Research

Navigation by light polarization in clear and turbid waters

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Certain terrestrial animals use sky polarization for navigation. Certain aquatic species have also been shown to orient according to a polarization stimulus, but the correlation between underwater polarization and Sun position and hence the ability to use underwater polarization as a compass for navigation is still under debate. To examine this issue, we use theoretical equations for per cent polarization and electric vector (e-vector) orientation that account for the position of the Sun, refraction at the air–water interface and Rayleigh single scattering. The polarization patterns predicted by these theoretical equations are compared with measurements conducted in clear and semi-turbid coastal sea waters at 2 m and 5 m depth over sea floors of 6 m and 28 m depth. We find that the per cent polarization is correlated with the Sun's elevation only in clear waters. We furthermore find that the maximum value of the e-vector orientation angle equals the angle of refraction only in clear waters, in the horizontal viewing direction, over the deeper sea floor. We conclude that navigation by use of underwater polarization is possible under restricted conditions, i.e. in clear waters, primarily near the horizontal viewing direction, and in locations where the sea floor has limited effects on the light's polarization.

Keywords: underwater; turbidity; navigation

1. INTRODUCTION

(a) *Using sky and underwater polarization as a compass for navigation*

von Frisch [1] was the first to describe the use of light polarization by animals, namely as a navigational compass for bees. Sunlight is partially polarized by single scattering by air molecules. This single scattering results in a fixed polarization pattern that moves with the Sun's position, making the sky polarization pattern a useful compass when single scattering by molecules dominates, i.e. in clear skies. It was shown that in the field, desert ants choose the sky polarization pattern or even part of it as a primary compass for navigation even when the Sun disc is visible [2]. Other insects, such as spiders [3] and field crickets [4], have also been shown to use sky polarization for navigation. Migratory birds were found to use the sky polarization at sunrise and sunset in the autumn and spring to calibrate their magnetic compass while passing between different latitudes [5–7]. Some even claim that the Vikings, with the aid of a 'sunstone' as a natural polarizer, used the sky's polarization to help them navigate the seas [8].

Recently, several species were found to project and/or detect circular polarization [9,10]. However, under water, circular polarization is mainly generated by internal reflection from the water surface and is found only at the margins of Snell's window [11]. We therefore restrict our discussion to linear polarization (a state in which the electric vector (e-vector) (the angle between the plane of vibration (PV) of the electric field and a reference plane) traces out a line in a fixed spatial plane as the light propagates). The linear polarization state has two attributes, the per cent polarization (otherwise known as the 'degree of polarization' or 'partial polarization') and the e-vector orientation.

In the ocean, direct light from the Sun (the fraction of sunlight that reaches the water surface without having being scattered by atmospheric molecules) is first partially polarized by refraction at the air–water interface and then further partially polarized by scattering by water molecules and other suspended matter (e.g. plankton, silt). The maximum per cent polarization of light in the clear ocean is generally 50–60% [12–14] near the water surface, which is less than the maximum per cent polarization in the atmosphere. One explanation for the difference between the maximum per cent polarization in the ocean versus the atmosphere is the difference in polarizability (the change in the shape of the electron cloud around a molecule in response to an applied electromagnetic field) of water molecules versus air molecules. Nonetheless, relatively high

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values of per cent polarization are sustained to great depths in the ocean, reaching as high as 40 per cent at depths exceeding 100 m [15]. This fact makes polarization a potentially advantageous visual cue, since light intensity decreases exponentially with depth (see discussion in [16]). Although more than 70 marine and fresh water species have been found to possess polarization sensitivity [13,17], and some of them have been shown to orient in a set direction according to a polarized light stimulus [18–24], the question of whether marine species can navigate using light polarization, especially in open waters, is still open to debate [25].

(b) How can per cent polarization be used as a compass?

The pattern of per cent polarization, known as the per cent polarization phase function (PPPF), is highly sensitive to the shape and size of the scatterers (relative to the wavelength of light), to the refractive index of the scatterers and to the order of scattering (the number of scattering events). If the content of the scatterers in a medium is constant, then the PPPF should not change, and the polarization pattern or even part of it can be used as a compass [26]. Such is the case when first-order (single) Rayleigh scattering (by scatterers with radii $R \ll 1 \mu\text{m}$ for wavelengths in the visual range [27]) dominates. In the Rayleigh scattering regime, the pattern of charge separation inside the scatterers is a dipole. The resulting PPPF is a bell-like

Figure 1. Illustration of the radiance angles in water. S, Sun, V, viewer (sensor) position, SW, Snell's window (dark grey area), N = north. The solar zenith angle (SZA) is represented by θ_s , the solar azimuthal angle by ϕ_s , the sensor or viewing zenith angle (VZA) by θ_p , the sensor azimuthal angle by ϕ_p , the angle of refraction into the water by θ_r , and the scattering angle by θ_{sca} . Note that the azimuthal angles are measured clockwise from the north. The angular difference between the Sun and the sensor bearings is defined by $\Delta\phi = \phi_s - \phi_p$.

Figure 2. Per cent polarization phase function (PPPF; per cent polarization versus scattering angle) measured at a depth of 2 m, (a–c) in clear and (d–f) semi-turbid waters at three solar zenith angles (SZA). Wavelength = 450 nm. SZA; (a,d) 0° – 30° ; (b,e) 30° – 60° ; (c,f) 60° – 90° .

Figure 3. Numerical solutions of equation (1.2) for the e-vector orientation, ψ , presented in the viewing (sensor) zenith angle (VZA = θ_p) and the sun-viewing azimuthal difference ($\Delta\phi = \phi_s - \phi_p$) plane. The colour bar represents the calculated e-vector orientation, in the range of $\pm 90^\circ$ relative to the horizon. (a,d) angle of refraction into the water $\theta_r = 48.4^\circ$ (solar zenith angle $\theta_s = 90^\circ$), (b) $\theta_r = 31.9^\circ$ ($\theta_s = 45^\circ$) and (c) $\theta_r = 7.5^\circ$ ($\theta_s = 10^\circ$). Pixels for which $\theta_r - \delta < \psi < \theta_r + \delta$, where δ is the detection resolution, are coloured in white. (a–c) $\delta = 0.1^\circ$, (d) $\delta = 1^\circ$. All cases assume a water refractive index of 1.337 at wavelength $\lambda = 450$ nm. Black pixels indicate convergence or discontinuity of ψ (e.g. values of -90° or 90°). Owing to the symmetry of the solution, $\Delta\phi$ is presented in the range 0 – 180° only.

curve, with values of 0 per cent polarization at 0° and 180° scattering angle (the angle between the viewer and the direction of incident light), and maximal per cent polarization at 90° scattering angle. This bell curve is represented by the theoretical equation [14]

$$P = P_{\max} \left(\frac{\sin^2 \theta_{\text{sca}}}{1 + \cos^2 \theta_{\text{sca}}} \right), \quad (1.1)$$

where P is the per cent polarization at scattering angle θ_{sca} (figure 1) and $P_{\max}$ is the maximum per cent polarization.

In the Mie scattering regime (scatterers with radii $R \approx 1 \mu\text{m}$ for wavelengths in the visual range; [27]), the pattern of charge separation inside of the scatterers is more complicated, and interference effects occur. The resulting PPPF differs from a simple bell curve, with the maximum per cent polarization shifted from 90° to higher scattering angles [13,28,29] and fluctuations in per cent polarization occurring at other scattering angles. Furthermore, Mie scattering often occurs in optically dense (turbid) media, accompanied by higher order (multiple) scattering effects, which cause an overall decrease in per cent polarization [30]. Indeed, sky polarization measured under overcast conditions can be lower than 10 per cent [8,31], making it impossible for most animals' visual systems to detect (with a possible exception of insects such as the field cricket [32]).

(c) How can e-vector orientation under water be used as a compass?

Measurements at 2 m depth under clear skies show that the e-vector orientation pattern inside of Snell's window is similar to the one in the sky [33]. However, this e-vector orientation pattern is easily distorted by waves [34] and does not hold at greater depths [12,35]. Furthermore, in many cases, mostly but not exclusively along the coasts, scattering by larger particles occurs along with Rayleigh scattering [36].

Under conditions in which the dominant processes are refraction of direct light from the Sun followed by Rayleigh single scattering in the water, the PV of the e-vector under water is perpendicular to the plane of scattering (PS; the plane defined by the direction of incident light propagation and the viewing direction). Under such conditions, the pattern of e-vector orientation goes according to the following theoretical equation [37]:

$$\tan \psi = \frac{\tan \theta_r \sin \Delta\phi}{\sin \theta_p - \tan \theta_r \cos \theta_p \cos \Delta\phi}, \quad (1.2)$$

where ψ represents the e-vector orientation angle relative to the horizon, θ_r and θ_p are the angle of refraction and the zenith angle of the sensor in the water, respectively, and $\Delta\phi$ is the difference between the azimuthal angles of the Sun and the sensor (figure 1). In fact, it was argued ([25] and references within, see also drawings by Hawryshyn [38]) that as sea waters are

Figure 4. Linear regression (a) slope, (b) intercept and (c) coefficient r between the measured e-vector orientation and the e-vector orientation calculated using equation (1.2) for each sensor viewing zenith angle (VZA, θ_p), in clear (open symbols) and semi-turbid (close symbols) waters, at 2 m (circle, rectangle) and 5 m (triangle) depth. $r = 1$, slope = 1 and intercept = 0, represents the exact equivalence of ($y = x$) of the measured and calculated e-vector orientation. See table 1 for statistical details. Data represented by the open circles were measured over a 6 m sea-floor depth, while all other data were measured over a 28 m sea-floor depth. The case turbid2m is chosen as representative of the tendency of all of the cases and is therefore emphasized with a solid curve. open circles, clear2m (shallow floor); open squares, clear2m; open triangles, clear5m; filled circles, turbid2m; filled triangles, turbid5m.

predominantly clear, the underwater e-vector orientation pattern is always similar to that generated by refraction and Rayleigh single scattering only, i.e. according to equation (1.2). However, in turbid conditions, in which multiple Mie scattering occurs, the PV is no longer perpendicular to the PS, and equation (1.2) fails to predict the e-vector orientation [37]. In such a circumstance, the pattern tends to vary strongly with optical depth (which by definition depends on the light's attenuation coefficient and on the geometric depth into the water). Therefore, on theoretical grounds alone, we predict that the e-vector orientation is less useful for navigation in turbid conditions outside of Snell's window as is the case inside of Snell's window.

Aside from the full e-vector orientation pattern when refraction followed by Rayleigh single scattering dominates, the maximum value of the e-vector orientation angle in the horizontal viewing plane may be used for navigation via its connection to the angle of refraction [25,37]. Equation (1.2) predicts that in the horizontal viewing plane, the absolute value of ψ does not exceed the angle of refraction θ_r and equals the angle of refraction in the azimuthal plane perpendicular to the Sun's bearing. As such, a navigator only needs to scan the horizontal plane in order to detect the angle of refraction and hence the Sun's position.

(d) Aims of the present study

In the present study, measurements similar to those of Sabbah & Shashar [39] were conducted outside of Snell's window in clear and semi-turbid waters. The potential for using polarization as a navigational compass (mostly outside of Snell's window) is evaluated by examining all three possible uses of polarization for navigation mentioned above: (i) the stability of the PPPF (its likeness to that predicted by equation

(1.1)), (ii) the stability of the e-vector orientation pattern (its likeness to that predicted by equation (2)), and (iii) the location and value of the maximum in ψ .

2. MATERIAL AND METHODS

(a) Light polarization measurements at sea and data analysis

Polarization measurements were conducted at a coral reef of the Gulf of Eilat at the tip of the Red Sea in front of the Steinitz Marine Biology Laboratory (29°30'070" N, 34°56'024" E), Eilat, Israel, during July 2003. Per cent polarization and e-vector orientation were measured under water from sunrise to sunset. Three sets of measurements were conducted. The first set was taken in clear waters at 2 m depth near the shore with a shallow bottom depth of 6 m, at viewing zenith angles (VZAs) of 30°, 70° and 90° (see figure 1 for a description of the angles), and at viewing azimuthal angles of 0°, 45°, 90°, 135° and 180° (see the detailed description of this set in [39]). The second set was taken in clear waters at 2 and 5 m depth, approximately 40 m from shore, with a bottom depth of 28 m (although this bottom depth should not be considered deep by any measure, it was deep enough to significantly reduce any sea-bottom effects), at the horizontal viewing direction (90° sensor zenith angle) and at eight azimuthal angles of 8°, 53°, 98°, 143°, 188°, 233°, 278° and 323° defined from the north towards the east. The third set was taken in semi-turbid waters (turbidity caused by a bloom of unicellular algae) at the same location and depth as the second set, at VZAs varying from 0° to 180° at 30° intervals and at viewing azimuthal angles of 8°, 53°, 98°, 143° and 188° only. A total of 5439 polarization measurements were obtained in all measurement sessions. Throughout these sessions, the sea was very calm, with wave

amplitude not exceeding 10 cm, and the sky was clear blue without any clouds.

The measurements were taken with an underwater spectral polarimeter previously used by Sabbah *et al.* [33], based on a three-channel spectrophotometer (Ocean Optics ADC-1000-USB). The polarimeter included three optic fibres (Ocean Optics UV/VIS 600 μm) with a 5° acceptance angle restrictor housed in PVC tubes. Linear polarizers (Polaroid H'NPB UV/VIS) were attached in front of the fibres at three orientations of 0° , 45° and 90° offset. On top of each polarizer, a polarizing neutral filter (Rosco Supergel no. 02-Bastard Amber) was mounted to flatten the natural spectra. For the deep-bottom sampling sets (sets 2 and 3), the polarimeter was mounted on a 25 m long submersed tripod. Sun zenith and azimuthal angles were obtained from the US Navy website (<http://aa.usno.navy.mil/-data/docs/AltAz.html>).

Per cent polarization and e-vector orientation were calculated from each set of three readings following the equations used by Sabbah *et al.* [33]. The scattering angle for each set of readings was calculated using the cosine equation [13]. Since the tripod was fixed during sampling, the polarimeter depth varied with the tide. However, the maximum difference between high and low tides (measured during each measurement day) was less than 1 m. The effect of a ± 50 cm change in depth at a wavelength of 450 nm over different sensor angles is equivalent to a standard deviation of ± 4.32 per cent in the per cent polarization and a standard deviation of $\pm 4.68^\circ$ in the e-vector orientation, respectively. Although our system could measure a wide spectral range (300–800 nm UV radiance was not available as it was absorbed by the filters), only measurements taken at a wavelength of 450 nm were analysed in this study (for simplicity and since 450 nm wavelength is often within the visual range of marine animals).

(b) Statistical analysis

To compare the measured e-vector with the values predicted by the theoretical equation (1.2), linear regression was used. Regression lines were fitted using major axis type-II regression analysis according to a MATLAB code provided by Peltzer [40], which is adequate for comparing datasets of the same size and scale.

3. RESULTS

(a) Stability of the per cent polarization phase function

The PPPFs (per cent polarization versus scattering angle) measured at 2 m depth over a 28 m deep sea floor and at all solar zenith angles (SZAs) in clear and semi-turbid water conditions are shown in figure 2. In clear waters (figure 2a–c), the PPPF is symmetric around the 90° scattering angle where the maximum polarization is achieved, for all Sun elevations, as described by equation (1.1). However, in semi-turbid waters (figure 2d–f), the symmetry around the 90° scattering angle is preserved only at low SZAs (figure 2d, $\text{SZA} < 30^\circ$); at other angles, the symmetry breaks and the maximum per cent

polarization shifts to other scattering angles. Therefore, the PPPF is consistent with the Sun's elevation in clear waters only.

(b) Stability of the e-vector orientation pattern

In figure 3, the e-vector orientation, ψ , calculated using equation (1.2), which accounts for refraction of the direct light from the Sun into the water and single Rayleigh scattering within the water only, is presented for different SZA ($\text{SZA} = \theta_s$) related to the different angles of refraction into the water, θ_r . Note that this theoretical calculation is considered to be more potentially relevant outside of Snell's window than inside of Snell's window, since it does not account for refraction of radiation that was already scattered in the atmosphere into the water. Nevertheless, for completeness, the solution is presented for all viewing (sensor) zenith angles, θ_p , and for all differences between the azimuthal angle of the Sun and the sensor, $\Delta\phi$. Owing to the symmetry of the solution, $\Delta\phi$ is presented in the 0 – 180° range only. The colour bar represents the values of e-vector orientation calculated with respect to the horizon. In general, the $(\Delta\phi, \theta_p)$ points at which the e-vector orientation equals the angle of refraction vary with the Sun's elevation. However, at horizontal viewing directions, in a plane perpendicular to the Sun's bearing ($\Delta\phi = 90^\circ$, $\theta_p = 90^\circ$), ψ equals θ_r at all Sun elevations. As the Sun's elevation increases, the e-vector field becomes more and more horizontal (figure 3a–c).

Note that one must consider the angular resolution capability of the observer. In figure 3, pixels in which $\theta_r - \delta < \psi < \theta_r + \delta$, where δ represents the detection resolution, are coloured white. Increasing δ (i.e. allowing lower detection resolution) would decrease the precision of the prediction of the Sun's position and with it the accuracy of the compass.

A linear regression model was applied to fit the measured e-vector orientations to the e-vector orientations calculated according to equation (1.2). The slope and intercept of the regression, and the correlation coefficient r , are presented in figure 4 as a function of the VZA (see statistical details in table 1), where maximum correlation is achieved for slope = 1, intercept = 0 and $r = 1$. (Note that all three parameters, slope, intercept and correlation coefficient, are necessary, as a deviation of any one of them from its maximum correlation value will suggest involvement of a different scattering mechanism than the one assumed.) Although maximum correlation was not achieved at any VZA, as the parameter values did not attain the 95% confidence level (95 CI; table 1), the highest prediction was achieved under the clear conditions at 5 m depth (95 CI of slope = 1.01–1.03, intercept = 5.81–5.93, $r = 0.85$ and $p < 0.001$). In general, in both water types at both depths, the correlation was high in the horizontal viewing direction ($\text{VZA} = 90^\circ$; mean $\pm$ 95 CI of the slope = 1.0 ± 0.2 , intercept = 0.0 ± 5.93 and $r > 0.8$, $p < 0.001$), and decreased towards the viewing zenith/nadir. In the horizontal viewing direction ($\theta_p = 90^\circ$; table 1), the fitted slope in clear waters at 2 m depth over the shallow sea floor (mean $\pm$ 95 CI

Figure 5. e-vector orientation versus absolute solar zenith angle ($SZA = \theta_s$) measured in clear waters at eight azimuthal angles of 8° , 53° , 98° , 143° , 188° , 233° , 278° and 323° defined from the north towards the east. (a,b) Viewing zenith angle ($VZA = \theta_p$) = 30° and 70° , respectively, at 2 m depth (sea-floor depth = 6 m), and (c) $VZA = 90^\circ$ at 5 m depth (sea-floor depth = 28 m). The red line represents the horizon, the green lines represent angle of refraction into the water (for real refractive index = 1.337, wavelength = 450 nm), and the blue lines represent the margins of Snell's window $\pm 48.4^\circ$. Measurements at $VZA = 90^\circ$ at 2 m depth are not presented, as they exhibit negligible differences from the measurements at 5 m depth.

Table 1. Major axis type-II linear regression line estimates of the correlation between the measured e-vector orientation and the e-vector orientation calculated using equation (1.2) for different water types and viewing directions. n = number of measurements per sampling set, θ_p = viewing (sensor) zenith angle, r = Pearson linear regression coefficient, s.d. = standard deviation, 95 CI = 95% confidence interval, p = p -value for r . n.s. = $p > 0.05$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Note that the e-vector orientation measured in the horizontal direction ($\theta_p = 90^\circ$) in clear conditions at 5 m depth exhibits the best correlation with equation (1.2).

sampling set	θ_p	n	slope			intercept			r	p
			mean	s.d.	95 CI	mean	s.d.	95 CI		
<i>sea-floor depth 6 m</i>										
clear2m	30°	1488	3.22	0.28	0.02	−31.61	2.33	0.12	0.29	***
clear2m	70°	666	2.68	0.17	0.02	50.53	4.20	0.32	0.53	***
clear2m	90°	1514	0.67	0.01	0.01	4.70	0.30	0.02	0.79	***
<i>ocean-floor depth 28 m</i>										
clear2m	90°	492	0.89	0.03	0.01	1.74	0.60	0.05	0.82	***
clear5m	90°	392	1.02	0.03	0.01	5.86	0.68	0.07	0.85	***
turbid2m	0°	63	0.26	0.20	0.05	8.52	5.35	1.31	0.16	n.s.
turbid2m	30°	57	0.53	0.18	0.05	26.00	5.15	1.35	0.36	**
turbid2m	60°	65	0.63	0.18	0.05	15.39	3.24	0.78	0.40	***
turbid2m	90°	70	0.81	0.07	0.02	−3.36	1.70	0.40	0.81	***
turbid2m	120°	69	0.65	0.07	0.02	−1.63	1.87	0.45	0.75	***
turbid2m	150°	67	0.14	0.08	0.02	20.18	2.91	0.69	0.20	n.s.
turbid2m	180°	65	0.09	0.06	0.02	32.02	3.12	0.75	0.17	n.s.
turbid5m	0°	66	0.41	0.18	0.05	16.62	5.33	1.28	0.28	*
turbid5m	30°	50	2.22	0.91	0.25	−58.17	28.61	7.93	0.33	*
turbid5m	60°	59	0.91	0.26	0.08	13.46	4.25	1.10	0.41	**
turbid5m	90°	64	0.91	0.08	0.02	−0.91	1.83	0.44	0.83	***
turbid5m	120°	66	0.65	0.08	0.02	2.85	2.19	0.53	0.70	***
turbid5m	150°	65	0.13	0.07	0.02	22.79	2.61	0.63	0.24	n.s.
turbid5m	180°	61	−0.04	0.04	0.01	34.55	1.87	0.48	0.13	n.s.

of the slope = 0.67 ± 0.01 , $p < 0.001$) is significantly lower than all other slopes at both the 2 m depth and the 5 m depth over the deeper sea floor. In the deeper sea-floor sets, all slopes are significantly different from each other, except that in clear waters at 2 m depth and that in semi-turbid water at 5 m depth

(mean $\pm$ 95 CI of the slope = 0.89 ± 0.01 and 0.91 ± 0.02 , $p < 0.001$, respectively). The slope in semi-turbid water at 5 m depth over the deeper sea floor is significantly lower than the other slopes over that sea-floor depth (mean $\pm$ 95 CI of the slope = 0.81 ± 0.02 , $p < 0.001$).

Figure 6. Same as figure 5 for e-vector orientations measured in semi-turbid waters at 5 m depth with sensor viewing zenith angles (VZA, θ_p) directed from zenith to nadir at 30° intervals and at azimuthal angles of 8°, 53°, 98°, 143° and 188°. Measurements conducted at 2 m depth did not differ from the ones conducted at 5 m depth and are therefore not presented.

(c) Using the e-vector orientation in the horizontal viewing plane to detect the angle of refraction

Using the e-vector orientation (ψ) to detect the angle of refraction requires that the absolute maximum value of the orientation angle perceived does not exceed the absolute angle of refraction into the water θ_r , and that the absolute maximum value of the orientation angle equals θ_r at at least one azimuthal direction at the moment of detection. e-vector orientations measured in clear and semi-turbid waters, respectively, at different VZAs are plotted in figures 5 and 6 against the SZA and against θ_r (denoted by the green line, calculated for refractive index in

water = 1.337 and wavelength = 450 nm). In clear waters (figure 5), the above requirements are met completely at all SZAs in the horizontal viewing direction (VZA = 90°, figure 5c) and at VZA = 70° for SZA < 75° (figure 5b). At VZA = 30° (figure 5a), ψ exceeds the absolute value of θ_r . This is to be expected, since this VZA is within Snell's window, and therefore the predictions of equation (1.2) are considered less relevant, even in clear waters (see above). In semi-turbid waters (figure 6), the above requirements are not met at any VZA, not even near the horizon. The absolute maximum of ψ differs from θ_r , and the difference between the two increases with increasing absolute VZA (looking away from the horizon).

4. DISCUSSION

(a) *Using per cent polarization as a compass tool under water*

Both attributes of the linear polarization field, namely the per cent polarization and the e-vector orientation, can be used as a sun-related compass for navigation outside of Snell's window in certain circumstances. We found that the pattern of per cent polarization (the PPPF) is stable and consistent with the Sun's location at depths of 2 and 5 m in clear waters only. In semi-turbid waters, in this case caused by an algae bloom, the PPPF measured was close to the Rayleigh bell shape only at midday (high Sun elevation) but was not stable and varied throughout the day. Therefore, using the per cent polarization pattern under water is possible in clear waters but less so in semi-turbid and turbid conditions.

Note that while the position of the maximum in the per cent polarization varied significantly between the clear water case (in which it was stable) and the semi-turbid water case (in which it was not stable), the value of the maximum in per cent polarization ($P_{\max}$) did not vary significantly between the clear and semi-turbid cases (figure 2), as it should according to the Mie scattering theory and atmospheric measurements in turbid conditions [8,30,31]. This could be due to two possible reasons. First, since the semi-turbid waters were only semi-turbid and not highly turbid (as we determined by qualitative inspection), the multiple scattering that often accompanies turbidity and is partly responsible for the lowering of the value of $P_{\max}$ may not have occurred. Second, the size of the algae could have been in the geometric optics regime (with radii $R > 50 \mu\text{m}$ for visible light). Geometric optics scatterers do not depolarize light as strongly as Mie scatterers ($R \approx 1 \mu\text{m}$ for visible light; [13]), but they may still significantly alter the e-vector orientation, as we observed (compare figures 5 and 6). Unfortunately, we lack quantitative information on the exact level of turbidity (the concentration of the algae present during our measurements) and on the size distribution of the algae necessary to confirm either or both of these two possible explanations.

(b) *Using e-vector orientation as a compass tool under water*

Inside of Snell's window in clear waters without waves and at shallow depths, the full pattern of e-vector orientation can be used similar to the way it is used on land. Outside of Snell's window, we found that the pattern of e-vector orientation at all viewing angles is fairly stable (coincides with the theoretical equation (1.2)) only in clear waters and at 5 m depth. However, the pattern of e-vector orientation in the horizontal viewing direction is fairly predictable (by the theoretical equation) in both clear and semi-turbid waters at both 2 m and 5 m depth over both shallow and deeper sea floors, though most predictable in clear waters over the deeper sea floor. We also found that using the maximum value of the e-vector orientation angle as an indicator of the angle of refraction and hence of the SZA is possible only in clear waters, near the horizontal viewing direction. Under such conditions, the angle of refraction can be

detected most of the day (except when the Sun is at the zenith or very close to it and the e-vector is horizontally aligned at all viewing directions) and may even be detected when the Sun is obscured, as long as some direct (unscattered) light from the Sun reaches the ocean surface within the field of view. However, we lack underwater measurements under overcast skies to support this last conjecture.

(c) *Visual adaptations to overcome limitations in the use of the polarization compass*

It should be noted that at lower Sun elevations (high SZA), the polarization cues are especially strong (highly directional) in the water. Though the signal-to-noise ratio is low at lower Sun elevations, high polarization sensitivity may help to overcome this limitation [16]. Hence, we expect that polarization cues, under the specific conditions mentioned above, could be used by marine animals for navigation (e.g. salmonids [41]) or for magnetic field calibration (e.g. tunas [42]) under water, during their daily vertical migration at sunset and at sunrise. In addition to high polarization sensitivity, high spatial resolution, as exhibited by, e.g. cuttlefish adults [43], would improve the detection of the refraction angle and expand the use of the compass to include hours closer to midday.

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