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New directions in biological research on polarized light

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Research

Polarization sensitivity as a contrast enhancer in pelagic predators: lessons from *in situ* polarization imaging of transparent zooplankton

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Because light in the pelagic environment is partially polarized, it has been suggested that the polarization sensitivity found in certain pelagic species may serve to enhance the contrast of their transparent zooplankton prey. We examined its potential during cruises in the Gulf of Mexico and Atlantic Ocean and at a field station on the Great Barrier Reef. First, we collected various species of transparent zooplankton and micronekton and photographed them between crossed polarizers. Many groups, particularly the cephalopods, pelagic snails, salps and ctenophores, were found to have ciliary, muscular or connective tissues with striking birefringence. *In situ* polarization imagery of the same species showed that, while the degree of underwater polarization was fairly high (approx. 30% in horizontal lines of sight), tissue birefringence played little to no role in increasing visibility. This is most likely due to the low radiance of the horizontal background light when compared with the downwelling irradiance. In fact, the dominant radiance and polarization contrasts are due to unpolarized downwelling light that has been scattered from the animal viewed against the darker and polarized horizontal background light. We show that relatively simple algorithms can use this negative polarization contrast to increase visibility substantially.

Keywords: polarization sensitivity; camouflage; zooplankton; transparency; birefringence; visual predation

1. INTRODUCTION

Polarization sensitivity and polarization vision have been documented in diverse taxa and serve a variety of functions including orientation [1–3], celestial navigation [4–6], intraspecific communication [7–9], water detection [10–13] and contrast enhancement [14–16]. While poorly documented, there is general consensus that this last function is significant, particularly in pelagic species. Several factors make contrast enhancement a particularly attractive hypothesis in the water column. First, many pelagic species use transparency for camouflage [17–22]. While transparent animals are indeed quite cryptic in the featureless pelagic environment, they can theoretically be detected by predators with polarization sensitivity because transparent tissues may either depolarize or change the polarization of the transmitted background light. In addition, because the primary tissues that alter the polarization of light are birefringent muscle and connective tissue fibres, polarization sensitivity not only serves to find prey but to find prey with a high food value.

Second, it has been demonstrated that knowledge of the polarization characteristics of certain images can be used to significantly increase their contrast. Early work on underwater visibility showed that, because circularly polarized light reflected by extended surfaces behaves differently than the same light reflected by suspended particles, imaging with circularly polarized light significantly increases contrast [23–25]. More recently, Schechner *et al.* [26] and Schechner & Karpel [27] developed an algorithm that uses the linear polarization characteristics of an image to nearly eliminate the spacelight (i.e. haze) in an image and thus increase contrast. The need for contrast enhancement in aquatic environments and the simplicity of this algorithm suggests that these algorithms (or some derivation of them) may be used by pelagic predators with polarization sensitivity.

Contrast enhancement is also an attractive functional hypothesis because other hypotheses do not fit well in this environment. While the polarization of the underwater light field retains information about the location of the Sun at shallow depths, this information becomes lost with increasing depth, as the light field (and its polarization) becomes cylindrically symmetrical [28]. Therefore, celestial navigation via polarization becomes less promising and so far has not been demonstrated in any open-ocean taxa.

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Intraspecific communication via polarization is still a potential hypothesis, but again has only been demonstrated in terrestrial and benthic species [7,8,29]. Therefore, contrast enhancement is often the default hypothesis, left to explain why pelagic arthropods, cephalopods and certain pelagic fish have polarization sensitivity.

However, despite its appeal and default status, the contrast enhancement hypothesis has received very little attention from biologists. To our knowledge, only two studies, both laboratory-based studies involving coleoid cephalopods, have directly tested whether polarization sensitivity increases prey capture [15,16]. In addition, no studies have examined the *in situ* polarization properties of pelagic species. This is critical, because much of the contrast enhancement hypothesis has relied on a few images of birefringence in transparent zooplankton (e.g. [15]). These images, while striking, were taken in a light environment quite different from what exists underwater.

This study explores the viability of the contrast enhancement hypothesis via analytical models and laboratory-based and *in situ* polarization imagery. Its primary purpose is to assess the underlying assumption of the hypothesis, that transparent zooplankton viewed under natural conditions are more visible to animals with polarization sensitivity.

2. METHODS

(a) General principles

One of the first considerations in any analysis of visibility is whether to use Weber or Michelson contrast. If L_d is the radiance of an object (viewed at a distance d) and L_b is the radiance of the background, then its Weber contrast is

$$C_d = \frac{L_d - L_b}{L_b}, \quad (2.1)$$

and its Michelson contrast is

$$C_d^M = \frac{L_d - L_b}{L_d + L_b}. \quad (2.2)$$

There are advantages and disadvantages to both definitions, but the Weber form is by far the simpler to use when analysing the attenuation of contrast. For example, the Weber contrast of an object viewed at a distance d is the simple exponential equation

$$C_d = C_o e^{-cd}, \quad (2.3)$$

where C_o is the Weber contrast of the object at zero distance, also known as the inherent Weber contrast, and c is the beam attenuation coefficient of the water (see appendix A). Compare this with the relatively unwieldy, equivalent equation using Michelson contrast:

$$C_d^M = \frac{C_o^M e^{-cd}}{1 - C_o^M (1 - e^{-cd})} \quad (2.4)$$

(see appendix A). Therefore, we will use the Weber contrast formulation for all that follows. However, calculations using both formulations are given in appendix A for completeness. It is also critical to note that all the following equations are wavelength-dependent.

Suppose an animal is being viewed horizontally against a water background in a pelagic environment (figure 1). Its apparent radiance is composed of two parts: (i) the radiance of the animal, and (ii) the radiance of the light scattered into the path between the animal and the viewer (referred to hereafter as path radiance). As the distance between the viewer and the animal increases, the radiance of the animal decreases and the path radiance increases, both exponentially:

$$L_d = L_o e^{-cd} + L_b (1 - e^{-cd}), \quad (2.5)$$

where L_o is the inherent radiance of the animal (i.e. radiance at zero viewing distance) [30,31]. As can be seen from equation (2.5), as d increases, the path radiance eventually dominates the total radiance, and the animal becomes indistinguishable from the background.

If the animal is transparent, its inherent radiance L_o is composed of two parts: (i) horizontal background radiance L_b partially transmitted through the animal, and (ii) environmental light scattered by the animal towards the viewer. Because the overhead light is generally at least two orders of magnitude brighter than light from other directions [32], this second component is dominated by the scattering of the downward radiance by the less-transparent components of the animal. So, roughly,

$$L_o = L_b T + L_d S, \quad (2.6)$$

where T is the transparency of the animal, L_d is the downward radiance and S is the fraction of downward radiance that is scattered horizontally towards the viewer. So,

$$L_d = L_b T e^{-cd} + L_d S e^{-cd} + L_b (1 - e^{-cd}). \quad (2.7)$$

This last equation suggests that estimating the polarization characteristics of a transparent animal can be quite complicated. Not only does one have to consider the relative contributions of these three terms to the radiance (the scattering term S in particular is nearly impossible to estimate), but the polarization of each must also be incorporated. The third term of equation (2.7), representing the contribution of the path radiance, is straightforward, but the other two terms are not. The first term, representing light transmitted through the animal, is problematic because the polarization may either be unaffected, diminished if the tissue is depolarizing or altered if the tissue is birefringent (figure 1). Apart from internal reflections, light scattered by structures significantly larger than a wavelength of light is unpolarized, so the polarization of the second term is generally zero or very low. However, because it is essentially impossible to model scattering in something as complex as animal tissue, the total contribution to the polarization (which is related to the radiance) is again difficult to estimate. In fact, it can only be solved for a few limiting cases.

Two important limiting cases are: (i) a highly polarized signal viewed in water with low background polarization (e.g. polarized reflections from stomatopods or cuttlefish thought to be used for signalling), and (ii) an unpolarized signal viewed in water with a high degree of background polarization (e.g. light

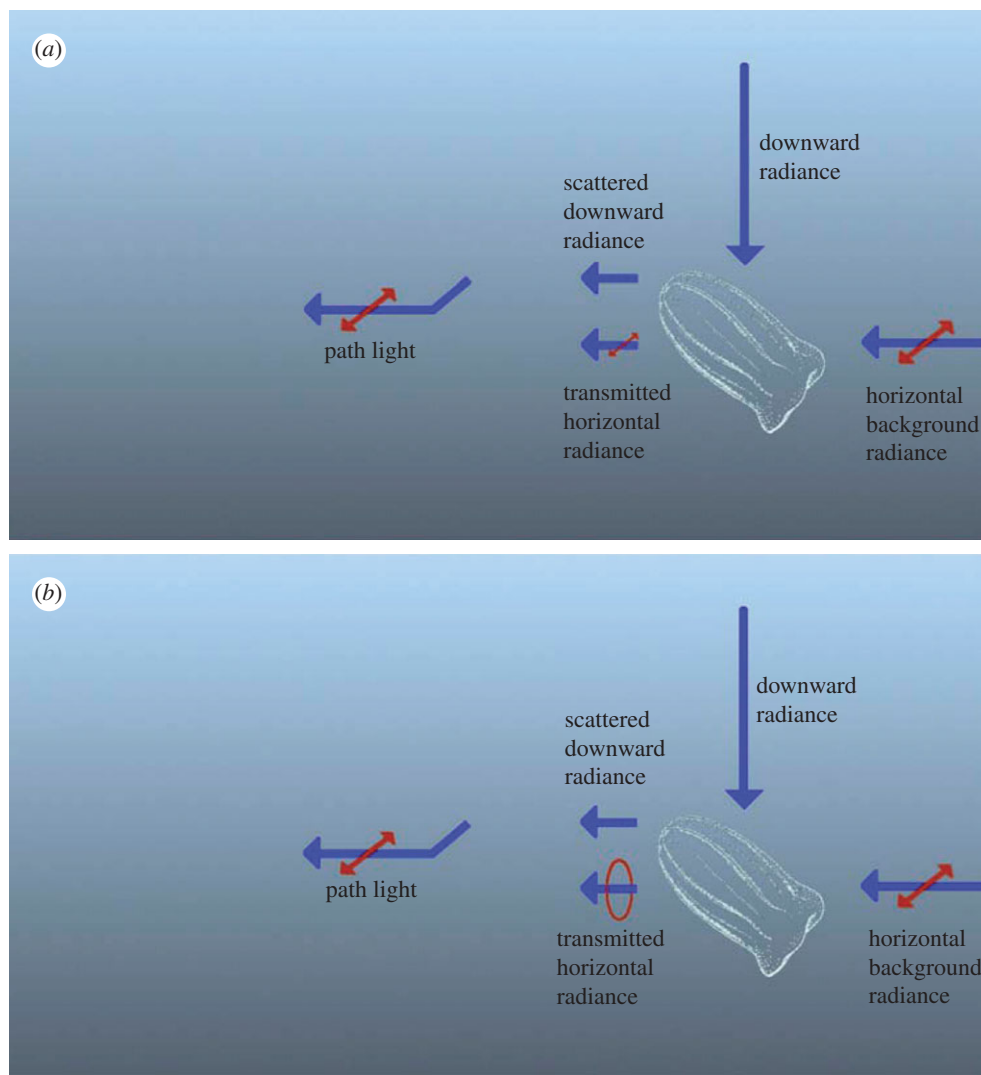


Figure 1. Schematic diagram of the contributions to polarization and radiance when viewing a transparent object horizontally in a pelagic environment. Blue lines denote radiance, red lines denote polarization (including its angle of polarization). (a) Case where the primary polarization contrast is due to reduction of the degree of polarization of the background light after passing through the tissue. (b) Case where the primary polarization contrast is due to the alteration of the polarization of the background light (from linear to elliptical) after passing through birefringent tissue. The viewer is assumed to be on the left side of each panel, looking to the right.

scattered from zooplankton in the open ocean). The first case was examined by Shashar *et al.* [33] and was found to display a simple exponential attenuation of the degree of polarization with increasing viewing distance. The second limiting case, which we feel is important in explaining the presence of polarization sensitivity in pelagic species, is examined analytically in this study. The general case (where the signal has an unknown radiance and polarization) can only be investigated via analysis of *in situ* imagery.

There are at least four ways in which linear polarization sensitivity can be used to increase contrast in a pelagic environment with high background polarization. Polarization information can be used to:

1. detect the change of degree of polarization of the background light transmitted through birefringent tissue,
2. detect the change of angle of the polarization of light after being transmitted through otherwise transparent tissue,
3. increase contrast by subtracting the polarized path radiance and background radiance, and
4. increase contrast by subtracting the polarized path and background radiance and compensating for the attenuation of the directly transmitted light from the animal (e.g. [26]).

Option 1 is driven by the striking images of transparent zooplankton between crossed polarizers, but has not been examined *in situ*. Option 2 is unlikely because few transparent tissues are known to rotate the polarization of light. Option 3 is the basis of several technological approaches to increasing underwater visibility, and option 4 is an extension of this that further increases contrast by compensating for the attenuation of direct light. An even simpler version of option 3 is to simply view the scene through a single polarization channel which is oriented so that the polarized background and path radiance are minimized, thus increasing the contrast of less-polarized foreground objects.

The primary goal of this study is to determine the viability of these various possibilities for pelagic species.

(b) *Birefringence imaging of zooplankton*

Shipboard birefringence images of zooplankton were taken during four research cruises on the *RV Seward Johnson*: two to the northern Gulf of Mexico (7–17 July 2004 and 19 August to 4 September 2005) and two to the Bahamas (17–28 August 2007 and 20–31 July 2009). Specimens were collected at depth (3–20 m) in water-filled glass jars using standard blue-water diving techniques [34,35] and photographed immediately after.

In 2004, the camera used was a medium format Mamiya 645 with a Megavision S3 digital back (3072×2048 pixel CCD with $12 \mu\text{m}$ pixel size, 12 bits per colour; 36-bit RGB; ISO 100–400) fitted with a Mamiya-Sekor Macro C 80 mm f/4. In 2005 and 2007, the camera was a Canon Rebel EOS 300D (3088×2056 pixel CMOS). The lens was a Canon 18–55 mm f/3.5–5.6. In 2009, the camera was a Canon EOS 50D (4752×3168 pixels CMOS) fitted with a Canon EF MP-E 65 mm f/2.8 1–5 macro lens. The same photo stand was used on all four cruises. Organisms were placed in sea water in glass photo tanks. A sheet of polarizing gel larger than the tank base was placed between the tank and the glass top of the photo stand. A white reflective surface was placed 15 cm beneath the glass top and a focusing light directed at it. The polarizing filter on the lens of the camera was then rotated until all light was extinguished. A Vivitar 283 flash was directed at the same white surface and was used to photograph specimens with the polarizers crossed and with the polarizers uncrossed. In some instances, unpolarized images were taken with side lighting against a black velvet background. Animals were rotated to maximize the effect of any birefringence.

(c) *In situ polarization imaging of zooplankton*

In situ imaging was performed on the four cruises described above and in the waters surrounding Heron Island, Australia on the Great Barrier Reef (June 2008). Two different camera systems were deployed. One was an underwater polarizing video camera based on a design by Wolff & Andreou [36]. In brief, the video frame-sync signal is used to drive a polarizing, nematic crystal switch-plate, such that alternate frames are taken through vertical and then horizontal polarizing filters. This half-video rate (25 Hz) is not an instantaneous capture of horizontal and vertical polarized views. However, if the subject does not move too much and is tracked carefully, between-frame movement artefacts can be minimized. A Sony PD150P (PAL) camera within an underwater housing (Bluefin Model, Light and Motion Inc.) was used for underwater deployment of the system. The window of the housing was confirmed to have low birefringence and the camera's linearity in manual mode was tested over a range of three optical density units.

In addition to *in situ* imaging of zooplankton, we also used the video system to measure the polarization of the horizontal radiance as a function of depth by

deploying it from within the front passenger sphere of the Johnson-Sea-Link submersible in the Gulf of Mexico (during the 2004 cruise). Before the dive, the acrylic of the passenger sphere was confirmed to have little to no birefringence for the selected horizontal angle of view.

Because video cameras have limited spatial resolution and because some animals moved significantly even over the $1/25$ th s interval required to take one complete polarization image, simultaneous pairs of still images were also taken using two small waterproof cameras (Stylus 1030 SW, Olympus Inc.) mounted such that their lenses were as close together as possible (figure 2). Both lenses were covered with a polarizing filter (HN 38, Polaroid Corp.), with one polarizer oriented such that the axis of maximum transmission was horizontal and the other oriented such that the axis of maximum transmission was vertical. The cameras were set to the same exposure and the shutters were tripped manually and simultaneously.

When being deployed, both the video and the still cameras were oriented so that one of the two polarizers was aligned with the e-vector axis of the background radiance in order to simplify the calculation of the degree of polarization. This orientation was done by maximizing 'flicker' in the video camera and difference between test images in the still camera. However, because only two polarizer orientations were used instead of three, only the degree of polarization could be calculated [37]. The angle of the e-vector was unknown. This limitation was necessary to preserve frame rate (in the case of the video camera) and to minimize parallax error (in the case of the still camera). However, we did examine whether zooplankton significantly turned the polarization of the light (rather than simply depolarizing it), by rotating the camera systems over a range of angles (no significant polarization rotation was observed). Circular polarization was not examined.

Degree of linear polarization was calculated from both the video and still captures using a simple algorithm written in Matlab (Mathworks, Natick, MA, USA). For each of the red, green and blue channels, the degree of polarization for each pixel (x, y) was calculated as

$$P(x, y) = \frac{I^{\max}(x, y) - I^{\min}(x, y)}{I^{\max}(x, y) + I^{\min}(x, y)}, \quad (2.8)$$

where $I^{\max}$ is the image viewed through the polarizer that was aligned parallel to the e-vector of the background light (and thus had the brightest image) and $I^{\min}$ is the image viewed through the polarizer that was aligned perpendicular to the e-vector of the background light (and thus had the dimmest image). While equation (2.8) would not give an accurate result for the degree of polarization of an object that rotated the angle of polarization, preliminary investigations found that none of the zooplankton tissues rotated polarization. However, given that tissue can rotate the plane of polarization in certain special cases (generally over short path lengths; e.g. [38]), it is worth analysing in future imaging studies.



Figure 2. (a) Schematic diagram of the still camera system used to take simultaneous pairs of images in two orthogonal polarizations. The white arrows show the angle of maximum transmission of the polarizer over each lens.

(d) Three analyses of contrast enhancement

The polarization video and still images were analysed in three different ways to explore various techniques for contrast enhancement. The first and simplest was to compare the unpolarized image (i.e. the sum of the images taken in two perpendicular polarizations) to $I^{\min}$, the image in which the polarizer was oriented such that the background was the darkest. Because the brightest signals from the animal were generally unpolarized (or at least far less polarized than the background), their contrast against the background was higher in $I^{\min}$. The contrast in $I^{\min}$ depends on both the initial radiance contrast and the degree of polarization of the background and (from appendix A) is given by

$$C_d^{\min} = \frac{C_o + P_{\infty}}{1 - P_{\infty}} e^{-cd}, \quad (2.9)$$

where P_{∞} is the degree of polarization of the background light. It can be seen that, as the background polarization approaches unity, the contrast of the object in $I^{\min}$ increases without bound. This happens because the background in $I^{\min}$ becomes black, and the Weber contrast of an object on a black background is infinite.

The second analysis is the method developed by Schechner *et al.* [26]. It assumes that any polarization in an image is due to the path radiance and uses the degree of polarization to subtract this veiling light. It also uses the polarization of the path radiance to estimate the distance of each point in the image. This information can then be used to at least partially invert the attenuation of the directly transmitted light. The fundamental equation of this ‘dehazing’ algorithm is

$$L_{\text{dehaze}} = \frac{L_d - L_{\text{path}}}{1 - (L_{\text{path}}/L_b)}, \quad (2.10)$$

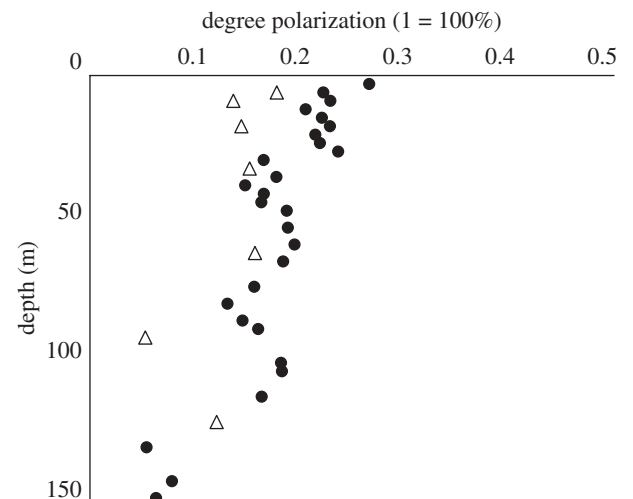


Figure 3. Degree of polarization of horizontal background light as a function of depth. Filled circles denote data taken while the submersible was diving, open triangles denote data taken when submersible was surfacing.

where the path radiance L_{path} is estimated to be $(L_d^{\max} - L_d^{\min})/P_{\infty}$ [26]. The numerator of equation (2.10) accomplishes the veiling light subtraction, and the denominator performs the inversion of attenuation. The algorithm depends critically on the choice of P_{∞} and L_b . We found that, in the pelagic environment, we achieved the best results by measuring both parameters for each horizontal pixel row of the image, because both polarization and radiance of the background light varied systematically with the viewing angle.

However, because we also found that the attenuation inversion was highly sensitive to initial conditions and noise (as many inversion algorithms are), and because we felt that the algorithm may

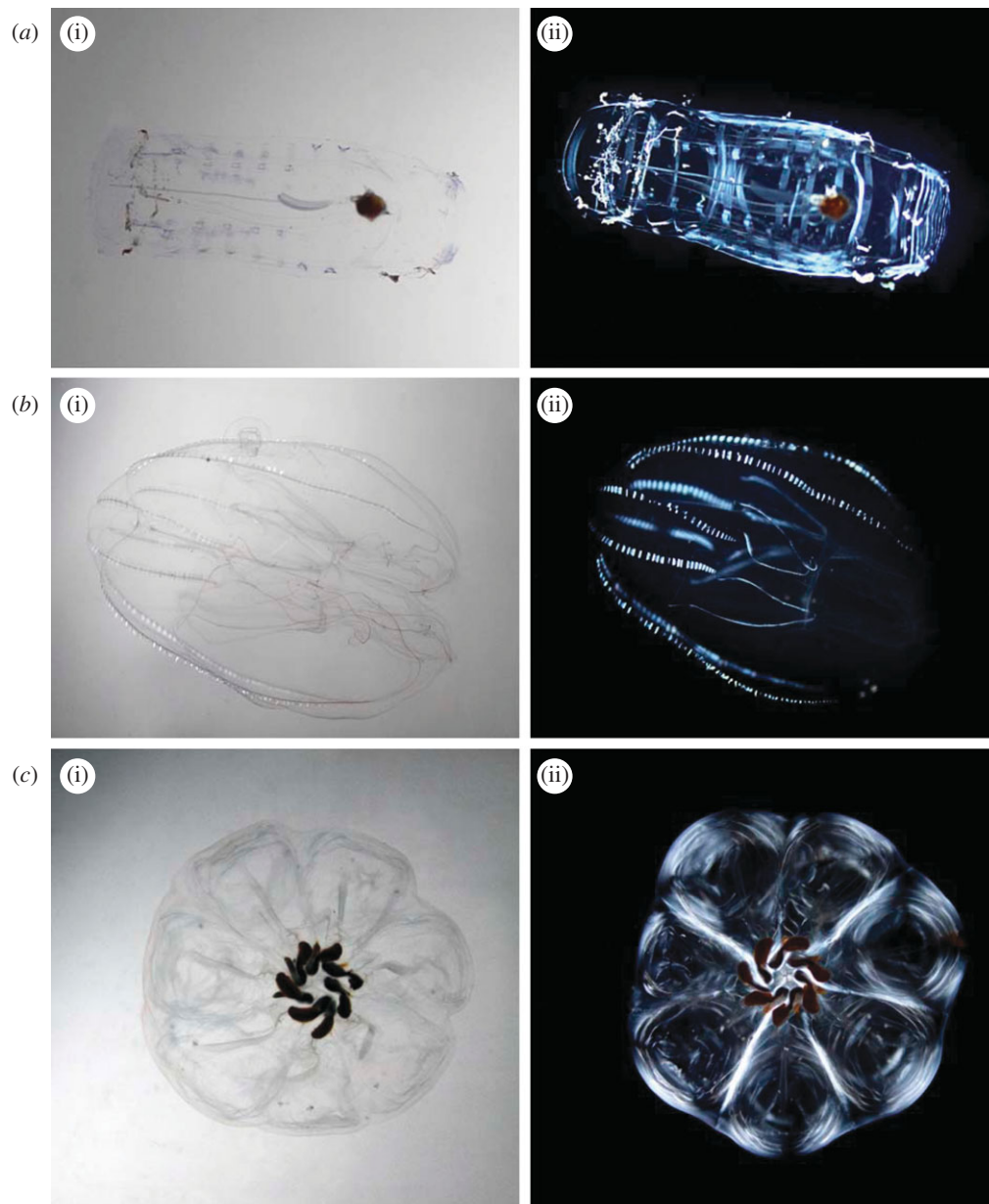


Figure 4. Selected images of transparent organisms viewed between (i) parallel polarizers filters and (ii) crossed polarizers. (a) The salp *Salpa cylindrica* (solitary form). (b) The lobate ctenophore *Bolinopsis* sp. (c) A chain of the salp *Cyclosalpa floridana*. All three animals were collected during blue-water dives in waters surrounding the Bahamian Islands between 20 July and 31 July 2009.

have been too complex to be plausible for pelagic visual systems, we also used a simpler algorithm, where only the path radiance subtraction was performed. We further simplified this by considering only the differences between polarization channels rather than the more abstract concept of the degree of polarization. This led to

$$L_{\text{sub}} = L_d \left(1 - \frac{L_d^{\text{max}} - L_d^{\text{min}}}{L_b^{\text{max}} - L_b^{\text{min}}} \right), \quad (2.11)$$

where L_d is the total radiance of the object at distance d (which equals $L_d^{\text{max}} + L_d^{\text{min}}$).

While the contrast of a single region can be easily quantified, the improvement of the visibility of a complex object is more subjective. Therefore, we chose to present the results of these analyses via a few selected

images. However, all the laboratory-based and *in situ* images and the Matlab-based algorithms that were used to process them are available from the authors upon request.

(e) Attenuation of polarization contrast in pelagic environments

As mentioned above, preliminary results showed that the primary polarization signature of most transparent zooplankton was due to downwelling light scattered horizontally by more opaque structures, such as comb plates on ctenophores and radial canals on medusae. Because this scattered light was unpolarized and viewed against the polarized horizontal light, we analysed the general case of the attenuation of the polarization contrast of unpolarized signals viewed horizontally at increasing distances.

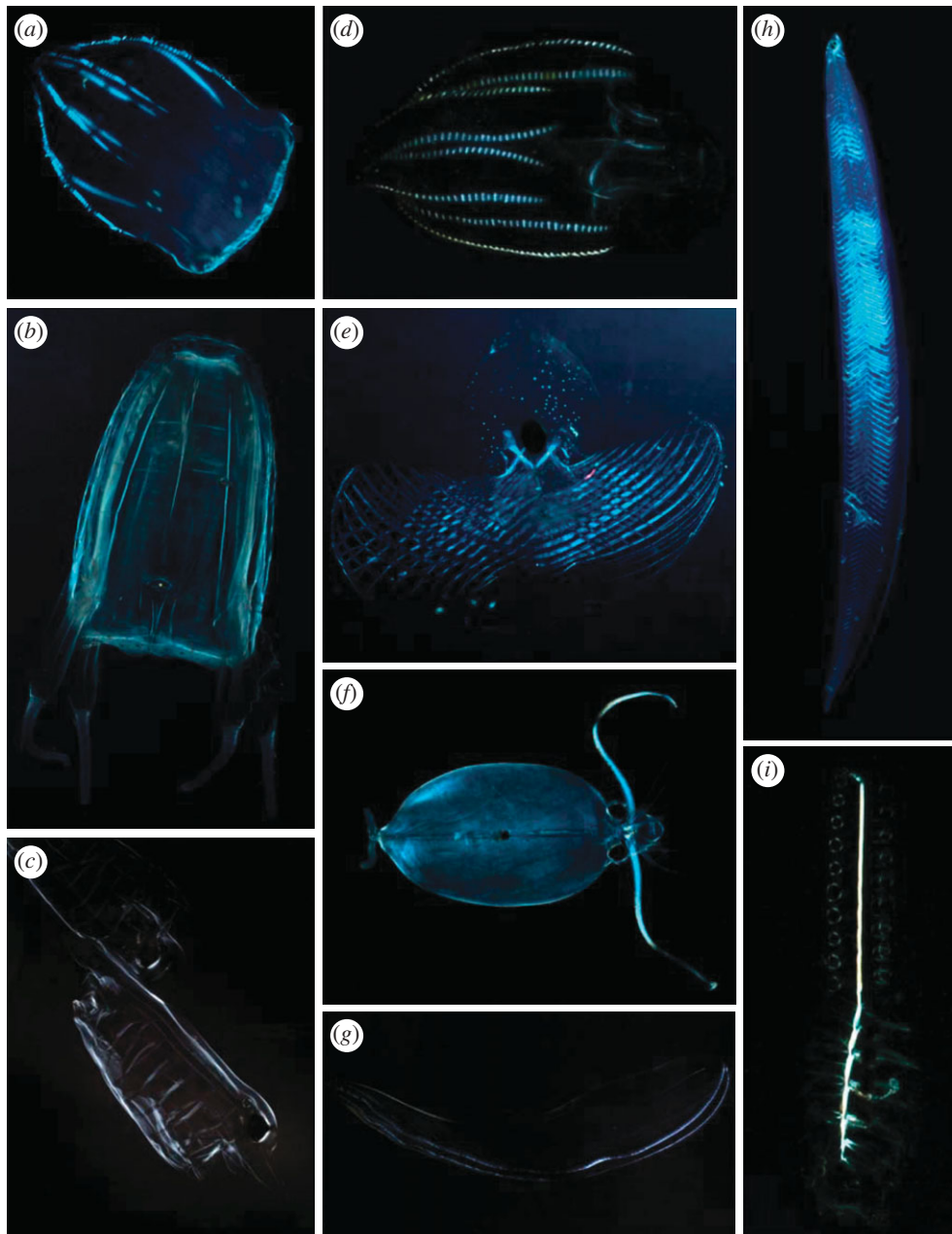


Figure 5. Selected images of transparent species viewed only between crossed polarizers. (a) The beroid ctenophore *Beroë ovata*. (b) The cubozoan medusa *Tamoya haplonema*. (c) The salp *Salpa maxima*. (d) The lobate ctenophore *Eurhamphea vexilligera*. (e) The pseudothecosomatous pteropod *Corolla spectabilis*. (f) The cranchid squid *Heliocranchia pfefferi*. (g) The cestid ctenophore *Cestum veneris*. (h) Leptocephalus eel larva. (i) The physonekt siphonophore *Agalma okeni*.

The polarization of an inherently unpolarized animal viewed horizontally underwater slowly increases as it is viewed from an increasingly larger distance. This happens because polarized background light enters the path between the object and the viewer. From appendix A, the degree of linear polarization of the animal viewed at distance d is given by

$$P_d = P_\infty \frac{e^{cd} - 1}{e^{cd} + C_o}. \quad (2.12)$$

Therefore, polarization rises from zero at zero distance to asymptotically approach P_∞ at large distances. How quickly it rises is inversely proportional to the inherent radiance contrast of

the object. The contrast of this polarization with the polarization of the background light is

$$C_{\text{pol}}(d) = \frac{P_d - P_\infty}{P_\infty} = -\frac{1 + C_o}{e^{cd} + C_o} \quad (2.13)$$

(see appendix A). This contrast approaches zero as viewing distance increases and the radiance of the object becomes dominated by the intervening polarized path radiance. Note that it is always negative, because the polarization of an inherently unpolarized object in this situation can never be greater than the polarization of the background light.

This is all based on the assumption that the path radiance has the same degree of polarization as the background radiance (see appendix A). In certain

Table 1. Degree of birefringence observed in various pelagic, transparent species. One, two and three asterices denote minor, moderate and striking birefringence, respectively.

species	birefringence	location
Cnidaria		
<i>Aequorea forskalea</i>	*	tentacles, radial canals
<i>Agalma okeni</i>	***	siphosome, nectophore muscle
<i>Aurelia aurita</i>	*	circumferential muscle
<i>Orchistoma pileus</i>	none	
<i>Cordagalma sp.</i>	***	siphosome, nectophore muscle
<i>Tamoya haplonema</i>	***	multiple muscle bands, tentacles
Ctenophora		
<i>Beroë ovata</i>	***	comb rows
<i>Bolinopsis vitrea</i>	***	comb rows
<i>Cestum veneris</i>	**	comb rows
<i>Eurhamphea vexilligera</i>	***	comb rows, lobes edges
<i>Mnemiopsis sp.</i>	***	comb rows
<i>Ocyropsis maculata</i>	***	comb rows, lobe muscles
<i>Velamen parallelum</i>	*	comb rows
Mollusca		
<i>Cavolinia uncinata</i>	**	wing musculature
<i>Corolla spectabilis</i>	***	wing musculature, spots on pseudoconch shell
<i>Cuvierina columnella</i>	***	
<i>Helicocranchia pfefferi</i>	***	mantle musculature, tentacles (not arms)
<i>Phylliroe atlantica</i>	**	rhinophores, gut
Annelida		
Alciopid worm	***	gut musculature, connective tissue
Crustacea		
Stomatopod larva	***	tail musculature, edges of carapace
Echinodermata		
<i>Pelagothuria sp.</i> (Larva)	**	body (not tentacles)
Urochordata		
<i>Cyclosalpa floridana</i>	***	muscle bands
<i>Salpa cylindrica</i>	***	muscle bands
<i>Salpa maxima</i>	***	muscle bands, test
<i>Thalia democratica</i>	*	test
Chaetognatha		
<i>Sagitta sp.</i>	***	body wall connective tissue
Hemichordata		
Tornaria larva	***	cilia
Chordata		
Leptocephalus larva	***	swimming muscle

cases though, in particular when a large opaque object is viewed at close distances near the surface, the path radiance may have a higher degree of polarization than the background radiance (Y. You & G. Kattawar 2010, unpublished data). This situation however does not apply to oceanic zooplankton because the unpolarized, scattering regions of the organism are quite small.

The radiance and polarization contrasts (as well as the ratio of the two) were calculated for eight different ratios of inherent radiance of object to inherent radiance of the background (i.e. L_o/L_b): 0, 0.25, 0.75, 1, 2, 5 and 10. The contrasts are presented as a function of attenuation length ($=1/c$), rather than absolute distance, to allow for easy translation from one water type to another or one wavelength to another. It is critical to remember that the beam attenuation coefficient depends strongly on water composition and wavelength.

For example, one attenuation length for blue–green 480 nm light in the clearest oceanic water is about 20 m. One attenuation length for red 650 nm light in relatively clear, but more productive, coastal water is about 2 m. Close to shore, attenuation lengths can be less than 0.1 m.

3. RESULTS

(a) Polarization of horizontal background radiance

Even in extremely clear Bahamian and Gulf of Mexico waters (Jerlov type I), the polarization of the horizontal radiance was not as high as expected. The submersible-based measurements were generally in the 25 per cent range near the surface, decreasing with depth to about 10 per cent at 150 m (figure 3).

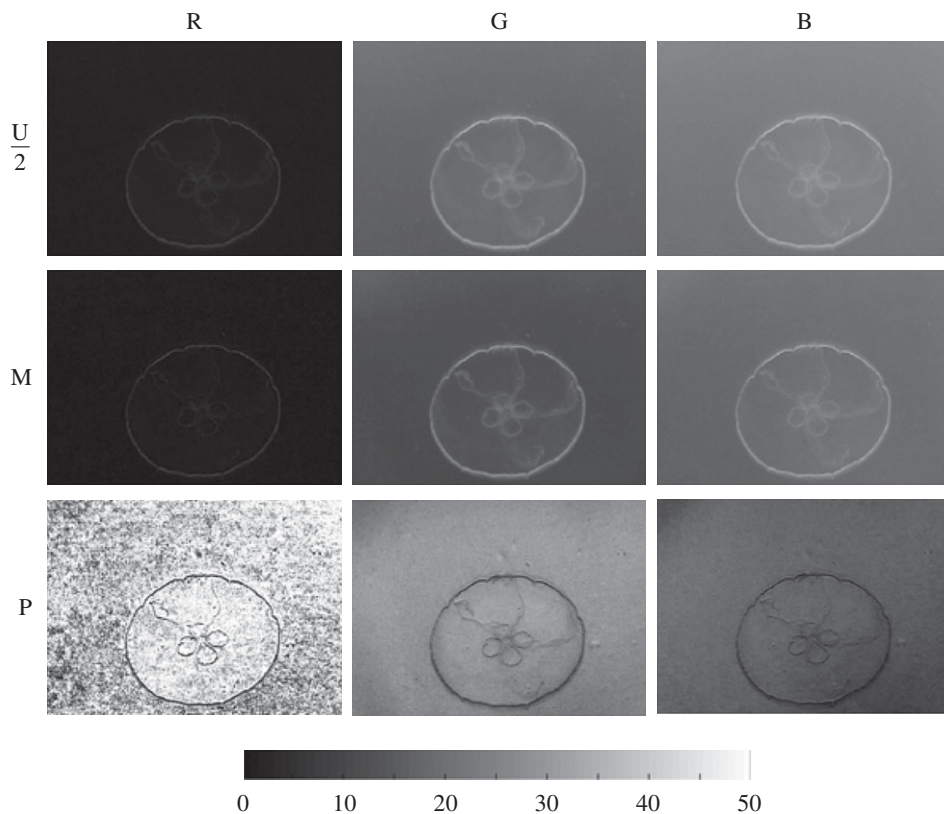


Figure 6. Example of a polarization and channel analysis of an *in situ* image. Animal shown is the scyphomedusa *Aurelia aurita*. The columns show each of the R, G and B colour channels from the camera. The rows show the unpolarized image ($U/2$), the image when the polarizer was oriented so that the background light was minimized (M) and an image of the degree of polarization (P; the horizontal bar is the grey code of the degree of polarization.). The grey values in the unpolarized images were halved to increase legibility given the limited dynamic range of printed paper (i.e. to prevent the unpolarized image from appearing too bright or the minimum image from appearing too dim).

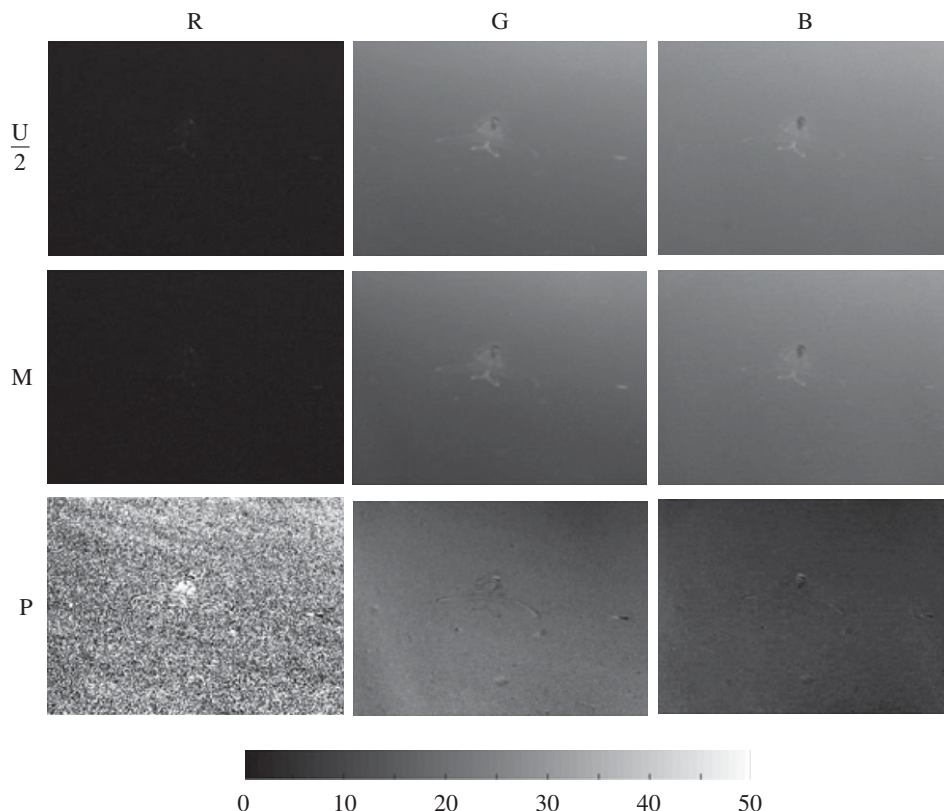


Figure 7. Example of a polarization and channel breakdown of an *in situ* image. Animal shown is the pseudothecosomatous pteropod *Corallia spectabilis*. See figure 6 caption for further details.

In situ polarization video and still shots at multiple locations and depths confirmed that the degree of polarization never rose above 30 per cent. As expected, the angle of polarization (as determined by the angle of the video camera that resulted in maximum flicker between frames) was approximately horizontal, though the exact angle depended on solar elevation and azimuth and water type. Both angle and degree of polarization were in general agreement with the

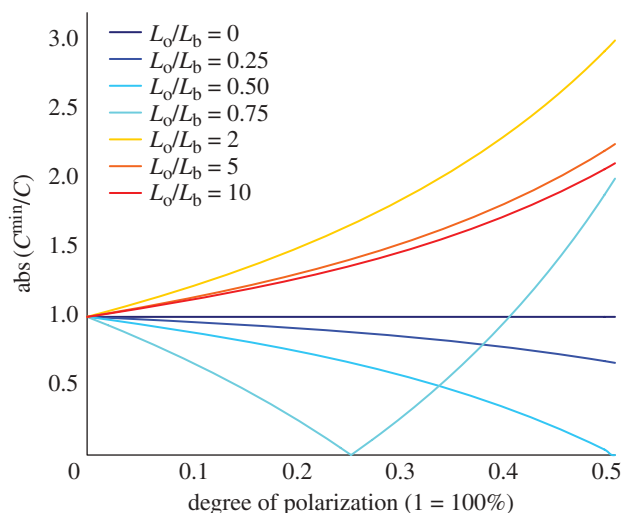


Figure 8. The Weber contrast of a nearby object viewed through a polarizer oriented to minimize background radiance compared with its contrast when viewed without a polarizer. The y-axis gives the absolute value of the ratio of the two, so the curve for $L_o/L_b = 0.75$ has a kink because it would otherwise change sign when the degree of polarization of the background is 25%.

recent and previous measures of underwater polarization, some of which used three polarizer angles for e-vector analysis [39–42].

(b) *Birefringence images of zooplankton*

Of the transparent species examined, approximately 25 displayed some birefringence, about 15 of which showed marked birefringence (figures 4 and 5, table 1). As expected, the most striking birefringence was found in the comb plates of ctenophores; the ciliary structures of larvae; the muscle bands of pteropods, crustaceans and salps; and the circumferential muscle of certain medusae. However, in certain species, gut cavities, radial canals, siphosomes and tentacles showed marked birefringence, likely due to sheets of connective tissue and/or longitudinal muscle fibres. The axial musculature of leptocephalus eel larvae were particularly impressive under crossed polarizers (figure 5). Oddly, the bodies of certain thecosomatous pteropods also appeared to display some birefringence, though, in this case, their brightness between crossed polarizers may actually be due to depolarization of the transmitted light by the translucent tissues.

(c) *In situ polarization images of zooplankton*

Surprisingly, even strikingly birefringent structures, such as the banded musculature of pteropods and salps, were not apparent *in situ*. Instead, the primary polarization contrast generated by transparent zooplankton was due to unpolarized light from scattering structures (e.g. comb plates, radial canals, siphosomes), the very same structures that produced the primary radiance contrast (e.g. figures 6 and 7). In fact, the

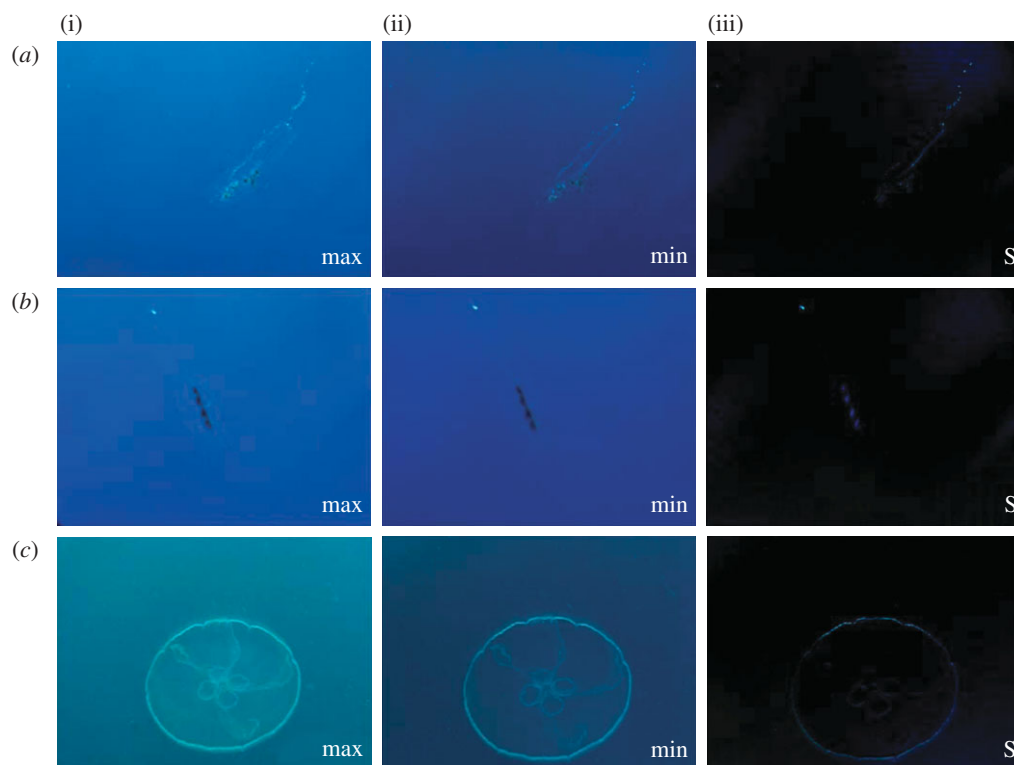


Figure 9. Examples of increased object contrast in $I^{\min}$ and path radiance subtraction for three specimens. (i) and (ii) $I^{\max}$ and $I^{\min}$, respectively. (iii) Each pair of images processed using equation (2.11) to remove the path and background radiance. (a,b) Two different specimens of the physonect siphonophore *Agalma okeni*. (c) The scyphomedusa *Aurelia aurita*.

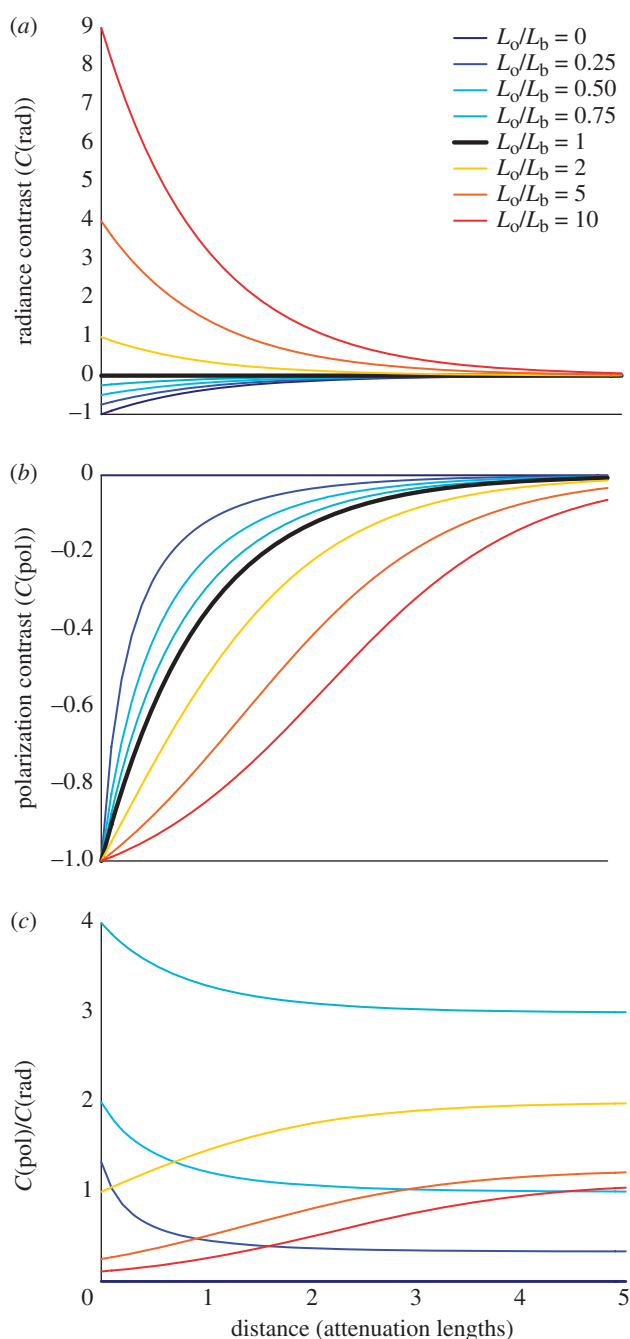


Figure 10. (a) The radiance Weber contrast of an object viewed horizontally (computed using equation (2.3)). (b) The polarization Weber contrast of an inherently unpolarized object viewed horizontally against a polarized background (computed using equation (2.13)). (c) The absolute value of the ratio of the polarization and radiance contrasts.

polarization images from most zooplankton were essentially 'negatives' of their radiance images, with no new structures becoming apparent via polarization.

As expected, the red channel was the darkest and had the highest radiance contrast due to the lack of long wavelength light in the horizontal background and its presence in the downwelling light scattered by the animal towards the camera. The blue and green channels were generally of roughly equal brightness, though the green channel invariably had a greater degree of background polarization, even in clear blue waters. The red channel may have had the greatest degree of polarization, but because the total amount

of light was low in this channel, the difference between two images with perpendicular polarizations was small and obscured by noise.

(d) Results of the three contrast enhancement techniques

Whether $I^{\min}$ (i.e. the image viewed through a polarizer that was oriented to minimize background radiance) had a higher contrast than the same image viewed without any filter depended on the radiance contrast of the animal (figure 8). If the animal was darker than the background, then its contrast in $I^{\min}$ dropped. How much it dropped depended on the degree of polarization and the initial contrast (the closer the contrast was to zero, the larger the effect). If the animal was brighter than the background, then its contrast increased. This again depended on the degree of background polarization and was greater for lower contrasts. In general, the increase in contrast for objects brighter than the background was significant at the observed levels of background polarization (approx. 25%). At these levels, the contrast of an unpolarized object that was twice as bright as the background was 66% higher when viewed through a polarizer that minimized background radiance when compared with that viewing without a polarizer.

The Schechner and path radiance subtraction algorithms (equations (2.10) and (2.11)) gave nearly the same results, though, as expected, the Schechner algorithm was more sensitive to noise. Both algorithms were able to essentially eliminate both the background and path radiance, dramatically increasing the contrast of any unpolarized or less-polarized foreground objects (figure 9).

(e) Attenuation of polarization contrast in pelagic environments

For unpolarized objects darker than the polarized background, the polarization contrast was generally greater than the radiance contrast at all viewing distances, with the exception of very dark objects (i.e. with contrast close to -1 ; figure 10). The ratio of the two was particularly high when the inherent radiance contrast was low. For unpolarized objects brighter than the polarized background, the polarization contrast was generally lower than the radiance contrast at short viewing distances. It increased with the distance to eventually become greater than the radiance contrast in many cases, but only at distances where both polarization and radiance contrast would be below the threshold for detection (approx. four attenuation lengths for black objects [30]).

4. DISCUSSION

(a) Laboratory-based versus in situ imagery

Many optical characteristics of aquatic species are far more apparent in controlled lighting situations than *in situ*. For example, fluorescence images are generally made by lighting and viewing the animal in narrow and non-overlapping wavebands (e.g. [43]). Similarly, ultraviolet images often exclude the remainder of the spectrum (e.g. [44,45]), and images of the iridescence of ctenophore comb rows, polychaete setae and other

structures use highly directional light. Images created by these methods are impressive, but can also be misleading because they do not match the underwater light field. For example, fluorescence and ultraviolet coloration are far less dramatic when viewed under natural illumination and the iridescence of ctenophores is seldom apparent more than 2 m from the surface (J. Marshall & S. Johnsen 2001–2008, personal observations). For this reason, one must be careful about assigning ecological significance to various optical traits before actually determining how apparent they are under natural light to a relevant viewer (e.g. [46]).

In the case of birefringence and zooplankton, the central issue is the difference between the intensities of the downward and horizontal radiance. Ten metres below the surface in clear ocean water, the downward radiance is two to three orders of magnitude greater than the horizontal radiance [32]. As depth increases or the Sun sets, this ratio drops, but it is still at least 50. Most scattering structures on transparent species have scattered horizontal radiances on the order of 1 per cent of the downward radiance (e.g. [47]). While this is a relatively low fraction, the relative intensity of the downward radiance is such that the scattered radiance is still greater than the background radiance, especially near the surface of the ocean. Thousands of collective hours underwater by the authors confirm that the primary signal from transparent zooplankton viewed horizontally is not an attenuation of the background horizontal light but instead the scattering of downwelling light.

With few exceptions, the birefringent tissues we observed are the same tissues that scatter the most light, generally because these tissues are composed of connective tissue and muscle fibres, which both have relatively high refractive indices. Therefore, the primary polarization signal coming from these structures is not an alteration of the background horizontal polarization via birefringence, but unpolarized scattered downwelling light viewed against a polarized background. This leads to the situation where the degree of polarization image of the animals is essentially the inverse of the radiance image.

Thus, we conclude that the often impressive birefringence we observed shipboard is not significant *in situ*. However, there is a significant inverse polarization signal due to scattered light, a general principle that holds for many non-transparent organisms as well.

(b) Contrast enhancement via polarization information

While it has long been known that polarization information can be used to increase underwater contrast, most of the methods employed required polarized artificial lights or relatively complex algorithms that may not be implemented in animal visual systems. In this study, we showed that, because the primary signal from transparent animals was unpolarized, two simple algorithms could be used to boost visibility. First, simply viewing the scene through a polarizer oriented to minimize background light could significantly increase the contrast. While this method does not work for objects that are darker than the

background, nearly all transparent zooplankton are equal to or brighter than the background, with the unpolarized portions being the brightest. This is also the case for fish using silvery camouflage and fish that may attempt camouflage by otherwise matching the background radiance of mid-water [48].

How much this increase in contrast increases sighting distance depends on the contrast sensitivity of the viewer [19], but can be substantial, particularly if the viewer's contrast vision is not optimal. For this reason, it would be interesting to investigate whether any zooplanktivorous pelagic species either have all the rhabdoms in their retinas aligned such that their sensitivity is minimal to the horizontally polarized light or have vertically oriented polarizing filters in their eyes. While either arrangement does not provide true polarization sensitivity, it nevertheless would be advantageous in the open ocean, where background polarization levels are highest.

Using polarization information to subtract both the background radiance and the path radiance has an even greater effect on object contrast, essentially removing all light except that which is scattered from above (figure 9). However, it is not known whether any visual systems actually implement a strategy of this sort. To be successful, the visual system would have to determine the polarization of the background, compare it with the polarization of each location in the image, and then scale the perceived radiance accordingly. Interestingly, the retinas of both crustaceans and cephalopods, which make up a substantial proportion of pelagic visual predators, are known to possess orthogonally arranged rhabdoms [49,50]. Where known, these are generally arranged with half the rhabdoms oriented vertically and the other half horizontally (see [51]), precisely the required orientation for the contrast-enhancement mechanisms we invoke here, and one that provides a parsimonious solution to viewing polarized light [52]. These animals are also capable of rotational eye movements that could theoretically optimize the signal difference between channels in the same way as we did by rotating the camera systems. Opponency, or signal comparison, between the horizontal and vertical channels is known, at least for the crustaceans and cephalopods [53–55], pointing towards a neural correlate of the algorithms we have developed. This remains to be tested neurophysiologically or behaviourally.

Certain fish are also known to possess polarization sensitivity [56,57], however the details of this sense are not well-known enough in pelagic species to speculate how it could be used in this environment. Similarly, while polarization sensitivity could theoretically allow diving birds to minimize sea-surface glare, our knowledge of polarization sensitivity in this group is largely limited to navigation tasks [58].

(c) Attenuation of polarization information

Given its fundamental importance to both ocean optics and aquatic ecology, surprisingly little work has been done on the attenuation of underwater polarization. Theoretical and laboratory-based studies suggest that the polarization of unscattered

and weakly scattered light remains unchanged (e.g. [59,60]), which implies that polarization information attenuates at least as slowly as the direct beam (i.e. the attenuation coefficient of polarization equals the beam attenuation coefficient). Measurements by Shashar *et al.* [33] of the attenuation of a polarized signal in coral reef water found that, when corrected for the polarization of the veiling light, it attenuated with a coefficient of 0.46 m^{-1} at one location and 0.25 m^{-1} at another. While the authors interpreted this as being different from the general beam attenuation coefficient, these two coefficients (corresponding to sighting distances of 8 and 16 m) are not unreasonable for benthic coral reef water. Therefore, it is possible that all three studies mentioned above agree, and that the polarization of a polarized signal on an unpolarized background attenuates at roughly the same rate as its direct radiance. However, this is a topic that clearly demands further research, particularly given the demonstration of polarized signals in aquatic species (e.g. [7,9]).

In this study, we examined the simpler case of the attenuation of an unpolarized signal viewed against a polarized background. This is less relevant to polarization signalling, but, as mentioned above, important for the detection of zooplankton and other prey. We found that the polarization contrast between the animal and the background was only higher than the radiance contrast when the animal was slightly darker than the background or slightly brighter than the background and viewed at distances that are likely beyond the sighting distance. Neither situation is relevant for transparent zooplankton that are viewed horizontally. In addition, it is unlikely that the contrast threshold for the degree of polarization is as low as the threshold for radiance. Aquatic species are known to have contrast thresholds on the order of 1 per cent (reviewed by [61]), while recently determined thresholds for distinguishing two stimuli with different degrees of polarization are on the order of a few per cent [62–64]. Therefore, it is unlikely that the polarization image of an animal (e.g. a map of its degree of polarization) is detectable from a farther distance than its radiance image. However, as mentioned in the previous section, the polarization information is nevertheless advantageous, because it can be input into relatively simple algorithms that do increase visibility. The central question now is whether any zooplanktivorous species make use of this potential.

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APPENDIX A

(a) Derivation of attenuation equations for Weber and Michelson radiance contrast

From equations (2.1) and (2.5) in the main text, the Weber contrast of an object viewed at a distance d is

$$C_d = \frac{L_o e^{-cd} + L_b(1 - e^{-cd}) - L_b}{L_b} = \frac{(L_o - L_b)e^{-cd}}{L_b} = C_o e^{-cd}, \quad (\text{A } 1)$$

The calculation of the attenuation of Michelson contrast is more complex. From equations (2.2) and (2.5) in the main text,

$$C_d^M = \frac{L_o e^{-cd} + L_b(1 - e^{-cd}) - L_b}{L_o e^{-cd} + L_b(1 - e^{-cd}) + L_b} = \frac{(L_o - L_b)e^{-cd}}{(L_o + L_b)e^{-cd} + 2L_b - 2L_b e^{-cd}}. \quad (\text{A } 2)$$

Dividing the top and bottom by $L_o + L_b$ gives

$$C_d^M = \frac{C_o^M e^{-cd}}{e^{-cd} + 2L_b(1 - e^{-cd})/(L_o + L_b)}, \quad (\text{A } 3)$$

where C_o^M is the inherent Michelson contrast of the object. Substituting $1 - C_o^M$ for $2L_b/(L_o + L_b)$ gives

$$C_d^M = \frac{C_o^M e^{-cd}}{e^{-cd} + (1 - C_o^M)(1 - e^{-cd})} = \frac{C_o^M e^{-cd}}{1 - C_o^M(1 - e^{-cd})}. \quad (\text{A } 4)$$

(b) Derivation of the inherent radiance contrast of an unpolarized object viewed through a polarizer that minimizes background radiance

An unpolarized object will have a higher contrast against a polarized background if it is viewed through a polarizer that minimizes the radiance of this background. From equation (2.8) and the fact that $L_b^{\max} + L_b^{\min} = L_b$, the degree of polarization of the background is

$$P_\infty = \frac{L_b^{\max} - L_b^{\min}}{L_b^{\max} + L_b^{\min}} = \frac{L_b^{\max} - L_b^{\min}}{L_b} = \frac{L_b - 2L_b^{\min}}{L_b}. \quad (\text{A } 5)$$

Solving for $L_b^{\min}$ gives

$$L_b^{\min} = \frac{L_b}{2}(1 - P_\infty). \quad (\text{A } 6)$$

If the object is unpolarized, then $L_o^{\min} = L_o/2$, $L_o^{\min} = L_o/2$, so

$$C_o^{\min} = \frac{L_o^{\min} - L_b^{\min}}{L_b^{\min}} = \frac{\frac{1}{2}L_o - \frac{1}{2}L_b(1 - P_\infty)}{\frac{1}{2}L_b(1 - P_\infty)} = \frac{L_o - L_b(1 - P_\infty)}{L_b(1 - P_\infty)} = \frac{L_o - L_b + L_b P_\infty}{L_b(1 - P_\infty)}. \quad (\text{A } 7)$$

Dividing the numerator and denominator by L_b gives

$$C_o^{\min} = \frac{((L_o - L_b)/L_b) + P_\infty}{1 - P_\infty} = \frac{C_o + P_\infty}{1 - P_\infty}. \quad (\text{A } 8)$$

A lengthy, but straightforward, analysis shows that this contrast attenuates in the usual manner:

$$C_d^{\min} = \frac{C_o + P_\infty}{1 - P_\infty} e^{-cd}. \quad (\text{A } 9)$$

(c) Derivation of the attenuation of polarization contrast from an inherently unpolarized object viewed against a polarized background

As discussed in the main text, it is often important to determine how the degree of polarization of an inherently unpolarized object changes as it is viewed from a distance in a polarized light field, such as is found in clear water. From equations (2.5) and (2.8) in the text and the fact that path radiance has a constant degree of polarization [26], the degree of polarization of the object viewed at a distance is

$$P_d = \frac{(L_o^{\max} e^{-cd} + L_b^{\max} (1 - e^{-cd})) - (L_o^{\min} e^{-cd} + L_b^{\min} (1 - e^{-cd}))}{(L_o^{\max} e^{-cd} + L_b^{\max} (1 - e^{-cd})) + (L_o^{\min} e^{-cd} + L_b^{\min} (1 - e^{-cd}))}. \quad (\text{A } 10)$$

Because we have assumed that the light from the object is unpolarized, $L_o^{\max} = L_o^{\min} = L_o/2$, this simplifies equation (A 10) to

$$P_d = \frac{(L_b^{\max} - L_b^{\min})(1 - e^{-cd})}{(L_b^{\max} + L_b^{\min})(1 - e^{-cd}) + L_o e^{-cd}}. \quad (\text{A } 11)$$

Dividing the top and bottom by $(L_b^{\max} + L_b^{\min}) = L_b$ gives

$$\begin{aligned} P_d &= \frac{P_\infty (1 - e^{-cd})}{(1 - e^{-cd}) + (L_o/L_b) e^{-cd}} \\ &= \frac{P_\infty}{1 + (L_o/L_b)(e^{-cd}/(1 - e^{-cd}))} \\ &= \frac{P_\infty}{1 + (L_o/L_b)(1/e^{cd} - 1)}. \end{aligned} \quad (\text{A } 12)$$

Now

$$\frac{L_o}{L_b} = 1 + C_o = \frac{1 + C_o^M}{1 - C_o^M}. \quad (\text{A } 13)$$

So, in terms of inherent Weber contrast,

$$P_d = \frac{P_\infty}{1 + (1 + C_o)/(e^{cd} - 1)} = P_\infty \frac{e^{cd} - 1}{e^{cd} + C_o}, \quad (\text{A } 14)$$

and in terms of inherent Michelson contrast,

$$P_d = \frac{P_\infty}{1 + (1 + C_o^M)/((1 - C_o^M)(e^{cd} - 1))}. \quad (\text{A } 15)$$

The last thing to consider is the polarization contrast between the object and the background. As with radiance, this can be defined in two ways, analogous to the Weber and Michelson formulations, i.e.

$$C_{\text{pol}}(d) = \frac{P_d - P_\infty}{P_\infty} \text{ in Weber formulation} \quad (\text{A } 16)$$

and

$$C_{\text{pol}}^M(d) = \frac{P_d - P_\infty}{P_d + P_\infty} \text{ in Michelson formulation.} \quad (\text{A } 17)$$

A lengthy, but straightforward, set of algebraic substitutions shows that:

$$\begin{aligned} C_{\text{pol}}(d) &= -\frac{1}{1 + ((1 - C_o^M)/(1 + C_o^M))(e^{cd} - 1)} \\ \text{or } &-\frac{1 + C_o}{e^{cd} + C_o} \text{ and} \end{aligned} \quad (\text{A } 18)$$

$$\begin{aligned} C_{\text{pol}}^M(d) &= -\frac{1}{1 + 2((1 - C_o^M)/(1 + C_o^M))(e^{cd} - 1)} \\ \text{or } &-\frac{1}{1 + (2/(1 + C_o))(e^{cd} - 1)}. \end{aligned} \quad (\text{A } 19)$$

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