

Lifting the Cloak of Invisibility: The Effects of Changing Optical Conditions on Pelagic Crypsis¹

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SYNOPSIS. While transparency, cryptic coloration, and counterillumination are all highly successful cryptic strategies for pelagic species, they become less effective when confronted with varying optical conditions. Transparent species are susceptible to detection by reflections from their body surface, particularly at shallow depths. Colored and mirrored species are vulnerable to detection when viewed from certain angles, or at certain times of day. Counterilluminating species must cope with the changes in the angular distribution and spectra of downwelling light at different depths. In all cases the vulnerabilities are more pronounced at shallow depths and essentially negligible at depths greater than 200 m. The results suggest interesting adaptations both for crypsis (e.g., anti-reflection coatings, variable coloration, variable filters for photophores) and for visual detection (e.g., circling, crepuscular predation), all of which are potentially fruitful topics for future research.

INTRODUCTION

Pelagic species appear to have converged on four major strategies for crypsis: transparency, mirroring, cryptic coloration, and counterillumination (reviewed by Herring and Roe, 1988; Herring, 1994; Johnsen, 2001; Widder, 2001). All four strategies have, in some instances, evolved to the point where, under ideal conditions, they provide essentially perfect crypsis when viewed by most visual systems. However, a cryptic animal may be perfectly camouflaged under one set of optical conditions, but highly visible under a different set. This is a serious limitation, because the aquatic light environment changes dramatically with depth, viewing angle, time of day, and water turbidity.

This paper, derived from a presentation given at the 2003 annual meeting of the Society of Integrative and Comparative Biology, integrates recent research and previously unpublished material to compare the robustness of the four major cryptic strategies under varying optical conditions. This is done by assuming that a particular strategy is perfect (i.e., affords complete crypsis) under one set of optical conditions, and then determining the visibility of an animal employing that strategy as these conditions are altered. It will be shown that none of the four strategies are obviously more robust, and that the most robust strategy depends on how the optical environment changes. The advantages and disadvantages of the various strategies also suggest various additional strategies for both crypsis and detection.

TRANSPARENCY

Research on the physiology, morphology, and potential costs of transparency has been recently reviewed (Johnsen, 2001). Therefore, the following discussion will be limited to situations potentially leading to failure of this form of camouflage.

Because a transparent animal directly transmits a high

percentage (ideally 100%) of the background light, transparency is a highly robust form of camouflage. Changing viewpoint, time of day, or water type has no effect on a transparent animal's visibility, with one important exception. If a portion of the animal has a substantially different refractive index from the rest, it will scatter light. Because this scattered light is usually a very small fraction of the total transmitted light, it will have little effect on visibility if the animal is viewed from below against the bright overhead illumination. However, because downward radiance underwater can be several orders of magnitude brighter than radiance in other directions (Jerlov, 1976; Johnsen, 2002), even the small fraction of light scattered from the downward radiance can be brighter than the background radiance in other directions (Figs. 1, 2a). It is for this reason that the glinting reflection from a window is obvious from the outside of a house, but generally undetectable from the inside (and why the situation is reversed at night). This scattered light can make an otherwise transparent animal quite conspicuous when viewed laterally or from above (Chapman, 1976). The effect is most prominent at shallow depths, where the light field is usually asymmetric, due to highly directional and intense solar radiance.

Even if a transparent animal is free of internal refractive index inhomogeneities, the body itself has a higher refractive index than the surrounding water and so will also scatter light. This scattered light is most easily interpreted as surface reflection. Its radiance L_r is given by:

$$L_r = \frac{1}{2} L_i \left\{ \left[\frac{\cos \theta - \sqrt{m(m - \sin^2 \theta)}}{\cos \theta + \sqrt{m(m - \sin^2 \theta)}} \right]^2 + \left[\frac{\cos \theta - \frac{1}{m} \sqrt{\frac{1}{m}(m - \sin^2 \theta)}}{\cos \theta + \frac{1}{m} \sqrt{\frac{1}{m}(m - \sin^2 \theta)}} \right]^2 \right\} \quad (1)$$

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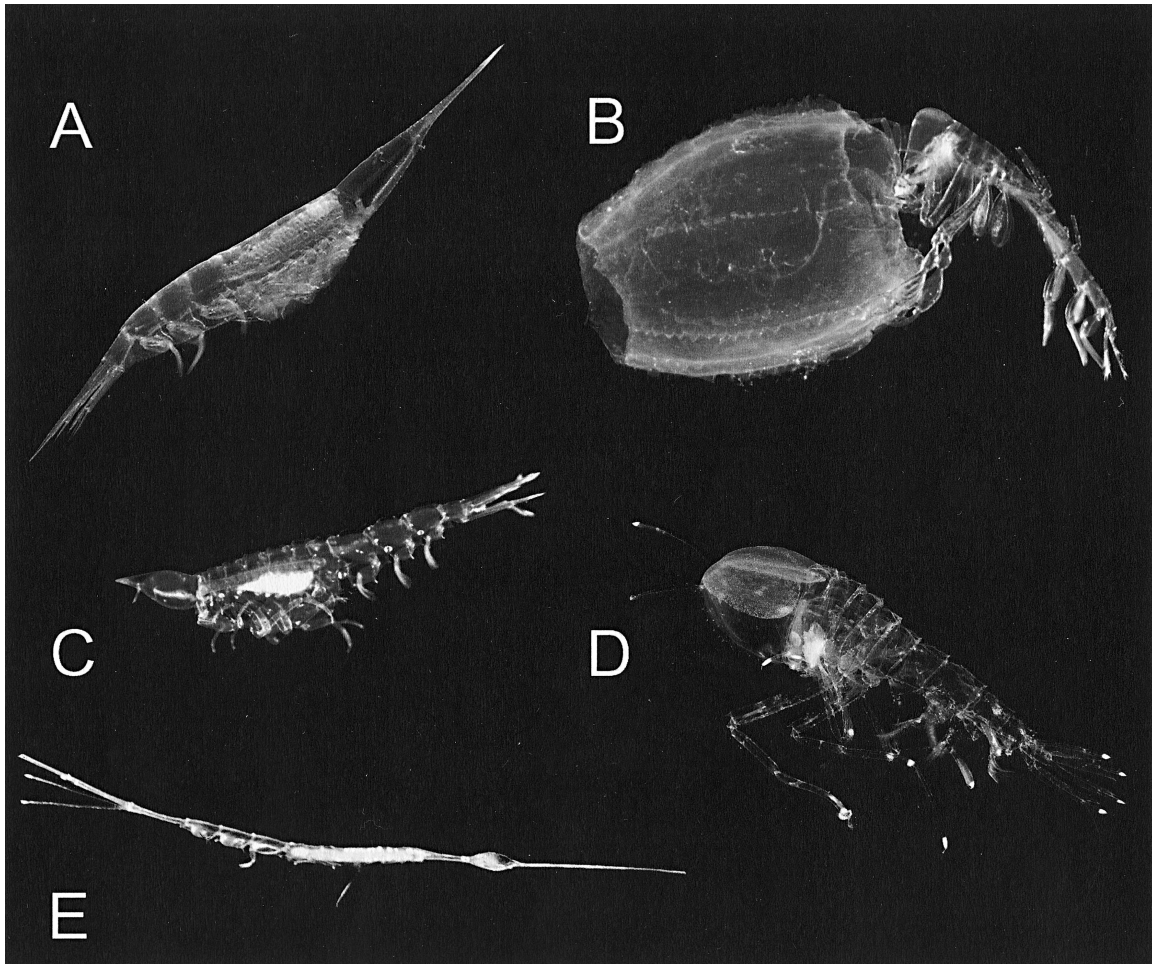


FIG. 1. Transparent species of hyperiid amphipods. A) *Streetsia* sp. B) *Phronima sedentaria* with house made from hollowed-out salp. C) *Oxycephalous* sp. D) *Cystisoma* sp. E) *Rhabdosoma* sp. While all five animals are highly transparent and difficult to detect under normal illumination, they are quite visible when side-lit by a bright light (in this case a photographic flash) and viewed against a dark background.

where L_i is the incident irradiance (assumed to be unpolarized), θ is the angle of incidence (0° is perpendicular to surface) and m is the relative refractive index $n_{\text{tissue}}/n_{\text{water}}$ (Hecht, 1998). The refractive index of biological tissue is roughly proportional to density and ranges from 1.35 (cytoplasm) to approximately 1.55 (densely packed protein) (Charney and Brackett, 1961; Chapman, 1976). The refractive index of seawater depends on temperature and salinity, but is generally about 1.34. The percentage of incident radiance that is reflected depends strongly on relative refractive index m , but is relatively independent of incident angle for angles less than 45° (however it rises sharply for angles $>45^\circ$) (Fig. 2b). When the ratio of the background radiance to the radiance of the incident light equals the reflection (e.g., $R = L_b/L_i$), the reflected radiance (RL_i) equals the background radiance (L_b). In a transparent animal, the background radiance is also transmitted through the reflective region of the tissue (and thus adds to the total animal radiance), thus the animal has twice the radiance of the background and should be highly visible (humans and fish can just detect an ob-

ject that is only 2% brighter than the background). By modeling the underwater radiance distribution from inherent optical properties (Mobley *et al.*, 1993; Johnsen, 2002), one can determine at what wavelengths this is most likely to occur as a function of depth, viewing angle, and refractive index (Figs. 2c, d). Mesogleal tissue, due to its low refractive index ($n \approx 1.35$), does not appear to be vulnerable to surface reflection, even at the surface of the ocean. Muscular tissue ($n \approx 1.4$) however, reflects a significant amount of light at longer wavelengths at shallow depths (from 600 to 700 nm at the ocean surface, from 630 to 650 nm at 10 m depth, both for horizontal viewing [Fig. 2c]). The wavelength range is somewhat larger when the animal is viewed from above (Fig. 2d). Tissue consisting primarily of lipid ($n \approx 1.48$), creates strong reflections at medium to long wavelengths (with the exact range depending on depth and whether the tissue is viewed horizontally or from above) at depths down to 20 m for horizontal viewing and 40 m for downward viewing. Chitin, due to its high refractive index ($n \approx 1.55$), creates strong reflections down to 40 m over an even

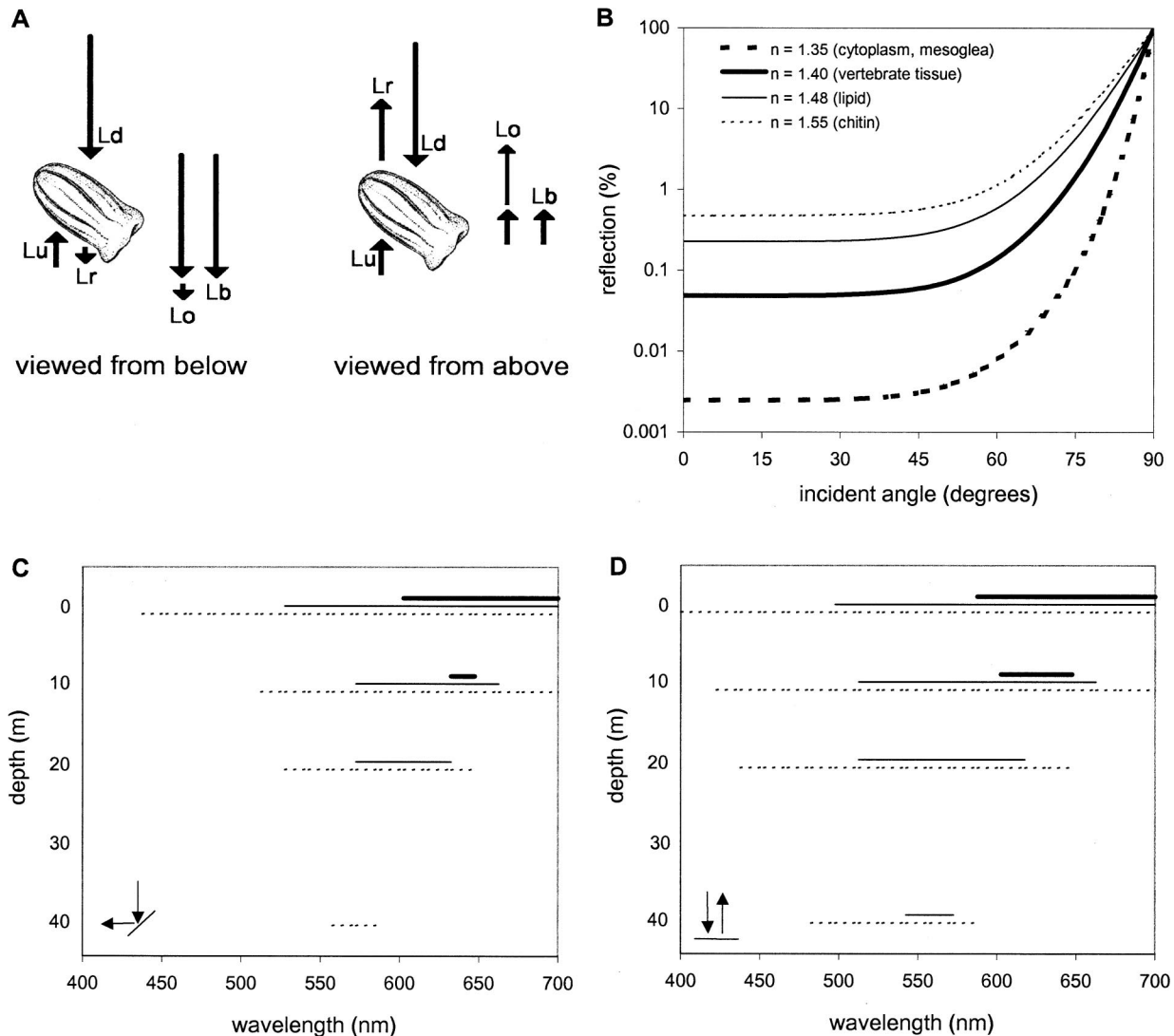


FIG. 2. A) Analysis of the visibility of reflections from two different viewing angles, assuming a reflectance of 50%. When viewed from below, the background radiance L_b (which equals the downward radiance L_d) is high, while the reflected radiance L_r is low (because it is 50% of the relatively low upward radiance L_o). The difference between the object radiance L_o (which, because the tissue is transparent, equals $L_d + L_r$) and the background radiance L_b is quite small and difficult to detect. When viewed from above, however, the background radiance L_b (which equals the upward radiance L_o) is quite low, while the reflected radiance L_r is high (because it is 50% of the relatively high downward radiance L_d). The difference between the object radiance $L_o (= L_d + L_r)$ and the background radiance L_b is now large and easy to detect. B) Percent reflection as a function of angle of incidence from submerged transparent surfaces made from different materials (from equation 1). Incident light is randomly polarized. Because this is specular reflection, the angle of the reflected light equals the angle of incidence. C) The wavelengths at which reflections from different tissue components (assuming a 45-degree angle of incidence) are highly visible (*i.e.*, double the brightness of the background) when viewed horizontally underwater as a function of depth. D) The wavelengths at which reflections from different tissue components (assuming a perpendicular angle of incidence) are highly visible when viewed from above. The radiance ratios were calculated from measured inherent optical properties and chlorophyll concentrations from the Equatorial Pacific (see Johnsen, 2002). The legends in C) and D) are the same as in B), and the lines at each depth are separated from clarity.

wider range of wavelengths. The reflections are naturally most noticeable under direct sunlight, thus diffuse surface illumination due to cloud cover reduces their prominence.

Reflections are more prominent at longer wavelengths because these wavelengths are absorbed more and scattered less by the water, resulting in a far lower background radiance in lines of sight away from the sun. While long-wavelength vision is extremely rare at depth, it is relatively common near the surface

(Lythgoe and Partridge, 1989). While long-wavelength vision likely serves many purposes, one that has not yet been considered is its advantage in detecting the reflective glints from transparent species. It would be particularly interesting to determine if there is a correlation between long-wavelength vision and a preference for transparent prey.

Surface reflections can be reduced or eliminated by covering the surface with sub-microscopic protrusions (Miller, 1979; Wilson and Hutley, 1982) (Fig. 3a). The

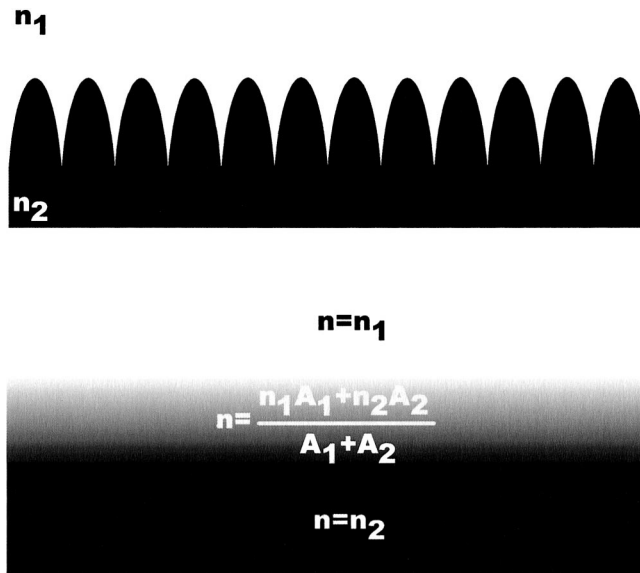


FIG. 3. Photons impinging from above on an irregular surface with protrusions smaller than half a wavelength of light experience a gradual change in refractive index, rather than a sharp discontinuity. n_1 is the refractive index of the external medium, n_2 is the index of the surface of the organism (e.g., cuticle). The refractive index at a given horizontal plane within the protrusion layer equals the average refractive index, which is given by the equation in the figure, where A_1 and A_2 are the respective areas of the external and organismal regions in that plane. The gradual shift in refractive index can reduce or eliminate surface reflections.

array of protrusions does not scatter light, but instead mimics a material with a graded refractive index. At the distal tips of the protrusions, the observed refractive index is that of the external medium. At the base of the protrusions, the index is that of the tissue. At intermediate positions, the index depends on the relative cross-sectional areas of the protrusions and the external medium at that position (Fig. 3b). These structures, known as “moth eyes,” are found on the wings of transparent lepidopterans, and in certain species (e.g., *Cephanodes hylas*) have been shown to reduce their visibility (Yoshida *et al.*, 1997). Interestingly, similar arrays of protrusions have been found on the surfaces of the tests of transparent salps (Hirose, personal communication), though their presence on sedentary, opaque ascidians casts some doubt on their cryptic function.

COLORS AND MIRRORS

Two other common cryptic strategies in the pelagic environment involve altering the reflective properties of the surface, either through the use of pigments or structural colors (reviewed by Cott, 1940; Denton, 1970; Herring and Roe, 1988; McFall-Ngai, 1990; Herring, 1994). The physiological advantages of these strategies over those that involve either the production of light (counterillumination) or the modification of the entire interior of the animal (transparency) are obvious and will not be discussed here. Again, we will

concern ourselves only with the robustness of these strategies under changing optical conditions.

While the coloration of benthic and near-shore species displays an astounding and bewildering diversity, particularly in tide pools and coral reef communities, coloration in the pelagic environment follows a more predictable pattern that appears to be primarily driven by selection for crypsis (Herring and Roe, 1988; Johnsen, 2002). In general, near-surface species are blue in the ocean and green in coastal waters, and darkest on the dorsal surface, fading to white on the ventral surface (Herring, 1967). With increasing depth, coloration changes first to “half-red” (red coloration of opaque tissues) and then to red and/or black uniformly distributed over the body surface. Mirroring (*i.e.*, reflective sides) is far more common in vertebrates than invertebrates, with highly reflective regions in invertebrates generally confined to guts and eyes. Even in vertebrates, mirroring is primarily confined to the lateral surfaces. The mirrored surfaces are generally highly reflective and spectrally neutral (though a golden colored reflectance is found in some deep-sea teleosts). While some species are either diffusely colored or mirrored and completely colorless, the majority of non-transparent species tend to have a complex reflectance that includes both diffuse (colored) and specular (mirrored) components.

One crucial difference between pelagic and benthic coloration, is that, in the former, the spectra of the irradiance illuminating the animal and the background radiance can change independently of each other. This is different from the benthic case, where any change in the spectrum of the illuminant has an equal effect on the background. For example, a white ball on white paper is just as cryptic under blue light as it is under green light, because the spectral radiance of both the ball and the paper are identically altered as the illuminant changes. However, because the background radiance in the pelagic environment is a complex result of multiple scattering and absorption events, its spectrum changes independently of the illuminant. For this reason, cryptic coloration in the pelagic realm is far less robust than it is in benthic environments.

It is important to note that cryptic animals must be correctly colored, even when being viewed by species without color vision. One might assume that it is only necessary to match the perceived brightness of the background; *i.e.*

$$\int L_o(\lambda)V(\lambda) d\lambda = \int L_b(\lambda)V(\lambda) d\lambda \quad (2)$$

where $V(\lambda)$ is the spectral sensitivity curve of the viewer and L_o and L_b are the radiance of the animal and the background respectively. However, a target spectrum that satisfies equation 2 for one visual system is unlikely to satisfy it for a different system with a different spectral sensitivity curve, unless $L_o = L_b$ for all relevant wavelengths (Johnsen, 2002). Given that marine visual systems present a diverse array of spec-

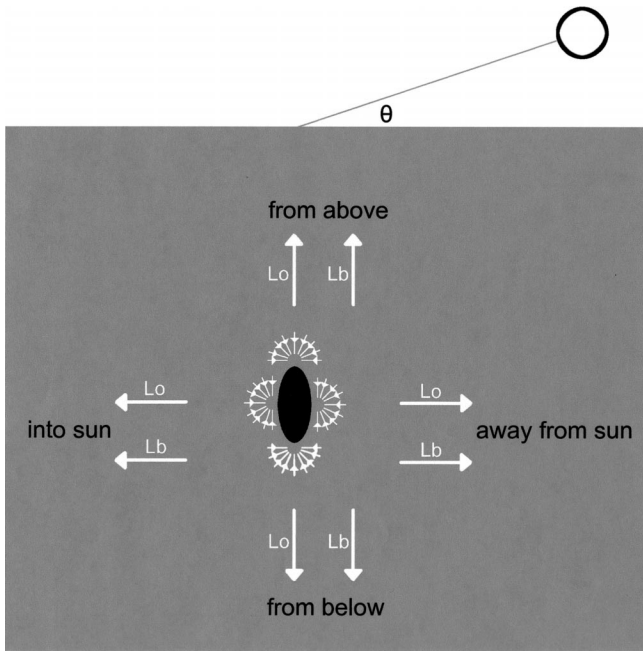


FIG. 4. The four different viewing angles analyzed in Johnsen (2002) and Johnsen and Sosik (2003). L_o is the radiance of the surface of the target, L_b is the radiance of the background. The clusters of inward pointing arrows denote the irradiance illuminating each surface (which is related to the radiance of the surface). The circle denotes the sun (which is in the plane of the figure). The angle θ is the solar elevation angle.

tral responses (Bowmaker, 1990; Marshall *et al.*, 1999; Muntz, 1999), any organism interacting with multiple species is unlikely to be cryptic to all of them unless $L_o = L_b$ at all wavelengths where sufficient illumination for vision exists. Indeed, one can consider an animal interacting with different monochromatic visual systems from multiple species as interacting with a single super-organismic color visual system.

Johnsen (2002) and Johnsen and Sosik (2003) determined the ideal reflectance for colored surfaces in both oceanic and coastal waters (Figs. 4, 5) and the ideal reflectance for mirrored surfaces in coastal waters (Fig. 6). The ideal reflectance depended strongly on water type, depth and the angle of view (*i.e.*, looking up at the ventral surface of the animal vs. looking down at the dorsal surface). The ideal reflectance depended less strongly on solar elevation and viewing azimuth (horizontal viewing direction), but significant differences were still noted due to the asymmetry of the light field, which has a higher radiance in the direction of the sun. Johnsen and Sosik (2003) quantified the effect of these differences on crypsis by considering four mismatch conditions: 1) an organism perfectly cryptic in oceanic water that is now viewed in coastal water, 2) an organism cryptic near noon (solar elevation 80°) that is now viewed near sunset (solar elevation 10°), 3) an organism cryptic in one azimuth that is now viewed horizontally in the opposite azimuth, and 4) an organism cryptic at 50 m depth that is now viewed at shallower depths. Because the ideal

coloration/mirroring depended on the optical conditions and viewing angle, these mismatches resulted in a breaking of the camouflage. Using the visual parameters of a fish native to the studied waters (Atlantic Cod, *Gadus morhua*), it was determined how far away the mismatched animal would be visible (*i.e.*, its sighting distance) depending on its size.

The mismatched animals were highly visible, with the sighting distances on the order of 5–10 m for large individuals (1 m body length) and 0.5–1.0 m for small individuals (6 mm body length). Mirrored organisms generally had shorter sighting distances when viewed under mismatched conditions than colored organisms, with two exceptions: 1) changing time of day and 2) changing depth when viewed backlit by the sun (Table 1). The first exception is due to the fact that, while mirrored organisms can be perfectly cryptic in a cylindrically symmetric light field (Denton, 1970), they cast strong reflections when viewed under the highly asymmetric conditions present at sunset (because they reflect the direct light of the setting sun). The second exception arises because mirrored organisms can never be completely cryptic when backlit by the sun since this requires the reflectance to be greater than one—a physical impossibility (Johnsen and Sosik, 2003). For this reason, while a colored, diffusely reflective surface can be completely cryptic at 50 m depth when viewed against the sun, a mirrored surface will still be visible. In the case of changing depth, this disadvantage is greater than the advantages that mirrored surfaces have under changing optical conditions.

Johnsen and Sosik (2003) showed that cryptic individuals are particularly vulnerable to detection when being viewed at different azimuths. Suppose that the light field is asymmetric due to low solar elevation and that an animal's lateral surface is cryptic when viewed away from the sun (Fig. 7). As the viewing azimuth changes, perhaps due to circling behavior of the viewer, the background radiance increases and the animal's radiance decreases (due to lower irradiance at its surface). Unless the animal increases its reflectance, it will appear as a dark target on a light background. This vulnerability to azimuthal changes is particularly troublesome because, while organisms can control their depth, water type, and the time of day at which they are active, they have little control over the azimuth from which they are viewed. While the light field at depths >200 m is essentially cylindrically symmetrical, at shallower depths the azimuthal asymmetry is quite pronounced, especially at sunrise and sunset (Johnsen, 2002).

One possible compensatory strategy is orientation towards or away from the sun. In this orientation, the lateral surfaces of the animal are equally illuminated and seen against equal backgrounds and thus can be simultaneously cryptic. This orientation also minimizes the effects of wave-induced lensing on the large lateral surfaces (see Loew and McFarland, 1990). Certain fish species are known to orient and migrate using a solar compass (*e.g.*, Levin *et al.*, 1992), but it is not

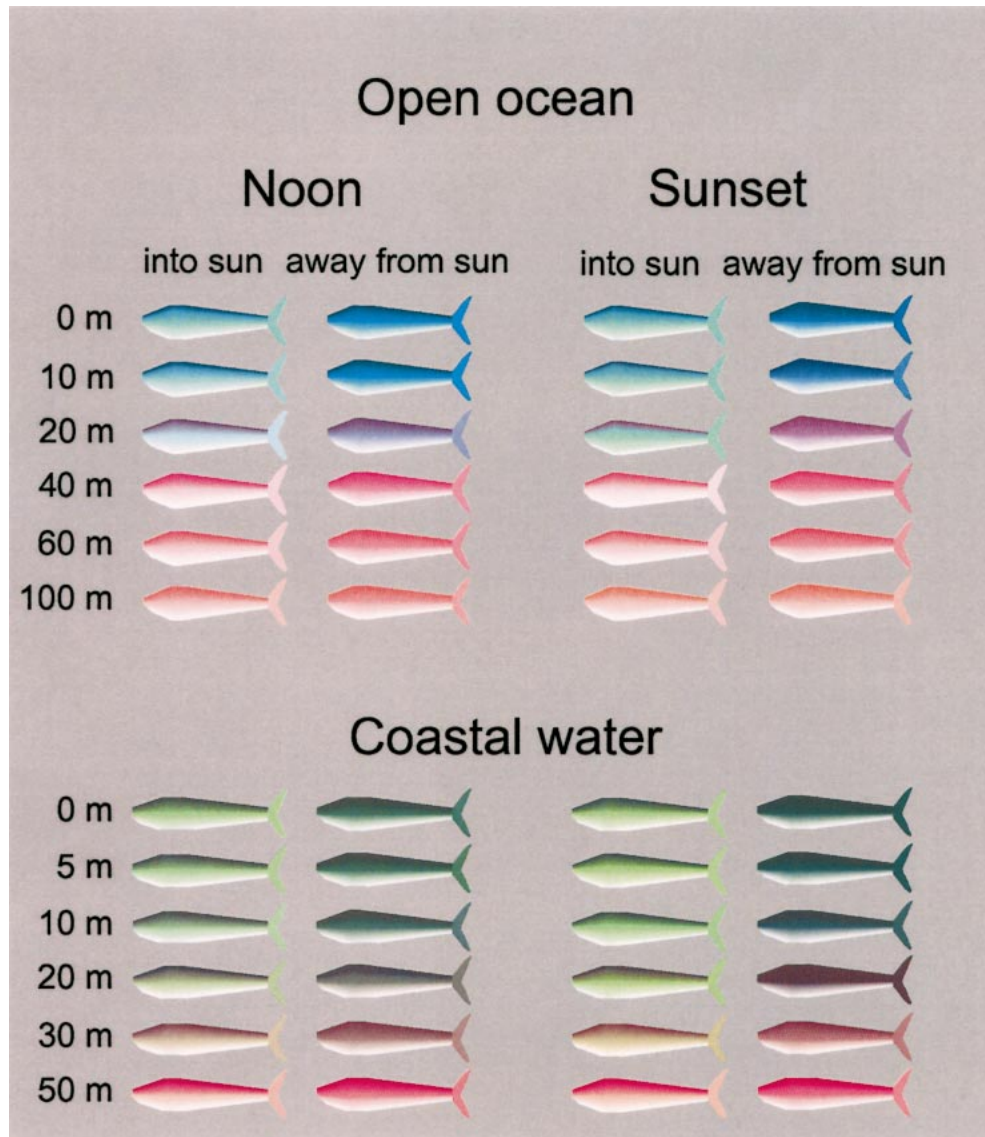


FIG. 5. Cryptic coloration for colored fish represented as human-perceived color (viewed under northern daylight). Predicted reflectance spectra for oceanic and coastal waters are converted to CIE XYZ coordinates using standard methods (Wyszecki and Stiles, 1982), and then converted to RGB coordinates using color conversion software (Munsell Conversion Program, GretagMacbeth Inc.). Dorsal, lateral, and ventral coloration are from Johnsen (2002) and Johnsen and Sosik (2003). Coloration at intermediate locations is given by linear interpolation. The surface of the animal is assumed to be diffusely reflective. Note that while the white ventral surface in each case is the best possible, it is not ideal, because the required reflectance for perfect ventral crypsis is several orders of magnitude higher than one.

known whether any species employ sunward orientation as a cryptic strategy.

Given the factors that reduce the crypticity of colored and mirrored animals, several predatory search strategies suggest themselves. First, the effect of azimuthal changes suggests a circular search strategy, particularly near the surface during crepuscular periods. A predator orbiting a volume of water will at some point arrive at a viewpoint in which the reflectance of the cryptic individual is badly mismatched. A second strategy involves searching at low solar elevations (*e.g.*, dawn and dusk) to take advantage of the asymmetry of the underwater light field. Finally, once an organism is detected, it is likely to become more

visible if it is driven towards the surface. All three tactics have been documented in pelagic predators, though it is not known if their primary purpose is in breaking crypsis (Ikehara *et al.*, 1978; Gallo Reynoso, 1991; Similae, 1997; McFarland *et al.*, 1999).

The results of Johnsen (2002) and Johnsen and Sosik (2003) suggest that adaptive color change in pelagic species may be a fruitful topic of research. However, while numerous studies have demonstrated adaptive and cryptic color changes in benthic species, pelagic species have received far less attention. It is known that certain pelagic crustaceans change color depending on depth or time of day (Herring and Roe, 1988), and that some anadromous fish develop mir-

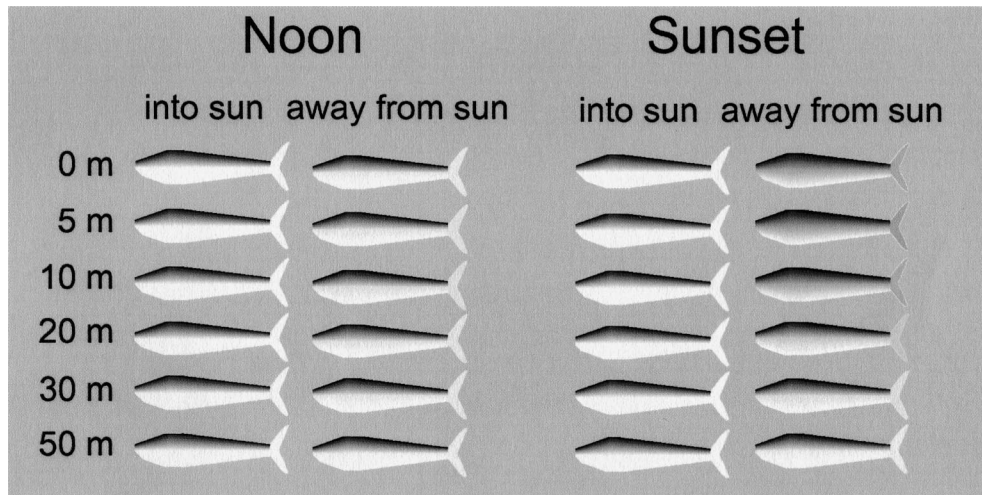


FIG. 6. Cryptic reflectance for mirrored fish in coastal waters represented as human-perceived brightness (viewed under northern daylight). See Figure 4 caption for more details. The white lateral surfaces when viewed into the sun and the white ventral surfaces in all cases are the best possible, but not ideal, because the required reflectance in both cases is greater than one.

rored sides before entering the ocean (reviewed by Herring, 1994). However, aside from anecdotal reports of color changes in various pelagic fish, particularly billfish, little else is known.

COUNTERILLUMINATION

Although white ventral coloration in aquatic animals has often been thought to be cryptic (*e.g.*, Cott, 1940), measurements and models of the underwater light clearly show that this cannot be the case. Even in deep water, where the light field is the most diffuse, the upward radiance is only 0.5% of the downward radiance (Denton, 1990). Therefore, even if the ventral surface reflected 100% percent of the upward radiance, it would still be silhouetted against the much brighter downward radiance. Near the surface, the situation is more extreme, with the downward radiance exceeding the upward radiance by many orders of magnitude. In

fact, while a white ventral surface is theoretically more cryptic than a black one, Johnsen (2002) showed that the difference is insignificant. Because unpigmented, opaque tissue tends to be white (due to multiple light scattering), the white ventral surface in many instances may simply be a default condition, with no adaptive value. Indeed, when one examines surface and cave populations of the same species, their dorsal and lateral coloration differs sharply, but their ventral coloration is identical (Fig. 8). However, in certain cases, white ventral coloration is obviously adaptive. For example, many polar species (*e.g.*, penguins, killer whales) have striking white coloration that appears to be used for crypsis in ice.

Because a colored or mirrored ventral surface always casts a silhouette, it will be visible from below. This is especially troublesome for any animal attempting to remain unseen because objects seen from below are more visible than seen from any other angle for two reasons. First, the zenith is generally the brightest portion of the underwater light field, so visual performance, in particular contrast sensitivity, is best in that direction. Second, the contrast of the silhouetted animal decreases very slowly relative to other directions. The distance at which an object can be seen not only depends on its contrast and size, but also on how quickly this contrast decreases. Mertens (1970) and others have shown that the sighting distance d is proportional to:

$$d \propto \frac{1}{c - K_L} \quad (3)$$

where c is the beam attenuation coefficient of the water and K_L is the attenuation coefficient of the background radiance. For upward viewing K_L is positive (because the background radiance decreases as the viewer moves down and away from the animal) and can be

TABLE 1. Summary of results from the mismatch studies in Johnsen and Sosik (2003).*

Condition	Time	Large animal		Small animal	
		Into	Away	Into	Away
Changing water type		M	M	M	M
Changing time of day		C	C	C	—
Changing azimuth	(noon)	M	M	M	M
	(sunset)	—	M	—	M
Changing depth	(noon)	C	M	C	M
	(sunset)	C	M	C	M

* A cell containing "M" denotes that mirroring was the more robust strategy under the given mismatch conditions. A cell containing "C" denotes that diffuse coloration was the more robust strategy. "Into" and "away" refers to whether the target animal was viewed backlit by the sun, or with the sun behind the viewer. The "large" animal was 1 m long. The "small" animal was 6 mm long. The underwater radiance distribution was modeled from inherent optical properties measured at a site 80 km from the coast of Portsmouth, New Hampshire (42°47'N 70°05'W, 11:06 local time, 30 June, 2000).

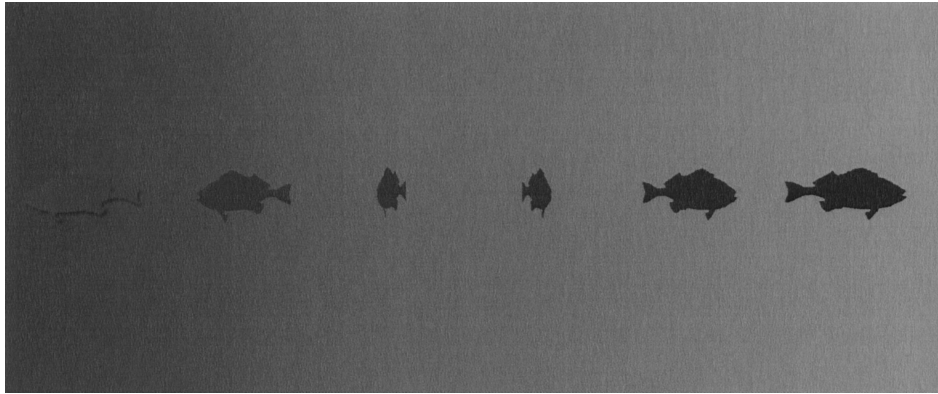


FIG. 7. Appearance of a fish viewed in the azimuth in which it is perfectly cryptic (left-most image) and at 36°, 72°, 108°, 144°, and 180° from that azimuth (in which crypsis is lost). In this case, the fish is cryptic when viewed away from the sun (where the horizontal background radiance is the least). As the viewpoint rotates around the fish, the background radiance increases, but the irradiance illuminating the fish decreases (because the viewed side of the fish is rotating away from the sun). This results in a large radiance mismatch (and thus high visibility) when the fish is viewed from the opposite azimuth (right-most image). Fish is viewed in the coastal water studied in Johnsen and Sosik (2003) at a depth of 5 m with a solar elevation of 10° (*i.e.*, near dawn or dusk).

quite close to the value of c . Therefore d can be quite high.

The inability to cryptically color the ventral surface, coupled with the visual advantages of viewing it, make this region highly vulnerable to detection. Indeed, a large number of mesopelagic animals have eyes that permanently view the upward direction for just this reason. The only successful countermeasure (aside from being transparent) is counterillumination, in which the ventral surface is covered with photophores that emit light to match the direct downward radiance and thus erase their silhouette. Most counterilluminators, in addition to matching the direct downward radiance, produce light with a particular angular distribution, so they can match radiance at other viewpoints and erase their silhouette from a large range of viewing angles. The diversity, physiology, and complexity of counterillumination have been well reviewed (*e.g.*, Latz, 1995; Harper and Case, 1999; Widder, 1999).

In considering the effects of changing optical conditions on the success of counterillumination, the primary issues are: the effects of depth on 1) the spectrum and 2) the angular distribution of the downwell-

ing light. Although inelastic light scattering complicates the picture somewhat (Marshall and Smith, 1990), the ocean generally acts as a monochromator, dramatically narrowing the spectral distribution with increasing depth. The longest and shortest wavelengths are attenuated rapidly, followed by a progressively slower narrowing of the wavelength range of the remaining light (Fig. 9a, b). Therefore, if the counterilluminator changes depth, it must change the spectral composition of the light emitted by its photophores.

During the day, these spectral changes likely have little impact because counterilluminating animals are found at depths greater than 200 m, where the spectrum changes quite slowly. However at night, counterilluminators are found closer to the surface, where the spectrum of the downward radiance changes rapidly with depth (Harper and Case, 1999). They also must compensate for the changing spectrum of the skylight due to the presence or absence of moonlight. Moonlight is not significantly different from sunlight, but starlight is shifted towards longer wavelengths, with a large peak at about 550 nm due to airglow (Munz and McFarland, 1977). These effects, generally overwhelmed by the absorption properties of the water at depth, can have significant influence in shallow water.

As discussed above (see COLORS AND MIRRORS), a counterilluminating organism in theory needs to match the actual downward radiance spectrum and not just the perceived brightness to remain cryptic to species with differing spectral sensitivities. However, many deep-sea species have extremely thick retinæ with large numbers of visual pigments. This essentially gives them sensitivity curves with very broad peaks, so their visual systems are nearly spectrally neutral (see Herring, 1983). Therefore, color mismatches are less costly for crypsis than they are for species facing shallow-water visual systems.

As the spectral distribution narrows with depth, the

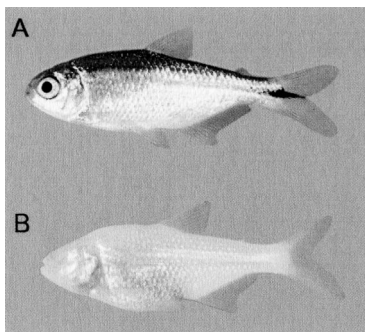


FIG. 8. The Mexican Blind Cavefish *Astyanax mexicanus*. A) Individual from surface population. B) Individual from cave population. Note that while the dorsal coloration differs between the two, the ventral coloration remains approximately identical.

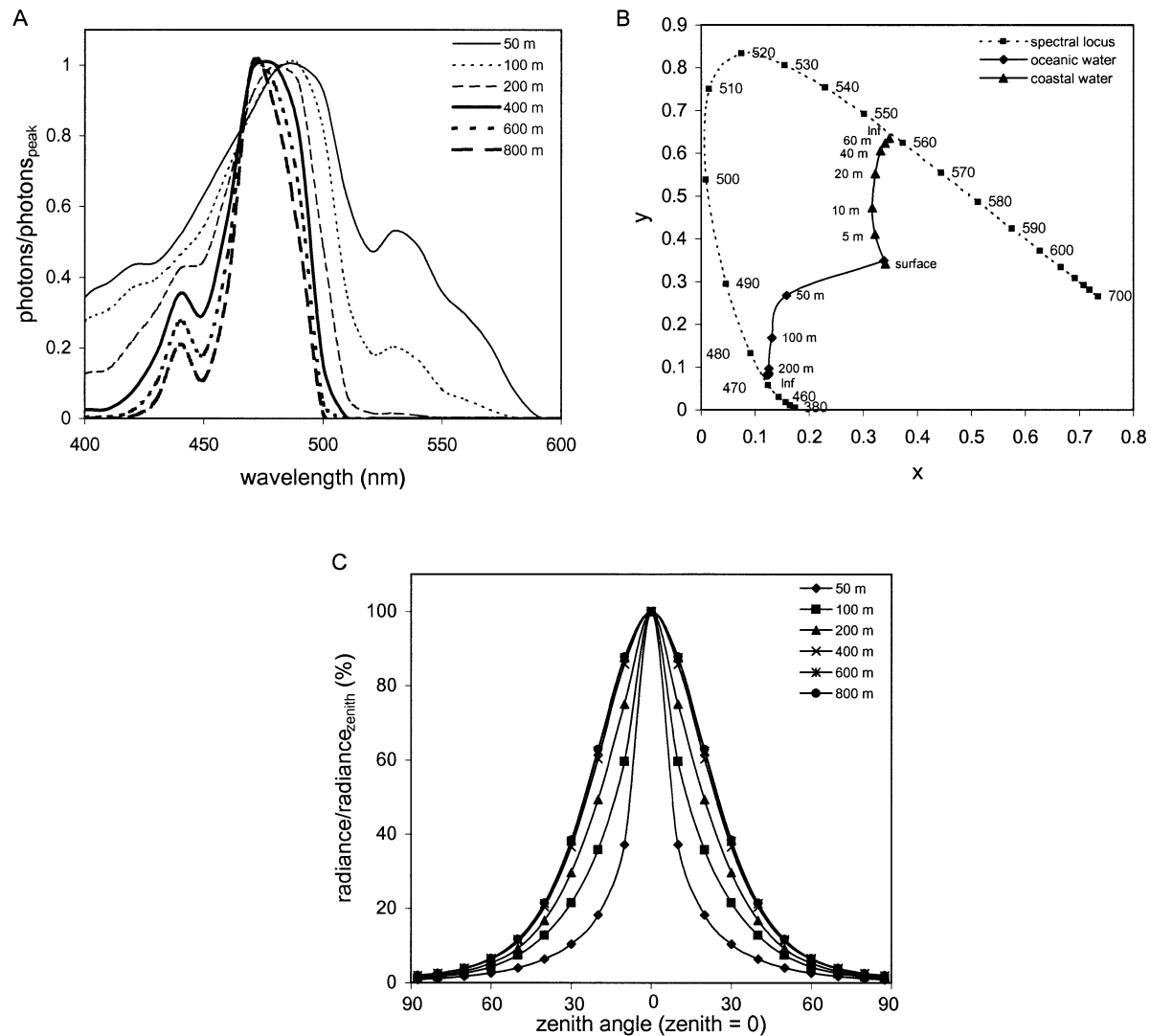


FIG. 9. A) Direct downward spectral radiance as a function of depth in clear oceanic water (modeled using inherent optical properties from the equatorial Pacific obtained from Barnard, Pegau, and Zaneveld). Spectra are normalized by the radiance at the peak wavelength to highlight changes in spectral composition. It is the direct downward spectral radiance that must be matched by counterilluminating organisms. Small peak at 440 nm is artifactual. B) Chromaticity of direct downward radiance as a function of depth in oceanic and coastal waters. While chromaticity is based on human color perception and not directly applicable to other visual systems, it provides a good index of relative spectral change. C) Angular distribution of downwelling light in the clear oceanic water from (A) as a function of depth. Sun is at zenith and so the light field is cylindrically symmetric at all depths.

angular distribution of the downwelling light broadens. Near the surface the radiance distribution has a strong peak in the direction of the sun. With increasing depth, multiple scattering events create a more diffuse light field (Fig. 9c). At a certain depth, known as the asymptotic depth, the angular distribution of the underwater light field no longer changes with depth. In extremely clear, oceanic waters, this occurs at approximately 200–400 m. Again, while this is not an important issue for animals counterilluminating during the day (due to their great depths), it requires that individuals found closer to the surface (typically at night) change the angular distribution of their emitted light to remain cryptic. If they do not, they will remain

cryptic from directly below, but become visible when viewed from other angles.

The effects of depth on the spectra and angular distribution of downwelling light are particularly troublesome for the many counterilluminating species that undergo diel vertical migration. These species undergo large changes in depth, many traveling from mesopelagic depths (>200 m) to the surface in the evening and then descending before dawn (Lampert, 1993). This strategy, which is generally considered to be a cryptic defense against visual predation, would be substantially less effective if the individual were not able to compensate for the changes in the color and angular structure of the light it is trying to match. While many

deep-sea species have flat visual sensitivity curves (see above), certain species possess visual adaptations that increase blue-green hue discrimination, suggesting that at least these species use potential color mismatches to their advantage (Munz, 1976; Denton and Locket, 1989; Douglas and Thorpe, 1992).

Due to the chemical processes involved, the ability of species to fine-tune the spectra of the chemiluminescent reaction is itself limited. However, many species then alter the spectra of the emitted light using spectral filters and reflectors (Denton *et al.*, 1972; Herring, 1983; reviewed by Widder, 1999). Some species are known to change the spectra of their emitted light as a function of depth, one example being the squid *Abralia trigonura*, which broadens its emission spectrum in shallow water by adjusting variable interference filters and reflectors and by turning on additional photophores (reviewed by Widder, 1999). It is not known whether any counterilluminating species change the angular distribution of their emitted light as a function of depth, though it is known that certain species (*e.g.*, the squid *Abralia trigonura*) take great care to maintain the vertical orientation of their photophores, either by maintaining body posture, or by counter-rotating the photophores as the body rotates (Young and Mencher, 1980). This is another promising area of future research, although experimental manipulation of counterillumination in laboratory conditions presents a formidable challenge.

CONCLUSIONS

The pelagic environment is a wonderful, natural laboratory for visual ecology. First, it is a realm where vision is important and where many special visual abilities have evolved (Waterman, 1981; Lythgoe, 1984; Bowmaker and Kunz, 1987; Muntz, 1990; Loew *et al.*, 1993; Browman *et al.*, 1994; Shashar *et al.*, 1998). Second, it has the double advantage of being a highly variable environment, while remaining tractable to modeling and analysis. Also, only in the underwater optical environment do the illuminant and background change independently of each other, creating complex problems for crypsis. Finally, for historical reasons, the physiology and ecology of oceanic species is in its infancy compared to what is known about terrestrial and coastal species.

Crypsis is just one example of interesting physiological issues in pelagic species. Recent research has shown that even straightforward solutions such as transparency, coloring, mirroring, and counterillumination have many complexities and also weaknesses that can be exploited by visual predators. Currently this work raises far more questions than it answers, which hopefully will be taken up by many future students of this fascinating subject.

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