ULTRAVIOLET PHOTORECEPTION CONTRIBUTES TO PREY SEARCH BEHAVIOUR IN TWO SPECIES OF ZOOPLANKTIVOROUS FISHES

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Summary

We tested the hypothesis that ultraviolet photoreception contributes to prey search in small juvenile rainbow trout (*Oncorhynchus mykiss*) and pumpkinseed sunfish (*Lepomis gibbosus*) while foraging on *Daphnia pulex*. Small individuals of these species are ultraviolet-photosensitive zooplanktivores. For both species, prey pursuit distances and angles were larger under full-spectrum illumination than under ultraviolet-absent illumination. The same was true for the distances and angles associated with repositioning movements (i.e. those not leading to the location of a prey item). Thus, ultraviolet photoreception contributes to prey search and detection in these fishes. We argue that the most likely mechanism underlying this enhancement of prey search abilities is improved target contrast.

Introduction

Ultraviolet photosensitivity has been documented in aquatic crustaceans (Cronin and Marshall, 1989; Cronin, 1990; Smith and Macagno, 1990), insects (Goldsmith and Bernard, 1985; Menzel and Backhaus, 1991), reptiles and amphibians (Jacobs, 1992), fishes (Douglas *et al.* 1989; Douglas and Hawryshyn, 1990), birds (Jacobs, 1992) and some mammals (Jacobs, 1992). All of these animals possess an independent retinal photoreceptor mechanism sensitive in the near ultraviolet (340–400 nm).

For vertebrates, evaluations of the possible adaptive roles of ultraviolet photoreception are rare (Burkhardt, 1982; Finger and Burkhardt, 1994). In some invertebrates and fishes, and possibly birds, the ultraviolet photoreceptor is involved in the detection of, and orientation to, the e-vector of the polarized light field (Rossel and Wehner, 1986; Wehner, 1989; Waldvogel, 1990; Hawryshyn, 1992; Parkyn and Hawryshyn, 1993). In addition, the ultraviolet photoreceptor extends the range of wavelengths and intensities over which

colour discriminations can be made (Jacobs, 1992; Neumeyer, 1992; Coughlin and Hawryshyn, 1993; Finger and Burkhardt, 1994). Several authors have proposed that the ultraviolet photoreceptor mechanism also contributes to the detection of prey during visually guided foraging behaviour, perhaps through contrast enhancement between an ultraviolet-absorbing target (e.g. a zooplankter) and a background rich in ultraviolet veiling illumination (e.g. the upper layers of non-dystrophic water bodies) (Bowmaker and Kunz, 1987; Douglas and Hawryshyn, 1990; Loew and McFarland, 1990; Novales-Flamarique et al. 1992; Novales-Flamarique and Hawryshyn, 1993; Loew et al. 1993). It is this latter issue that we address in this paper.

Small juvenile rainbow trout [*Oncorhynchus mykiss* (Walbaum)] and pumpkinseed sunfish [*Lepomis gibbosus* (Linnaeus)] possess a retinal photoreceptor mechanism sensitive to ultraviolet wavelengths (λ_{max}=360–370 nm) (Hawryshyn *et al.* 1989; Hawryshyn and Harosi, 1994, for rainbow trout; E. R. Loew, personal communication, for pumpkinseed). Small juveniles of these species are zooplanktivorous (Johnson and Ringler, 1980; Vinyard, 1980; Lazzaro, 1987), and our preliminary observations indicated that both species search for prey using a pause–travel movement pattern. Pause–travel searchers scan for prey throughout the scan space, but only during the brief stationary periods that punctuate repositioning movements. If prey are not located, the animal moves a short distance, stops, and scans again (see Tye, 1989; Bell, 1990; O'Brien *et al.* 1990). For pause–travel searchers, the pattern of movements (distances and angles) associated with prey locations (i.e. 'pursuits'), and with repositioning movements (i.e. 'moves' not associated with prey locations), are strongly correlated with their visual abilities (O'Brien *et al.* 1989, 1990; Bell, 1990; Browman *et al.* 1990). When prey items are larger and/or more visible, the distances and angles at which they are located increase (Bell, 1990; Browman *et al.* 1990; O'Brien *et al.* 1990). Typically, the pattern of repositioning movements – the distances and angles associated with the many changes of position along a search trajectory – is also related to prey size and visibility (Bell, 1990; O'Brien *et al.* 1990).

Following from these observations, we hypothesized that, if ultraviolet photoreception contributes to prey search, then (1) prey location distances and angles should be greater under full-spectrum illumination than under ultraviolet-absent illumination; (2) repositioning move lengths and angles should also be greater under full-spectrum illumination than under ultraviolet-absent illumination. These hypotheses were tested in the experiments reported here.

Materials and methods

Experimental protocol

We used small juvenile rainbow trout (3.8±0.1 cm total length) and pumpkinseed sunfish (3.4±0.1 cm total length) in these experiments. Three fish (starved for 24 h prior to the experiment) were placed in a 30 cm×30 cm×30 cm all-glass observation tank at least 1 h prior to each experiment. Three replicate experiments were conducted for each of the two illumination conditions, ultraviolet-present compared with ultraviolet-absent (see below). In each experiment, foraging behaviour was videotaped for 30 min.

The observation tank was filled to a depth of 15 cm and its sides were covered with black plastic. Water temperature was 15±1 °C. At the beginning of an experiment, prey items (*Daphnia pulex*) were introduced to the observation aquarium at an abundance of 1001^{-1}, determined by counting them individually. Prey were uniformly distributed when introduced and no clumping of prey was apparent during the experiments. To ensure uniformity of prey size in all experiments (before their introduction), *Daphnia* were serially sieved and the carapace lengths of ten individuals were measured under a dissecting microscope using an ocular micrometer.

The *D. pulex* used in the rainbow trout experiments were 1.25±0.16 mm (mean ± 1 S.E.M.) and 1.28±0.16 mm for the ultraviolet-present and ultraviolet-absent conditions, respectively. The *D. pulex* used in the pumpkinseed experiments were 1.17±0.27 mm and 1.21±0.30 mm for the ultraviolet-present and ultraviolet-absent conditions, respectively.

Light environment

All experiments were conducted in a completely dark room in which the only illumination was provided by a tungsten lamp (250 W quartz tungsten halogen bulb). For experiments conducted under full-spectrum illumination (ultraviolet-present), the tungsten lamp was positioned so that it illuminated the observation aquarium uniformly. For experiments conducted in the absence of ultraviolet illumination (ultraviolet-absent), the tungsten source was projected through a 450 LP interference filter (Corion). Total photon flux in both of these situations was matched by altering the voltage delivered to the tungsten source. Total irradiance being delivered to the aquarium during each experiment was measured using a radiometer (Photodyne Inc.), and the exact spectral composition of the lighting conditions produced in these two situations was measured using a Li-Cor LI-1800 underwater spectroradiometer (Biggs, 1984).

Total photon fluxes in the ultraviolet-present and ultraviolet-absent lighting conditions were 18.89 and 18.90 log photons $m^{-2} s^{-1}$, respectively. The integrated irradiance (below 450 nm) for the ultraviolet-present condition was 16.53 log photons $m^{-2} s^{-1}$, while that for the ultraviolet-absent condition was 15.89 log photons $m^{-2} s^{-1}$. Thus, the spectral composition of the two light environments was such that the probability of a photon being absorbed by the ultraviolet photoreceptor was higher in the ultraviolet-present than in the ultraviolet-absent condition (Fig. 1).

Observations and analysis of foraging and search behaviour

Silhouette (shadow) video photography was used to record the foraging and prey search behaviour of juvenile rainbow trout and pumpkinseed sunfish. This method has several advantages over standard cinegraphic or video techniques. First, it can be used to make detailed observations of small transparent organisms such as small fish and their prey (e.g. Arnold and Nutall-Smith, 1974; Drost, 1987; Browman and O'Brien, 1992*a,b*). Second, events can be filmed in a large depth of field (approximately 15 cm) with a relatively large field of view (18 cm); free-swimming predators and their prey can be viewed under laboratory conditions. Third, magnification is independent of distance from
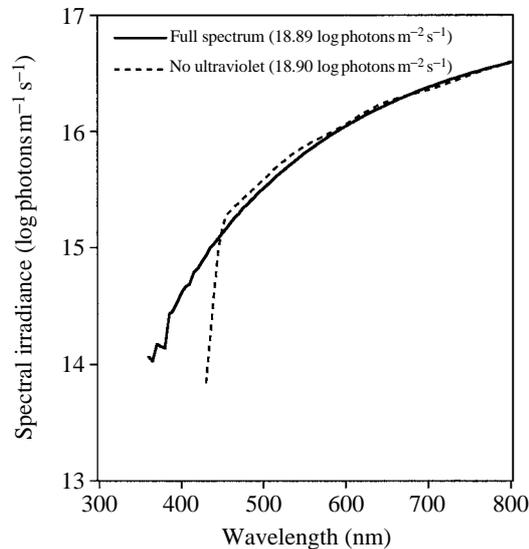
Fig. 1. Spectral composition of the lighting conditions in the ultraviolet-present *versus* ultraviolet-absent experiments, measured with a Li-Cor LI-1800 spectroradiometer.

the camera, and the resolution of the system is extremely good; objects as small as 0.2 mm in diameter can be resolved. The system was configured for imaging in the vertical plane (from above). Only images from the central 15 cm of the 30 cm observation tank were analyzed. More complete technical details on the system used here have been published elsewhere (Browman *et al.* 1989).

The videotapes were analyzed frame-by-frame on a video monitor using a Panasonic AG-1950 video tape machine. All time intervals were measured in increments of 0.033 s. For each experiment, a videotaped ruler established conversions from monitor units to millimetres. Sequences in which movement in the vertical plane exceeded 5–10 ° from horizontal were not included in the analysis (approximately 5 % of all sequences).

Search behaviour was analyzed by assigning the activities of the fish to one of the components of their predation cycle: move or prey pursuit (Fig. 2A). A move is operationally defined as a repositioning (i.e. swimming) movement that neither precedes a prey location nor ends in an attack on a prey item. Thus, move distances are the lengths of swim paths that connect two changes in direction (Fig. 2B). A pursuit is a swimming movement that follows a prey location and ends in an attack. The distance between the point at which the fish first reacts to a prey item and the position of the prey itself is the pursuit distance. Thus, operationally and for the purposes of this analysis, pursuit distance is interpreted as being equivalent to prey location distance.

Move and pursuit distances and angles were measured (Fig. 2B). The longitudinal body axis of the fish was defined as the central axis of the forward-directed visual field (i.e. 0 ° from forward-directed). Thus, pursuit angle is defined as the angle between the central axis of the fish prior to pursuit and the line connecting the fish's rostrum to the
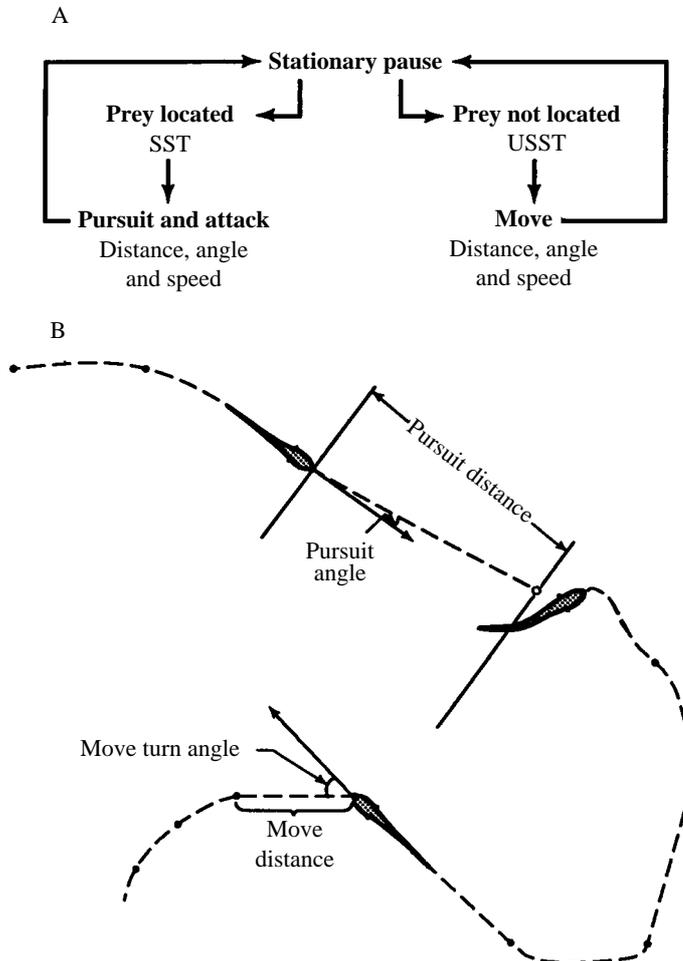
A

Stationary pause

Prey located
SST

Prey not located
USST

Pursuit and attack
Distance, angle
and speed

Move
Distance, angle
and speed

B

Pursuit distance

Pursuit
angle

Move turn angle

Move
distance

Fig. 2. (A) Flow chart of the predation cycle for juvenile zooplanktivorous rainbow trout and pumkinseed sunfish. SST, successful search time; USST, unsuccessful search time. Note that these variables were not measured in this study. (B) A typical search path and attack sequence for rainbow trout and pumpkinseed sunfish, illustrating the measurements drawn from it. The solid dots along the dashed line represent stationary pauses. The open dot represents a prey item. (Reprinted, with the permission of the publisher, from Browman and O'Brien, 1992*a*, Fig. 1.)

position of the prey, both of which are clearly visible on the screen (Fig. 2B). Move turn angles were measured as the angle between the fish's body axis at one position and the position of its rostrum just prior to the next change of direction (Fig. 2B).

We used the Kolmogorov–Smirnov two-sample test (SPSS, procedure K-S, two-tailed) to evaluate whether there was a difference in the frequency distributions of move and pursuit distances and angles under ultraviolet-present *versus* ultraviolet-absent light conditions.

Results

Both rainbow trout and pumpkinseed sunfish employed a typical pause–travel movement pattern while searching for prey. Repositioning movements and prey locations (pursuits) were always preceded by stationary pauses during which individuals scanned for prey. Further, the frequency distributions of repositioning move distances and angles were related to those for pursuit distances and angles (Figs 3–6).

For rainbow trout, the frequency distributions of pursuit distances in the ultraviolet-present *versus* the ultraviolet-absent conditions were not statistically different (Kolmogorov–Smirnov $Z=1.131$, two-tailed $P=0.154$, $N=141$) (Fig. 3A). The frequency distributions of move distances under the two lighting conditions were statistically different (Kolmogorov–Smirnov $Z=1.344$, two-tailed $P=0.054$, $N=134$): there were relatively more long move distances in the presence of ultraviolet illumination (Fig. 3B).
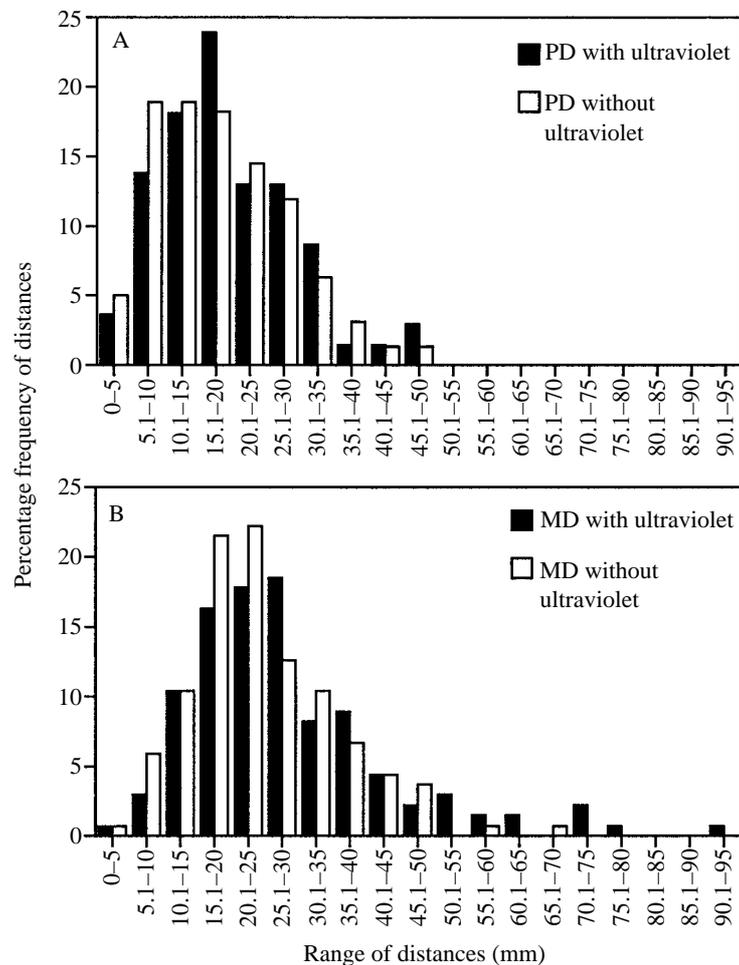

Fig. 3. Frequency distributions of (A) pursuit distances (PD) and (B) move distances (MD) for small juvenile zooplanktivorous rainbow trout foraging under full-spectrum or ultraviolet-absent illumination.

The frequency distributions of pursuit angles under the two lighting conditions were statistically different (Kolmogorov–Smirnov $Z=1.565$, two-tailed $P=0.015$, $N=138$): pursuit angles were larger under ultraviolet illumination (Fig. 4A). The same was true for move angles (Fig. 4B; Kolmogorov–Smirnov $Z=1.894$, two-tailed $P=0.002$, $N=134$).

For pumpkinseed sunfish, the frequency distributions of pursuit distances in the ultraviolet-present *versus* the ultraviolet-absent conditions were statistically different (Kolmogorov–Smirnov $Z=2.268$, two-tailed $P<0.0001$, $N=111$): pursuit distances were longer in the presence of ultraviolet illumination (Fig. 5A). The frequency distributions of move distances under the two lighting conditions were statistically different (Kolmogorov–Smirnov $Z=1.907$, two-tailed $P=0.001$, $N=133$), with longer move distances occurring in the presence of ultraviolet illumination (Fig. 5B). Pursuit angles were also larger under ultraviolet illumination (Fig. 6A), and the frequency distributions
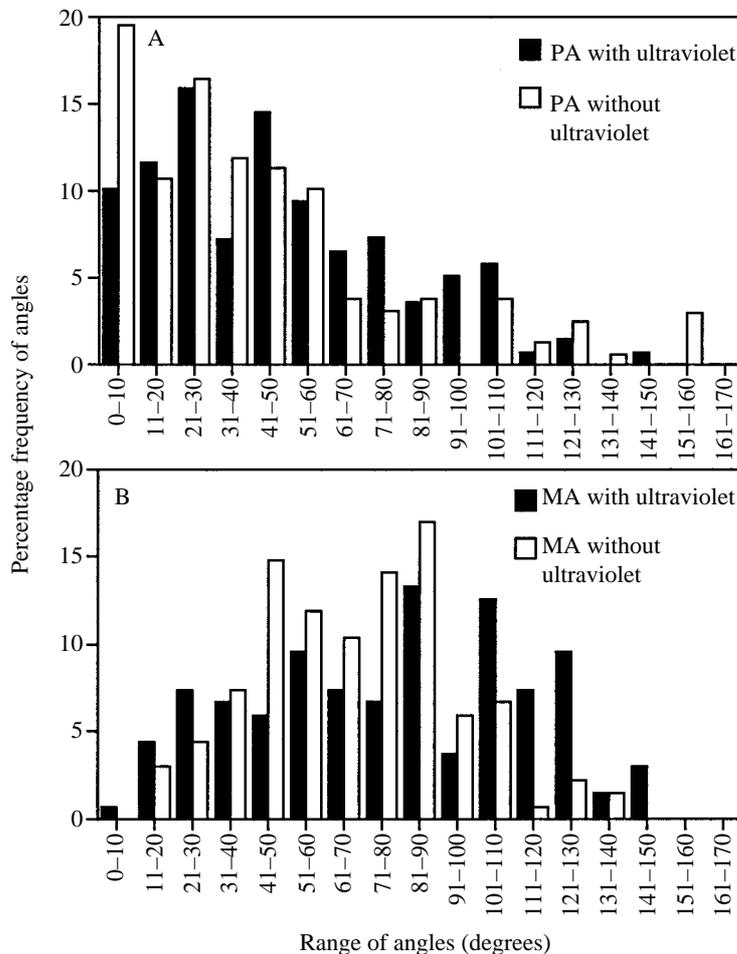
Fig. 4. Frequency distributions of (A) pursuit angles (PA) and (B) move angles (MA) for small juvenile zooplanktivorous rainbow trout foraging under full-spectrum or ultraviolet-absent illumination.
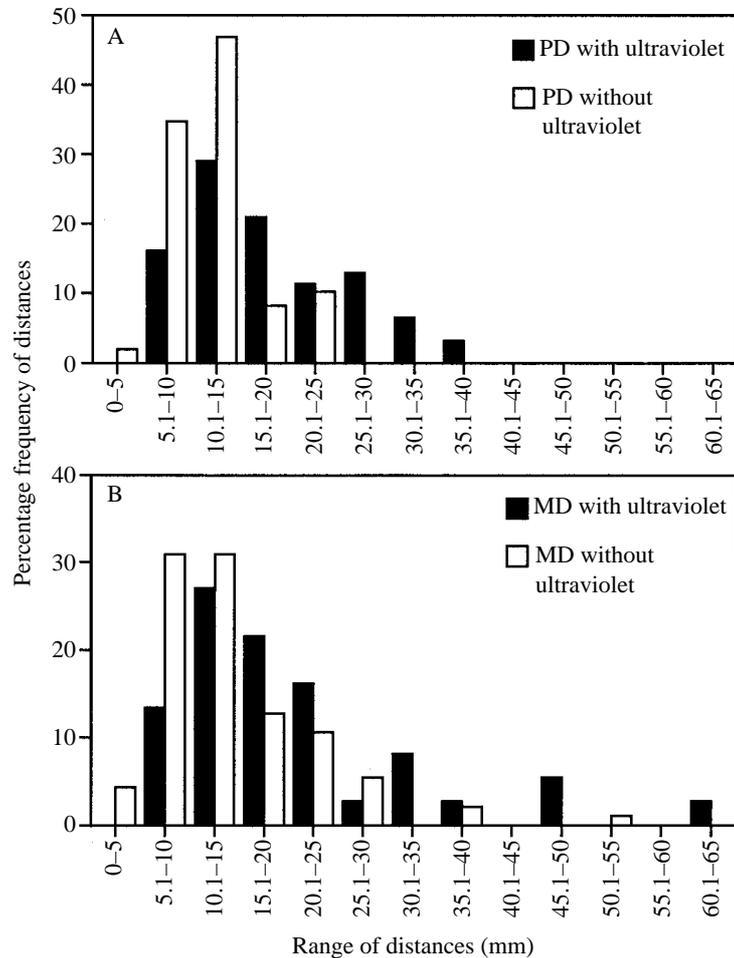
Fig. 5. Frequency distributions of (A) pursuit distances (PD) and (B) move distances (MD) for small juvenile zooplanktivorous pumpkinseed sunfish foraging under full-spectrum or ultraviolet-absent illumination.

of pursuit angles under the two lighting conditions were statistically different (Kolmogorov–Smirnov $Z=2.668$, two-tailed $P=0.0001$, $N=109$). The same was true for move angles (Fig. 6B; Kolmogorov–Smirnov $Z=1.321$, two-tailed $P=0.061$, $N=135$).

Discussion

These results are consistent with the hypothesis that ultraviolet photoreception contributes to prey search in small zooplanktivorous fishes. Although they can certainly search for and locate prey items in the absence of ultraviolet illumination, absorption of ultraviolet radiation by the retina of juvenile rainbow trout and pumpkinseed sunfish improves their prey search performance. Further, juvenile yellow perch (*Perca*
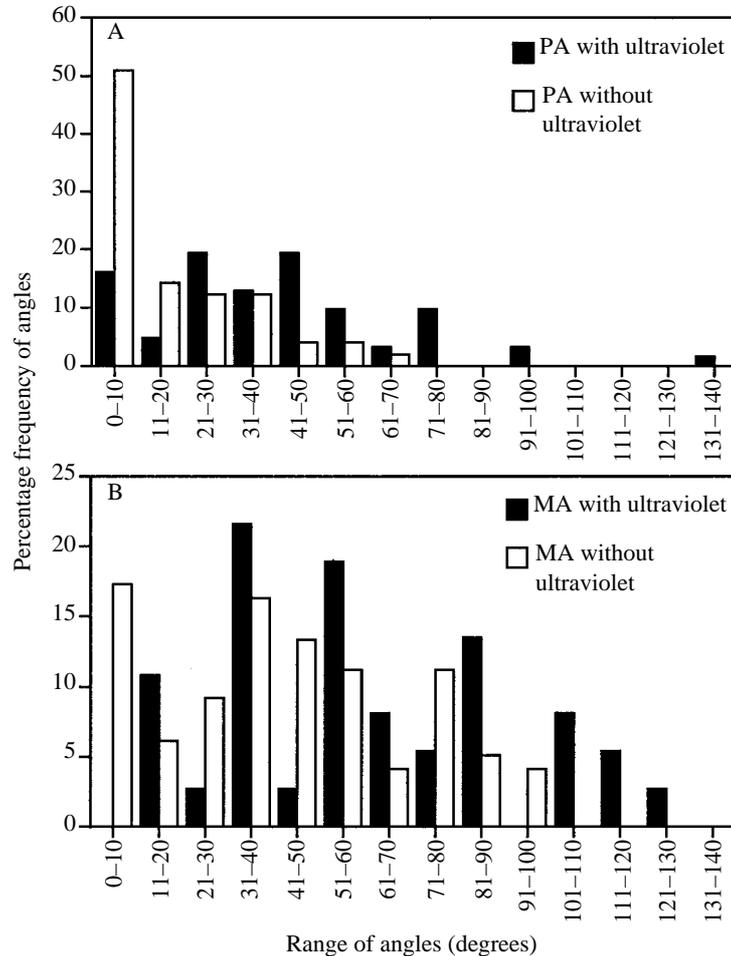
Fig. 6. Frequency distributions of (A) pursuit angles (PA) and (B) move angles (MA) for small juvenile zooplanktivorous pumpkinseed sunfish foraging under full-spectrum or ultraviolet-absent illumination.

flavescens), whose retina possesses an ultraviolet photoreceptor, are able to locate, pursue and attack prey items while foraging under monochromatic ultraviolet illumination (Loew *et al.* 1993). These observations support the contention that, in fishes that possess it, the ultraviolet photoreceptor plays a direct role in prey search and detection.

Under the experimental conditions that we used, the contribution of the ultraviolet photoreceptor to the prey search pattern of rainbow trout was not as clear as that for pumkinseed sunfish. A clearer response might have been generated through a three-dimensional analysis of search paths and/or by having generated a greater difference in the number of ultraviolet photons available in the ultraviolet-present *versus* the ultraviolet-absent conditions.

The high degree of scatter of ultraviolet photons by water significantly degrades

the quality of images produced by ultraviolet photoreceptors (Loew and McFarland, 1990; Novales-Flamarique *et al.* 1992; Novales-Flamarique and Hawryshyn, 1993). Further, the spatial acuity of the ultraviolet cone mechanism in fishes is poorer than that for the other cone mechanisms (Hawryshyn, 1991). Thus, for these fishes, the ultraviolet photoreceptor's role in prey detection is probably one of target contrast enhancement, through a combination of luminance and colour contrast (see Hawryshyn *et al.* 1988).

There are at least two mechanisms through which the ultraviolet cone mechanism could improve prey contrast. A prey item that differentially absorbs ultraviolet radiation will appear as a dark object against a background rich in ultraviolet photons. This effect would be most pronounced when the target is viewed from below, since downwelling light is relatively rich in ultraviolet radiation (see Novales-Flamarique *et al.* 1992; Novales-Flamarique and Hawryshyn, 1993). Alternatively, a prey item that differentially scatters ultraviolet radiation will appear brighter against a background poorer in ultraviolet photons. This latter effect would be particularly pronounced if the target (i.e. the prey item) were located from above, since upwelling light contains less ultraviolet radiation (see Novales-Flamarique *et al.* 1992; Novales-Flamarique and Hawryshyn, 1993). Electrophysiological recordings from ultraviolet-sensitive fibres in the rainbow trout visual system demonstrate that ultraviolet-sensitive cells respond primarily to increments in light intensity, i.e. with ON responses (Beaudet *et al.* 1993; Coughlin and Hawryshyn, 1993). Thus, ultraviolet-sensitive visual units are well-suited to detect targets against backgrounds of different luminance and/or colour.

It is noteworthy that a common prey item for juvenile zooplanktivorous fishes, the phantom midge (*Chaoborus* sp.), which rises to the surface from the bottom sediments of lakes and is located and captured by fishes along the way, possesses a carapace that is highly reflective of ultraviolet radiation (Giguere and Dunbrack, 1990). Further, many aquatic crustaceans absorb ultraviolet radiation and some, including *Daphnia magna*, themselves possess an ultraviolet photoreceptor (Smith and Macagno, 1990). Thus, for a fish foraging in open water, there are a number of possible target contrast mechanisms operating in the ultraviolet part of the spectrum that may serve to enhance their prey detection abilities.

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