination as a cryptic strategy. *Biol. Bull.* 207:1–16

Jordan TM, Partridge JC, Roberts NW. 2012. Non-polarizing broadband multilayer reflectors in fish. *Nat. Photonics* 6:759–63

Lampert W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Beih. Ergeb. Limnol.* 39:79–88

Land MF, Nilsson DE. 2012. *Animal Eyes*. Oxford, UK: Oxford Univ. Press. 2nd ed.

Levenson DH, Eckert SA, Crognale MA, Deegan JF II, Jacobs GH, Douglas ME. 2004. Photopic spectral sensitivity of green and loggerhead sea turtles. *Copeia* 4:908–14

Levin LE, Belmonte P, González O. 1992. Sun-compass orientation in the characid *Cheirodon pulcher*. *Environ. Biol. Fishes* 35:321–25

Levy-Lior A, Shimoni E, Schwartz O, Gavish-Regev E, Oron D, et al. 2010. Guanine-based biogenic photonic-crystal arrays in fish and spiders. *Adv. Funct. Mater.* 20:320–29

Losey GS, Cronin TW, Goldsmith TH, Hyde D, Marshall NJ, McFarland WN. 1999. The UV visual world of fishes: a review. *J. Fish Biol.* 54:921–43

Lythgoe JN. 1979. *The Ecology of Vision*. London: Clarendon

Mackie GO. 1996. Defensive strategies in planktonic coelenterates. In *Zooplankton: Sensory Ecology and Physiology*, ed. PH Lenz, DK Hartline, JE Purcell, DL Macmillan, pp. 435–46. Amsterdam: Overseas Publ. Assoc.

Marshall BR, Smith RC. 1990. Raman scattering and in-water ocean optical properties. *Appl. Opt.* 29:71–84

McFall-Ngai MJ. 1990. Crypsis in the pelagic environment. *Am. Zool.* 30:175–88

McKenzie DR, Yin Y, McFall WD. 1995. Silvery fish skin as an example of a chaotic reflector. *Proc. R. Soc. Lond. A* 451:579–84

Mertens LE. 1970. *In-Water Photography: Theory and Practice*. New York: Wiley & Sons

Mobley CD. 1994. *Light and Water: Radiative Transfer in Natural Waters*. San Diego: Academic

Muntz WRA. 1976. On yellow lenses in mesopelagic animals. *J. Mar. Biol. Assoc. UK* 56:963–76

Partridge JC, Cummings ME. 1999. Adaptation of visual pigments to the aquatic environment. In *Adaptive Mechanisms in the Ecology of Vision*, ed. SN Archer, MBA Djamgoz, ER Loew, JC Partridge, S Vallerga, pp. 251–84. Boston: Kluwer

Perilloux BE, Fischer DG. 1988. *Polarization preserving reflector and method*. US Patent No. 4,746,202

Ruxton GD, Sherratt TN, Speed MP. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford, UK: Oxford Univ. Press

Schechner YY, Karpel N. 2005. Recovery of underwater visibility and structure by polarization analysis. *IEEE J. Ocean. Eng.* 30:570–87

Schechner YY, Narasimhan SG, Nayar SK. 2003. Polarization-based vision through haze. *Appl. Opt.* 42:511–25

Seapy RR, Young RE. 1986. Concealment in epipelagic pterotracheid heteropods (Gastropoda) and cranchiid squids (Cephalopoda). *J. Zool. Soc. Lond. A* 210:137–47

Shashar N, Hagan R, Boal JG, Hanlon RT. 2000. Cuttlefish use polarization sensitivity in predation on silvery fish. *Vis. Res.* 40:71–75

Shashar N, Hanlon RT, Petz A. 1998. Polarization vision helps detect transparent prey. *Nature* 393:222–23

Stavenga DG, Stowe S, Siebke K, Zeil J, Arikawa K. 2004. Butterfly wing colours: scale beads make white pierid wings brighter. *Proc. R. Soc. Lond. B* 271:1577–84

Stavn RH, Wiedemann AD. 1988. Raman scattering in ocean optics: quantitative assessment of internal radiant emission. *Appl. Opt.* 9:1294–303

Tyrrell T, Holligan PM, Mobley CD. 1999. Optical impacts of oceanic coccolithophore blooms. *J. Geophys. Res.* 104:3223–41

Vogel S. 1996. *Life in Moving Fluids: The Physical Biology of Flow*. Princeton, NJ: Princeton Univ. Press. 2nd ed.

Wagner HJ, Douglas RH, Frank TM, Roberts NW, Partridge JC. 2009. A novel vertebrate eye using both refractive and reflective optics. *Curr. Biol.* 19:108–14

Warrant EJ. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vis. Res.* 39:1611–30

Warrant EJ, Locket NA. 2004. Vision in the deep sea. *Biol. Rev.* 79:671–712

Webb TJ, Vanden Berghe E, O'Dor R. 2010. Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLoS ONE* 5:e10223

Widder EA. 1999. Bioluminescence. In *Adaptive Mechanisms in the Ecology of Vision*, ed. SN Archer, MBA Djamgoz, ER Loew, JC Partridge, S Vallerga, pp. 555–81. Boston: Kluwer

Young RE, Mencher FM. 1980. Bioluminescence in mesopelagic squid: diel color change during counterillumination. *Science* 208:1286–88

Young RE, Roper CFE. 1976. Bioluminescent countershading in mid-water animals: evidence from living squid. *Science* 191:1046–48

Young RE, Roper CFE. 1977. Intensity regulation of bioluminescence during countershading in living mid-water animals. *Fish. Bull.* 75:239–52

Zylinski S, Johnsen S. 2011. Mesopelagic cephalopods switch between transparency and pigmentation to optimize camouflage in the deep. *Curr. Biol.* 21:1937–41