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FORAGING AND PREY-SEARCH BEHAVIOUR OF SMALL JUVENILE RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) UNDER POLARIZED LIGHT

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Summary

Several fish species appear to be polarization sensitive, i.e. to be able to discriminate a light source's maximum plane of polarization from any other plane. However, the functional significance of this ability remains unclear. We tested the hypothesis that polarized light improves the prey location ability of free-swimming rainbow trout (*Oncorhynchus mykiss*) in laboratory aquaria. We found that prey location distances increased while the vertical component of prey location angle decreased under polarized compared with unpolarized (diffuse) illumination. The average frequency distribution of the horizontal component of prey location angle was more bimodal under polarized than unpolarized illumination. These results indicate that polarization sensitivity enhances prey location by juvenile rainbow trout.

Key words: polarization, salmonid, rainbow trout, *Oncorhynchus mykiss*, zooplankton, ultraviolet light, target contrast, foraging, prey-search behaviour.

Introduction

In addition to colour (wavelength) and intensity (irradiance), light has another physical attribute, termed its polarization (Shurcliff, 1962), which some animals are able to detect and use (Wehner, 1983). The polarization of a light source is a measure of the degree to which the photons comprising it vibrate in the same plane. Light that is 100 % linearly polarized has all its photons vibrating in the same plane, whereas diffuse (unpolarized or 0 % polarized) light has the same amount of photons vibrating in any given direction (Shurcliff, 1962). Sunlight reaching the Earth's atmosphere is diffuse, but it becomes partially polarized in a variety of ways that include molecular scattering, reflection at interfaces and passage through optically active materials (see Hecht and Zajac, 1974). Both terrestrial and aquatic invertebrates use the polarization of light for orientation and navigation (Wehner, 1983; Goddard and Forward, 1991; Schwind, 1999; Novales Flamarique and Browman, 2000), and for object recognition (Moody and Parriss, 1961; Shashar and Cronin, 1996; Shashar et al., 1998; Marshall et al., 1999). To date, however, there is no definitive evidence for a functional use of polarization discrimination by a vertebrate (although see Groot, 1965; Hawryshyn and Bolger, 1990; Hawryshyn et al., 1990, for experimental tests of the orientation hypothesis in fish).

Most of the polarization-related investigations using vertebrates have concentrated on fish, and in particular on the rainbow trout *Oncorhynchus mykiss* (see Parkyn and Hawryshyn, 1993; Coughlin and Hawryshyn, 1995). Like most fishes during the early life stages, the rainbow trout (or its anadromous morph, the steelhead trout) is a visual predator that feeds on zooplankton. The majority of these prey organisms contain lipids and carotenoid pigments (Lee et al., 1970) that preferentially absorb ultraviolet and short wavelengths (Fig. 1A–D). As such, zooplankton become more visible to an ultraviolet-sensitive predator, like the rainbow trout (Hawryshyn and Hárosi, 1994), when the background illumination contains ultraviolet/short wavelengths (Browman et al., 1994), as is the case in nature (Novales Flamarique and Hawryshyn, 1997). Perhaps as a result of this enhanced contrast, several zooplankton species, including the genus *Daphnia*, have evolved cuticle layers that preferentially reflect short wavelengths (Giguère and Dunbrack, 1990), thereby reducing their contrast. Zooplankton may be further conspicuous to polarization-sensitive predators because of the pronounced birefrigence that their calcium carbonate exoskeletons exhibit (Fig. 1E–H). Polarized light traversing their bodies will be scattered and/or retarded depending on the wavelength and path of the light, and the angle that the maximum plane of polarization, E_{max}, makes with the orientations of optical axes going through the various birefringent structures. Under polarized light illumination, zooplankton may therefore exhibit higher contrast to a polarization-sensitive predator (Fineran and Nicol, 1978).

The purpose of this study was to test whether polarized light

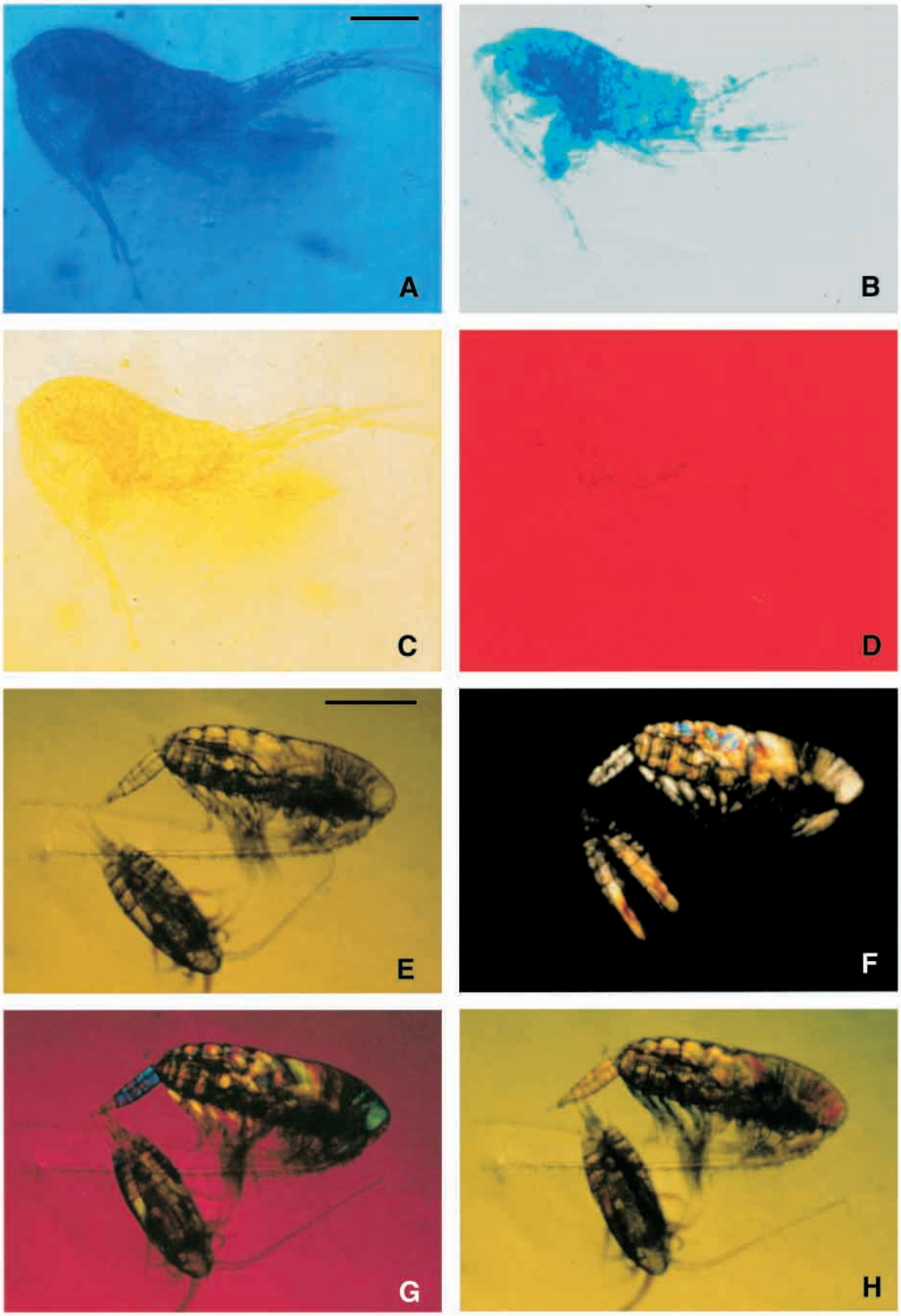
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Fig. 1. Images of copepods taken under different spectral and polarized light illuminations. All images were taken using an Ektachrome-type colour slide film with nearly uniform sensitivity in the range 320–700 nm (Kodak Color Films and Paper Manual, 1986). (A–D) The copepod *Metridia pacifica* (length=2.6 mm) was photographed with a Zeiss Universal microscope equipped with Balzer filters with the following peak transmissions: (A) ultraviolet (λ_{max}=368 nm), (B) short-wavelength (λ_{max}=432 nm), (C) middle-wavelength (λ_{max}=544 nm) and (D) long-wavelength (λ_{max}=646 nm) light. The light source was a halogen lamp. All photographs share the same exposure (70 s); this exposure was selected because it gave the highest contrasts under middle- and long-wavelength illumination (with the progressive disappearance of the copepod at lower or higher exposures). The copepod is most conspicuous under ultraviolet- and short-wavelength illumination; under these conditions, the animal remained highly visible from 1–90 s of exposure. Scale bar, 0.5 mm. (E–H) The copepods *Calanus pacificus* (larger animal, length=2.6 mm) and *Aetidius divergens* (smaller animal, length=1.6 mm) were photographed using the same microscope but equipped with (E) a polarizer but no analyzer, (F) a polarizer oriented perpendicular to the analyzer, (G) a polarizer oriented perpendicular to the analyzer but with a quarter-wave plate (Zeiss Quarz 1, total retardation 140 nm) oriented at 45° to the polarizer and prior to the specimen, and (H) a polarizer oriented parallel to the analyzer with the quarter-wave plate in the same configuration. The light source here was a short-arc mercury vapor lamp (Osram). The animals are more conspicuous when an analyzer of polarized light is present in the light path. In this fashion, prey may become more conspicuous to a polarization-sensitive predator by diffusing (depolarizing) the incident polarization and, for animals that possess pre-retinal analyzers (e.g. the iridescent corneas of some fishes, perhaps; see Lythgoe, 1975), by the changes in intensity and colour patterns that may arise from transduction of polarization in the animal's visual system. Scale bar, 1 mm.

improves prey location in small juvenile rainbow trout. To this end, we observed rainbow trout foraging freely on *Daphnia magna*, a cladoceran present in some water bodies that salmonids inhabit. Experiments were carried out under two white light illuminations of low intensity (one diffuse, the other 100 % linearly polarized) and under low-intensity short-wavelength illumination of varying percent polarization. Foraging performance was assessed by measuring prey location distance, and the vertical and horizontal components of prey location angle for each attack on prey. If polarized light increases prey contrast, then the frequency distributions of prey location distance and angles should be different under polarized and unpolarized illumination. Likewise, the frequency distributions under low percent polarizations (those below the fish detection threshold) should be different from those under higher percent polarizations (those that fall within the fish's detection threshold).

Materials and methods

Imaging system

We used silhouette (shadow) video photography (SVP) (Arnold and Nutall-Smith, 1974; Edgerton, 1977; Browman et al., 1989) to record the foraging behaviour of rainbow trout (*Oncorhynchus mykiss*) feeding on *Daphnia magna* under light fields of differing polarization content. Silhouette video photography is superior to standard cinematographic or video imaging techniques in various ways. First, it allows filming of events in a large depth of field (approximately 15 cm) with a relatively large field of view (limited only by the size of the collimating lens, in these experiments 14.5 cm). Second, magnification is independent of distance from the cameras and the resolution is very good (objects approximately 0.2 mm in size can be resolved). Third, image quality is unaffected by ambient light levels, and only a very low-intensity point source of light (well below that which could confound the results) is required to achieve the silhouette effect. Thus, foraging behaviour can be observed under relatively natural conditions.

The SVP observation and motion-analysis system consisted of two orthogonally oriented optical rails, with the observation aquarium placed at their intersection (see Fig. 1 in Novales Flamarique et al., 2000, for a description of a similar system). The imaging optics on each rail comprised a far-red light-emitting diode (LED) placed at the focal point of a 14.5 cm diameter biconvex collimating lens whose output passed through the aquarium. Shadow images were collected by a lens (Tamron 70–210 mm zoom) attached to a 1.25 cm CCD sensor video camera (Panasonic WV-BL730) and recorded using an S-VHS video tape recorder (Panasonic AG-6730). The optical components on each rail were aligned prior to the experiments using helium–neon lasers, which allowed the vertical viewing heights and orthogonal orientation of the two rails to be established precisely. The synchronously recorded orthogonal views allowed for exact determination of the three-dimensional positions of objects that appeared in both fields of view simultaneously.

The outermost 10 cm of the aquarium walls were covered with black plastic (matte-surface) contact paper. This restricted the field of view to the central 20 cm^3 volume of water and ensured that the behaviours observed were not influenced by surface or edge effects; only animals swimming freely in the water column were imaged and their displacements analyzed.

Illumination system

The illumination system consisted of a light-intensity-controlled 1000 W Xenon arc lamp connected to a black L-shaped tube. The bend in the tube housed a mirror, oriented at 45°, that reflected the incident light onto the aquarium. A filter holder was attached to the end of the tube, and a rotatable holder housing a quarter-wave plate could be connected to it. The filter holder always contained two KG-3 type quartz substrate heat filters (Melles Griot). For experiments with diffuse white light illumination, the heat filters were followed by a UV-grade HNP'B linear polarizer (Polaroid) and a wax paper diffuser. The position of the polarizer and wax paper diffuser were interchanged for experiments under 100 % linearly polarized white light illumination. We also performed experiments with short-wavelength light that varied in percent polarization from 52 % to 97 %. In these experiments, the heat filters were

followed by a diffuser, a 400±10 nm NB filter (Melles Griot), the polarizer and a rotatable Mica quarter-wave plate (Melles Griot). Percent polarizations for various rotations of the quarter-wave plate were computed from intensity measurements at the maximum (E_{max}) and minimum (E_{min}) planes of polarization (determined visually at the level of the aquarium with an Oriel E-vector finder) using a 100 mm diameter submersible integrating sphere (OL-IS-470-WP) attached, via a quartz fiber optic cable, to a scanning spectroradiometer (OL 754-O-PMT, Optronic Laboratories Inc.). Percent polarization (P) was computed as: $\%P=100(I_{Emax}-I_{Emin})/(I_{Emax}+I_{Emin})$, where I_{Emax} and I_{Emin} are the intensities in the maximum and minimum planes of polarization, respectively. The light field formed a cone of approximately 74° aperture that projected a 30 cm diameter circle into the aquarium. This optical configuration minimized the non-illuminated volume of water and, hence, the chances of edge effects during the experiments. From the rainbow trout's point of view, the illumination was that of a point source subtending an angle of approximately 13°. The intensity (5.62×10^{16} photons m^{-2} s^{-1}) and spectral distribution (340–700 nm) of the white light were chosen to mimic spectra obtained in mesotrophic waters during crepuscular periods (Novales Flamarique et al., 1992; Novales Flamarique et al., 2000), times when the relative contribution of the ultraviolet cone to photopic vision is highest (Novales Flamarique and Hárosi, 2000). We chose the short-wavelength filter for percent polarization studies because we could then attain relatively low (52 %) polarizations with the Mica quarter-wave plate available and because the spectral content of the field was within the absorption range of all the cone visual pigments present in small rainbow trout. The intensity and spectral distribution of the short-wavelength field were 4.23×10^{16} photons m^{-2} s^{-1} and 390–413 nm, respectively.

Experiments and analysis

For each experiment, 20 rainbow trout of approximately the same size [mean mass=0.085±0.003 g, total length= 1.55±0.12 cm, measurements from 50 individuals chosen randomly at the beginning of the study; means ± S.D.] were removed from the rearing tank 16 h prior to a given experiment. Following this starvation period, the animals were placed in a 30 cm×30 cm×30 cm glass aquarium filled with 25 l of water (from the tanks in which they were reared) and allowed to acclimate for 30 min. *Daphnia magna* (N=250) were then gently introduced into the aquarium, and videotape recordings were made for the next 35 min. Attacks during the first 5 min, when the prey had not yet distributed evenly throughout the aquarium and feeding did not require substantial searching, were not considered in the analysis.

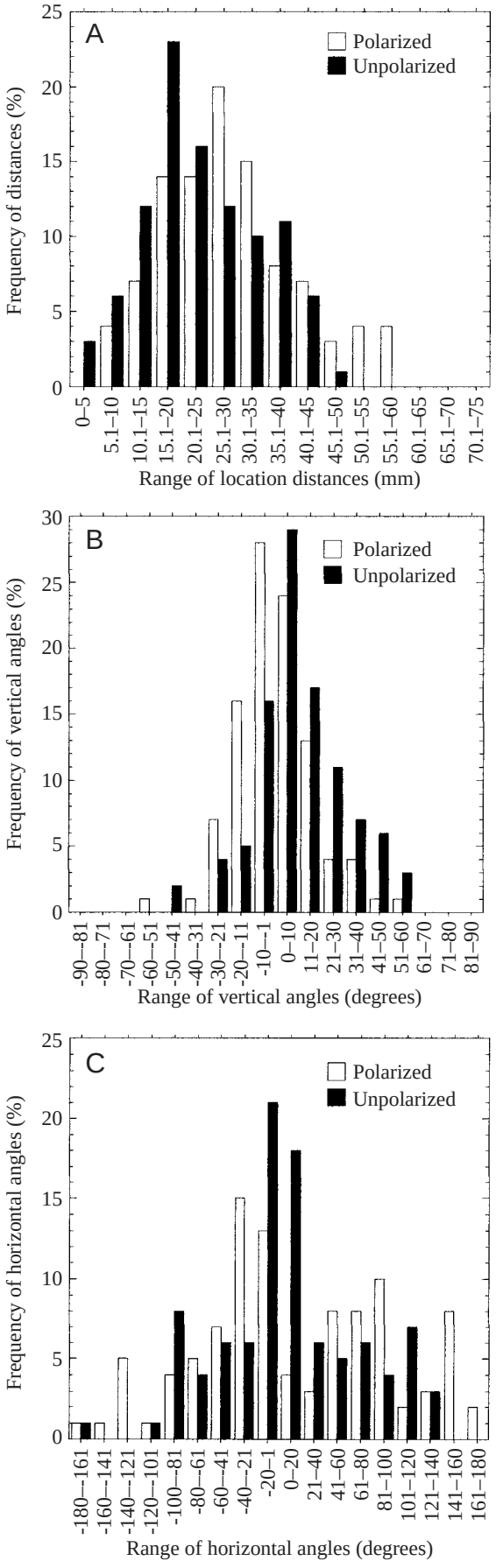

Fig. 2. Frequency distributions of (A) prey location distance, (B) the vertical component of prey location angle and (C) the lateral component of prey location angle for rainbow trout foraging under 100 % linearly polarized or unpolarized (diffuse, 0 %) light. Individual frequencies are percentage totals from three trials per light condition.

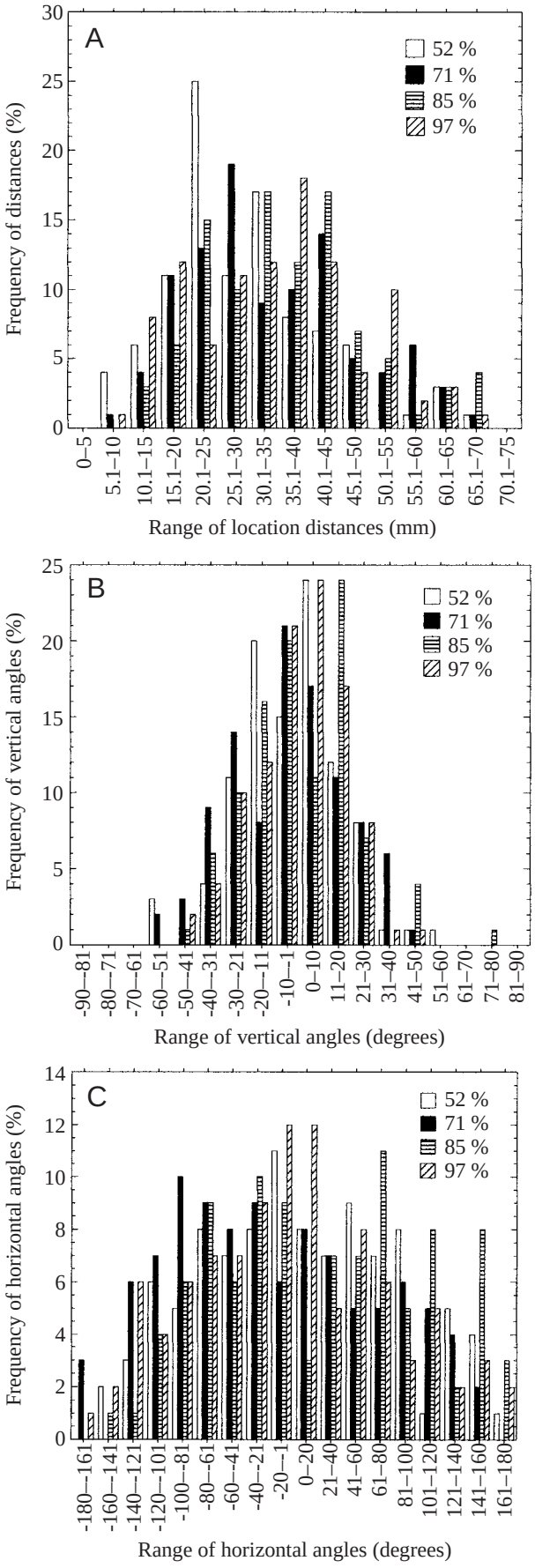

Fig. 3. Frequency distributions of (A) prey location distance, (B) the vertical component of prey location and (C) the lateral component of prey location angle for rainbow trout foraging under short-wavelength light of varying percent polarization (97 %, 85 %, 71 % or 55 %). Individual frequencies are percentage totals from three trials per light condition.

To ensure uniformity of prey size, *Daphnia magna* were serially sieved prior to use. The mean length of the animals' carapace was not significantly different between treatments at α=0.05 level of significance ($F_{5,89}$=1.505, P=0.197, one-way analysis of variance, ANOVA; 15 *Daphnia magna* were measured at the start of experiments during the first 6 days, N=90). The mean carapace length for all measurements was 0.89±0.05 mm (mean ± S.D.).

Videotaped observations of rainbow trout attacks on *Daphnia magna* were analyzed frame-by-frame using tracking software (TRAKFISH; Racca Scientific Consulting) that extracted the three-dimensional path coordinates of each animal simultaneously present on both camera views during the experiment. For every attack, we measured the distance at which the prey was first spotted and the attack launched (prey location distance) and the horizontal and vertical angles of prey location (see Browman et al., 1994). The procedure used to obtain these measurements (from the videotaped experiments) involved the following steps. First, the experimenter visually identified an attack on prey that was visible simultaneously in both camera views. Once an attack had been identified, the videotapes were rewound to determine the exact moment, within 0.01 s resolution, at which the prey was first located (this was clearly identifiable by the posture that the rainbow trout exhibits prior to launching an attack, see Fig. 2B in Browman et al., 1994). At this moment, the distance between predator and prey was measured to obtain prey location distance and angles. Prey location distance and the vertical and horizontal angles between the fish's body axis and the prey item were measured using software (MEASURE; Racca Scientific Consulting) that allowed the spatial three-dimensional orientation of the fish's trunk (its pitch and yaw) to be established relative to the prey item (on a computer screen that displays both orthogonal views simultaneously). The observer then uses the computer's mouse to establish the distance from the fish's snout to the prey item that was attacked (by pointing and clicking at both objects). The software computes the prey location distance and the related prey location angles. Horizontal prey location angles were assigned values of –180° to 180° relative to a straight line along the fish's body axis (0° is straight ahead): a positive angle corresponds to a prey item located to the fish's right, while a negative angle corresponds to a prey item located to the left. Vertical prey location angles were assigned values of –90° to 90° relative to the fish's body axis: a negative angle corresponds to a prey item located below the body axis, while a positive angle corresponds to a prey item located above the body axis.

Three replicate experiments were conducted for each light treatment. For each replicate, attack variables were obtained

for 25 prey-location events. Thus, for a given light treatment, we analyzed 75 attacks on prey.

Statistical analyses

The frequency distributions obtained under white light illumination were analyzed using the Kolmogorov–Smirnov two-sample test (SPSS; procedure K–S, two-tailed) to detect any differences between the polarized and unpolarized conditions. To analyze overall differences between treatments in the percent polarization experiments, we performed a Kruskal–Wallis test on the frequency distributions. If a significant difference was identified, the Kolmogorov–Smirnov two-sample test was then applied to frequency distribution pairs. Watson's two-sample test with ties (Zar, 1999) was applied, in an analogous manner, to the location angle data (vertical and horizontal). In these analyses, every attack sequence was considered an independent observation. This assumption is based on the observation that, once an attack has been launched, the attack sequence is the same irrespective of whether the fish is alone or with others in the aquarium (at least within the predator densities used in this study).

Results

Prey location distances were significantly longer under white polarized compared with white unpolarized light conditions (Fig. 2A; Table 1). The frequency distributions of the vertical component of prey location angle were significantly different between the two conditions (Fig. 2B; Table 1, Table 2); vertical angles of attack were directed more below the body axis under polarized light. The frequency distributions of the horizontal component of prey location angle were only significantly different when compared by circular statistics (Table 2). The average frequency distribution under the polarized condition was more bimodal (with peaks in the ranges –20° to –80° and 20° to 80°) than the corresponding one under the unpolarized condition (which showed maxima near 0°, Fig. 2C).

Under short-wavelength illumination of varying percent polarization, location distances were significantly longer under 97 % and 85 % polarizations than under 52 % polarization (Kruskal–Wallis test, χ^2=11.26, d.f.=3, P=0.01; Table 1, Fig. 3A). The frequency distributions of the vertical (Fig. 3B) and horizontal (Fig. 3C) components of prey location angles were not statistically different [Kruskal–Wallis test (vertical angle), χ^2=2.06, d.f.=3, P=0.56; Kruskal–Wallis test (horizontal angle), χ^2=5.91, d.f.=3, P=0.12; Table 2].

Table 1. *Summary of the Kolmogorov–Smirnov two-sample test applied to the variables measured for rainbow trout alevins foraging under different illumination conditions*

Variable	Illumination	Pol comparison (%)	Z (K–S)	P (two-tailed)	N
Distance	White light	100 *versus* 0	1.535	0.018	150
va	White light	100 *versus* 0	1.594	0.012	150
ha	White light	100 *versus* 0	1.109	0.171	150
Distance	Short wave	97 *versus* 85	0.735	0.653	150
Distance	Short wave	97 *versus* 71	0.735	0.653	150
Distance	Short wave	97 *versus* 52	1.633	0.010	150
Distance	Short wave	85 *versus* 71	0.980	0.292	150
Distance	Short wave	85 *versus* 52	1.715	0.006	150
Distance	Short wave	71 *versus* 52	1.143	0.147	150

Short wave, the short-wavelength (390–413 nm) illumination; Pol, polarization; va and ha, vertical and horizontal components of prey location angle, respectively.

Discussion

Under 100 % linearly polarized illumination, the frequency distribution of prey location distances is skewed towards longer distances compared with that obtained under unpolarized light of the same intensity and spectral distribution. This is as would be expected from foraging theory if prey contrast improves under polarization conditions. Our results therefore support the hypothesis that polarization sensitivity in fishes improves under polarization conditions.

The observation that significantly more attacks were directed downwards than upwards under polarized than unpolarized illumination is consistent with the higher densities of ultraviolet cones in the dorsal retina of young rainbow trout (I.N.F., unpublished observations) and the presumed role of these cones in polarization sensitivity (see Hawryshyn et al., 1990; Parkyn and Hawryshyn, 1993). If the ultraviolet cone is fundamentally involved in polarization sensitivity, then the locations and numbers of this cone type suggest that the

Table 2. *Results of Watson's two-sample test with ties applied to the vertical and horizontal components of attack angle*

Variable	Illumination	Pol comparison (%)	U^2 (Watson)	N
va	White light	100 *versus* 0	0.201	150
ha	White light	100 *versus* 0	0.209	150
va	Short wave	97 *versus* 85	0.067	150
va	Short wave	97 *versus* 71	0.030	150
va	Short wave	97 *versus* 52	0.092	150
va	Short wave	85 *versus* 71	0.061	150
va	Short wave	85 *versus* 52	0.122	150
va	Short wave	71 *versus* 52	0.069	150
ha	Short wave	97 *versus* 85	0.067	150
ha	Short wave	97 *versus* 71	0.021	150
ha	Short wave	97 *versus* 52	0.074	150
ha	Short wave	85 *versus* 71	0.077	150
ha	Short wave	85 *versus* 52	0.149	150
ha	Short wave	71 *versus* 52	0.048	150

Abbreviations as in Table 1.

Only Pol comparisons with $U^2 > U^2_{0.05,75,75}$=0.187 are significantly different from each other.

majority of attacks would be directed in the horizontal and downwards directions (as they are).

The significant difference in the shape of the horizontal angle distribution between polarized and unpolarized conditions may indicate a preferred retinal area for polarization detection. Indeed, the bimodal distribution under polarization illumination with maxima in the range 20–80 ° on either visual field, in combination with the vertical angle results, suggests that the centro–temporo–dorsal retina is the primary site for polarization detection. This suggestion is consistent with anatomical and microspectrophotometric evaluations of the potential for polarization detection by double and corner (ultraviolet) cones in this area of the retina (Novales Flamarique et al., 1998).

The results from the experiments that used short-wavelength illumination of varying percent polarization are more difficult to interpret. The illumination used in this case could not have induced similar potential photon catches for the ultraviolet-, the middle- and the long-wavelength cone mechanisms. Since this balance of inputs from all polarization-sensitive mechanisms appears to be crucial to obtain strong polarization responses, at least during electrophysiological experiments (see Coughlin and Hawryshyn, 1995), the absence of significant differences in the majority of our results may be a consequence of the uneven stimulation of all polarization receptor types. Nonetheless, we did find a significant difference in the frequency distributions of prey location distances between those from the two highest polarizations (97 % and 85 %) compared with that from the lowest one (52 %). Previous electrophysiological (Novales Flamarique and Hawryshyn, 1997) and behavioural (Hawryshyn and Bolger, 1990) experiments have indicated that the threshold for polarization discrimination in rainbow trout is around 60 %. The 52 % polarization used in our experiments may have been below that detectable by the animals. The observation that the frequency distribution of attack distances under 71 % polarization is similar to the frequency distributions of both the low (52 %) and high (85 % and 97 %) polarization conditions (Table 1) may reflect an intermediate point (under the short-wavelength illumination used) at which the advantages of polarization sensitivity start to be lost.

It is important to note that these experiments were carried out under a point-source illumination, a situation that is never encountered in nature (except if detecting light flashes from animals that emit or reflect polarized light). The differences observed between 100 % linearly polarized and unpolarized (or less polarized) light might have been more pronounced if a wide-angle downwelling polarization background had been used instead of a point source. This is because a larger area containing polarization receptors would have been illuminated with a wide-angle background. In nature, the highest percent polarizations occur under such a background, during crepuscular periods (Novales Flamarique and Hawryshyn, 1997). Coincidently, it is during these periods that young salmonids feed intensely on crustacean zooplankton near the water surface (Scarsbrook et al., 1978; Browman and Marcotte, 1986; Marcotte and Browman, 1986), where the percent polarization is sufficiently high for it to be perceived and used (Novales Flamarique and Hawryshyn, 1997).

Polarization sensitivity may provide salmonids with an improved means of locating prey at specific developmental stages, when feeding performance is of primary importance (e.g. at the alevin/parr and reproductive stages). However, it should be emphasized that this is only one small part of a complex sensory system that is used, in part, to locate prey. Young salmonid smolts, with diminished ultraviolet cone populations and, presumably, no polarization sensitivity (Parkyn and Hawryshyn, 1993; Hawryshyn et al., 1990), also feed successfully on crustacean zooplankton. The same is true for many zooplanktivorous freshwater fishes that lack ultraviolet cones after the larval stages (e.g. the sunfishes). Thus, ultraviolet sensitivity and polarization sensitivity are not essential to the foraging success of most fish species: fishes can certainly feed and survive without these sensory capabilities. Understanding the role of ultraviolet and polarization sensitivities in visual function begins by realizing that these sensory channels are not in any way special on their own, but that they complement (and are an integrated part of) the processing taking place in the entire visual system.

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