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Comparative study of the spectral sensitivities of mesopelagic crustaceans

Abstract The spectral sensitivities of 12 species of mesopelagic crustaceans were studied by means of electrophysiological recordings. Nine of the species are vertical migrators, while 3 are not, and 9 species possess bioluminescent organs, while 3 are not bioluminescent. All species had a single peak of spectral sensitivity with maxima between 470 nm and 500 nm. There was no apparent correlation between sensitivity maxima and daytime depth distribution, migratory behavior, or the presence or absence of bioluminescent organs. With the exception of the hyperiid amphipod *Phronima sedentaria*, the spectral sensitivities of these mesopelagic crustaceans demonstrate a better match for maximum sensitivity to bioluminescence than to downwelling light.

Key words Mesopelagic · Crustacean Electrophysiology · Vision · Deep-sea

Abbreviations *ERG* electroretinogram · *FWHM* full width at half maximum · λ_{max} wavelength of peak absorbance · *MSP* microspectrophotometry

Introduction

Frank and Case (1988a) reported the discovery of UV sensitivity in four species of deep-sea shrimp (*Systellaspis debilis*, *Oplophorus gracilirostris*, *O. spinosus* and *Janicella spinacauda*) in the family Oplophoridae. These shrimp occupy daytime depth ranges of 500–900 m, well below the depth at which UV wavelengths from the surface were thought to be "visible". At these depths, the majority of the remaining downwelling light is a very narrow spectrum centering on 475 nm (Jerlov 1976). Thus, it had been assumed that the visual systems of organisms from these depths (barring anomalies such as visual adaptations for detecting red-emitting photophores) would be monochromatic, possessing a single visual pigment with maximum absorption in the blue-green region of the spectrum (Bayliss et al. 1936; Clarke 1936; Goldsmith 1972; reviewed by Cronin 1986). Early microspectrophotometric work on one of these oplophorid shrimp, *S. debilis*, did not identify a near-UV visual pigment (Hiller-Adams et al. 1988), but a subsequent study was able to isolate it in the eighth and enlarged rhabdomere of the ommatidium (Cronin and Frank 1996). Subsequent behavioral experiments (Frank and Widder 1994a, b) demonstrated that the four mesopelagic species with a UV-sensitive visual pigment were clearly able to see and respond to UV wavelengths, while mesopelagic species lacking the near-UV visual pigment were not.

Distinguishing characteristics of the four species of crustaceans with UV-sensitive visual pigments are that they all undergo well-established vertical migrations, and they possess bioluminescent organs. Whether this short-wavelength sensitivity is a widespread phenomenon amongst crustaceans that share one or both of these characteristics is not known because, in addition to the species mentioned above, the published data on deep-sea crustacean visual pigments are limited to several species of euphausiids (Fisher and Goldie 1960; Boden et al. 1961; Denys and Brown 1982; Widder et al. 1987), and several species of sergestid shrimp (Hiller-Adams et al. 1988; Lindsay et al. 1999).

This paper describes the results of electrophysiological studies, using electroretinograms (ERGs), on the visual systems of deep-sea crustaceans. ERGs, which represent the summed mass activity of a large number of receptor cells, can reveal the presence of several classes of receptor cells, can be measured onboard ship (an important consideration when working on fragile and sometimes rare organisms), and most importantly, are an efficient way of identifying major evolutionary differences in spectral sensitivity (Neitz and Jacobs 1984;

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Chen and Goldsmith 1986; Jacobs and Neitz 1986). Twelve species in five families that cover a wide depth range were examined, including bioluminescent and non-bioluminescent species, as well as vertical migrators and non-migrators. The data presented here indicate that UV sensitivity in deep-sea crustaceans is not a common phenomenon, and may be restricted to members of the family Oplophoridae. In addition, these results indicate that the visual systems of most of the species in this study are better adapted for sensitivity to bioluminescence than to downwelling light.

Materials and methods

Animal collections

Specimens (with the exception of *Euphausia superba*) were collected with a Tucker trawl fitted with a thermally insulated, light-tight closing collecting container. The collecting container was closed at depth, and opened at the surface in a light-tight room under dim red light. Specimens were sorted under dim red light, and maintained in aerated light-tight containers of seawater at 2–10 °C, depending on species, for at least 24 h before being used for experiments. Each species was kept at a temperature that corresponded to one found within its daytime depth range. Specimens were collected in the following locations:

- *Funchalia villosa*: Gulf of Mexico and off south coast of Cuba
- *Meganyctiphanes norvegica*: Wilkinson Basin, Gulf of Maine and Oceanographer Canyon, south edge of Georges Bank
- *Pasiphaea multidentata*: Wilkinson Basin and Oceanographer Canyon
- *Phronima sedenteria*: Gulf of Mexico
- *Nematobrachion boopis*: off coast of southern California
- *N. sexspinosus*: off south coast of Cuba
- *Sergestes arcticus*: Cape Hatteras
- *S. corniculum*: Gulf of Mexico and Northwest Providence Channel, Bahamas
- *Sergia grandis*: Gulf of Mexico
- *Stylocheiron maximum*: off coast of southern California and off south coast of Cuba
- *Thysanopoda orientalis*: off east coast of Oahu

E. superba was collected at night in surface Antarctic waters with a dip net, placed in light-tight containers, and shipped to the U.S. on ice by a commercial courier.

Electrophysiological recordings

Experiments were conducted onboard ship or in a shore-based laboratory using the same apparatus. Live specimens were mounted on a Plexiglas holder, and placed in a chilled (2–10 °C) seawater bath with the dorsal surface of the eye just above the level of the water. In this configuration, their pleopods were free to paddle and generate respiratory water currents across the gills. Differential electrophysiological recordings of the ERG were conducted by placing metal microelectrodes (10-μm tip; F. Haer and Co.) subcorneally in both eyes, with the reference eye shielded from all light by covering it with black petroleum jelly. A silver chloride-coated wire grounded the water bath. As these were a.c. recordings, data were analyzed for peak to peak response heights using a program written in LabView (National Instruments), digitized and stored to disk for later analysis.

Light stimuli

Monochromatic test flashes (Instruments SA, Model H-20 Monochromator) were delivered to the test eye via a bifurcated light guide composed of randomized fibers. The light guide was placed at a set distance away, such that the beam of light bathed the entire eye. Flash duration (100 ms) was controlled by a Uniblitz Shutter (Model VS14 S) under computer control. Irradiance, which was controlled with a neutral-density wheel driven by a stepper motor under computer control, was calibrated at 10-nm intervals with a UDT Optometer (Graseby Optronics) and calibrated radiometric probe.

For photoadaptation experiments, an adapting light illuminated the eye through one branch of the bifurcated light guide, while test flashes were delivered through the other branch, ensuring that both the adapting light and test light impinged on the same photoreceptors. The adapting light was a white light filtered with a 380-nm (Ealing 35–3094) or 480-nm (Ealing 35–3458) interference filter (FWHM bandwidth 10 nm). Irradiance was controlled by neutral-density filters.

Experimental procedure

The specimens were prepared for experiments under dim red light (>690 nm). Even though deep-sea crustaceans are very insensitive to these wavelengths (Frank and Case 1988a), some degree of light adaptation still occurred. Therefore, experiments were not started until the response to a dim test flash had not changed for 1 h.

The eye was stimulated with 100-ms test flashes of monochromatic light adjusted for irradiance until a defined criterion response was obtained at each wavelength tested (usually every 10 nm from 400 nm to 580 nm). The criterion was set at 20 μV above background noise for each preparation, to ensure that the irradiance of the light flashes was near the threshold sensitivity of the animal, and would therefore not isomerize a sizable fraction of the visual pigment. The criterion response was never above 100 μV, which is less than 5% of the potential maximum ERG voltage of 3–5 mV that can be recorded with this electrophysiological set-up. To ensure that the eye remained in the same state of dark-adaptation during the experiment, the response to a standard test flash of set wavelength and irradiance was tested periodically throughout the experiment. If the response to the test flash started changing during the experiment, the experiment was terminated and these data were not used in the analysis.

Species with bilobed eyes

Several species of euphausiids in this study have bilobed eyes. In these specimens, the eye was aligned so that both lobes were oriented towards the light guide. The light guide, with its large-diameter fiber-optic bundle (4 mm), presented light over a large visual field, incorporating the field of view of both lobes. The recording electrode was placed in either the upper or lower lobe of the test eye, and a spectral sensitivity series was recorded, as described above. At the end of the spectral sensitivity run, if the preparation was still viable, the electrode was removed from this lobe and placed in the other lobe under dim red light. Once the test flash indicated that the eye was again fully dark-adapted, a spectral sensitivity curve was recorded from the other lobe. The position of the light guide was not moved between electrode placements.

Rhabdom lengths

Eyes were excised from specimens that had been preserved in 10% formalin in seawater. Each eye was bisected, and several rhabdoms from the center of the eye (where the largest rhabdoms are found) were measured in each specimen by an ocular micrometer with a dissecting microscope. In most cases, the crustaceans that were used for the ERG experiments were used for these determinations. When these were not available, measurements were made from specimens that covered the same size range as those used in the ERG experiments.

Data analysis

Spectral sensitivity data were plotted as the reciprocal of the irradiance (units: photons s^{-1} cm^{-2}) required to produce the criterion response at each wavelength. Absorptance curves were fit to the spectral sensitivity data from visual pigment templates (Stavenga et al. 1993). In order to calculate these curves, values for rhabdom length, specific absorbance (optical density of the visual pigment per micrometer of rhabdom) and λ_{max} (wavelength of peak absorbance) of the visual pigment must be entered. For this study, the mean rhabdom lengths (Table 2) from the center of the eye were used. Since the specific absorbance and λ_{max} of the visual pigments are not known for most of these species, these variables were simultaneously varied, within reasonable physiological limits, until the best sum-of-squares fit to the spectral sensitivity data was obtained.

Results

The species studied are shown in Table 1. Eight of the species undergo pronounced vertical migrations, while three species are not known to be vertical migrators. One species, *P. sedenteria,* was difficult to classify, as it has a wide vertical range during the day, and is not an abundant, and therefore easily quantifiable, species. However, several authors have shown that the bulk of the population appears to be shallower at night than during the day (Brusca 1967; Shih 1969; Franqueville 1971; Thurston 1976), so it will be considered a vertical migrator. Nine of the species in this study possess photophores or organs of Pesta, which are both sources of bioluminescence, while three species are not bioluminescent.

Spectral sensitivity data for the various species are shown in Fig. 1. All the species had a single spectral sensitivity maximum peaking in the blue-green region of the spectrum, which is indicative of the presence of a single receptor class (Table 2).

Chromatic adaptation experiments were conducted on *E. superba*, *P. sedenteria*, *F. villosa*, *N. sexspinosus*, *T. orientalis*, *P. multidentata*, *S. arcticus*, *S. corniculum* and *S. grandis*, with blue-green (480 nm) and/or UV (380 nm) adapting lights. A representative example of these experiments is shown in Fig. 2, for the euphausiid *M. norvegica*. Chromatic adaptation during exposure to 480-nm light did not produce a wavelength-specific effect on the shape of the spectral sensitivity curve with respect to the dark-adapted curve (Fig. 2A). In addition, the waveform responses at short, middle and long wavelengths were identical, both in the dark-adapted eye and the same eye under blue-green chromatic adaptation (Fig. 2B). Identical results were obtained after chromatic adaptation with UV light. Similarity of the waveform responses in the dark-adapted eye, together with the failure of the adapting lights to produce a wavelength-specific effect on either the shape of the spectral sensitivity curve or the response waveforms, are strongly suggestive of a single receptor class being present in the above-mentioned species.

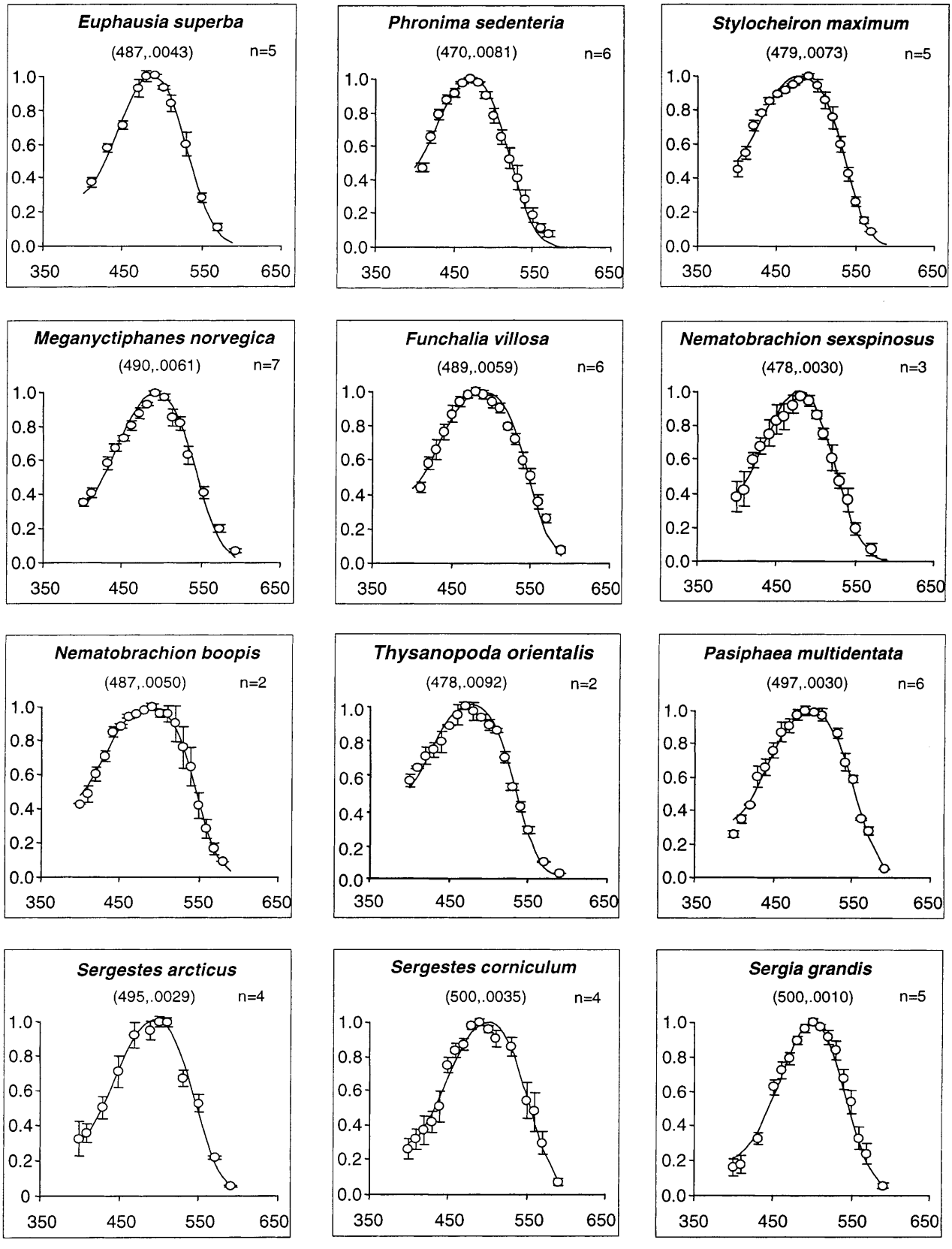
Chromatic adaptation experiments could not be completed for *S. maximum* and *N. boopis* due to lack of sufficient material and/or the fragility of the species involved. However, these species also had relatively narrow spectral sensitivity curves with a single maximum, indicative of a single visual receptor class, and the response waveforms were of uniform shape across the spectrum. In a previous ERG study of deep-sea crustaceans, those species with two visual pigments consistently showed wavelength dependent shifts in the shapes of the response waveforms (Frank and Case 1988a, b). The uniformity of response waveforms in these two species, together with a single sensitivity maximum in the dark-adapted spectral sensitivity curve, supports the supposition that these species also have a single class of visual receptor.

Maximum sensitivities ranged from 470 nm for the hyperiid amphipod *P. sedenteria* to 500 nm for the sergestids *S. corniculum* and *S. grandis* (Table 2). In Table 2, the species are listed according to a rough approximation of their daytime depth range, from shallowest (*E. superba*) to deepest (*S. grandis*). *N. boopis*, whose daytime

Table 1 Approximate daytime depth ranges, migratory behavior, and bioluminescence of adult mesopelagic crustaceans

Family	Species	Daytime depth (m)	Vertical migrator	Bioluminescent organs	Water type[17]
Euphausiidae	*Euphausia superba*	0–100[1,2]	*	*	1A–lll[18,19,20]
	Meganyctiphanes norvegica	300–500[3,4]	*	*	lB
	Stylocheiron maximum	250–500[5]		*	l,lA,lB
	Nematobrachion sexspinosus	350–600[5,6,7]		*	l,lA,lB
	Nematobrachion boopis	400–600[5,6,8]		*	l,lA,lB
	Thysanopoda orientalis	450–800[5,9]	*	*	l,lA,lB
Hyperiidae	*Phronima sedenteria*	100–1000[10,11,12]	*		lA,lB
Pasiphaeidae	*Pasiphaea multidentata*	500–800[3]	*		lB
Penaeidae	*Funchalia villosa*	300–550[13]	*		1A
Sergestidae	*Sergestes arcticus*	450–600[3]	*	*	lB
	Sergestes corniculum	600–800[3,14]	*	*	I,lA,lB
	Sergia grandis	600–900[14,15,16]	*	*	l,lA,lB

[1] Witek et al. 1981; [2] Mauchline and Fisher 1969; [3] Sardou et al. 1996; [4] Frank and Widder 1998; [5] Roger 1978; [6] Brinton 1967; [7] Baker 1970; [8] Kinsey and Hopkins 1994; [9] Brinton 1962; [10] Brusca 1967; [11] Thurston 1976; [12] Franqueville 1971; [13] Hopkins et al. 1994; [14] Donaldson 1975; [15] Donnelly et al. 1993; [16] Flock and Hopkins 1992; [17] Jerlov 1976; [18] Tilzer et al. 1983; [19] Palmisano and Sullivan 1983; [20] Smith et al. 1992


Euphausia superba
(487,.0043) n=5
Phronima sedenteria
(470,.0081) n=6
Stylocheiron maximum
(479,.0073) n=5
Meganyctiphanes norvegica
(490,.0061) n=7
Funchalia villosa
(489,.0059) n=6
Nematobrachion sexspinosus
(478,.0030) n=3
Nematobrachion boopis
(487,.0050) n=2
Thysanopoda orientalis
(478,.0092) n=2
Pasiphaea multidentata
(497,.0030) n=6
Sergestes arcticus
(495,.0029) n=4
Sergestes corniculum
(500,.0035) n=4
Sergia grandis
(500,.0010) n=5
Relative Sensitivity or Absorptance
Wavelength (nm)

◀

Fig. 1 Spectral sensitivity of 12 species of mesopelagic crustaceans. Species are arranged according to their daytime depth distributions, from shallowest to deepest. The *open circles* represent averaged normalized spectral sensitivity data; the number of specimens measured for each species is indicated on each graph. For those species with bilobed eyes, the data shown are from the upper lobe. The *solid curves* represent calculated best-fit absorptance curves for 400 through 590 nm (see Materials and methods). The *numbers in parenthesis* are the calculated best-fit wavelength of peak absorbance (λ_{max}) (nm) and specific absorbance (μm^{-1}). Error bars represent standard errors

depth range covers 400–600 m, was placed with the species occurring primarily above 500 m because the adults are most abundant during the day between 400 m and 500 m (Brinton 1967; Kinsey and Hopkins 1994). It is clear from this table that there is no correlation between daytime depth and the peak spectral sensitivity. The full width at half maximum sensitivity (FWHM) of the calculated absorptance curves, which would be broadened by high visual pigment densities, and narrowed by absorption by screening pigments, was also determined; again, there is no apparent correlation between this parameter and daytime depth distribution (Table 2).

Three species in the study, *P. sedenteria*, *F. villosa* and *P. multidentata* are not bioluminescent. Their respective spectral sensitivities peaked at wavelengths of 470, 489, and 497 nm, and covered the range of spectral sensitivities measured in this study, with a mean of 485 ± 8.0 nm. The other nine species are bioluminescent, and their spectral sensitivities cover almost as wide a range, from 478 nm to 500 nm, with a mean of 488 ± 2.9 nm. The difference between the means is not statistically significant (two-sample *t*-test, $P = 0.34$), indicating that there is no significant correlation between the presence or absence of bioluminescent organs and spectral sensitivity.

Three species, *S. maximum, N. sexspinosus* and *N. boopis*, are not vertical migrators, while the other nine species undergo substantial nocturnal migrations covering hundreds of meters. While the calculated absorbance maxima of the visual pigments from the vertical migrators were, in general, at longer wavelengths than those of the non-migrators (mean $\lambda_{max} = 489 \pm 3.4$ nm for migrators versus 481 ± 2.8 nm for non-migrators), the difference between the means was not statistically significant (two-sample *t*-test, $P = 0.11$). Similarly, while the FWHMs were, in general, narrower for the vertical migrators (120 ± 3.8 nm) than for the non-migrators (129 ± 8.5 nm), this difference was also not statistically significant (two-sample *t*-test, $P = 0.16$). These results indicate that there is no significant difference between the spectral sensitivities of species that undergo regular vertical migrations and those that do not.

Crustaceans with bilobed eyes

Several species of euphausiid shrimp in this study, *S. maximum, N. sexspinosus and N. boopis,* possess bilobed eyes. The upper lobe is directed towards brighter downwelling light, while the lower lobe is directed towards dimmer upwelling light. Since the spectral peak of downwelling and upwelling light are similar at the depths at which these species live (McFarland and Munz

Table 2 Characteristics of the visual systems of adult mesopelagic crustaceans. Species are arranged according to a rough approximation of their depth distribution, from shallowest to deepest. Length data for euphausiids refer to body length; length data for other species refer to carapace length. Numbers in parentheses next to species names are number of specimens measured for morphological data. Numbers in parentheses next to length measurements are standard errors. λ_{max} (wavelength of peak absorbance) is the hypothesized peak absorbance of visual pigment based on spectral sensitivity data. FWHM is the width of the calculated absorptance curve at half maximum sensitivity

Minimum daytime depth range (m)	Mean carapace or body* length (mm)	Rhabdom length (μm)	λ_{max}	FWHM
< 500 m				
Euphausia superba (4)	*31.4 (±1.5)	47 (±3.0)	487	108
Phronima sedenteria (5)	*31.8 (±0.72)	55[1]	470	118
Stylocheiron maximum (5)				
Upper lobe	*25.2 (±1.15)	108 (±9.3)	479	131
Lower lobe	*25.2 (±1.15)	78 (±6.0)	479	118
Meganyctiphanes norvegica (4)	*31.2 (±0.94)	68 (±3.8)	490	118
Funchalia villosa (3)	16.9 (±1.0)	137 (±17.9)	489	137
Nematobrachion sexspinosus (2)	*24.0 (±2.0)	110 (±2.5)	478	113
Nematobrachion boopis (3)				
Upper lobe	*24.7 (±1.9)	182 (±14.7)	487	142
Lower lobe	*24.7 (±1.9)	123 (±3.5)	488	126
> 500 m				
Thysanopoda orientalis (2)	34.5 (±1.0)	87 (±4.5)	478	134
Pasiphaea multidentata (4)	29.5 (±2.8)	207 (±10.6)	497	129
Sergestes arcticus (3)	14.0 (±0.74)	141 (±17.3)	495	118
Sergestes corniculum (2)	17.7 (±1.7)	126 (±18.1)	500	119
Sergia grandis (3)	20.9 (±2.5)	161 (±11.1)	500	104

[1] Data from Ball 1977

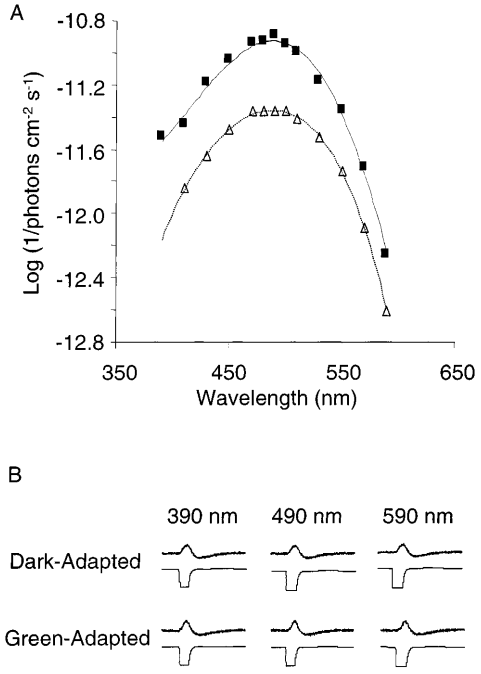


Fig. 2 A Spectral sensitivity of *Meganyctiphanes norvegica* while dark adapted (*filled squares*) and under chromatic adaptation (*open triangles*). **B** Response waveforms at three different wavelengths in dark-adapted and chromatically adapted eyes. The *upper trace* is the electroretinogram (ERG); the *lower trace* is the light stimulus

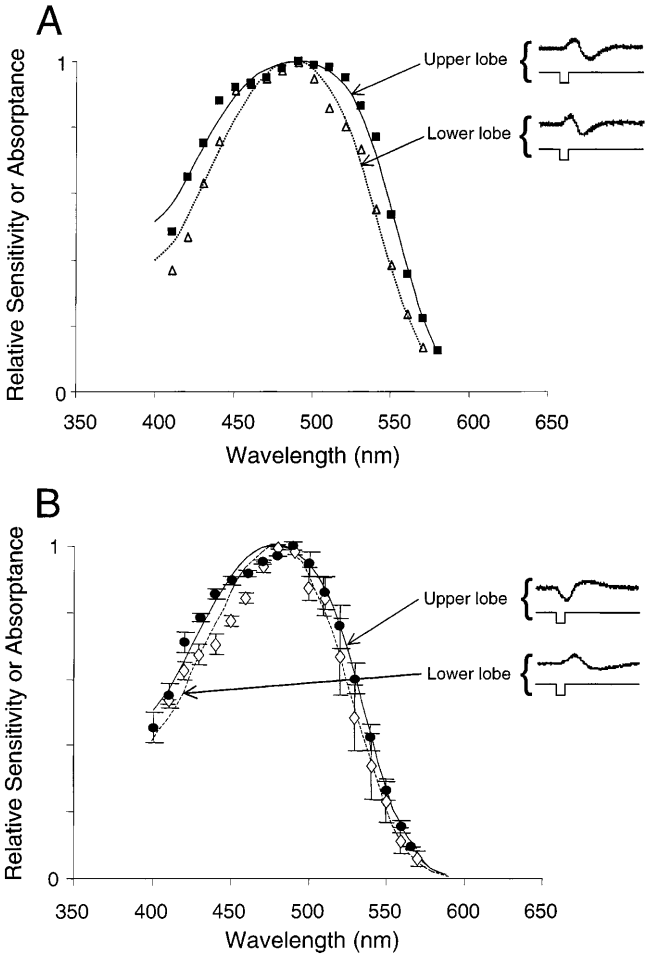


Fig. 3A Dark-adapted spectral sensitivity from the upper (*filled markers*) and lower lobes (*open markers*) of the eyes of two species of euphausiids. Curves are calculated best-fit absorptance curves. Response waveforms to 490-nm stimuli are shown in *upper right*; *upper trace* is the response recorded from the eye; *lower trace* is the light stimulus. **A** *Nematobrachion boopis* – data are from one animal. **B** *Stylocheiron maximum* – *filled circles* represent averaged normalized data from five specimens; *open diamonds* represent averaged normalized data from three specimens. Error bars are standard errors

1975; Jerlov 1976), one might anticipate that the spectral sensitivities of these two lobes would be similar, and results from *N. boopis* and *S. maximum* indicate that this is indeed the case. The spectral sensitivity of both the upper and lower lobes of *N. boopis* peaked between 487 and 488 nm (Table 2, Fig. 3A). The calculated absorptance curve of the upper lobe (FWHM = 142 nm) was considerably broader than that of the lower lobe (FWHM = 126 nm). The same tendency is true for *S. maximum* – the spectral sensitivity of both the upper and lower lobe peaked at 479 nm, while the calculated spectral absorptance curve was broader in the upper lobe than in the lower lobe (131 nm and 118 nm, respectively; Table 2, Fig. 3B). Comparisons of sensitivity between the two lobes were not possible because the instrumentation could not emit enough light to complete a V/log I curve. The response waveforms for the one specimen of *N. boopis* for which data were obtained in both the upper and lower lobes were of the same polarity, and the response kinetics were slightly faster in the lower lobe than in the upper lobe (Fig. 3). However, the response waveforms between the two lobes of *S. maximum* were consistently different. Responses were obtained from both the upper and lower lobes in five specimens, and the responses from the upper lobe were always of a different polarity from those of the lower lobe.

In addition to the three species of euphausiids, the hyperiid amphipod, *P. sedenteria*, also possesses a bilobed eye. Each eye is split into a dorsally oriented medial and ventrally oriented lateral eye, with separate retinas for each. The crystalline cones in the medial eye of *Phromina* are also remarkably elongated, producing huge bulbous lobes on the dorsal surface (Ball 1977). Placing the electrode subcorneally on the dorsal side of the upper lobe did not elicit any discernible response to light. Rather, the electrode had to be inserted at the level of the retinae in order to elicit a measurable response. In this orientation, the electrode was between the two retinae. Due to the extremely narrow visual field of the dorsal eye (Land 1989), and the large size of the eyes relative to the size of the light guide, it is likely that most, if not all, of the ERG came from the retina of the ventral eye, which has a much larger field of view (Land 1989). The spectral sensitivity curve was consistent for each specimen (Fig. 1), and the waveform responses were always of the same polarity.

Discussion

When attempting to correlate visual adaptations of oceanic species with their daytime depth distributions, it is important to take into account not only their depth range, but also the clarity of the water they occupy. For example, a species living in the Gulf of Mexico with relatively clear Jerlov's Type 1A water would be exposed to a substantially higher light intensity at 500 m depth than a species living in the mid Atlantic off the coast of Africa, which has murky Jerlov's Type III water. Assuming equal surface light intensities, species living in Jerlov's Type III water at 156 m depth would be exposed to the same light intensity (at 480 nm) as species living at 500 m depth in Jerlov's Type 1A water. For this reason, the depth distributions given in Table 1 were chosen, when possible, for locations that have similar water types. In addition, the species classification by depth in Table 2 is broad enough that corrections for equal optical depths between Jerlov's Type 1, 1A and 1B water would not affect their depth classification in this table. This holds true for *E. superba* as well, which is found in the Southern Ocean off Antarctica, where the water type ranges from Jerlov's Type 1A to Jerlov's Type III, depending on location as well as season (Tilzer et al. 1983; Smith et al. 1992). In Jerlov's Type III water, a depth of 100 m corresponds optically to a depth of 378 m in Jerlov's Type 1 water, so *E. superba* would still be classified as a species that is found primarily above 500 m water depth.

The spectral sensitivity curves were calculated based on the assumption that the concentration of metarhodopsin, and hence its intracellular spectral filtering, was negligible, as the animals were all dark adapted, and experiments were conducted using test flashes close to the threshold sensitivity of the photoreceptor. In the absence of filters or shielding pigments, the spectral sensitivity should by equivalent to the absorptance spectrum of the visual pigment. However, there are screening pigments in the photoreceptors of all these species, and as the density and absorbance of these pigments are unknown, their effects could not be accounted for. Previous studies have demonstrated that the peak of spectral sensitivity can be shifted by 10–35 nm from the λ_{max} of the visual pigment due to the filtering effects of longwave-pass screening pigments (Wald and Hubbard 1957; Kennedy and Bruno 1961; Fernandez 1965; Wald and Seldin 1968; Goldsmith and Fernandez 1968; Wald 1968; Goldsmith 1978; Cummins and Goldsmith 1981). In other crustaceans, the presence of the screening pigments had no effect on the spectral peak, but did narrow spectral sensitivity with respect to the absorptance spectrum of the visual pigment (Stowe 1980). Therefore, the calculated absorptance curves based on the spectral sensitivity data in this study may not match the actual absorptance curve of the visual pigment. However, for purposes of assessing the fitness of a photoreceptor to its environment, the spectral sensitivity peak is probably superior to the λ_{max} of the visual pigment in providing the most physiologically relevant evaluation.

Table 3 Comparison of previous and current studies

Species	λ_{max}	Method	Reference
Meganyctiphanes norvegica	460–465	Extract	Fisher and Goldie 1960
	460, 490, 515	ERG	Boden et al. 1961
	488	MSP	Denys and Brown 1982
	490	ERG	Current study
Euphausia superba	485	Extract	Denys and Brown 1982
	487	ERG	Current study
Stylocheiron maximum	470	Extract	Fisher and Goldie 1960
	479	ERG	Current study
Sergestes arcticus	475	Extract	Fisher and Goldie 1960
	495	ERG	Current study

Comparison with previous studies

The spectral sensitivity data indicate that the euphausiids *M. norvegica* and *E. superba* have single receptor classes with sensitivity peaks around 490 nm and 487 nm, respectively. These data are in excellent agreement with absorbance λ_{max} values measured from the rhodopsins of these two species by Denys and Brown (1982) (Table 3). These values for *M. norvegica* are at substantially longer wavelengths than that reported by Fisher and Goldie (1960) (Table 3), but their results are thought to be incorrect due to contaminating factors present in euphausiid eyes that were not known at the time of their work (Denys 1982). This may also explain why Fisher and Goldie's reported λ_{max} for the euphausiid *S. maximum* is considerably lower than the 479-nm peak suggested by the ERG data in the current study (Table 3). The ERG results from *M. norvegica* by Boden et al. (1961), which showed three peaks of spectral sensitivity (Table 3), are puzzling, as the data from the specimens used in the current study ($n = 7$) consistently showed a single peak near the λ_{max} of the visual pigment in both dark-adapted and chromatically adapted individuals. Boden et al. (1961) state that a spectral sensitivity curve can be generated by "exposing the eye to wave bands of equal energy". If they erroneously calibrated their light source for energy rather than photons, this would very likely produce a sensitivity peak at the wrong location, as photoreceptors are photon counters (Dartnall 1975), but should not have given them three peaks of sensitivity. Unfortunately, not enough information is given in their paper to allow determination of whether they made other errors in calibrating their light source.

Fisher and Goldie (1960) report a λ_{max} of 475 nm for rhodopsin extracted from the rhabdoms of *S. arcticus*, which is considerably lower than the 495-nm peak suggested by the ERG data. However, their value is also considerably lower than those of all other sergestid

visual pigments (493–497 nm) that have been studied to date via MSP (Hiller-Adams et al. 1988; Kent 1997), and again, it appears that their methodology might be at fault. They may not have been working on a photoreceptor that was fully dark adapted, which would shift the absorbance maximum of rhodopsin to shorter wavelengths due to contamination of metarhodopsin in the extract (Hiller-Adams et al. 1988). In addition, the absorbance spectra of visual pigments in extracts may peak at considerably lower wavelengths than those measured via MSP or electrophysiology (Goldsmith and Fernandez 1968; Goldsmith 1972; Fernandez 1973; Bruno and Goldsmith 1974).

If the data from the problematical studies are discounted, then it is clear that there is a close match between the spectral sensitivity peaks and the visual pigment absorbance peaks for those species for which both data sets are available, namely *M. norvegica*, *E. superba,* and by comparison to closely related species, *S. arcticus*. This close match indicates that for these species, pre-retinal dioptric structures and/or screening pigments are not significantly affecting their peak spectral sensitivity. This does not imply that the shape of the spectral sensitivity curve matches the absorptance curve of the visual pigment, but only that their relative maxima are the same.

There are no data available to determine how well the specific absorbances calculated to fit the spectral sensitivity data in the current study reflect the true specific absorbances of the visual pigments.

Crustaceans with bilobed eyes

Several species of euphausiids in this study have eyes that are divided into an upper and lower lobe. Optically, the lower eye has a wider visual field and lower resolution than the upper eye (Land et al. 1979), and this assessment is supported by differences in temporal resolution between the upper and lower eyes as well (T.M. Frank, unpublished observations). There are no differences between the peak spectral sensitivities of the two lobes in either *N. boopis* or *S. maximum*. However, in both species the calculated absorptance curve fitting the data from the upper lobe was broader than the absorptance curve fitting the data from the lower lobe. This may be because the rhabdoms are longer in the upper lobes than in the lower lobes (Table 2), allowing for more self-screening to occur, resulting in a greater broadening of the spectral sensitivity curve. In *N. boopis*, the calculated specific absorbances were identical ($0.005\ \mu m^{-1}$), lending support to this supposition. In *S. maximum*, the calculated specific absorbance in the upper lobe was $0.0073\ \mu m^{-1}$, while in the lower lobe, it was $0.0058\ \mu m^{-1}$, suggesting that, in addition to being longer, the upper lobe rhabdoms also contain a higher concentration of visual pigment. The difference in response waveforms between the two lobes of *S. maximum* is perplexing, as the facets from each lobe report to their own retina, rather than to a single retina (Kampa 1965). In both lobes, the electrode was placed subcorneally and distal to the retina, and therefore should have been in the same orientation with respect to each retina. In addition, the light guide was placed such that both lobes were bathed in the circle of light radiating from the end of the light guide, and the position of the light guide was not moved during the course of an experiment. While the response waveform is somewhat dependent on the depth of the electrode in the photoreceptor, in the five specimens in which responses were recorded from both the upper and lower lobes, the response waveforms recorded from the upper lobe were always of a different polarity from those recorded from the lower lobe. It is unlikely that chance differences in electrode depth produced such consistently different responses, and therefore, it appears that there is something unusual about the processing of the visual signal in the eye of *S. maximum*.

Ecological considerations

The ERG data indicate that all the species in this study have single visual receptor classes with sensitivity maxima between 470 nm and 500 nm. This is substantially lower than the 490-nm to 550-nm range that has been reported for shallow water species (reviewed by Goldsmith 1972; Cronin 1986) and mirrors the hyposochromatic shift that has been found in deep-sea fish visual pigments when compared to their shallow water or terrestrial relatives (Lythgoe 1972; Partridge 1989; Partridge et al. 1988, 1989; reviewed by Crescitelli et al.1985; Douglas et al.1998). It may be tempting to conclude that such a blue shift might confer a sensitivity benefit to these mesopelagic species, as the light at deeper depths is also blue shifted (Jerlov 1976). However, several investigators have argued that at the high pigment densities generally present in the eyes of these deeper living organisms, the benefits of a blue-shifted visual pigment are trivial (Munz 1965; Hiller-Adams et al. 1988; Crescitelli 1991; Bowmaker 1995). In the deep-sea, however, where every photon counts, the possibility that even such seemingly trivial benefits might provide an adaptive advantage cannot be discounted.

The Sensitivity Hypothesis, as first stated by Clarke (1936) and Bayliss et al. (1936), suggests that the visual pigments of deep-sea organisms would be blue shifted for maximum absorption of the available downwelling light, as the residual downwelling sunlight in the deep-sea is largely blue. The Sensitivity Hypothesis also predicts that there should be a shift towards shorter wavelength pigments with depth, but this is clearly not the case in deep-sea fish (reviewed by Douglas et al. 1998) or the deep-sea crustaceans in this study. In addition, calculations (Douglas et al. 1998; J.C. Partridge, unpublished observations) have shown that deep-sea fish should have λ_{max} values shorter than 474 nm in

Jerlov's Type 1B, 1A and I waters for greatest sensitivity to downwelling light, and the same case could be made for the crustaceans in this study, as they occupy the same photic environment. However, their spectral sensitivity and/or visual pigment maxima, and those of most other deep-sea crustaceans that have been studied to date (Frank and Case 1988a; Hiller-Adams et al. 1988, Kent 1997), are at longer wavelengths. Clearly, most deep-sea crustaceans are not optimally adapted for maximum sensitivity to downwelling light. However, even though a visual pigment that is spectrally matched to the downwelling irradiance is best for the detection of dark targets against a light background (Lythgoe 1966, 1968; Loew and Lythgoe 1978), in the deep-sea there is the added complication of bioluminescence. Bioluminescence is considered by some to be the major visual stimulus in the deep-sea (Beebe 1935; Clarke and Hubbard 1959; Jervlov 1976; Widder 1999), and species that specialize on bioluminescent prey would be scanning for lighter objects against a darker background. A visual pigment that is offset from the wavelength of maximum irradiance is superior to a spectrally matched pigment for discerning this type of contrast (Lythgoe 1966, 1968; Loew and Lythgoe 1978). Calculations by Partridge (Douglas et al. 1998, J.C. Partridge, unpublished observations) indicate that the λ_{max} values which will provide maximum sensitivity to bioluminescence range from 468 nm to 490 nm, which coincides with the peak rhodopsin absorbance or spectral sensitivity of most deep-sea crustaceans that have been studied to date. Thus, it appears that the spectral sensitivities of most deep-sea crustaceans are also better tuned for the detection of bioluminescence than downwelling light.

P. sedenteria appears to be the exception to this generalization, as its 470-nm spectral sensitivity maximum indicates that its visual system may be adapted for greatest sensitivity to downwelling light. This conjecture can be supported by examining its lifestyle. *Phronima* sp. use salps, pyrosomes, siphonophores and medusae as food sources, brood chambers, and feeding platforms (Laval 1980; Schaadt 1982). Although they also eat small crustaceans, gelatinous zooplankton make up the major portion of their diet (Repelin 1970), and therefore they are challenged with the task of imaging an object of low contrast against the downwelling light field. Land (1992) was able to demonstrate that *Phronima* would react to a dark square passing overhead in a behavioral tank. In this situation, possessing a pigment with maximum sensitivity to the downwelling light field might be considered an adaptive advantage. This observation underscores the importance of examining the lifestyle and diet of organisms, particularly those that live in the mesopelagic realm where bioluminescence is so prevalent, as well as their depth distributions and the downwelling irradiance at these depths, when attempting to draw conclusions about the fitness of visual pigments to the photic environment.

Phylogenetic constraints

Among deep-sea fish, there appears to be some degree of phylogenetic conservatism with respect to λ_{max} (Partridge et al. 1988, 1989, 1992; Douglas and Partridge 1997), and the same appears to be true for sergestid crustaceans. The three species of sergestids that have been studied here, as well as those studied via microspectrophotometry (Hiller-Adams et al. 1988; Kent 1997; Lindsay et al. 1999), all have spectral sensitivity and/or visual pigment absorbance maxima clumped between 495 nm and 500 nm, even though their depth distributions range from 300 m to 900 m. However, the same trend does not appear to hold for crustaceans in the family Euphausiidae. The spectral sensitivities within this family differ by 12 nm, ranging from 478 nm for *N. sexspinosus* to 490 nm for *M. norvegica*. Three of the species possess bilobed eyes (*N. sexspinosus, N. boopis,* and *S. maximum*), but this does not appear to be related to spectral sensitivity, as the spectral sensitivity peaks for these three species range from 478 nm to 487 nm. There is some indication that temporal resolution of some euphausiid species may be related to dietary preferences (Frank 1999), but a similar correlation cannot be made with respect to spectral sensitivity. *N. boopis* and *N. sexspinosus* both possess bilobed eyes and prefer copepods (primarily bioluminescent *Pleuromamma* sp.) and protozoan prey (Kinsey and Hopkins 1994), yet their spectral sensitivities differ by 10 nm. Currently, there is not enough information available about the predatory behavior of the sergestids and the euphausiids, or about the characteristics of their prey, to determine why there appears to be phylogenetic conservation among the sergestids but not the euphausiids.

The data on the 12 species of crustaceans in this study indicate that, as stated earlier, there is a single receptor class present in each species, with maximum sensitivity in the blue-green region of the spectrum. There was no evidence of a secondary near-UV receptor class, as has been found in several species of bioluminescent, vertically migrating oplophorid crustaceans. In these oplophorid species, as well as in several shallow living decapod crustacean species, the UV visual pigment is localized in an enlarged eighth retinula cell, which forms a secondary rhabdom lying distal to the main rhabdom secreted by the other seven retinula cells (Cummins and Goldsmith 1981; Cummins et al. 1984; Gaten et al. 1992; Cronin and Frank 1996) . In several species of the oplophorid *Acanthephyra*, which do not have UV sensitivity, the R8 cell is either missing or too small to be easily identified (Gaten et al. 1992). Looking at what little is known about the structure of the eyes of the species in the current study, neither *Phronima* (Ball 1977) nor euphausiid (Chun 1896; Kampa 1965; Meyer-Rochow and Walsh 1978; Hallberg and Nilsson 1983; Denys et al. 1983) ommatidia possess an eccentric cell that forms a distal rhabdom, which matches the physiological data that they lack UV sensitivity. While a shallow water sergestid species, *Acetes*, has an R8 cell

which forms a distal rhabdom (Ball et al. 1986), there are no reports on the structure of the rhabdoms in deep-sea sergestid species, but it is likely that their R8 cells would be degenerate or missing, similar to those species of deep-sea oplophorids which lack UV sensitivity. In summary, it appears that UV sensitivity is not an ubiquitous characteristic of deep-sea crustacean visual systems, but is a relatively rare phenomenon that, based on the data currently available, is found only in several bioluminescent species in the family Oplophoridae. The data presented here indicate that the photoreceptors of deep-sea crustaceans in general have single receptor classes with maximum sensitivities that are blue-shifted with respect to those of their shallow water relatives, and appear to be adapted for greater sensitivity to bioluminescence than downwelling light.

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