



FAU Institutional Repository

<http://purl.fcla.edu/fau/fauir>

This paper was submitted by the faculty of FAU's Harbor Branch Oceanographic Institute

Notice: ©2001 Springer-Verlag. This manuscript is a version of an article with the final publication found online at <http://www.springerlink.com> and may be cited as: Widder, E. A. and T. M. Frank (2001) The speed of an isolume: a shrimp's eye view, *Marine Biology* 138:669-677 doi: 10.1007/s002270000504

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

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 isolumes (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 isolumes (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

Communicated by N. H. Marcus, Tallahassee

E. A. Widder (✉) · T. M. Frank
Harbor Branch Oceanographic Institution,
Fort Pierce, FL 34946, USA

Tel.: +1-800-3334264315; Fax: +1-561-4680757
e-mail: Widder@HBOI.edu

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°20'N; 68°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 auto-calibration circuit. LoLAR sensitivity extends from 10^{-2} to 10^{-8} $\mu\text{W cm}^{-2}$, 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 μm 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 m^2 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

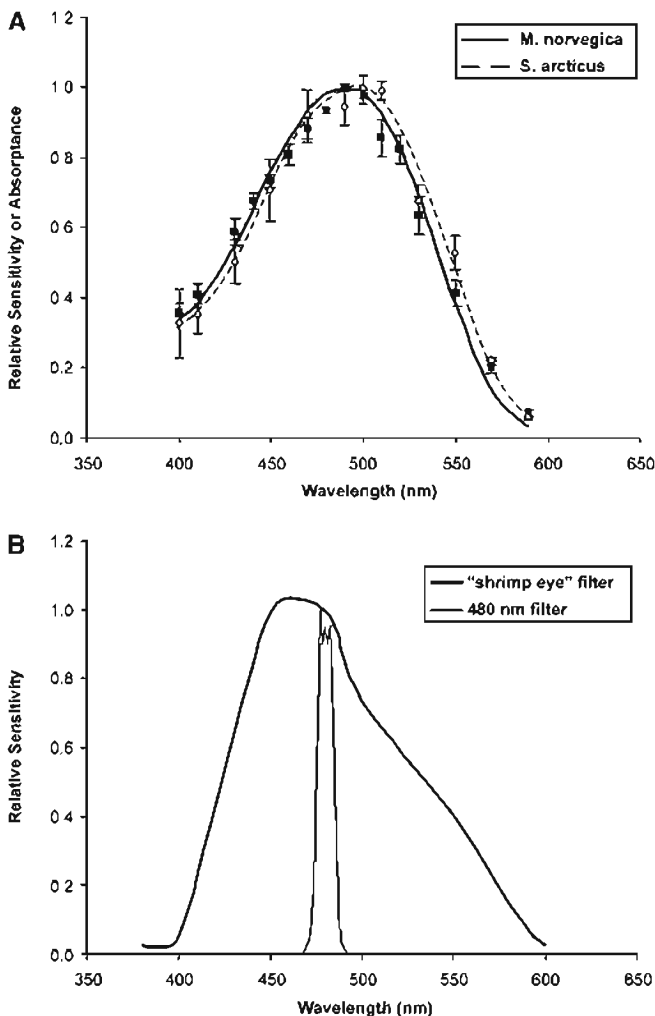


Fig. 1 A Spectral sensitivity of the euphausiid *Meganyctiphanes norvegica* (solid line) and the sergestid shrimp *Sergestes arcticus* (dashed line) as measured by electroretinogram. B Spectral responsivity of the LoLAR with the "shrimp filter" in place (thick line) as compared with the 480 nm interference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

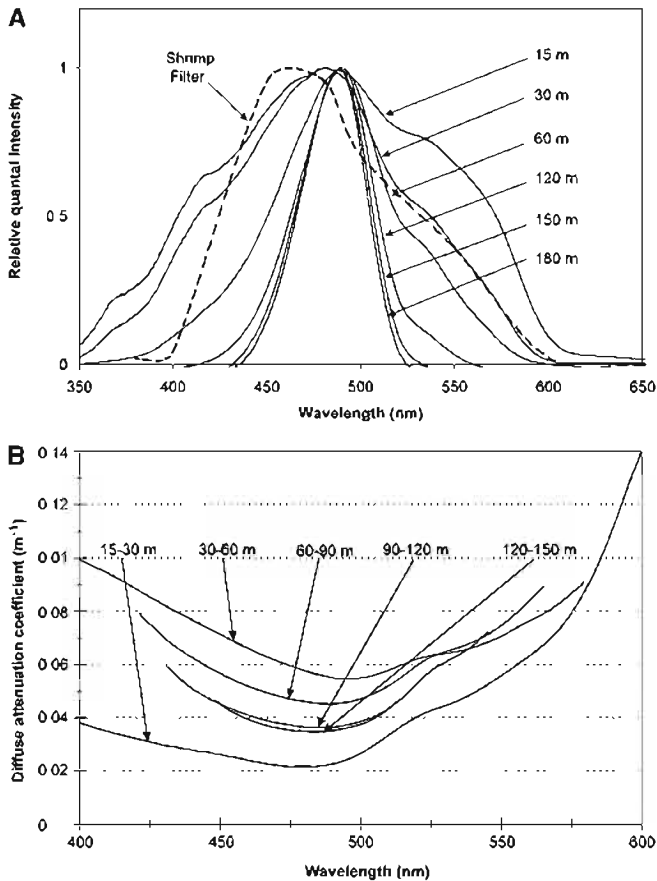


Fig. 2 A Variation of spectral distribution of downwelling light with depth in Oceanographer Canyon, as measured with fiber optic spectrometer from the submersible. The *dashed line* is the spectral responsivity of the LoLAR with the "shrimp filter" in place. **B** Variation of diffuse attenuation with 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

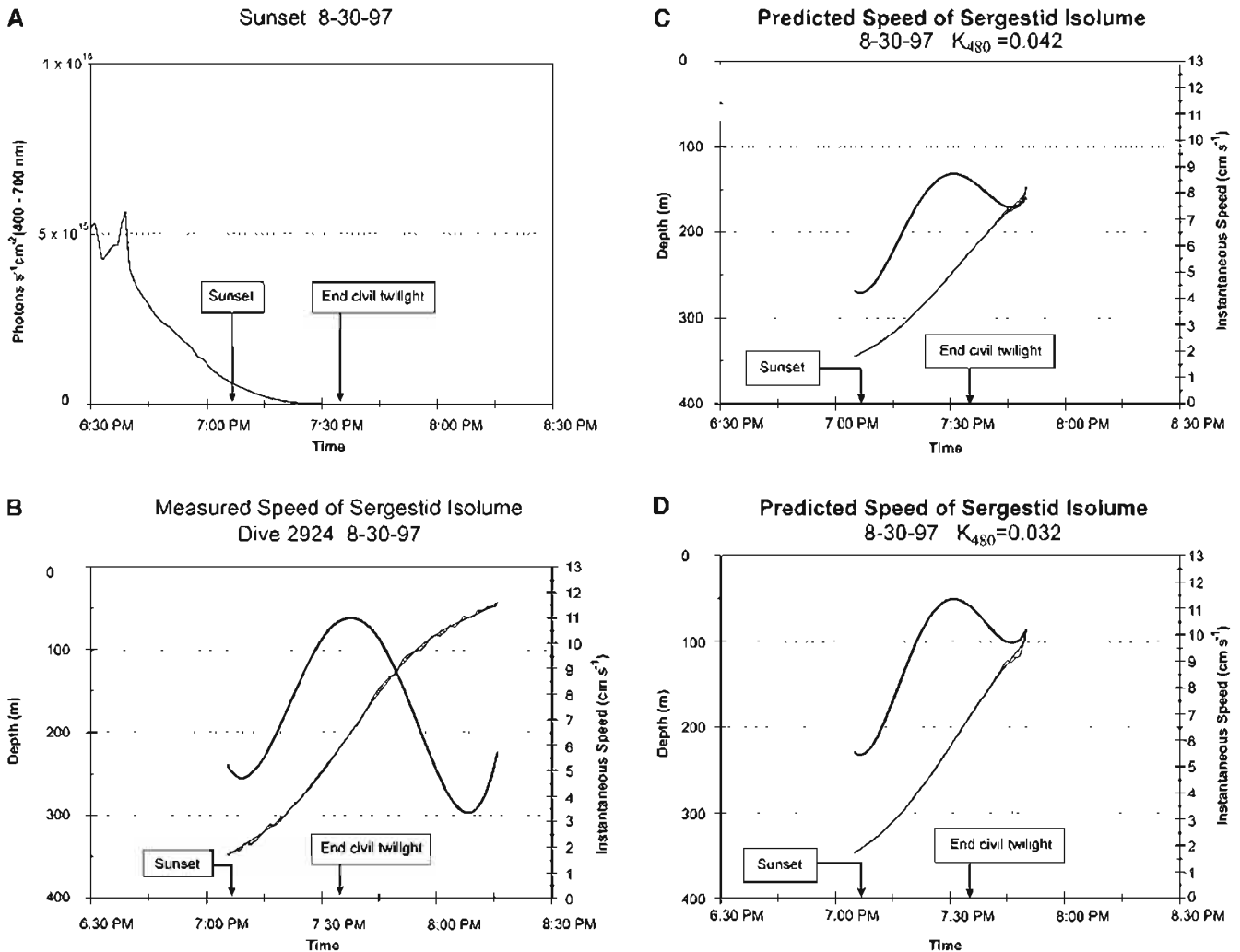


Fig. 3 **A** Time course of change in surface irradiance at sunset, as measured by a dock-mounted LiCOR light meter on 30 August 1997. **B** The measured speed of the sergestid isolume. The raw data and the fifth order polynomial fit to these data are indicated by *thin lines*, which are plotted as time 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-

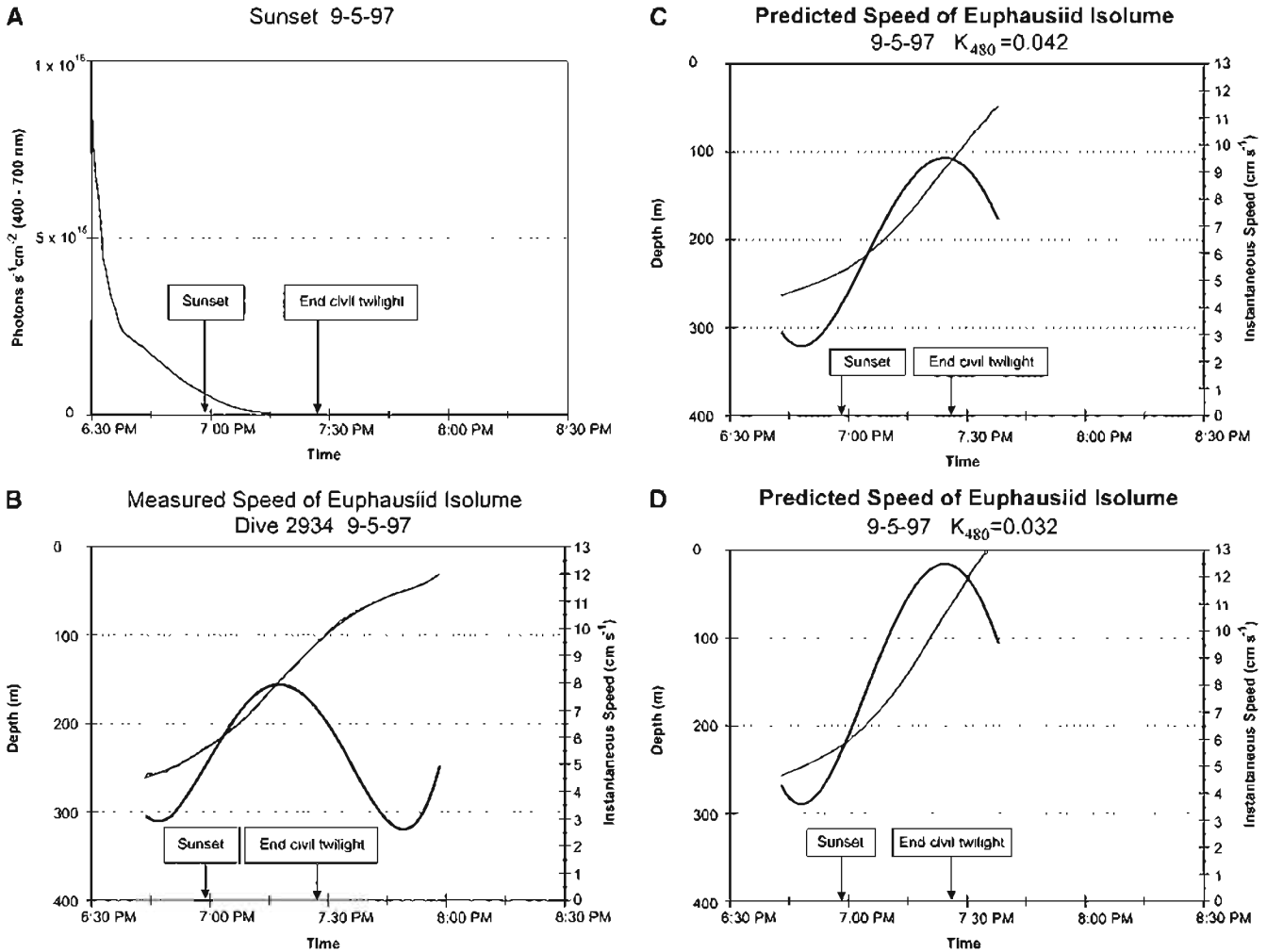


Fig. 4 A Time course of change in surface irradiance at sunset, as measured by a deck-mounted LICOR light meter on 5 September 1997. B The measured speed of the euphausiid isolume. The raw data and the fifth order polynomial fit to these data are indicated by *thin lines*, which are plotted as time versus 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

Table 1 Speed and depths of measured versus calculated isolumines

Sergestid isolume		Euphausiid isolume					
Date	30 August 1997	5 September 1997					
Sunset	7:07 p.m.	6:58 p.m.					
End civil twilight	7:35 p.m.	7:25 p.m.					
	Avg. speed (cm s ⁻¹)	Time (p.m.)	Depth (m)	Avg. speed (cm s ⁻¹)	Time (p.m.)	Depth (m)	Max. speed
Measured isolume	8.8	7:07-7:47	344-142	6.7	6:58-7:38	232-71	8
Calculated ($K_{480} = 0.042$)	7.2	7:07-7:47	342-170	7.8	6:58-7:38	237-48	9.5
Calculated ($K_{480} = 0.032$)	9.4	7:07-7:47	341-114	10.3	6:58-7:38	228-20	12.5
		Time (p.m.)	Depth (m)		Time (p.m.)	Depth (m)	
		7:38	200		7:17	153	
		7:31	246		7:24	122	
		7:31	215		7:24	77	

(1994) used a remote operating vehicle to make in situ observations of the sergestid shrimp *Sergestes similis*, for which he estimated an average swimming speed of 7.4 cm s⁻¹ and a maximum swimming speed of 13.1 cm s⁻¹. Smith et al. (1989) used an acoustic Doppler current profiler to measure the migration of the deep scattering layer off Southern California, where *S. similis* is abundant, and determined the speed of the sunset migration as 5.8 cm s⁻¹. These values suggest that our measured average speed of 8.8 cm s⁻¹ and maximum speed of 11 cm s⁻¹ for the sergestid isolume can be attained by the sergestids. Similarly, euphausiid swimming speeds estimated in the field with MOCNESS sampling as 2.8-5.4 cm s⁻¹ (Wiebe et al. 1992) and measured in the laboratory as 9.7 cm s⁻¹ (Torres and Childress 1983) mean that euphausiids should be able to keep up with the euphausiid isolume, moving at a measured average speed of 6.7 cm s⁻¹ and maximum speed of 8 cm s⁻¹.

There is no denying that animal distribution patterns are strongly influenced by light, but the question is how. Roe (1983) rejected the preferendum hypothesis in large part because he found that the populations he examined were not vertically discrete, i.e. were not maintained within a narrow light regime. However, there is no reason to presume that all individuals within a population must be locked onto the same isolume. Individuals may follow different isolumines due to differences in internal modifying factors such as sex and age in addition to dealing with conflicting drives to optimize foraging while minimizing predator impact. Therefore, while a hungry individual might push the upper limit of the light envelope in order to have a better chance of spotting prey, a well-fed individual might remain deeper in order to reduce the chances of being spotted by a predator. Both euphausiids (Herring and Locket 1978) and sergestids (Warner et al. 1979) use downward-directed bioluminescence to camouflage their silhouettes against downwelling light. Production of bioluminescence is energetically costly and there is an upper limit above which an animal cannot replace the light absorbed and reflected by its body with an equivalent amount of bioluminescence. If an individual attempts to ascend above that maximum, it will become highly visible against the downwelling light field and therefore easy prey for visual predators. The resulting selection pressure would impose a clearly defined upper light limit on a migrating population, while the restrictions on lower limits are less clearly defined. Interestingly, some of the strongest evidence for the association of sound scattering layers with specific isolumines comes from instances where investigators have looked at the relationship between changing light levels and the leading edge of the scattering layer (see for example Boden and Kampa 1967). Therefore, while the light level associated with an individual organism might be fairly discrete and correctly referred to as an isolume, the light levels associated with a population could encompass a much broader range. Consequently, the only reliable test of the preferendum

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.

Acknowledgements We are indebted to S. Bernstein who developed the data collection software and assisted with the fieldwork. We also thank the captain and crew of the R.V. "Edwin Link" and the pilots and crew of the "Johnson Sea Link". This work was funded by grants from the National Science Foundation (OCE-9313872 and OCE-9730073) and from the National Oceanic and Atmospheric Administration (subgrant UCAP-95-02b, University of Connecticut, award no. N-A76RU0060) to Drs. T.M.F. and E.A.W. This is Harbor Branch contribution no. 1397.

References

- Backus RH, Clark RC, Wing AS (1965) Behaviour of certain marine organisms during the solar eclipse of July 20, 1963. *Nature* 205: 989-991
- Blaxter JHS, Currie RI (1967) The effect of artificial lights on acoustic scattering layers in the ocean. *Symp Zool Soc Lond* 19: 1-14
- Boden BP, Kampa EM (1965) An aspect of euphausiid ecology revealed by echo-sounding in a fjord. *Crustaceana* 9: 155-173
- Boden BP, Kampa EM (1967) The influence of natural light on the vertical migrations of an animal community in the sea. *Symp Zool Soc Lond* 19: 15-26
- Bright T, Ferrari F, Martine D, Franceschini GA (1972) Effects of a total solar eclipse on the vertical distribution of certain oceanic zooplankters. *Limnol Oceanogr* 17: 296-301
- Buchanan C, Haney JF (1980) Vertical migration of zooplankton in the arctic. A test of the environmental controls. In: Kerfoot WC (ed) *Evolution and ecology of zooplankton communities, special symposium III*. University Press of New England, Hanover, N.H., pp 69-79
- Caruthers JW, Thompson RC, Novarini JC, Franceschini GA (1972) The response of deep scattering layers in the Gulf of Mexico total solar eclipse. *Deep-Sea Res* 19: 337-338
- Clarke GL (1930) Change in phototropic and geotropic signs in *Daphnia* induced by changes in light intensity. *J Exp Biol* 7: 109-131
- Clarke GL, Backus RH (1956) Measurements of light penetration in relation to vertical migration and records of luminescence of deep-sea animals. *Deep-Sea Res* 4: 1-14
- Clarke GL, Backus RH (1964) Interrelations between vertical migration of deep scattering layers, bioluminescence and changes in daylight in the sea. *Bull Inst Oceanogr Monaco* 64: 1-36
- Cowles DL (1994) Swimming dynamics of the mesopelagic vertically migrating penaeid shrimp *Sergestes similis*: modes and speeds of swimming. *J Crustac Biol* 14: 247-257
- Ewald WF (1910) Über Orientierung, Lokomotion und Lichtreaktionen einiger Cladoceren und deren Bedeutung für die Theorie der Tropismen. *Biol Zentbl* 30: 1-399
- Forward RB Jr (1985) Behavioral responses of larvae of the crab *Rhithropanopeus harrisi* (Brachyura: Xanthidea) during diel vertical migrations. *Mar Biol* 90: 9-18
- Forward RB Jr (1988) Diel vertical migration: zooplankton photobiology and behavior. *Oceanogr Mar Biol Annu Rev* 26: 361-393
- Franceschini GA, Bright TJ, Caruthers JW, El-Sayed SZ, Vastano AC (1970) Effects on migration of marine organisms in the Gulf of Mexico. *Science* 226: 1155-1156
- Frank TM, Widder EA (1996) UV light in the deep-sea; in situ measurements of downwelling irradiance in relation to the visual threshold sensitivity of UV-sensitive crustaceans. *Mar Freshw Behav Physiol* 27: 189-197
- Frank TM, Widder EA (1997) The correlation of downwelling irradiance and staggered vertical migration patterns of zooplankton in Wilkinson Basin, Gulf of Maine. *J Plankton Res* 19: 1975-1991
- Frank TM, Widder EA (1999) Comparative study of the spectral sensitivities of mesopelagic crustaceans. *J Comp Physiol A Sens Neural Behav Physiol* 185: 255-265
- Hamner WM (1988) Behavior of plankton and patch formation in pelagic ecosystems. *Bull Mar Sci* 43: 752-757
- Herring PJ, Locket NA (1978) The luminescence and photophores of euphausiid crustaceans. *J Zool (Lond)* 186: 431-462
- Heywood KJ (1996) Diel vertical migration of zooplankton in the northeast Atlantic. *J Plankton Res* 18: 163-184
- Jerlov NG (1963) Optical oceanography. *Oceanogr Mar Biol Annu Rev* 1: 89-114
- Kampa EM (1970) Underwater daylight and moonlight measurements in the eastern North Atlantic. *J Mar Biol Assoc UK* 50: 397-420
- Kampa EM (1975) Observations of a sonic-scattering layer during the total solar eclipse 30 June 1973. *Deep-Sea Res* 22: 417-423
- Kampa EM, Boden BP (1954) Submarine illumination and the twilight movements of a sonic scattering layer. *Nature* 174: 869-873
- Plueddemann AJ, Pinkel R (1989) Characterization of the patterns of diel migration using a Doppler sonar. *Deep-Sea Res* 36A: 509-530
- Ringelberg J (1964) The positively phototactic reaction of *Daphnia magna* Straus: a contribution to the understanding of diurnal vertical migration. *Neth J Sea Res* 2: 319-406
- Ringelberg J, Flik BJG, Lindenaar D, Royackers K (1991) Diel vertical migration in *Daphnia hyalina* (sensu *latiori*) in Lake Maarssenveen, part 1. Aspects of seasonal and daily timing. *Arch Hydrobiol* 121: 129-145
- Roe HSJ (1983) Vertical distributions of euphausiids and fish in relation to light intensity in the northeastern Atlantic. *Mar Biol* 77: 287-298
- Roe HSJ, Harris MJ (1980) A new acoustically telemetering deep-sea photometer with some observations on underwater light in the northeast Atlantic. *Deep-Sea Res* 27A: 181-195
- Rose M (1925) Contribution à l'étude de la biologie du plankton: le problèmes des migrations verticales journalières. *Arch Zool Exp Gen* 54: 387-542
- Russell FS (1926) The vertical distribution of marine macroplankton. IV. The apparent importance of light intensity as a controlling factor in the behavior of certain species in the Plymouth area. *J Mar Biol Assoc UK* 14: 415-440
- Smith PE, Ohman D, Eber LE (1989) Analysis of the patterns of distribution of zooplanktonic aggregations from an acoustic doppler current profiler. *Calif Coop Ocean Fish Investig Rep* 30: 88-103
- Smith RC (1969) An underwater spectral irradiance collector. *J Mar Res* 27: 341-351
- Stearns DE, Forward RB Jr (1984) Copepod photobehavior in a simulated natural light environment and its relation to nocturnal vertical migrations. *Mar Biol* 82: 91-100
- Swift MC, Forward RB Jr (1988) Absolute light intensity vs. rate of relative change in light intensity: the role of light in the vertical migration of *Chaoborus punctipennis* larvae. *Bull Mar Sci* 43: 604-619
- Tont SA, Wick GL (1973) Response of a deep scattering layer to the 1972 total solar eclipse. *Deep-Sea Res* 20: 769-771
- Torres JJ, Childress JJ (1983) Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. I. Effects of temperature and pressure. *Mar Biol* 74: 79-86
- Tyler JE (1960) Radiance distribution as a function of depth in an underwater environment. *Bull Scripps Inst Oceanogr Univ Calif* 7: 363-412
- Wagner-Dobler I (1990) Vertical migration of *Chaoborus flavicans* (Diptera, Chaoboridae): control of onset of migration and migration velocity by environmental stimuli. *Arch Hydrobiol* 177: 279-307

- Warner JA, Latz MI, Case JF (1979) Cryptic bioluminescence in a midwater shrimp. *Science* 203: 1109-1110
- Widder EA, Caimi FM, Taylor W, Tusting RF (1992) Design and development of an auto-calibrating radiometer for deep-sea bio-optical studies. In: *Proceedings of the Oceanic Engineering Society of the IEEE, OCEANS '92. Mastering the oceans through technology*, vol 1. Institute of Electrical and Electronics Engineers, New York, pp 525-530
- Wiebe PH, Copley NJ, Boyd SH (1992) Coarse-scale horizontal patchiness and vertical migration of zooplankton in Gulf Stream warm-core ring 82-H. *Deep-Sea Res* 39: 247-278
- Zaneveld JRV (1977) Optical parameters that may affect vertical movement of animals in the ocean. In: Anderson NR, Zahuranec BJ (eds) *Oceanic sound scattering prediction*. Plenum, New York, pp 147-158