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# Evidence for behavioral sensitivity to near-UV light in the deep-sea crustacean *Systellaspis debilis*

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**Abstract.** The role of UV light in the deep-sea environment has been discounted in the past, due to the assumptions that (1) there is insufficient UV light available for vision and, therefore (2) deep-sea organisms would not be sensitive to these wavelengths. A recent study that employed electrophysiological techniques on dark-captured deep-sea crustaceans demonstrated that several species of deep-sea crustaceans possess very high sensitivity to near-UV light. The current study was undertaken to determine if near-UV light would also elicit a behavioral response from these species. The species studied was *Systellaspis debilis*, an oplophorid shrimp whose daytime depth ranges from 600 to 700 m. A method for tethering shrimp was developed which allowed them to freely orient in response to changes in the ambient light field. Behavioral responses to changes in ambient light included changes in body tilt with respect to the horizontal plane, changes in swimming speed, and movement of the feeding appendages. These experiments, the first of their kind on a deep-sea organism, demonstrate that behaviorally, *S. debilis* is equally sensitive to very low intensities of blue-green and near-UV light.

## Introduction

Previous electrophysiological studies on the eyes of deep-sea shrimp determined that several species in the family Oplophoridae possess two peaks in their spectral sensitivities (Frank and Case 1988). One peak was in the blue-green (500 nm), as expected for organisms with daytime depths of 600 m, but the other peak was in the near-UV (370 to 400 nm), a surprising and puzzling discovery. The function of this near-UV photopigment is not known. However, it was noted that, of the species tested, those which possessed the near-UV photopigment shared two characteristics that were not consistently found in the species lacking this photopigment: (1) they possess bioluminescent photophores and (2) they are vertical migrators. Before further contemplating the functional significance

of near-UV sensitivity to either of these systems, it is necessary to demonstrate that these organisms will respond behaviorally to near-UV light. This requires laboratory studies with a controlled and calibrated light field, a difficult proposition for deep-sea pelagic species, which are profoundly disoriented by contact with surfaces. We have developed a methodology for tethering deep-sea crustaceans in such a way that they can freely orient to changes in the ambient light field without the disruptive influence of surface contacts. The species used in this study was *Systellaspis debilis*, a bioluminescent, vertically migrating shrimp which possesses the unusual high sensitivity to near-UV light mentioned above (Frank and Case 1988). We find that the behavioral sensitivity of *S. debilis* to near-UV light is approximately the same as its sensitivity to blue-green light.

## Materials and methods

### Collection

*Systellaspis debilis* was collected from Northwest Providence Channel, Bahamas, with an 8' × 6' (2.44 × 1.83 m) Tucker Trawl, fitted with an opaque, thermally protected collecting container. Collections were made on four cruises between March and November in 1992, within a 10 mile radius of 26°21'N and 78°17'W. The shrimp were collected at night from depths of 150 to 200 m. Both the net and collection container were closed at depth, preventing exposure of the organisms to damaging surface light. Previous electrophysiological experiments showed that exposure to moonlight or the ship's lights was sufficient to cause a lasting decrease in sensitivity (own unpublished data). The collection container was opened in the dark, shrimp were sorted out under dim red light, transferred to ~1-liter containers containing ambient (19°C) seawater, and maintained with aeration in light-tight boxes at 13°C for transport back to land.

### Maintenance

*Systellaspis debilis* was maintained in light-tight containers of seawater, with aeration, at 13°C. Due to their high metabolic rate, it was necessary to change the water on a daily basis, otherwise high rates of mortality occurred. They were fed frozen shrimp and fish

which were collected on the same trawls as *S. debilis*. Initial attempts at feeding by placing small chunks of shrimp or fish in contact with the mouthparts were unsuccessful. The food was rejected and all the shrimp died within two weeks. However, with subsequent experimentation, it was found that feeding responses could be stimulated by squirting a small volume of seawater, containing a slurry of mashed shrimp and fish, onto the feeding appendages. When chunks of food were subsequently placed in contact with the pleopods, the food was accepted and at least partially ingested. Observations on the production of fecal pellets the day after each feeding supported this conclusion. Feeding and water changes were carried out under dim red light. Under these conditions, most shrimp survived for 3 to 4 wk, although several survived for 5 wk. All experiments were conducted within the first 2 wk after collection.

## Experimental procedure

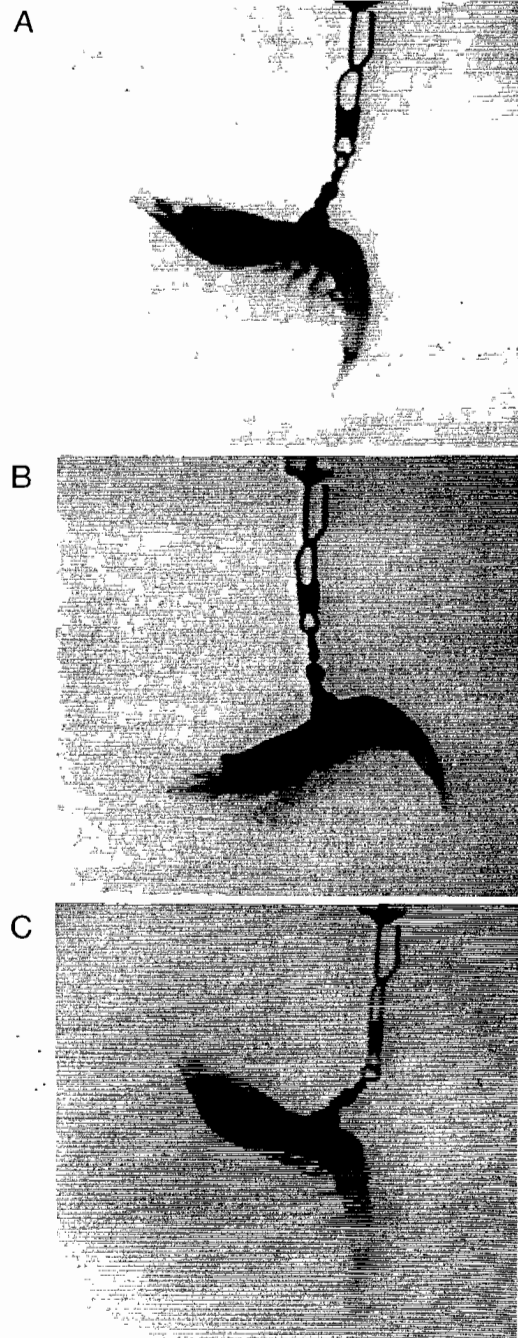
### Tethering

It is extremely difficult, if not impossible, to study behavioral responses of an unrestrained pelagic organism in laboratory tanks. These organisms come from an environment without surfaces, and contact with surfaces such as the walls or air/water interface in a tank disorient them. When introduced into a tank, *Systellaspis debilis* swims rapidly until it contacts a surface, and then plummets to the bottom of the tank, remaining there regardless of changes in ambient light, temperature or the introduction of food. In order to examine their behavioral responses to changes in the ambient light environment, we developed a method for tethering *S. debilis* that allowed them to rotate freely in both the vertical and horizontal planes without contacting a surface. Stainless steel swivels, removed from #1 Snap Swivels, were attached to the mid-dorsal surface of the shrimp with cyanoacrylic glue. The loop at the end of the swivel was suspended from a hook on a Plexiglas rod mounted in the lid of the experimental tank. A rigid tether that prevented vertical displacements was necessary because experimentation with a flexible tether, i.e., monofilament line, demonstrated that when the shrimp reached the end of the tether, it was disoriented by the sudden restraint. It jerked back in response to the restraint, momentarily stopped swimming, then resumed swimming until it reached the end of the tether, and repeated the cycle. Observations of five organisms indicated that this sudden restraint, regardless of the length of the tether, obliterated any meaningful responses to changes in the ambient light field. The snap-swivel arrangement allowed the shrimp freedom to tilt up or down, as well as roll and rotate around the horizontal axis. There was no increase in mortality after stainless steel swivels had been attached, but brass swivels proved to be uniformly toxic.

### Chamber

The experimental chamber was a Plexiglas box (30 × 30 × 30 cm), placed in the center of a much larger Plexiglas water bath (62 × 62 × 62 cm), such that the walls of the outer chamber were outside the critical angle as viewed from the position of the shrimp (after Forward et al. 1984). Both chambers were filled with seawater to the same level, and the temperature was kept at 13°C by chilling the water in the water bath.

The illumination was designed to produce a diffuse downwelling light field (after Forward et al. 1984). The light source was a slide projector, filtered with a heat filter and a 400 nm (Melles Griot, FWHM = 40 nm) or a 500 nm (FWHM = 40 nm) interference filter. The light was directed onto a mirror, which reflected the light down over the tank. A white Plexiglas (#2447) cover on the tank served as a diffuser. Irradiance was measured at the position of the shrimp with a LI-COR underwater quantum sensor. Corrections for wavelengths below 400 nm were made with a multichannel (1024 element CCD array) spectrometer (Ocean Optics Inc., Model S1000).



**Fig. 1.** *Systellaspis debilis*. Responses to changes in ambient light. (A) During 2 min interval between light stimuli, *S. debilis* remains in relatively level orientation with respect to horizontal, with pleopods beating; this photograph was taken 1 s before light stimulus. (B) In response to bright-light stimulus (500 nm,  $7.5 \times 10^8$  photons  $\text{cm}^{-2} \text{s}^{-1}$ ), *S. debilis* tilts downward, pleopods cease all movement, and feeding appendages become visible; this photograph was taken 1 s after initiation of light stimulus. (C) After cessation of light stimulus, pleopods start beating rapidly and *S. debilis* orients upward; this photograph was taken 1 s after cessation of light stimulus. Identical responses were observed in response to a bright 400 nm light

The shrimp was illuminated from the side of the tank with light filtered through a Kodak Wratten Infrared Filter (#89B), which passed wavelengths that were invisible to the shrimp. The responses of the shrimp were imaged with an IR video camera, displayed on a TV monitor, and recorded on video tape for later analysis.

The walls of the tanks were left transparent, and experiments were carried out in a light-tight room with black walls. The light sources and video system were placed behind light-tight partitions.

### Procedure

The swivels were attached several days prior to an experiment. The shrimp was removed from the holding chamber and tethered in the experimental chamber under dim red light. After a 1 h acclimation period, the responses of the shrimp to various irradiances of 400 or 500 nm light were tested. The test flash duration was 15 s and the period between test flashes was 2 min. The stimulus irradiances were randomized and tested repeatedly throughout an experiment.

### Data analysis

The video tapes were played back on a video editor, which allowed frame-by-frame analysis. After observing numerous responses to the stimulus flashes, it became apparent that there were three behaviors which could be correlated with a change in the ambient light field: change in swimming speed, change in the degree of tilt (with respect to the horizontal), and movement of the feeding appendages (3rd maxilliped, 1st and 2nd chelipeds). In order to quantify the response to the light stimulus, the behavior of the shrimp during the stimulus was compared to that recorded during the 5 s interval prior to, and the 5 s interval after, the light stimulus. The absolute magnitude of the change in tilt proved to be highly variable, and could not be correlated with irradiance levels. Therefore, only the direction of the tilt change – up or down – was recorded. Swimming speed was recorded as pleopod beats  $s^{-1}$ . Movement of the feeding appendages was not quantified, but merely recorded with respect to onset of movement.

### Results

We did not provide any type of Zeitgeber to maintain circadian changes in activity or visual sensitivity of *Systellaspis debilis*; the shrimp were maintained on a 24 h dark cycle. However, in order to determine if time of day affected the results of the experiment, five shrimp were tested twice, once during the day and once at night. The intervals between the first and second tests were 5, 9, 17, 19, and 81 h. No significant difference was found between tests conducted during the day and at night (Student's *t*-test;  $p \leq 0.05$ ). Therefore, the results of 14 experiments of 9 shrimp were combined for the analysis.

The behavioral responses to the light stimuli were a function of the intensity of the light. In the dark, *Systellaspis debilis* maintained a fairly level orientation with respect to the horizontal, slowly fanning its pleopods (Fig. 1A). At the highest intensities, *S. debilis* changed its angle of tilt with respect to the horizontal (Fig. 1B), ceased swimming completely, and initiated rapid movement of its previously immobile feeding appendages. When the light was extinguished, the shrimp responded with changes in tilt and swimming speed (Fig. 1C). Since feeding appendage activity usually ceased during the light stimulus, cessation of this activity was not considered a quantifiable response. At lower light intensities, the shrimp changed its angle of tilt and reduced its swimming speed, but did not cease swimming entirely. Feeding appendage activity was observed ~75% of the time. At the lowest intensities, only a change in tilt or swimming speed was observed in response to initiation of the light, and no responses were seen in response to cessation of the light stimulus. Based on these observations, the responses to the light stimuli were scored according to the following protocol:

Light on: change in degree of tilt = 1; change in swimming speed = 1; swimming ceases completely = 1; feeding appendages start to move = 1.

Light off: change in degree of tilt = 1; change in swimming speed = 1.

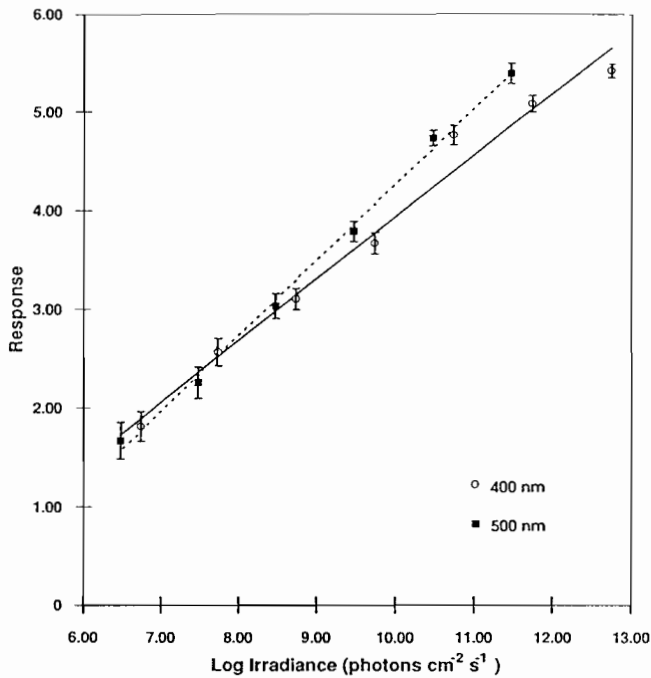
A maximum score of 6 was possible. As stated above, 5 or 6 of these behaviors were usually observed at the highest intensities, while only 1 or 2 were observed at the lowest intensities. Results of this analysis are shown in Table 1.

The data from Table 1 were plotted as response vs log irradiance. Regression equations were calculated for each data set utilizing an iterative process until the best fit was obtained (Zar 1974). The best fit in both cases was a simple regression (Fig. 2). The regression slopes and elevations were not significantly different at the  $p \leq 0.05$  level of significance (Student's *t*-test), indicating that under these conditions *Systellaspis debilis* has approximately the same sensitivity to near-UV light as to blue-green light.

In this analysis, any response to the initiation or cessation of the light stimulus was scored as a positive response. However, it became clear that the responses to the initiation of light were consistently different from those in re-

**Table 1.** *Systellaspis debilis*. Responses to different irradiances of light at two wavelengths. *N*: no. of experiments; Response: mean response utilizing scoring system described in "Results"; maximum score of 6 was possible

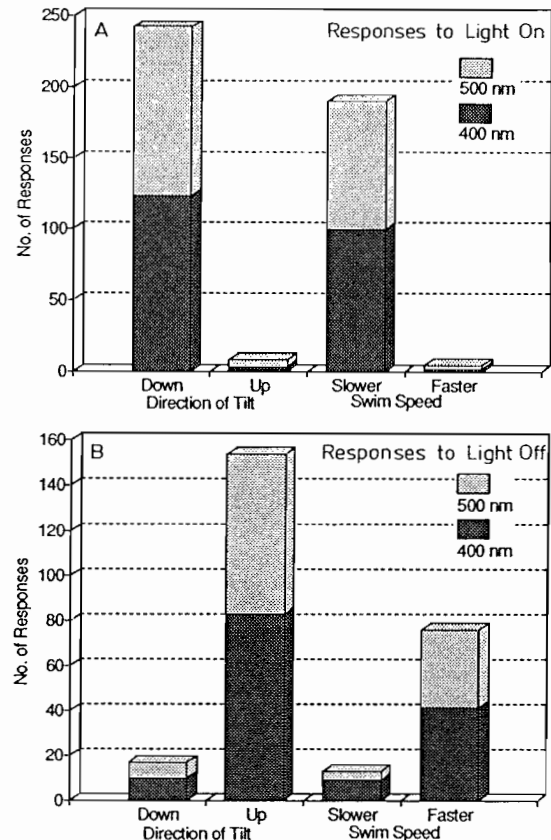
400 nm light			500 nm light		
( <i>N</i> )	Irradiance (photons $cm^{-2} s^{-1}$ )	Response (mean $\pm$ SD)	( <i>N</i> )	Irradiance (photons $cm^{-2} s^{-1}$ )	Response (mean $\pm$ SD)
(11)	$5.5 \times 10^{12}$	$5.42 \pm 0.070$	(12)	$3.0 \times 10^{11}$	$5.39 \pm 0.103$
(12)	$5.5 \times 10^{11}$	$5.08 \pm 0.085$	(12)	$3.0 \times 10^{10}$	$4.73 \pm 0.079$
(12)	$5.5 \times 10^{10}$	$4.76 \pm 0.097$	(12)	$3.0 \times 10^9$	$3.79 \pm 0.102$
(13)	$5.5 \times 10^9$	$3.67 \pm 0.107$	(12)	$3.0 \times 10^8$	$3.03 \pm 0.126$
(13)	$5.5 \times 10^8$	$3.10 \pm 0.108$	(12)	$3.0 \times 10^7$	$2.25 \pm 0.157$
(12)	$5.5 \times 10^7$	$2.56 \pm 0.141$	(12)	$3.0 \times 10^6$	$1.48 \pm 0.185$
(10)	$5.5 \times 10^6$	$1.81 \pm 0.148$			



**Fig. 2.** *Systellaspis debilis*. Response vs log irradiance at two wavelengths. Each data point represents mean  $\pm$  SE of 12 experiments. Total of 14 experiments were conducted, but meaningful data could not be obtained at every intensity in every experiment, primarily because the shrimps were occasionally in positions where pleopod beats could not be counted, or degree of tilt could not be clearly observed. Lines are calculated regression lines utilizing equation  $y = -2.327 + 0.626(x)$  for 400 nm data, and  $y = -3.397 + 0.766(x)$  for 500 nm data. Statistical analysis (Student's *t*-test) demonstrated that slopes are not significantly different at  $p \leq 0.05$  level of significance

response to the cessation of light. Out of 251 light (both 400 and 500 nm) stimuli that produced a discernible change in tilt, 242 (96%) of these were in the downward direction (Fig. 3A). Similarly, extinguishing the light produced a discernible response 171 times, and 154 (90%) of these were in the upward direction (Fig. 3B). A similar light-specific response was seen with respect to swimming speed. Turning the light on produced a slowing or cessation of swimming 97% of the time (190 out of 195 responses: Fig. 3A), while extinguishing the light resulted in increased swimming activity 85% of the time (76 out of 89 responses: Fig. 3B).

The lowest irradiance of 400 nm light that was repeatedly tested was  $5.5 \times 10^6$  photons  $\text{cm}^{-2} \text{s}^{-1}$ . A total of 6 individuals were tested at this irradiance, and 4 demonstrated behavioral sensitivity to this irradiance level. The lowest irradiance of 500 nm light repeatedly utilized was  $3.0 \times 10^6$  photons  $\text{cm}^{-2} \text{s}^{-1}$ , and 4 out of 6 individuals responded behaviorally at this irradiance. One specimen proved to be extremely sensitive, demonstrating distinct behavioral responses to both the initiation and cessation of 400 nm light at an irradiance of  $5.5 \times 10^4$  photons  $\text{cm}^{-2} \text{s}^{-1}$ , which was the lowest irradiance we were able to provide. The lowest possible irradiance of 500 nm light,  $3.0 \times 10^4$  photons  $\text{cm}^{-2} \text{s}^{-1}$ , also produced a response at the initiation of the light stimulus, but no response was seen at the cessation of the light.



**Fig. 3.** *Systellaspis debilis*. Differing responses to initiation and cessation of 400 and 500 nm light. Results are from same experiments and range of intensities shown in Table 1. (A) Initiation of light stimulus produced downward tilt with respect to horizontal together with decrease in swimming speed. (B) Cessation of light stimulus routinely produced opposite response – upward tilt together with increase in pleopod movements. No differences were discernible in the responses to 400 nm vs 500 nm light

## Discussion

Many crustaceans, such as crayfish (Goldsmith and Fernandez 1968, Wald 1968), estuarine shrimp (Goldsmith and Fernandez 1968, Wald and Seldin 1968), lobsters (Cummins et al. 1984), and shallow-water crabs (Wald 1968) possess photoreceptors with short-wavelength sensitivity. Although the function of these photoreceptors has not been established, these species live in shallow waters where UV light is expected to be a part of the ambient light field.

The discovery of near-UV spectral sensitivity in deep-sea crustaceans (Frank 1986, Frank and Case 1988) is remarkable in several respects. Firstly, the visual environment of the deep sea is generally described as being confined to a relatively narrow waveband, centered at 475 nm (Jerlov 1976, Denton 1990). Available light from bioluminescence is also confined to this transmission window; the luminescent emissions of most pelagic species have maxima in the range of 450 to 490 nm (Herring 1983, Widder et al. 1983). Secondly, as a general rule, there is a significant correlation between the photic environment and the  $\lambda_{\text{max}}$  values of the visual pigments of marine organisms

(for reviews see Lythgoe 1972, Dartnall 1974, Cronin 1986, Cronin and Forward 1988, Cronin et al. 1988). Thirdly, in intensity-limited environments such as the deep sea, eyes are generally optimized for maximum sensitivity and having more than one receptor type causes a reduction in sensitivity (Lythgoe 1979). Therefore, the simplest assumption would be that deep-sea crustaceans possess a single visual pigment with maximum absorption occurring between 460 and 490 nm. The current study, demonstrating strong behavioral responses to near-UV light as well as to blue-green light in a deep-sea crustacean, is at odds with this assumption.

Making meaningful assumptions about the visual capabilities of deep-sea organisms is difficult, because the light environment of the deep sea has not been well defined. Measurements of the spectral distribution of downward irradiance are generally made in the epipelagic zone; however, the optical properties of the ocean change with depth. Even slight differences in the diffuse attenuation coefficient can produce significant differences in the estimated available irradiance at great depths. For example, with a surface quantum irradiance of  $1.8 \times 10^{14}$  photons  $\text{cm}^{-2} \text{s}^{-1} \text{nm}^{-1}$  in the Bahamas (Tyler and Smith 1970), where *Systellaspis debilis* is found, and an attenuation coefficient of 0.028 for 400 nm light (Jerlov 1976), at a depth of 600 m (the daytime depth of *S. debilis*), the irradiance is  $9.1 \times 10^6$  photons  $\text{cm}^{-2} \text{s}^{-1} \text{nm}^{-1}$ . Using an attenuation coefficient for 400 nm light of 0.021 from Smith and Baker's (1981) more recent study, the irradiance at 600 m is  $6.4 \times 10^8$  photons  $\text{cm}^{-2} \text{s}^{-1} \text{nm}^{-1}$ , a 70-fold increase in available light.

The average behavioral threshold of *Systellaspis debilis* to 400 nm light determined in this study is  $5.5 \times 10^6$  photons  $\text{cm}^{-2} \text{s}^{-1}$ . Although the actual intensity of downwelling near-UV light at 600 m remains to be measured, the irradiances calculated utilizing the attenuation coefficients discussed above are well within the threshold sensitivity of *S. debilis*.

The function of this sensitivity to near-UV light, in deep-sea or shallow-water crustaceans, has not been established, although wavelength-dependent behavior has been established for some shallow-water crabs (Hyatt 1975) and the water mite *Unionicola* spp. (Dimock and Davids 1985). The four species of deep-sea crustaceans that have been shown to possess high sensitivity to near-UV light share two characteristics: they possess photophores, and they undergo diurnal vertical migrations. It is possible that this unusual visual pigment plays a role in discriminating between bioluminescent displays from different organisms (Frank and Case 1988) to assist in discriminating congeners from predators. We propose that this two-visual pigment system might also serve to discriminate changes in the ambient light environment which trigger the initiation of vertical migrations. Very little is known about the actual cues which trigger vertical migrations, but light is usually considered to be the most significant factor, since most vertical migrations occur at sunrise or sunset (for review see Forward 1988). However, the characteristics of the changing light field which trigger the migrations have not been established – it may be the change in absolute light intensity, the rate of change in

light intensity, or the change in the spectral composition of light which triggers the migrations. Between noon and twilight, the spectral distribution of surface light changes dramatically. At noon, there is more long-wavelength (500 nm) light compared to short-wavelength (400 nm) light, while at twilight, as the overall intensity of light decreases, the relative proportion of 400 nm light approaches that of 500 nm light (McFarland and Munz 1974, Jerlov 1976). For deep-sea crustaceans with two peaks of spectral sensitivity (400 and 500 nm), we suggest that it may be this change in the ratio of short-wavelength to long-wavelength light which triggers their migrations. In addition, due to the decrease in the spectral bandwidth of downwelling light with depth, this dual visual pigment system could function as a depth gauge, as suggested by Wald and Rappoport (1977) for the alciopid worm *Torrea candida*.

The behaviors exhibited by *Systellaspis debilis* in response to the light are consistent with the behavior one would expect to see in an organism whose migratory behavior is controlled by light. Observations on free-swimming individuals indicate that *S. debilis* is slightly negatively buoyant at sea level. A downward tilt and/or decreased pleopod activity, such as exhibited in response to the light stimulus, would lead to active or passive sinking. An upward tilt and/or increased pleopod activity, such as exhibited in response to cessation of the light stimulus, would lead to an ascent in the water column. The results presented here do not claim to provide information about vertical migrations in this species, but do suggest that the experimental paradigm described here can be used to study the cues triggering vertical migrations in deep-sea crustaceans. Further studies are currently under way to determine how *S. debilis* responds to gradual changes in the ambient light environment, such as those it would experience at dawn and dusk.

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