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The speed of an isolume: a shrimp's eye view

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Abstract Using data from electroretinogram recordings, we designed a submersible light meter with a spectral luminous efficiency comparable to that of a vertically migrating shrimp. Using this light meter on the “Johnson Sea Link” submersible, we were able to ascend with the isolumines (preferred light levels) associated with the sergestid and euphausiid shrimp layers. The speed of the submersible's movement was recorded and correlated with simultaneous measurements of surface irradiance. In situ measurements of the downwelling spectral distribution were also made with a fiber optic spectrometer. The average measured speed of the sergestid isolume was 8.8 cm s^{-1} , while that of the shallower euphausiid isolume was 6.7 cm s^{-1} . These values are different from those calculated using average diffuse attenuation coefficients and surface light measurements. This difference was due to the broadening of the spectral distribution of downwelling light above 120 m and to the variability of the diffuse attenuation coefficients with depth. These results clearly demonstrate that when investigating the relationship between light and vertical migration patterns, it is important that: (1) the light measurements be made in situ and (2) such measurements take into account the spectral sensitivity of the eyes of the migrators.

Introduction

Light is one of the primary determinants of animal distribution patterns in the ocean. Diurnal vertical migration (DVM), which has been described as the most

massive animal migration pattern on the planet (Hamner 1988), is a striking example. Although there is a vast body of literature documenting the fact that these movement patterns are synchronized with changing light/dark cycles, there is, as yet, no clear consensus as to how this synchronization is achieved. For the most common vertical migration pattern, which is known as nocturnal DVM, animals inhabit deep water during the day and ascend to shallower depths at night (Forward 1988). There are two leading hypotheses as to what aspect of the light field is triggering these migrations. One, known as the “rate of change” hypothesis, suggests that migrations are triggered by the rate and direction of change in light intensities (Clarke 1930; Ringelberg 1964), and field studies in shallow-water environments provide strong support for this hypothesis (Buchanan and Haney 1980; Stearns and Forward 1984; Forward 1985; Ringelberg et al. 1991). The other, known as the “preferendum” hypothesis, suggests that animals remain within a preferred light zone, known as an isolume (Ewald 1910; Rose 1925; Russell 1926). Studies on shallow-water organisms indicate that in general, these species are not following an isolume (Swift and Forward 1988; Wagner-Dobler 1990). However, the results of numerous studies attempting to relate changing submarine light levels to movement patterns of mesopelagic (200–1000 m depth) organisms have been equivocal and contradictory.

There are several factors that have undoubtedly contributed to this confusion. For example, many investigations have tracked the movement patterns of sound scattering layers (SSLs), and have found that, in some cases, the SSLs appear to follow isolumines (Kampa and Boden 1954; Backus et al. 1965; Blaxter and Currie 1967; Boden and Kampa 1967; Tont and Wick 1973; Kampa 1975), while others do not (Clarke and Backus 1956; Boden and Kampa 1965; Franceschini et al. 1970; Bright et al. 1972; Caruthers et al. 1972). However, the species make-up of the sonic scattering layers were for the most part not known, and therefore these differences may be attributed to the different taxonomic

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compositions of these layers. In addition, while some studies have depended on in situ light measurements in the SSLs using submarine photometers (Boden and Kampa 1965, 1967), others have extrapolated surface measurements to depth using transparency measurements made during the same investigation (Clarke and Backus 1964) or taken from historical data (Heywood 1996). Because attenuation varies with depth, such extrapolations can produce order of magnitude errors in irradiance (Zaneveld 1977), which could lead to erroneous conclusions as to whether or not a given SSL is following an isolume.

A number of investigators have attempted to identify the migrators using net-collected samples (e.g. Wiebe et al. 1992). One of the primary difficulties with this approach is that the net has to be continuously retrieved and deployed during a time when light intensities and animal distribution patterns are changing rapidly. Estimates of swimming speeds from such samples are consequently speculative (Wiebe et al. 1992). Additionally, making simultaneous, in situ light measurements is complicated by the fact that the ship is underway, therefore necessitating extrapolation from surface light measurements, which leads to additional ambiguities. Roe and Harris (1980) tried to circumvent this by mounting a light detector directly on the net. Since they judged a photomultiplier tube (PMT) to be too fragile and complicated for this application, they employed a silicon photodiode with a flat spectral response between 438 and 520 nm, which is different from the spectral sensitivity of a visual pigment. Besides having a broad spectral window, their light detector did not have a cosine collector or any way to ensure that it was oriented vertically. Making accurate in situ measurements of downwelling irradiance at low light levels is technically challenging, and the added requirement of also being able to identify the migrators further complicates the issue.

An additional variable that has not generally been addressed but may have helped contribute to some of the confusion is the spectral bandwidth of the photometers that have been used in these different investigations. For example, in some of the early work by Kampa and Boden (1954), they used a bare PMT that was mounted with the detector oriented so as to measure horizontal rather than vertical (downwelling) irradiance. In later work the PMT was oriented to measure downwelling irradiance and was fitted with a 502 nm interference filter (Boden and Kampa 1965) and then later still a 474 nm interference filter was used (Boden and Kampa 1967). [Also, it should be noted that prior to 1970 they did not account for temperature effects on the PMT (Kampa 1970).] Since the preferendum hypothesis actually refers to a preferred subjective light level for a particular organism, the isolume for that organism will depend on the spectral sensitivity of its eyes. Therefore, in order to test the preferendum hypothesis, it is important that the spectral bandwidth of the photometer reflect the spectral sensitivity of the organisms whose movement patterns are being tracked.

We have attacked these problems by using a mid-water submersible as both the measurement and observation platform. To accomplish this, we have developed a unique set of protocols for making in situ determinations of animal abundance, distribution and swimming behaviors (Frank and Widder 1996, 1997), in combination with instrumentation designed to make accurate in situ measurements of downwelling light (Widder et al. 1992). Prior to this investigation, we measured light within a narrowly defined waveband (480 ± 5 nm) that was chosen based on the spectral sensitivity peaks of the Crustacea whose migration patterns were being studied (Frank and Widder 1997, 1999). This is the accepted method of making such measurements (Jerlov 1963). However, the term isolume actually indicates that the subjective light level, i.e. the magnitude of the visual stimulus, remains constant. Calculations and measurements of the speed at which an isolume moves through the water have not taken into account the spectral sensitivity of the eyes of the migrators, but rather, the spectral sensitivity of a narrow-band interference filter. Using data from electroretinogram (ERG) recordings, we designed a submersible light meter with a spectral luminous efficiency comparable to that of a vertically migrating shrimp. With this methodology, we demonstrated that the speed of an isolume with respect to a shrimp eye is substantially different than that of an isolume measured with a narrow-band interference filter, or that calculated using average diffuse attenuation coefficients.

Materials and methods

Light measurements

Light measurements were made with the low light auto-radiometer (LoLAR), mounted on the "Johnson Sea Link" submersible, during a research cruise in the Gulf of Maine (Oceanographer Canyon, $40^{\circ}20'N$; $68^{\circ}08'W$) from 30 August to 8 September 1997. The LoLAR was developed to extend the lower limit of contemporary underwater irradiance detectors by using a PMT-based system that circumvents the temperature sensitivity and poor stability of the PMT with an autocalibration circuit. LoLAR sensitivity extends from 10^{-2} to 10^{-8} $\mu W\ cm^{-2}$, and the sample rate is 275 Hz. Additional sensors include depth, temperature and tilt, and data collection is to a laptop computer in the submersible.

LoLAR input optics were designed around a lens system, rather than the conventional optical diffuser, in order to optimize sensitivity. The incident photon flux is integrated over a 2π steradian solid angle, and the measured angular response of the system closely matches that of an ideal cosine collector. The error between the measured and ideal response was 7.5%, calculated using Tyler's (1960) data for radiance distribution at 66.1 m, according to the method of Smith (1969). The experimentally measured (based on Smith 1969) immersion-effect factor was 0.57. The lower responsiveness of the wet compared to the dry collector is primarily a result of the increased angular divergence of the light as it passes from the water to the air inside the dome and secondarily a result of decreased internal reflections within the dome. The initial calibration of the system, with a National Institute of Standards and Technology (NIST) referenced standard (model 310 multi-filter calibration source, Optronics Laboratory, Orlando, Fla., USA), is maintained by referencing the PMT output to the known quantum

flux from a radiophosphorescent source. The flux from the radiophosphorescent source is monitored with a high-stability silicon photodiode. During operation, periodic internal calibration sequences adjust the PMT responsivity calibration factor to correct for changes in PMT responsivity. The stability and reliability of the LoLAR are therefore based on the known temperature independence and excellent long-term stability of the silicon photodiode. (For further details on the theory of operation and calibration of LoLAR see Widder et al. 1992.)

LoLAR input optics also include a two-position filter wheel. In one slot a 480 nm interference filter (full width half-maximum intensity = 10 nm) was used to measure the diffuse attenuation coefficient. For this investigation, the second slot was fitted with a filter (Corion LG-420) selected such that the detector/filter combination would result in a weighted responsivity comparable to that of a vertically migrating mesopelagic shrimp. The shrimp responsivity function was based on ERG data collected from the euphausiid *Meganyctiphanes norvegica* and the sergestid shrimp *Sergestes arcticus* (Frank and Widder 1999). Figure 1A shows the spectral sensitivity of these shrimp as compared to that shown in Fig. 1B of the detector/filter combination as referenced to an NIST standard of discrete spectral irradiance (model 310 multi-filter

calibration source, Optronics Laboratory). The spectral sensitivity with the 480 nm interference filter is also shown for comparison.

Depth profiles of the changing spectral distribution through the water column were collected with an Ocean Optics PS1000 portable fiber optic spectrometer interfaced to a notebook computer inside the submersible. The fiber optic used for the pressure feedthrough was a 1000 μ m diameter silica fiber terminated with SMA connectors with O-ring seals. The spectrometer was optimized for maximum sensitivity by factory removal of the clad stripper and installation of a collection lens. In addition, the collection optics used for the fiber optic employed an optically flat window (in-water angular acceptance of 13°) rather than a diffuser in order to further enhance sensitivity. The spectrometer was wavelength calibrated using a low pressure mercury spectrum lamp (HG-1 mercury argon calibration source, Ocean Optics) and intensity calibrated using an NIST referenced calibration source designed for the calibration of detectors from 350 to 800 nm (model 310, Optronics Laboratory).

Both the LoLAR and the fiber optic light collector were mounted on a pan and tilt on top of the submersible. Accurate vertical orientation during measurements was established by reference to the LoLAR's two-axis tilt sensor. Measurements of surface irradiance were made during each dive with a deck-mounted Li-COR quantum sensor (400–700 nm).

Prior to sunset, the submersible was positioned in an isolume that was selected based on daytime animal distribution patterns. The isolume chosen was the irradiance measured at the shallowest depth at which statistically significant numbers of euphausiids or sergestids were found during the daytime dives. As sunset progressed, the position of the submersible was constantly adjusted in order to maintain a constant reading from the LoLAR with the "shrimp filter" in place. Time and depth were automatically logged by the LoLAR's data collection system. The times of sunset and the end of civil twilight indicated on the figures were for the latitude and longitude of Oceanographer Canyon as provided by the U.S. Naval Observatory. Sunset is defined as the point in time when the upper edge of the disk of the sun is on the horizon. Civil twilight is defined as the point in time when the center of the sun is geometrically 6° below the horizon. On a clear night, at the end of civil twilight, the brightest stars are visible in the sky.

Observations of organisms

Daytime distribution patterns of organisms were assessed by running visual transects with the submersible, as described in Frank and Widder (1997). Briefly, transects were run at a forward speed of 0.6 knots for 4 min. Organisms entering the 2.65 m² transect area were visually identified and recorded to tape by the scientist (E.A.W. or T.M.F.) seated in the front chamber of the "Johnson Sea Link" submersible, which is a 5'-Plexiglas sphere. Organisms were periodically caught with samplers on the front of the submersible (euphausiid crustaceans) or with a trawl net at night (euphausiid and sergestid crustaceans) to verify species identifications made during transects. The only species of *Sergestes* found in Oceanographer Canyon was *S. arcticus*. The euphausiids seen during transects were a mixture of three different species: *Thysanoessa gregaria*, *Nematoscelis megalops* and *Meganyctiphanes norvegica*. The upper edge of the euphausiid or sergestid layer is defined as the shallowest depth at which a statistically significant number of organisms was present. Animal distribution data were analyzed as described in Frank and Widder (1997).

Results

Figure 2A shows the variation of spectral distribution with depth in Oceanographer Canyon during this investigation. The broad spectral responsivity of the shrimp filter (indicated by the dashed line in the figure) had the greatest impact on the measured speed of the

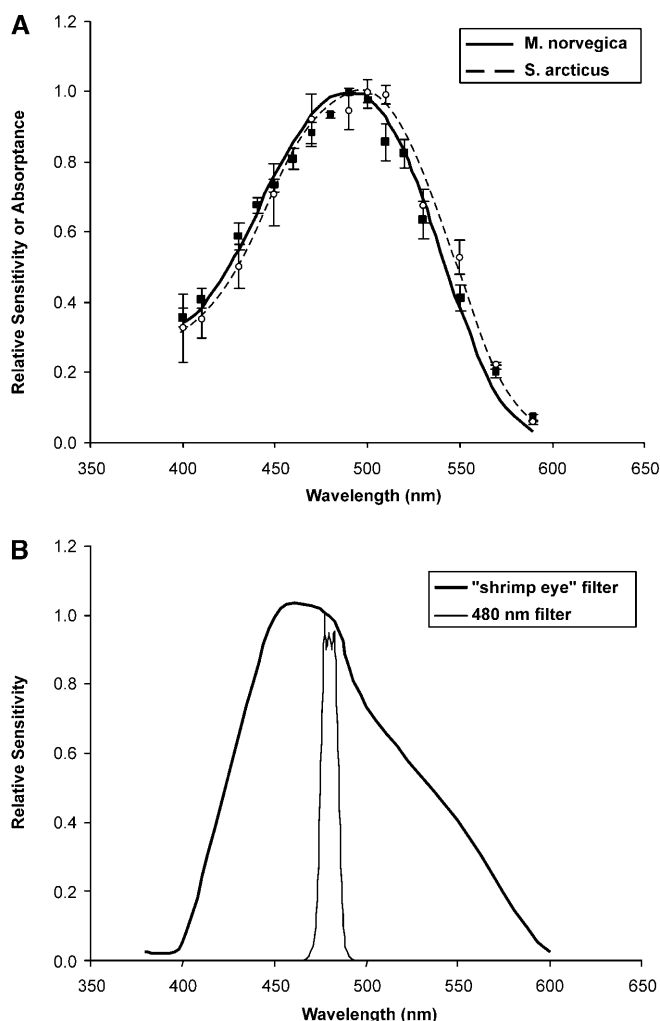


Fig. 1 A Spectral sensitivity of the euphausiid *Meganyctiphanes norvegica* (solid line) and the sergestid shrimp *Sergestes arcticus* (dashed line) as measured by electroretinogram. B Spectral responsivity of the LoLAR with the "shrimp filter" in place (thick line) as compared with the 480 nm interference filter in place

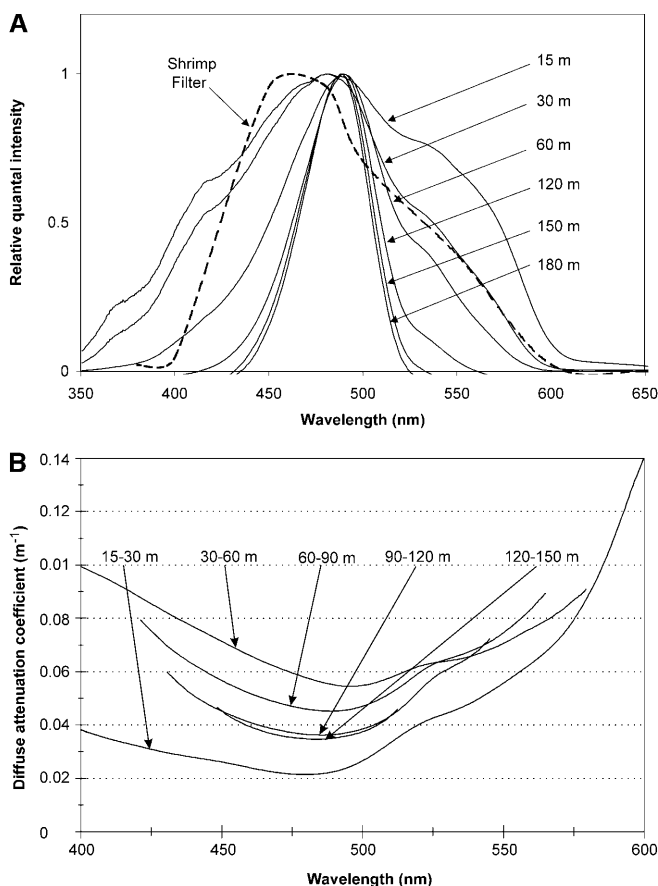


Fig. 2 **A** Variation of spectral distribution of downwelling light with depth in Oceanographer Canyon, as measured with fiber optic spectrometer from the submersible. The dashed line is the spectral responsivity of the LoLAR with the "shrimp filter" in place. **B** Variation of diffuse attenuation with depth in Oceanographer Canyon, calculated over the indicated depth intervals. The decreasing width of the plotted spectra with increasing depth is a consequence of the loss of a measurable signal at short and long wavelengths

isolume between 30 and 120 m. Below 120 m the spectral distribution changed slowly with depth.

Figure 2B shows the spectral variation of the diffuse attenuation coefficient with depth. There was a high degree of variability between the surface and 120 m, largely due to a loss of optical clarity between 30 and 90 m. This layer of reduced visibility was readily apparent to observers in the submersible. Below 90 m the diffuse attenuation coefficient remained relatively constant with depth.

Light was measured in situ at the upper limit of the sergestid daytime distribution using the LoLAR with the shrimp filter. The submersible was positioned at this same light level just prior to sunset on 30 August. At this depth (347 m) irradiance measured at 480 nm with the LoLAR was 3.8×10^6 photons $s^{-1} cm^{-2} nm^{-1}$. Skies were clear throughout the measurement period (Fig. 3A). Time of sunset was 7:07 p.m. and end of civil twilight was at 7:35 p.m.. Figure 3B shows the measured speed of this sergestid isolume.

The average speed of the measured sergestid isolume over the first 45 min after sunset was $8.8 cm s^{-1}$. Using the standard method of calculating the speed of an isolume based on surface light measurements and the average diffuse attenuation coefficient measured in the upper 100 m ($K_{480} = 0.042$), the calculated average speed was $7.2 cm s^{-1}$. This calculated value was 18% slower than the measured average speed (Fig. 3C). On the other hand, when this same calculation was made using the average diffuse attenuation coefficient measured between 100 and 300 m ($K_{480} = 0.032$), the calculated average speed of $9.4 cm s^{-1}$ was 7% faster than the average measured speed (Fig. 3D).

The maximum measured speed that animals would need to swim in order to keep up with the sergestid isolume was $11 cm s^{-1}$. This maximum occurred 3 min after the end of civil twilight (7:35 p.m.) at a depth of 200 m. The calculated maximum speed of the isolume was $8.7 cm s^{-1}$ using the average diffuse attenuation coefficient measured in the upper 100 m ($K_{480} = 0.042$). This maximum would have occurred prior (7:31 p.m.) to civil twilight at a depth of 246 m. Using the average diffuse attenuation coefficient measured between 100 and 300 m ($K_{480} = 0.032$), the predicted maximum speed of the isolume was $11.4 cm s^{-1}$, a close match to the measured maximum. However, this maximum would have occurred prior (7:31 p.m.) to civil twilight at a depth of 215 m.

Figure 4A–D shows measurements and calculations comparable to those in Fig. 3A–D, but for the shallower euphausiid isolume. In this case the isolume that was followed was the light level measured with the LoLAR with shrimp filter at the upper limit of the euphausiid daytime distribution. These measurements were made on 5 September during a period when there was no cloud cover (Fig. 4A). Sunset was at 6:58 p.m. and end of civil twilight was at 7:25 p.m.. The submersible was positioned in the euphausiid isolume just prior to sunset. At this depth (262 m) irradiance measured at 480 nm with the LoLAR was 4.4×10^7 photons $s^{-1} cm^{-2} nm^{-1}$. Figure 4B shows the measured speed of the euphausiid isolume.

The average speed of the measured isolume over the first 45 min after sunset was $6.7 cm s^{-1}$. This speed was 16% slower than the predicted average speed using $K_{480} = 0.042$ ($7.8 cm s^{-1}$) and 54% slower than the predicted average speed using $K_{480} = 0.032$ ($10.3 cm s^{-1}$).

The maximum measured speed of this isolume was $8 cm s^{-1}$, which occurred 8 min prior to civil twilight at 7:17 p.m. at a depth of 153 m. Using surface light measurements and the average diffuse attenuation coefficient measured in the upper 100 m, the calculated maximum speed of this isolume was $9.5 cm s^{-1}$. This maximum would have occurred 1 min prior to civil twilight at 7:24 p.m. at a depth of 122 m (Fig. 4C). Using the average diffuse attenuation coefficient measured between 100 and 300 m, the predicted maximum speed of the isolume was $12.5 cm s^{-1}$, which

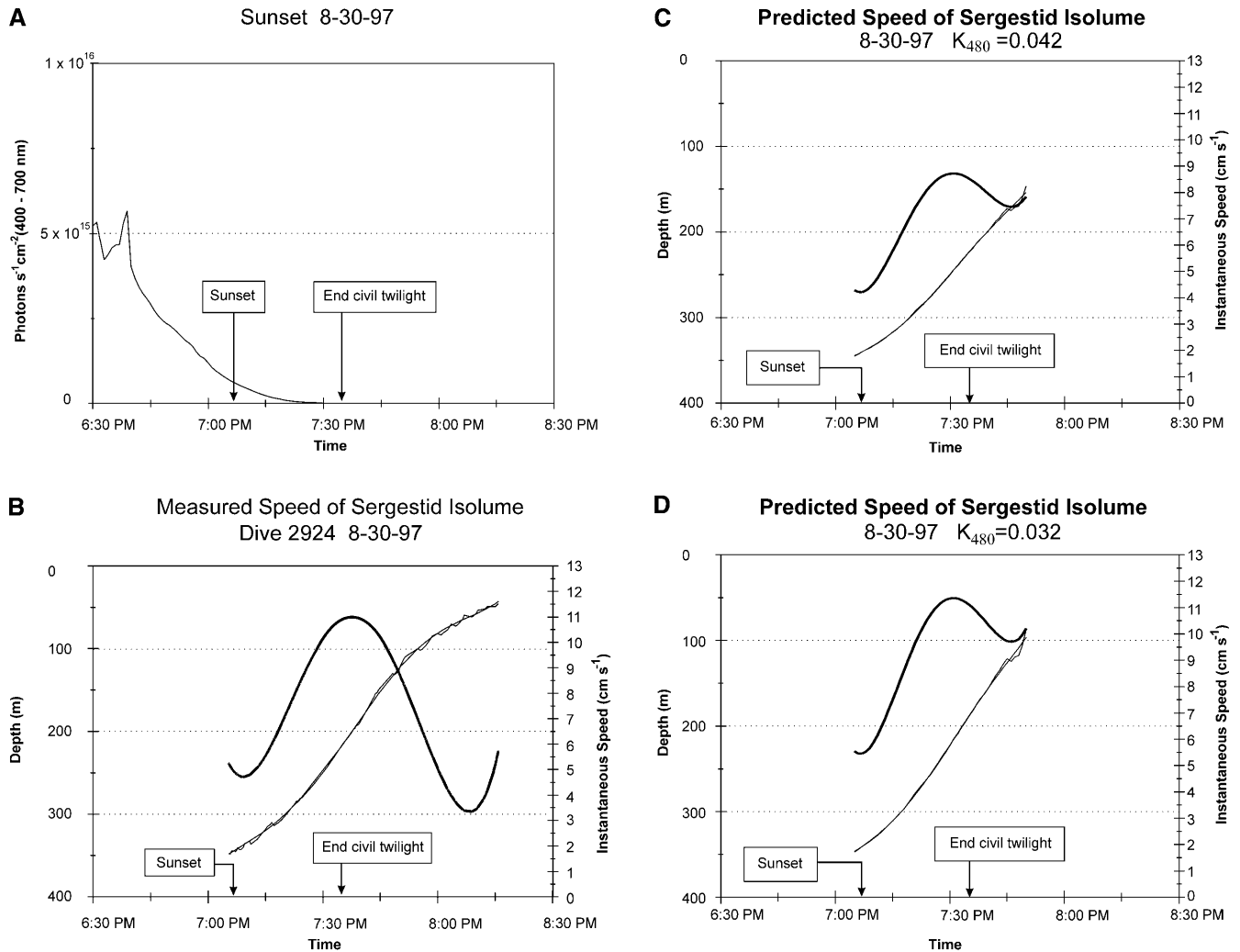


Fig. 3 **A** Time course of change in surface irradiance at sunset, as measured by a deck-mounted LiCOR light meter on 30 August 1997. **B** The measured speed of the sergestid isolume. The raw data and the fifth order polynomial fit to these data are indicated by *thin lines*, which are plotted as time versus depth (*left axis*). The *thick line* is the calculated first derivative of this function, which gives the instantaneous speed of the isolume throughout the measurement period plotted as time versus instantaneous speed (*right axis*). **C** The predicted speed of the sergestid isolume, as calculated using the surface light measurements from **A** and the diffuse attenuation coefficient of $K_{480} = 0.042$ measured between the surface and 100 m. **D** The predicted speed of the sergestid isolume, as calculated using the surface light measurements from **A** and the diffuse attenuation coefficient of $K_{480} = 0.032$ measured between 100 and 300 m

would have occurred at a depth of 77 m at 7:24 p.m. (Fig. 4D).

The differences between the measured and predicted values for the sergestid and euphausiid isolumes are summarized in Table 1.

Discussion

The speed at which a migrator must move in order to remain at a constant subjective light level will change with

depth because: (1) the spectral distribution of downwelling irradiance changes with depth and (2) the spectral responsivity of the eyes of vertical migrators is broad. As a result of the broadening of the spectral distribution at shallower depths, the speed will be slower on the ascent at sunset and faster on the descent at sunrise than would be predicted using just surface irradiance measurements and a constant diffuse attenuation coefficient. In addition, different isolumes will move at different speeds, depending on the rate of change in the spectral distribution with depth. In our measurements, using the LoLAR with the "shrimp filter", the deeper sergestid isolume moved faster than the shallower euphausiid isolume at sunset because of the greater rate at which downwelling spectral irradiance broadens near the surface. In this regard it is interesting to note that in a study by Plueddemann and Pinkel (1989), using Doppler sonar (67 kHz) to track the migration patterns of three daytime scattering layers at 300, 560 and 1000 m, they found that during the upward migration at sunset, the deeper layer migrated faster than the intermediate layer and the intermediate layer migrated faster than the shallow layer.

Even under the unlikely circumstance that the spectral diffuse attenuation coefficients remain con-

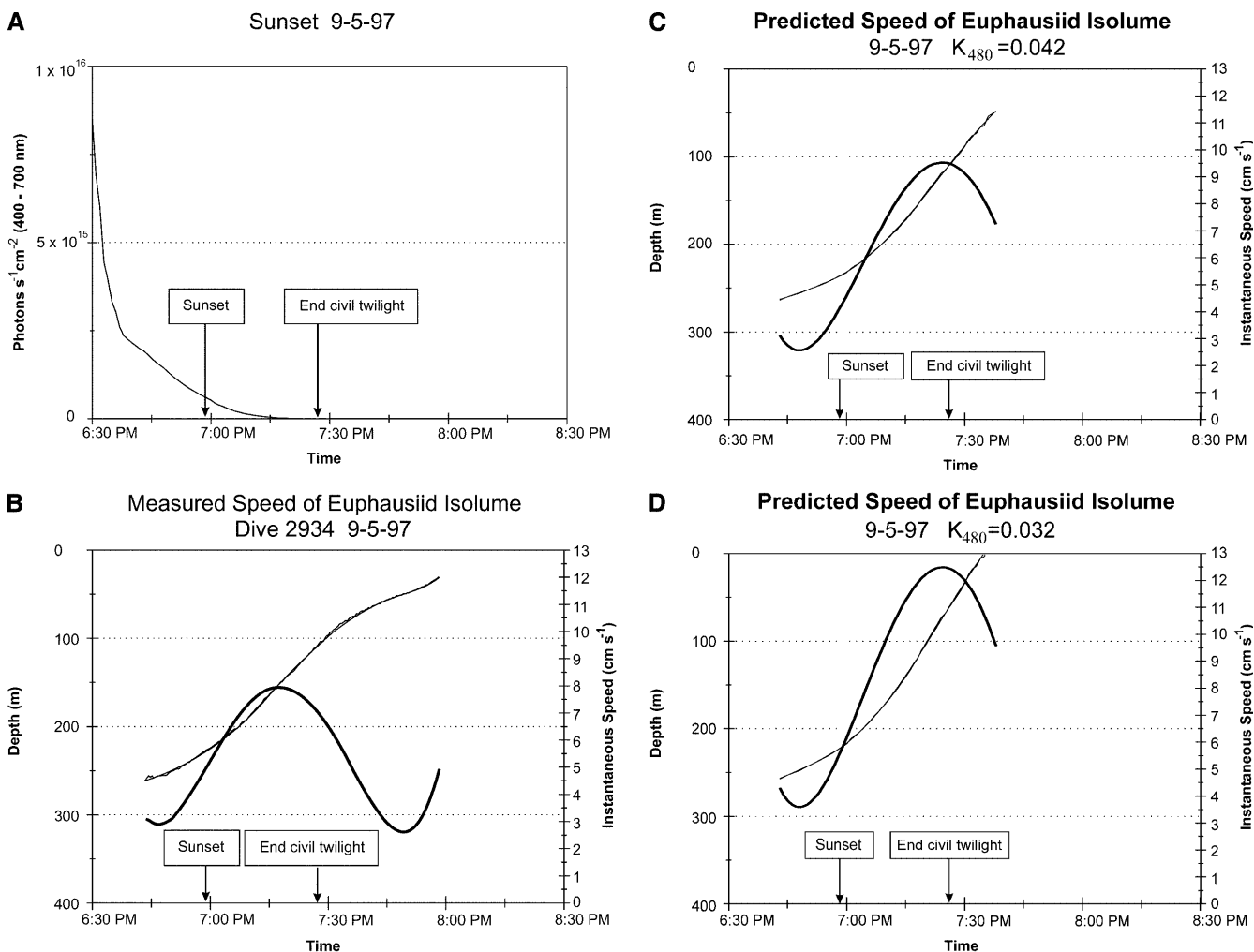


Fig. 4 **A** Time course of change in surface irradiance at sunset, as measured by a deck-mounted LiCOR light meter on 5 September 1997. **B** The measured speed of the euphausiid isolume. The raw data and the fifth order polynomial fit to these data are indicated by *thin lines*, which are plotted as time versus depth (*left axis*). The *thick line* is the calculated first derivative of this function, which gives the instantaneous speed of the isolume throughout the measurement period plotted as time versus instantaneous speed (*right axis*). **C** The predicted speed of the euphausiid isolume, as calculated using the surface light measurements from **A** and the diffuse attenuation coefficient of $K_{480} = 0.042$ measured between the surface and 100 m. **D** The predicted speed of the euphausiid isolume, as calculated using the surface light measurements from **A** and the diffuse attenuation coefficient of $K_{480} = 0.032$ measured between 100 and 300 m

stant, the wavelength dependence of light transmission through water in combination with the broad spectral responsivity of the eyes of vertical migrators must still be taken into account when trying to relate swimming speeds to surface light measurements extrapolated to depth. However, because diffuse attenuation coefficients are not constant with depth, such extrapolations are subject to large errors. For our investigation, the speeds of the predicted isolumes were very different depending on whether we used the average diffuse at-

tenuation coefficient measured in the upper 100 m or that measured between 100 and 300 m. Since, in reality, the diffuse attenuation coefficients varied continuously with depth, the most accurate extrapolations need to account for these variations. To do so requires correcting the surface solar spectrum by the average diffuse attenuation coefficient between the surface and each depth point and then integrating the photon flux in each waveband weighted by the relative visual sensitivity in that band. Obviously, because of the spatial and temporal variability of the optical environment, it is far better to depend on in situ measurements than extrapolations, and to use light sensors that provide the closest possible approximation to the eyes of the animals under study. By using a detector with a responsivity that has been weighted to reflect the spectral responsivity of the eyes of the migrators, measurements can be directly related to the magnitude of the visual stimulus regardless of the spectral variability of the light source.

In analyzing the present results in terms of previous observations, the first point to consider is whether or not the speeds of the isolumes that we measured can be attained by the sergestids and euphausiids. Cowles

hypothesis in the field will be to follow an individual migrator, while making in situ light measurements that account for the broad spectral responsivity of its eye.

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