

Does new technology inspire new directions? Examples drawn from pelagic visual ecology

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Synopsis Oceanography has seen the recent development of many new tools and techniques. The subfield of pelagic visual ecology in particular has benefited from the development of more reliable, portable, and economic tools and techniques that can be taken to sea including spectrometers, microspectrophotometry, electroretinography, and ultraviolet and polarization imaging systems. These advances have led to a relative wealth of data on the visual physiology of pelagic species and on the optical properties of these species and their environment. These data, particularly in combination with computational methods, have tested long-standing hypotheses in pelagic ecology and led to new hypotheses and research directions. While the ability to study pelagic species still lags far behind what is possible in terrestrial and coastal environments, a renaissance may be developing in the study of the integrative biology of pelagic species.

Introduction

It has often been said that many, if not most, new hypotheses and discoveries follow the development of new technologies and methods. For example, Einstein's special theory of relativity was in part an attempt to address the data from the first interferometer (Einstein 1961), and the cosmic microwave background radiation, the smoking gun of the Big Bang, was accidentally discovered after the development of more powerful radio receivers (Penzias and Wilson 1965). Over the past two decades, ocean biologists have seen the development of an impressive array of new tools including remote sensing by satellite, genomic and phylogenetic methods, submersibles and sampling systems of many types, and monitoring systems designed to cover entire tectonic plates. In addition, many older technologies are now portable and reliable enough to be taken to sea and even used underwater by submersibles or SCUBA divers. All this, combined with web-based data archives and the enormous rise of computational power, has led to an explosion of data comparable to that seen in molecular biology. However, have these new tools led to fundamentally new questions and discoveries in oceanic biology?

A similar increase of tools and data has occurred in the field of pelagic visual ecology. It is smaller in scope due to the smaller number of researchers and the relative difficulty of obtaining organismal data, but the increase is significant. While some new tools

have been developed in this field, the primary advance is in the portability and robustness of older technologies. Spectrometers that required nitrogen tanks and covered many square feet of precious shipboard laboratory space have been replaced by units the size of fat credit cards. Electrophysiology and microspectrophotometry have been adapted for shipboard use, and a host of more economical and user-friendly underwater light meters have been developed. The latter, combined with advances in computational power, allow the underwater light field to be measured and modeled with fair accuracy. A final, critical advance is the development of more delicate submersible and SCUBA-based collection techniques. This allows study of fragile, particularly gelatinous, species and the study of all species in more natural physiological states.

This article discusses a few of the many collections of optical and visual data on pelagic species and their environments. The emphasis is on camouflage, because it is an area of the author's expertise, and because it is another example of the extraordinary convergence found in many aspects of pelagic species (McFall-Ngai 1990; Hamner 1996; Johnsen 2001). While coloration in terrestrial and many aquatic habitats is highly variable and serves many purposes, coloration in the oceanic pelagic habitat appears to serve almost exclusively as camouflage and be primarily determined by depth (Johnsen 2002) (Fig. 1). This is, perhaps, not surprising, given the

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Fig. 1 The coloration and transparency of oceanic species as a function of depth. Images courtesy of Drs Steven Haddock, Larry Madin, Richard Harbison, Kevin Raskoff, Tamara Frank, Edith Widder, and Kerstin Fritsches.

exposure of species in the pelagic habitat, but is nevertheless striking. This convergence also allows for the rare opportunity to make general conclusions about disparate taxa. Data on the transparency, reflectance, and bioluminescence of organisms are discussed in relation to the visual abilities of potential viewers and the characteristics of the

underwater light field. Each section gives examples where new data and tools have led to new questions and directions.

Optical measurements of tissue

Until recently, the bulk and cost of spectrometers and the delicacy of many pelagic species have made

it difficult to measure their optical properties. This is unfortunate, because the reflectance and transparency of animals are critical factors in their visibility (Duntley 1952). With increasing distance, all underwater objects eventually resemble the background, but the distance at which this happens depends in part on the object's optical properties, particularly on their transparency and reflectance (i.e., color).

Now, however, these measurements are relatively simple and economical. One set of these is found in Fig. 2 (Johnsen and Widder 1998, 2001). Transparency is a versatile form of camouflage because a transparent organism automatically matches a changing background. It is difficult, however, to make complex or large tissues transparent, so this strategy is generally limited to slow-moving and/or small species (Johnsen 2001). Thus, one might expect smaller transparent animals to be more transparent than larger ones. Conversely, because the detectability of relatively small organisms is proportional to the product of their contrast and their angular area (Aksnes and Utne 1997), one might expect that selection might favor higher transparency in larger organisms. However, multiple measurements from each of ~200 individuals from 52 species over two orders of magnitude in size (none of which have obvious warning coloration) do not support either prediction. The molluscs and ctenophores show non-significant trends of increasing transparency with size, but other groups show no discernible relationship. One also might expect that animals found at depth would be less transparent than animals found nearer the surface, since vision is more challenging (and crypsis easier) at low light levels due to the loss of contrast sensitivity

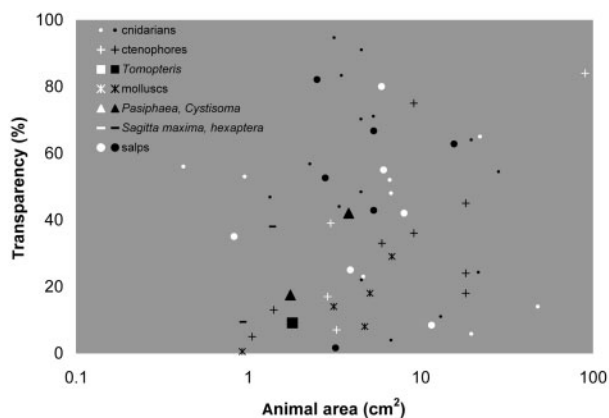


Fig. 2 The transparencies of various transparent zooplankton (at 480 nm, the wavelength of greatest light penetration) as a function of their greatest cross-sectional areas. Black symbols indicate mesopelagic species of a given taxon, white symbols indicate epipelagic species.

(Warrant 1999; Warrant and Locket 2004). Again, the data show no significant differences. In fact, many mesopelagic species are more transparent than is needed for complete crypsis at these depths (Johnsen and Widder 1998).

Some species may not be subject to visual predation, or some may be advertising toxicity in a non-obvious fashion, but the lack of any pattern is surprising, particularly given the relative constancy of transparency and size within a species in these studies. Perhaps, selection for increased transparency at larger size is balanced by the difficulty of achieving transparency at these sizes. Similarly, perhaps selection for increased transparency at shallow, brightly lit depths is balanced by the increased water content (and thus transparency) of deep-sea species forced to survive on lower concentrations of food. Another possibility is that percent transparency of the major tissue of an individual is not a useful estimate of visibility. It may be that the visibility of smaller, but more opaque tissues (e.g., guts, comb rows) primarily determines how conspicuous an individual is, or that visibility is primarily determined by scattering of downwelling light by the tissues.

Modern spectrometers also make it possible to measure the reflectance of opaque species. Figure 3A shows a set of measurements from ~150 individuals of 29 pelagic species (Johnsen 2005). These reflectances were taken to determine whether the coloration of pelagic species is more cryptic against the ambient background illumination or against bioluminescent searchlights (i.e., the ocular photophores of many fish and arthropods thought to be used for finding prey). Unlike benthic or terrestrial crypsis, the predictions for optimal cryptic reflectance are different depending on whether a searchlight is used or not. For crypsis against the background illumination, the predicted reflectances range from 30% to 60%, depending on wavelength and water clarity. For crypsis against a searchlight, the ideal reflectance is zero, because the background water reflects almost no light. The results show that the reflectances of the pelagic species are particularly low and have low variability in the range of wavelengths at which bioluminescent searchlights and deep-sea visual pigments operate, and also where the water is the clearest (Figs 3A and B). The reflectances are so low that the animals are essentially silhouetted against the background light, suggesting that crypsis against bioluminescence in the deep-sea is more important than crypsis against the background illumination. This has long been thought to be the case (Herring pers comm), but was difficult to demonstrate due to

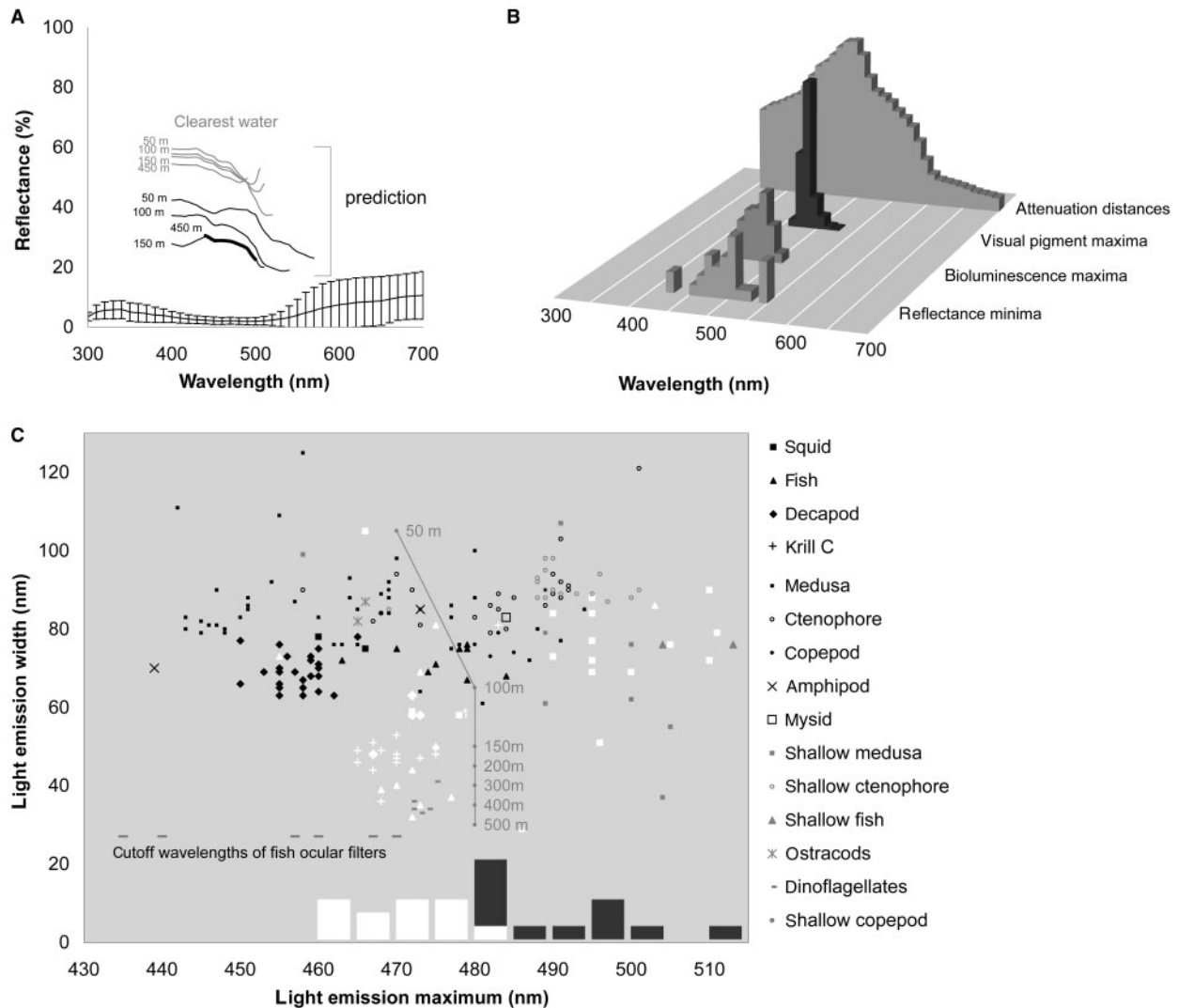


Fig. 3 (A) Predicted reflectances for the lateral surfaces of pelagic animals as a function of depth and wavelength. The black lines denote the predictions based on data from the Equatorial Pacific Ocean. The grey lines denote the predictions based on data from the clearest known natural waters (from Smith and Baker 1981). The predicted reflectance is zero for crypsis when viewed by bioluminescent searchlights. Panel adapted from Johnsen (2005). (B) Histograms of wavelengths of minimum reflectance of oceanic zooplankton (from Johnsen 2005), maxima of bioluminescent emissions and deep-sea visual pigments, and water clarity (from Johnsen 2002). (C) Peak wavelength versus emission width (full-width half-max, FWHM) for the bioluminescent emissions from various species. White symbols denote photophores involved in counterillumination. Black symbols denote photophores and other luminous sources used for other tasks (e.g., warning, luring). Grey symbols denote non-counterilluminating sources found at shallow depths. White line shows peak wavelength and FWHM for downwelling light as a function of depth. Bar chart is a histogram showing the absorption peaks of the visual pigments for the eyes of deep-sea fish known to have multiple pigments in the blue-green portion of the spectrum (data from Douglas et al. 1998). The white bars represent the short-wavelength pigments, the black bars the long-wavelength pigments. The grey symbols show the cut-off wavelengths for the filters in the ocular lenses of seven deep-sea species of fish (data from Douglas and Thorpe 1992). Photophore spectral data taken from Nicol (1960), Swift et al. (1973), Swift et al. (1977), Biggley et al. (1981), Herring (1983), Denton et al. (1985), Widder et al. (1983), Herring et al. (1992), Herring et al. (1993), and Haddock and Case (1999). Since the published bioluminescence spectra are calibrated in energy units (instead of quanta), the downwelling light curve is calibrated in relative energy units. Panel adapted from Johnsen et al. (2004).

the near impossibility of undisturbed observations and behavioral experiments.

Thus, the transparency measurements suggest new research into what actually determines visibility in these organisms and the reflectance measurements

help test a standing hypothesis. More generally, these measurements are critical for understanding the visibility of these organisms and hence visual predation and intraspecific communication. Their availability and the ease of gathering data on other

species opens new directions and allows for the testing of hypotheses that have long since been established in freshwater systems (e.g., Zaret and Kerfoot 1975; Endler 1991).

Spectral measurements of bioluminescence and visual sensitivity

The previous analysis of the function of the coloration of deep-sea species would not have been possible without measurements of the spectral sensitivities of the eyes and the spectral emissions of the photophores of dozens of species (Fig 3C) (>150 for eyes, >200 for photophores; see caption for references). The measurements of spectral sensitivity are due partially to the development of techniques and apparatus for performing microspectrophotometry (MSP) and electroretinography (ERGs) at sea (e.g., Hiller-Adams et al. 1988; Frank and Widder 1999). While shipboard MSP has proven to be impractical and is now generally done on shore using frozen material (reviewed by Partridge and Cummings 1999), ERG methods have developed further and are now used to measure temporal resolution and other aspects of visual physiology (e.g., Frank 1999). Together these techniques have shown that the visual systems of deep-sea species are tuned for maximal sensitivity (reviewed by Partridge and Cummings 1999). This is not surprising, but the discoveries of multiple visual pigments and even UV-sensitive visual pigments in mesopelagic species (e.g., Cronin and Frank 1996; Douglas et al. 1998) have led to a number of interesting hypotheses. For example, the UV photopigments of certain oplophorid shrimps appear to be ideally placed to help the animal distinguish between its two forms of bioluminescence (Cronin and Frank 1996), suggesting that multiple visual pigments in general may be used to distinguish one source of bioluminescence from another.

Measurements of bioluminescence were difficult until the development of relatively portable, high-sensitivity spectrometers (Widder et al. 1983). While still expensive and delicate, they can be used at sea. As with the visual measurements, the resulting data have confirmed certain hypotheses and suggested new ones. A quick glance at Fig. 3C suggests a number of testable questions and several puzzles. For example, while many counterilluminators (species that mask their silhouette using ventral photophores) have spectra that approximate that of the downwelling light at depth, a large number of squid have photophores that do not match. One squid species is known to increase the wavelength of its

counterillumination with increasing temperature (presumably to match the greener and warmer water found near the surface) (Herring et al. 1992). Are the green-shifted spectra of squid spectra (Fig. 3C) the result of the testing of squid with similar abilities in the warmer water of the shipboard laboratories? Also, certain species have bioluminescent emissions that peak at very low wavelengths, suggesting a luminous form of warning coloration. The spectral sensitivities of the pigments of the dichromatic deep-sea fish and the cutoff wavelengths of certain of the ocular filters suggest they may play roles in breaking the camouflage of counterillumination.

The data on bioluminescent emissions also present an interesting puzzle: the peak wavelengths of the counterilluminators do not match the peak wavelengths of the downwelling light, but are nevertheless closely clustered. Because the spectral responses of deep-sea visual systems are relatively flat near the peak absorption wavelength (due to a saturation of photon catch by the large number of visual pigments), this difference may not be seen as a color shift, even by fish with multiple visual pigments. Those with sharp cutoff filters in their eyes may be able to distinguish the difference between the counterillumination and the downwelling light (Munz 1976; Douglas and Thorpe 1992), but the difference is quite small. All this suggests that the match with the background need not be exact, but does not explain the close clustering. The clustering of non-counterilluminating decapod photophore emissions is similarly puzzling. Perhaps, both prevent potential predators from developing a species-specific search image. This would be analogous to the “selfish herd” effect, in which identical individuals in large aggregations reduce their chance of predation (Hamilton 1971; Bond and Kamil 2002).

As is the case for optical measurements, the data on the visual abilities and bioluminescence of deep-sea species raise more questions than they answer. Fortunately the data also provide a starting point for answering them.

Combining measurements

As can be seen from the previous sections, the wealth of measurements of different optical and visual properties of pelagic species and their environment (and the relative ease of gathering more) can be combined to suggest and test new hypotheses. Similar sets of measurements can also be combined to answer outstanding questions about visual predation.

In the pelagic realm, visual predation depends on sighting distance, the distance at which a prey (or predator) can be reliably separated from the background illumination (Mertens 1970). Due to the absorption and scattering characteristics of even clear water, sighting distance often depends more on the contrast of an organism than on its apparent size (Duntley 1952; Johnsen 2002). In this case, the sighting distance depends on the spectral radiance (i.e., intensity and color) of the viewed organism, the contrast sensitivity of the viewer, the background illumination, the turbidity of the water and the direction from which the organism is being viewed (Fig. 4) (Johnsen 2002). The spectral radiance of the organism depends in turn on its reflectance and on the illumination striking it (Palmer 1995). All of the above variables depend on wavelength, so general understanding of sighting distance for different species inhabiting different waters viewed by different organisms requires a large amount of disparate data. Due to advances in technology, however, there are now databases for most of these variables, particularly spectral sensitivities (reviewed by Partridge and Cummings 1999) and the optical properties of different waters (e.g., Capone et al. 2002). In addition, the contrast sensitivity for different species has also been measured and modeled, although not as extensively (Anthony 1981; Douglas and Hawryshyn 1990; Warrant 1999). Thus, one can address previously untenable

questions such as: (1) are certain visual search strategies more successful than others? (2) is mirrored camouflage more successful than color camouflage? (3) are there oceanic species that are visible to conspecifics but cryptic to predators with different visual systems? and (4) how dramatically does changing turbidity affect visual predation for different species? As is the case in genomics and remote sensing, these new data and tools have suggested more questions than we can perhaps answer.

Imaging in non-human sensory modalities

The ability of certain species to see things that are invisible to humans has always been fascinating. Two such abilities found in pelagic species are ultraviolet vision and polarization vision. The former has been documented in many pelagic species (reviewed by Leech and Johnsen 2003), the latter proven in only a few (Cronin et al. 2003) but considered to be relatively common, particularly in crustaceans and cephalopods. The partially overlapping hypotheses of function include navigation, orientation, avoidance of UV radiation, mate recognition, and contrast enhancement. The testing and developing of these hypotheses, however, have been limited by a lack of understanding of the UV and polarization characteristics of the organisms being viewed

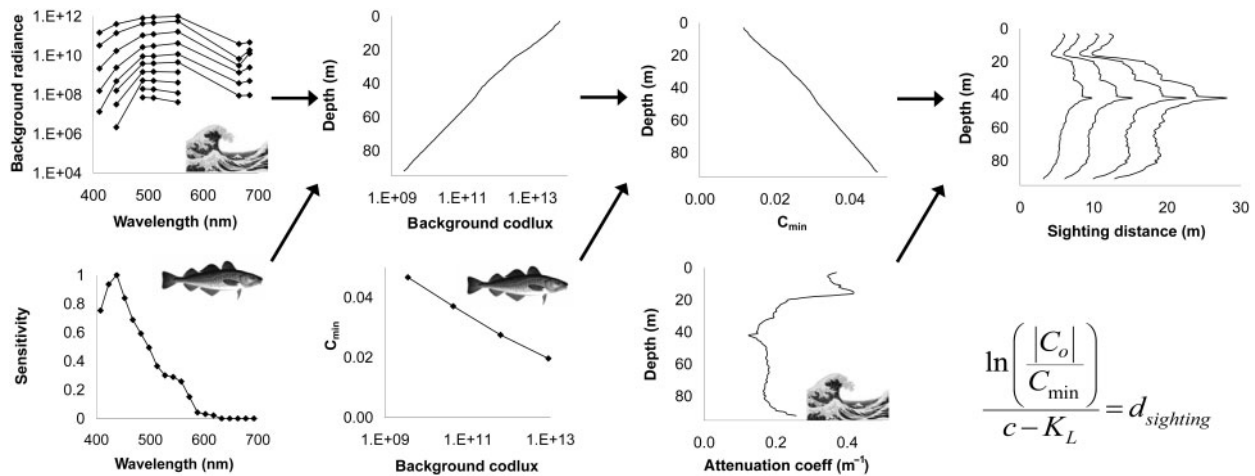


Fig. 4 Algorithm for determining the sighting distance of a large object when viewed by a given visual system (the atlantic cod, *Gadus morhua* in this example). Arrows indicate inputs needed for each graph. Moving from left to right, one starts with the modeled or measured background radiance and the spectral sensitivity of the viewer. In this example, the background radiance is modeled from measurements of the optical properties of water 80 km off the coast of New Hampshire, USA (Johnsen and Sosik 2003) and the spectral sensitivity of juvenile cod is taken from Anthony (1981). These are combined to determine perceived light intensity as a function of depth. This is then combined with contrast sensitivity as a function of perceived intensity (taken from Anthony 1981) to determine contrast sensitivity as a function of depth. This, along with the measured turbidity of the water (from Johnsen and Sosik 2003), gives the sighting distance as a function of depth for objects of various contrasts (10, 20, 50, and 100% from left to right) using the shown equation.

as well as of the underwater environment. Recent advances in both techniques and instrumentation however, have provided both quantitative and visual data for both. In both cases, surprising results have led to new hypotheses.

Ultraviolet measurements and imaging studies have shown that UV radiation is abundant in oceanic waters, so much so that it nearly constitutes the majority of the light in horizontal and downward directions near the surface (Fig. 5A) (reviewed by Losey et al. 1999). While this has obvious implications for UV damage that have been extensively explored, its effects on visual predation are still poorly understood (reviewed by Leech and Johnsen 2003). The bright UV background effectively silhouettes prey at these wavelengths and the need for pigments that protect against UV can render many otherwise transparent species opaque (e.g., Johnsen and Widder 2001). In addition, the high scattering and absorption of UV radiation limits its transmission and thus makes it a potentially useful short-range signal for mate recognition and other conspecific signaling. Thus, these new data, combined with measurements and images of the UV reflectances and absorption on organisms, have led to studies of UV as a communication channel and of the evolutionary trade-offs between protection from UV radiation and crypsis against UV visual predation.

Measurements and imaging studies of the polarization of the underwater light field, while less extensive, have also suggested new directions. These measurements have shown that polarization levels are significant in oceanic waters (reviewed by Waterman 1981 and Horvath and Varju 2004) and that many transparent organisms are highly birefringent (Johnsen and Marshall unpublished data) due to the presence of connective tissue and muscle (Fig. 5B). In addition, it has been shown that cephalopods are better able to detect transparent objects when they are also birefringent (Shashar et al. 1998). The polarized reflectance from silvered fish has also led to research that showed that some species use polarization vision to detect them as well (Shashar et al. 2000). Finally, current studies are examining whether polarization vision can be used to increase the contrast of underwater organisms by minimizing the clouding effect of scattered light much in the way that certain algorithms are now used to reduce atmospheric haze in terrestrial images (Schechner et al. 2003).

Conclusion

As is true of so many other subfields of oceanography, the study of the visual ecology of pelagic organisms has been limited by significant technological issues. Pressure, darkness, inaccessibility, expense, and many other factors have led many

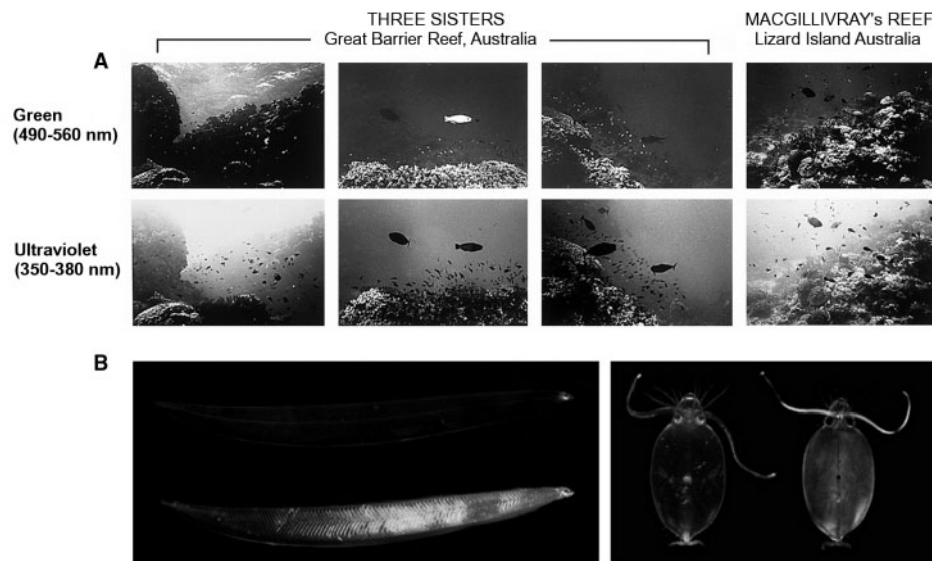


Fig. 5 (A) Upper eight panels: Simultaneous images taken at green (490–560 nm) and ultraviolet (350–380 nm) wavelengths. Note the bright background in the UV image that silhouettes fish strongly, even against the reef. Also note that distant items in the UV images have lower contrast than in the visible images. Images courtesy of Dr Thomas Cronin. (B) Lower two panels: Images of an eel leptocephalus larva and a cranchiid squid under parallel and crossed polarizers. The birefringence of the muscle and connective tissue in both animals results in higher contrast when viewed between crossed polarizers. This, combined with the relatively high polarization of background light in clear waters, suggests that polarization vision may be useful for detecting transparent animals that contain optically anisotropic materials. Images courtesy of Dr Edith Widder.

to state that we know more about the surface of the moon than we do about the depths of the ocean. While certain goals, such as the ability to observe the undisturbed behavior of pelagic species, remain out of reach, advances in physiological, optical, and sampling techniques now allow us to build circumstantial cases about the behavior and ecology of these organisms. This “forensic” biology is not entirely satisfying, but is a significant improvement over the state of the field twenty years ago. In addition to allowing the refining of established ideas, recently developed equipment and techniques have suggested new hypotheses and even new directions of research into the biology of this enormous and fascinating realm.

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