**Interspecific Variations in the Morphology and Ultrastructure of the Rhabdoms of
Oplophorid Shrimps.**

EDWARD GATEN¹, PETER M.J. SHELTON ¹ AND MARK S. NOWEL ²

¹Department of Biology, University of Leicester, Leicester LE1 7RH, UK

²Department of Biology, Providence College, Providence, Rhode Island 02918-0001,
USA

Pages – 20

Figures – 4

Short title: Rhabdom structure in oplophorid shrimps

Corresponding author: Dr E. Gaten

Department of Biology
University of Leicester
University Road
Leicester LE1 7RH, UK

Telephone +44 (0)116 2523387

FAX +44 (0)116 2523330

E-mail gat@le.ac.uk

Keywords: vision, Crustacea, deep-sea, rhabdom structure, distal rhabdom

ABSTRACT Interspecific variations in rhabdom structure between various oplophorid shrimps are described and the differences are related to the light environment at different depths within the mesopelagic zone. The ultrastructure of the distal rhabdom in these species is described for the first time. Quantitative measurements show that the proportion of the rhabdom layer occupied by the distal rhabdom varies from 3.5% to 25% in the dorso-ventral plane of the eye of *Systellaspis debilis*. The distal rhabdom occupies less than 1% of the rhabdoms in the eye of *Acanthephyra pelagica*, where it can only be seen using the electron microscope. It is suggested that the rhabdoms of those species that remain within the photic zone (such as *S. debilis*) are adapted to maximize contrast whereas in those whose depth ranges extend into the aphotic zone (such as *A. pelagica*) they are adapted for maximum sensitivity.

Daylight is modified by absorption and scattering to produce a light environment in the deep seas that is monochromatic, highly scattering and of low irradiance (Kirk, 1983). Light is also highly directional, downwelling irradiance being around 200 times greater than upwelling irradiance (Denton, 1990). Animals in the photic zone view their environment using the downwelling irradiance. At greater depths, bioluminescence becomes increasingly important until in the aphotic zone, below about 800 m, it is the only significant source of light. These factors have resulted in the eyes of deep-sea organisms being adapted for high absolute sensitivity (particularly to the wavelengths of maximum transmission) and, frequently, modified along the dorso-ventral plane in response to the directionally graded nature of the underwater light field. Although much of the work in this field has been carried out on fish (see Lythgoe, 1979), these adaptations are also observed in crustaceans living in the mesopelagic zone which extends from around 200 to 1,000 m. The eyes of euphausiids (Land et al., 1979), hyperiid amphipods (Land, 1989) and oplophorid shrimps (Gaten et al., 1992) show adaptations to the underwater light field. We have examined variations in rhabdom morphology in the eyes of mesopelagic decapod shrimps of the family Oplophoridae.

The eyes of adult decapod shrimps are generally of the reflecting superposition type (Gaten, 1998), in which the image is focused onto the light-absorbing rhabdoms by reflection within a distal layer of crystalline cones (Vogt, 1975; Land, 1976). The rhabdoms also act as light-collecting structures, retaining light by total internal reflection due to the difference in refractive index between the rhabdom and the surrounding cytoplasm. The typical decapod rhabdom consists of a single structure formed from interlocking bundles of microvilli (rhabdomeres) contributed by the eight retinula cells in each ommatidium, with rhodopsin molecules located within the microvillar membrane (Shaw and Stowe, 1982). The rhabdomeres of the eighth retinula cell (R8) are variable in appearance but usually differ

from those of the other retinula cells (R1 to R7). R8 forms a discrete distal part of the rhabdom, resulting in a tiered rhabdom structure. In many decapods, the microvilli from cells R3, R4, and R7 are orientated parallel to the shrimp's antero-posterior axis, while those from R1, R2, R5, and R6 are orientated parallel to the medio-lateral axis (Shaw and Stowe, 1982).

The cytoplasm of R8 does not contain shielding pigment granules and it is electron lucent (Shaw and Stowe, 1982). In the distal rhabdom the microvilli may all be oriented in one direction (e.g., *Pacifastacus* - Nüssel, 1976), arranged in two orthogonal directions (e.g., *Panulirus* - Meyer-Rochow, 1975) or sometimes randomly directed (e.g., *Leptograpsus* - Shaw and Stowe, 1982). R8 has been identified in the crayfish *Procambarus clarkii* as a violet receptor with maximum absorption near to 440 nm, whereas the rest of the rhabdom has an absorption maximum at 530 nm (Cummins and Goldsmith, 1981). Although sensitivity to UV light has been documented in shallow-water crustaceans (Storz and Paul, 1998; Marshall and Oberwinkler, 1999), evidence for sensitivity to short-wavelength light in mesopelagic species is limited. Using spectrophotometric methods, two photoreceptor classes have been described in the oplophorid shrimp *Systellaspis debilis* (Cronin and Frank, 1996). In the main rhabdom, maximum absorption is at 498 nm, whereas the distal rhabdom absorbs maximally at 410 nm. Electrophysiological (Frank and Case, 1988) and behavioral experiments (Frank and Widder, 1994a,b) have shown that some oplophorid shrimps are sensitive to both near-UV light and blue-green light.

All oplophorid shrimps have reflecting superposition eyes, although in some deep-sea species their eyes are modified through atrophy of the cone cell layer (Welsh and Chace, 1937, 1938; Gaten et al., 1992). Their eyes all possess a tapetum behind the rhabdom layer which reflects unabsorbed light back through the rhabdoms, although the extent of the tapetum varies between species (Shelton et al., 1992, 2000). Within the Oplophoridae there

is considerable variation in the appearance of the rhabdom, depending on the habitat depth and stage of development of the shrimp. Larval oplophorids have thin apposition-type rhabdoms in the zoeal stages, whereas those that hatch at postlarval stages have broader rhabdoms, tapering at both the proximal and distal ends (Gaten and Herring, 1995). Adult oplophorids from the upper mesopelagic zone, such as *Oplophorus spinosus* and *Systellaspis debilis*, show a gradient from spindle-shaped dorsal rhabdoms to larger, multi-lobed ventral rhabdoms (Gaten et al., 1992). Species normally inhabiting the deepest part of the mesopelagic zone, such as *AcanthePHYra pelagica*, possess a uniform layer of densely-packed lobed rhabdoms (Gaten et al., 1992).

The purpose of this study is to describe for the first time the ultrastructure of the distal rhabdom and its relative size in different regions of the eyes of a number of oplophorid shrimps, and to relate this to the depth and light environment inhabited by the various species. This work builds on the qualitative descriptions at the light microscope level previously published (Gaten et al., 1992).

MATERIALS AND METHODS

Specimen capture and preparation

Oplophorid shrimps (suborder Pleocyemata, infraorder Caridea, family Oplophoridae) were obtained during Cruise 195 of RRS Discovery in the eastern North Atlantic from depths of up to 1,000 m using the RMT 1+8 net system (Roe and Shale, 1979). There is considerable variation in the published depth ranges of the species used, due to differences in sampling technique, latitude, water quality and sampling time (several species of oplophorids undertake diel vertical migrations). To take account of these variations, the depth ranges quoted here are daytime depths from samples taken in the eastern North Atlantic where the water is Type I oceanic (Jerlov, 1976). The species used were *Oplophorus spinosus* (300-500

m Foxton, 1970), *Systellaspis debilis* (650-850 m Foxton, 1970), *S. cristata* (875-950 m Foxton, 1970), *Acantheephyra pelagica* (900-1200 m Domanski, 1986) and *Notostomus auriculatus* (600-1000 m present study). All of the specimens used in this study were taken from within the depth ranges given above.

Some of the shrimps used in this investigation were captured during the day, resulting in some light-induced damage being visible in the rhabdoms. Exposure to light rapidly causes the initiation of breakdown of the proximal rhabdom, leaving the distal rhabdom largely intact (Shelton et al., 1989). Although in its initial stages this does not change the volume of the rhabdom, the division between undamaged distal rhabdom and damaged proximal rhabdom can be distinguished more easily. Only those animals in which this division could be clearly seen were used for rhabdom analysis. The eyes were fixed as soon as possible after the capture of the animals using a mixture of 4% formaldehyde and 5% glutaraldehyde in phosphate buffer pH 7.4 (Karnovsky, 1965) for 3 to 12 h. Most of the eyestalks were removed to promote rapid penetration of the fixative, although some parts were left attached to assist in the orientation of the specimens. The eyes were post-fixed in 1% osmium tetroxide for 1.5 h, dehydrated in an acetone series and embedded in Spurr resin. Semithin (1 μ m) sections were taken and stained in 1% toluidine blue in 1% sodium borate. Ultrathin sections (ca. 0.1 μ m) mounted on grids were stained with uranyl acetate and lead citrate and observed on a Jeol 100CX electron microscope.

Image analysis

For examination by light microscopy, sections of the eyes of the following species were taken: *Oplophorus spinosus*, *Systellaspis debilis*, *S. cristata*, *Acantheephyra pelagica* and *Notostomus auriculatus*. Only those animals in which the distal and proximal rhabdoms could be clearly differentiated were used in this analysis. Although this resulted in rather

low numbers of specimens being used for the quantitative analysis, these appeared to be representative of each species. For each specimen, five sections in the dorso-ventral plane of the eye, where the rhabdoms were cut approximately longitudinally, were selected for further analysis. The sections were digitized using a Scion AG-5 frame grabber and an Apple Macintosh computer and analyzed using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). Five areas (dorsal, dorso-lateral, lateral, ventro-lateral and ventral) of each image were segmented manually and the lengths and areas of distal and proximal rhabdoms recorded. The mean values obtained from the five sections were then used to estimate the relative proportions of distal and proximal rhabdom in each area of the eye. These values were normalized using an arcsine transform and the resulting data tested for normality (no significant departure from normality when tested using Shapiro-Wilke) and homogeneity of variance (no departure from homoscedasticity, according to Bartlett-Box). ANOVA was used to show differences between areas, and Student-Newman-Keuls was employed to show the significance of these differences.

RESULTS

Gross anatomy of the oplophorid eye

The oplophorid shrimps used in this investigation have hemispherical eyes borne on short eyestalks. They are typical reflecting superposition eyes in which the distal crystalline cone layer and the proximal rhabdom layer are separated by a clear zone (Fig. 1A). In all species, the retinula cell nuclei are mainly located around the distal rhabdoms at the proximal margin of the clear zone, although in some regions of the eyes of *Notostomus auriculatus* these nuclei are located close to the basement membrane. The main difference between the eyes

Fig. 1. A: Light micrograph of a dorso-ventral section through the eye of *Systellaspis debilis* showing the crystalline cone layer (cc) and the rhabdom layer (r) separated by the clear zone (arrowed). B: The dorsal rhabdoms of *Oplophorus spinosus* exhibit a characteristic spindle shape with a small distal rhabdom (d) and a large proximal rhabdom (p). C: The ventral rhabdoms of the same species have a much larger distal rhabdom and multilobed proximal rhabdom. The rhabdoms of *AcanthePHYra pelagica* (D) and *Notostomus auriculatus* (E) are densely packed and interdigitating and they show no sign of a distal rhabdom. Scale bars A = 500 μm , B, C, D and E = 50 μm .

of the species investigated here lies in the structure of the rhabdoms. In *Oplophorus spinosus* and *Systellaspis debilis* there is a marked difference between the rhabdoms of dorsal and ventral parts of the eye. The dorsal rhabdoms are spindle shaped and have a relatively small distal rhabdom (Fig. 1B). The ventral rhabdoms consist of a larger distal rhabdom and a multilobed proximal portion (Fig. 1C). The distal rhabdom is clearly identifiable in these specimens as a more dense and non-striated region (Fig. 1B,C). In *S. cristata* the rhabdom structure throughout the eye is similar to that seen in the ventral part of the eye of *S. debilis*, and the distal rhabdom is clearly visible. The proportions of distal to proximal rhabdom are much more uniform throughout the eye. In contrast, a distal rhabdom is not seen at the light microscope level in the eyes of *Acantheephyra pelagica* or *Notostomus auriculatus*. The rhabdom layer in these species is uniform, consisting of multi-lobed and densely packed rhabdoms (Fig. 1D,E).

For each specimen, the maximum lengths of the distal and proximal rhabdoms were measured from 30 rhabdoms cut approximately axially (Table 1). Reconstruction of individual rhabdoms from the sections was not possible over most of the eye due to their interdigitating structure.

Fine structure of the distal rhabdom

The difference in structure between the distal and proximal rhabdoms can readily be seen in the dorsal rhabdoms of *Oplophorus spinosus* and *Systellaspis debilis* (Fig. 2). The proximal rhabdom consists of alternating layers of orthogonally directed bundles of microvilli, resulting in a banded appearance. In contrast, the distal rhabdom consists of microvilli that are not orientated in this orderly fashion (Fig. 2A). The vesiculation seen in some microvilli in the proximal rhabdom is typical of that found in the early stages of light-induced damage. The quadripartite cone cell tract separates just above the distal rhabdom

Table 1. Mean lengths (and standard deviations) of distal and proximal rhabdoms in five species of oplophorid shrimp, based on 30 measurements from each specimen.

eye region	rhabdom type	<i>Systellaspis debilis</i>		<i>Systellaspis cristata</i>		<i>Oplophorus spinosus</i>		<i>Notostomus auriculatus</i>		<i>Acantheephyra pelagica</i>	
		length (µm)	s.d.	length (µm)	s.d.	length (µm)	s.d.	length (µm)	s.d.	length (µm)	s.d.
dorsal	distal	21.2	4.3	35.8	-	20.6	5.4	-	-	-	-
	prox.	140.3	12.9	94.8	-	123.4	9.4	110.9	-	116.7	12.8
dorso-lateral	distal	34.2	3.6	36.3	-	21.6	7.7	-	-	-	-
	prox.	146.1	9.2	98.5	-	107.8	20.1	100.3	-	126.8	14.5
lateral	distal	37.6	4.4	51.3	-	25.3	9.8	-	-	-	-
	prox.	115.5	9.6	113.7	-	114.9	24.2	90.0	-	131.2	7.6
ventro-lateral	distal	44.7	6.6	41.6	-	28.8	16.2	-	-	-	-
	prox.	113.0	7.3	124.3	-	100.9	42.4	95.5	-	134.3	9.1
ventral	distal	40.0	7.4	48.9	-	27.4	7.9	-	-	-	-
	prox.	75.5	14.1	112.8	-	90.0	27.1	106.6	-	111.3	11.6
number of animals		4		1		2		1		1	

into four processes that pass around the sides of the rhabdom, terminating at the basement membrane. The cytoplasm of R8 occupies the region between the cone tract and the distal rhabdom (Fig. 2B). Four electron-lucent lobes of R8 extend proximally, surrounding the distal rhabdom (Fig. 2C). The lobes are joined by zonulae adherentes close to the rhabdom margin. More proximally, the four lobes of R8 line the sides of the distal rhabdom with each lobe contributing microvilli to one quarter of the distal rhabdom (Fig. 2D). At the base of the distal rhabdom, the other retinula cells (R1-7) are in close proximity to the cone cell processes, appearing larger in successive sections as the lobes of R8 get smaller (Fig. 2E).

Fig. 2. Electron micrographs showing rhabdom ultrastructure in *Systellaspis debilis*. A: Longitudinal section through the distal part of the rhabdom. The layered appearance of the proximal rhabdom (pr) is in sharp contrast to the homogeneous appearance of the distal rhabdom (dr). The vesiculation seen in the microvillar layers is an early sign of light-induced damage in the proximal rhabdom. One cone cell process is cut in longitudinal section (arrowed). B: Transverse section taken just above a rhabdom showing the four cone cell processes (*) separating around R8. C: Transverse section of the tip of the distal rhabdom showing four lobes of R8 surrounding the rhabdomal microvilli. D: In the

mid-region of the distal rhabdom the four lobes of R8 each contribute microvilli to one quarter of the rhabdom. E: Transverse section of the distal rhabdom close to its junction with the proximal rhabdom. The lobes of R8 are reduced and the cell bodies of the other seven retinula cells (arrowed) join the rhabdom around the cone cell processes (*). F: The proximal rhabdom is deeply lobed and is surrounded by a thin layer of retinula cell cytoplasm (rc). Tapetal cells (tc) are present between the rhabdoms at this level. Scale bars: A = 5 μm , B = 2 μm , C = 1 μm , D = 2 μm , E = 2 μm , F = 5 μm .

The main rhabdom, formed only by R1-7, is multilobed and partially surrounded by tapetal cells (Fig. 2F).

Although at the light microscope level no distal rhabdom could be seen in the eye of *Acantheephyra pelagica*, clear evidence of R8 is provided by electron microscopy. Its appearance at the point where the cone cell processes separate (Fig. 3A) is similar to that described in *Systellaspis debilis*. R8 then divides into four lobes extending proximally between the cone cell processes. In contrast to *S. debilis*, however, the microvilli arising from the lobes of R8 all run parallel to one another in this species (Fig. 3B). The proximal rhabdom, surrounded by R1-7, forms the vast majority of the rhabdom with microvilli that are not orientated consistently (Fig. 3C). In *Notostomus auriculatus* no distal rhabdom could be found, even at the distal tip of the rhabdom where instead the seven retinula cells could be observed (Fig. 3D). However, below the rhabdom an eighth retinula cell body could be seen towards the periphery of the ommatidium (Fig 3E).

Variations in rhabdom volumes

Those sections where the distal and proximal rhabdoms could be reliably distinguished were analyzed for regional variations in the relative size of the distal rhabdom. This included four specimens of *Systellaspis debilis*, two of *Oplophorus spinosus* and one of *S. cristata*. The relative volumes of distal and proximal rhabdom were calculated for each of the five regions of the eye in those specimens (Fig. 4).

Fig. 3. Electron micrographs showing rhabdom ultrastructure in *Acantheephyra pelagica* (A – C) and *Notostomus auriculatus* (D – E). A: Transverse section taken just above the rhabdom of *A. pelagica* showing R8 situated between the four cone cell processes (*). B: Transverse section of the small distal rhabdom contributed by the four lobes of R8 and still surrounded by cone cell processes (*). The microvilli are unidirectional. C: Proximal rhabdom, formed by R1-7 at the level of the retinula cell nuclei (rcn). The microvilli are orientated at various angles. D: The distal tip of the rhabdom of *Notostomus auriculatus* showing that seven retinula cells contribute to this portion of the rhabdom. E: Below the rhabdom, each ommatidium consists of rosettes of seven retinula cells, although an eighth cell body can be seen towards the periphery of the ommatidium. Cone cell processes (*) can be seen between the retinula cells. Scale bars: A = 1 μ m, B = 1 μ m, C = 2 μ m, D = 1 μ m, E = 2 μ m.

In *Systellaspis debilis*, the proportion of the rhabdom contributed by R8 increased from 3.7% in the dorsal region to 9.3% dorso-laterally. In the other three regions the proportion was between 21.9% and 23.9%. Very highly significant differences between groups were shown using ANOVA ($p < 0.001$). A Student-Newman-Keuls test showed that there were

highly significant differences ($p < 0.01$) between the dorsal region and all of the others and between the dorso-lateral region and all of the rest. The lateral, ventro-lateral and ventral regions formed a homogeneous sub-set showing no significant difference between them.

Fig. 4. Change in the relative proportion of distal (grey) and proximal (striped) rhabdoms in three species, *Systellaspis debilis*, *Systellaspis cristata* and *Oplophorus spinosus*. The inset shows the five regions of the eye sampled. d, dorsal; d-l, dorso-lateral; l, lateral; v-l, ventro-lateral; v, ventral.

In *Oplophorus spinosus*, the same general pattern was observed, with an increase in the relative size of the distal rhabdom along the dorso-ventral plane. The single specimen of *S. cristata* showed a higher proportion of distal rhabdom in all regions of the eye when compared to both *Systellaspis debilis* and *Oplophorus spinosus*. Results for *Acanthephyra*

pelagica and *Notostomus auriculatus* are not plotted because no distal rhabdom could be detected using light microscopy in any regions of the eyes of these species.

DISCUSSION

The descriptions of the oplophorid eyes presented here show that there is considerable variation in rhabdom size and structure, particularly with respect to variations in the size of the distal rhabdom, both between species and within a single eye. These differences may be correlated with the depth range over which the animals are normally found. However, quoted depth ranges are only of real value if the water quality is also known. For instance, the boundary between the mesopelagic and bathypelagic fauna may occur between 700 and 1300 m depending on water clarity (Lythgoe, 1979). Recorded depth distributions for individual species cover a wide range due not only to the natural intraspecific variation but also to the effects of water quality and sampling technique. In the eyes investigated here, the banded fusiform rhabdoms, typically seen in shallow water shrimps, are found only in the dorsal regions of the eyes of *Oplophorus spinosus* and *Systellaspis debilis*. These two species had the shallowest daytime range of the oplophorids investigated, usually being found at depths of less than 700 m (Foxton, 1970; Roe, 1984). Complex interdigitating rhabdoms were found in the ventral parts of the eyes of these shrimps and throughout the eyes of those from deeper water, such as *S. cristata* and *Acanthephyra pelagica*. The distal retinula cell (R8) was free of all shielding pigments and formed a conical distal rhabdomeric cap in those rhabdoms where it was present. The microvilli within the distal rhabdom were not aligned in orthogonal rows, as seen in some decapod eyes (Shaw and Stowe, 1982). The distal rhabdoms in *Acanthephyra pelagica* are so small as not to be discernible at the light-microscope level. None could be seen even at the electron-microscope level in the eyes of *Notostomus auriculatus*.

Within the eye of *Systellaspis debilis*, changes in rhabdom volume occur around the dorso-ventral plane. The dorsal rhabdoms are spindle-shaped, which enhances resolution (Warrant and McIntyre, 1991) but leads to a reduction in rhabdom volume and sensitivity to light. Over the rest of the eye, the rhabdoms fill all of the available space within the rhabdom layer, maximizing both rhabdom volume and sensitivity. However, the loss of a layer of retinula cell cytoplasm between adjacent rhabdoms must lead to a reduction in resolution due to an increase in the crossover of light into non-target rhabdoms. The lateral rhabdoms are shorter than the dorso-lateral and ventro-lateral rhabdoms in this species, although this is not true of other oplophorids (Table 1). The volume of the distal rhabdom, as a proportion of the rhabdom as a whole, is around 23% over the lateral and ventral regions of the eye. The values are significantly different for the dorso-lateral (9.4%) and dorsal (3.7%) regions of the eye. A similar trend of reduction of the distal rhabdom dorsally is seen in *Oplophorus spinosus* and *Systellaspis cristata*, although the difference is not so apparent in the latter species. In *Acantheephyra pelagica*, the distal rhabdom is considerably reduced with no detectable regional variation in volume.

A microspectrophotometric study (Cronin and Frank, 1996) has shown that the distal rhabdom of *Systellaspis debilis* contains a visual pigment that absorbs maximally at 410 nm in contrast to one absorbing at 498 nm in the proximal rhabdom. Behavioral sensitivity measurements (Frank and Widder, 1994a,b) show equal sensitivities to light at 400 and 500 nm in species of shrimp with two visual pigments. In those with only one pigment, up to one log unit more light was required to achieve a threshold response at 400 nm than at 500 nm. The behavioral experiments show that a number of oplophorids with obvious distal rhabdoms are using near-UV light and it has been shown that usable amounts of light at 380 nm are present at 600 m, within the daytime depth range of *Systellaspis debilis* (Frank and

Widder, 1996). However, the question remains: why do some shrimps maintain a gradient of distal rhabdom volume within the eye while others have abandoned it altogether?

The dorso-ventral structural and functional variations in the rhabdoms of *Systellaspis debilis* seem to be related to the variations in the light environment above and below the animal and in the visual tasks that need to be carried out by the different regions of the eye. The dorsal part of the eye is adapted for higher resolution and sensitivity to the downwelling light; this makes it ideal for picking out detail of silhouettes overhead. In the ventral and lateral regions, the rhabdoms are not spindle-shaped, are not separated by a layer of retinula cell cytoplasm of low refractive index and, therefore, are expected to have lower resolution (Warrant and McIntyre, 1991). However, the dense packing of rhabdoms and the enlarged distal rhabdom may result in increased contrast sensitivity, ideal for detecting light reflected or emitted from targets against the background spacelight. An analogous spatial variation in spectral sensitivity has been described in the eye of the squid *Watasenia scintillans* (Matsui et al., 1988) and in the fish *Diretmus argenteus* (Denton, 1990). Shrimps of the genus *Systellaspis* found in deeper water (such as *S. cristata*) have rhabdoms in the dorsal part of the eye that have adapted to the reduced downwelling light by abandoning the high resolution spindle-shaped rhabdoms. As a result all of the rhabdoms in this species are multi-lobed. However, they retain distal rhabdoms and we assume that this is because these shrimps may be relatively recent invaders of deeper water and have not yet adapted to their new habitat. They therefore retain the rhabdom structure of an ancestor active in shallower water.

The differences in rhabdom structure described here are attributed to depth-related changes in the light environment. Oplophorids active only within the photic zone have dorsal rhabdoms adapted for increased resolution whereas ventral and lateral rhabdoms are adapted for increased contrast sensitivity due to their enlarged distal rhabdom. Those

shrimps whose depth ranges extend into the aphotic zone (such as *Acanthephyra* spp. and *Notostomus auriculatus*) appear to have largely abandoned the distal rhabdom as a possible adaptation to increase the total quantum capture.

ACKNOWLEDGMENTS

This work was supported by NERC grant GR3/11212. MSN gratefully acknowledges sabbatical support from Providence College. We thank Barry Shepherd (Department of Biology, University of Leicester) for his invaluable help with the statistics.

LITERATURE CITED

- Bryceson KP. 1986. The effect of screening pigment migration on spectral sensitivity in a crayfish reflecting superposition eye. *J Exp Biol* 125: 401-404.
- Cronin TW, Forward RB. 1988. The visual pigments of crabs. I. Spectral characteristics. *J Comp Physiol* 162: 463-478.
- Cronin TW, Frank TM. 1996. A short-wavelength photoreceptor class in a deep-sea shrimp. *Proc Roy Soc Lond (Biol)* 263: 861-865.
- Cummins D, Goldsmith TH. 1981. Cellular identification of the violet receptor in the crayfish eye. *J Comp Physiol* 142: 199-202.
- Denton EJ. 1990. Light and vision at depths greater than 200 metres. In: Herring PJ, Campbell AK, Whitfield M, Maddock L. eds *Light and life in the sea*. Cambridge: University Press. p 127-148.
- Domanski PA. 1986. The Azores front: A zoogeographic boundary. In: Pierrot-Bults AC, van der Spoel S, Zahuranec BJ and Johnson RK, editors. *Pelagic biogeography*. The Netherlands: UNESCO. p. 73-83.
- Foxton P. 1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SOND cruise 1965. 1. The Caridea. *J Mar Biol Assoc U.K.* 50: 939-960.
- Frank TM, Case JF. 1988. Visual spectral sensitivities of bioluminescent deep-sea crustaceans. *Biol Bull* 175: 261-273.
- Frank TM, Widder EA. 1994a. Evidence for behavioral sensitivity to near-UV light in the deep-sea crustacean *Systellaspis debilis*. *Mar Biol* 118: 279-284.
- Frank TM, Widder EA. 1994b. Comparative study of behavioral-sensitivity thresholds to near-UV and blue-green light in deep-sea crustaceans. *Mar Biol* 121: 229-235.

- Frank TM., and 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 Fresh Behav Physiol* 27: 189-197.
- Gaten E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contrib to Zool* 67: 223-235.
- Gaten E, Herring PJ. 1995. The morphology of the reflecting superposition eyes of larval oplophorid shrimps. *J Morphol* 225: 19-29.
- Gaten E, Shelton PMJ, Herring PJ. 1992. Regional morphological variations in the compound eyes of mesopelagic decapods in relation to their habitat. *J Mar Biol Assoc U.K.* 72: 61-75.
- Hiller-Adams P, Widder E A, Case JF. 1988. The visual pigments of four deep-sea crustacean species. *J Comp Physiol* 163: 63-72.
- Jerlov NG. 1976. *Marine Optics*. Elsevier Oceanography Series. Amsterdam: Elsevier Scientific Publishing Co.
- Karnovsky MJ. 1965. A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *J Cell Biol* 27: 137A-138A.
- Kirk JTO. 1983. *Light and photosynthesis in aquatic ecosystems*. Cambridge: University Press.
- Land MF. 1976. Superposition images are formed by reflection in the eyes of some oceanic decapod Crustacea. *Nature* 263: 764-765.
- Land MF. 1989. The eyes of hyperiid amphipods: relations of optical structure to depth. *J Comp Physiol* 164: 751-762.
- Land MF, Burton FA, Meyer-Rochow VB. 1979. The optical geometry of euphausiid eyes. *J Comp Physiol* 130: 49-62.
- Lythgoe JN. 1979. *The ecology of vision*. Oxford: Clarendon Press.

- Matsui S, Seidou M, Horiuchi S, Uchiyama I, Kito Y. 1988. Adaptation of a deep-sea cephalopod to the photic environment. *J Gen Physiol* 92: 55-66.
- Marshall J, Oberwinkler J. 1999. The colourful world of the mantis shrimp. *Nature* 401: 873-874.
- Meyer-Rochow VB. 1975. Larval and adult eye of the Western Rock Lobster (*Panulirus longipes*). *Cell Tissue Res* 162: 439-457.
- Nässel DR. 1976. The retina and retinal projection on the lamina ganglionaris of the crayfish *Pacifastacus leniusculus* Dana. *J Comp Neurol* 167: 341-360.
- Roe HSJ. 1984. The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 2. Vertical migrations and feeding of mysids and decapod Crustacea. *Prog Oceanog* 13: 269-318.
- Roe HSJ, Shale DM. 1979. A new multiple rectangular midwater trawl (RMT 1+8M) and some modifications to the Institute of Oceanographic Sciences' RMT 1+8. *Mar Biol* 50: 283-288.
- Shaw SR, Stowe S. 1982. Photoreception. In: Atwood HL, Sandeman DC eds. *The biology of Crustacea* vol. 3. New York: Academic Press. p 291-367.
- Shelton PMJ, Gaten E, Herring PJ. 1989. Compound eye morphology, pigment migration and light-induced retinal damage in mesopelagic decapod crustaceans. *J Mar Biol Assoc U.K.* 69: 737.
- Shelton PMJ, Gaten E, Herring PJ. 1992. Adaptations of tapeta in the eyes of mesopelagic decapod shrimps to match the oceanic irradiance distribution. *J Mar Biol Assoc U.K.* 72: 77-88.
- Shelton PMJ, Gaten E, Johnson ML, Herring PJ. 2000. The 'eye-blink' response of mesopelagic Natantia, eyeshine patterns and the escape reaction. *Crust Issues* 12: 253-260.

- Storz UC, Paul RJ. 1998. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. J Comp Physiol 183: 709-717.
- Vogt K. 1975. Optik des Flubkrebsauges. Z Naturforsch 30c: 691.
- Warrant EJ, McIntyre PD. 1991. Strategies for retinal design in arthropod eyes of low F-number. J Comp Physiol 168: 499-512.
- Welsh JH, Chace FA. 1937. Eyes of deep-sea crustaceans. Acanthephyridae. Biol Bull 72: 57-74.
- Welsh JH, Chace FA. 1938. Eyes of deep-sea crustaceans. Sergestidae. Biol Bull 74: 364-375.