J. Mar. Biol. Ass. U.K. (2002), **82**, 835–842
Printed in the United Kingdom

Spectral sensitivities of five marine decapod crustaceans and a review of spectral sensitivity variation in relation to habitat

Magnus L. Johnson*‡, Edward Gaten† and Peter M.J. Shelton†

*Scarborough Centre for Coastal Studies, University of Hull, Filey Road, Scarborough, YO11 3AZ. †Department of Biology, University of Leicester, University Road, Leicester, LE1 7RH. ‡Corresponding author, e-mail: M.Johnson@hull.ac.uk

The spectral sensitivities of five species of decapod crustaceans have been determined by electroretinogram measurements. Their spectral sensitivities conform to the general picture for marine crustacea with high sensitivity to blue-green wavelengths and some showing sensitivity to violet/near ultraviolet. Two deep-water species (*Paromola cuvieri* and *Chaceon* (*Geryon*) *affinis*) have spectral sensitivity maxima below 500 nm, whereas the three coastal species examined (*Crangon allmani*, *Pandalus montagui* and *Nephrops norvegicus*) are maximally sensitive to light of longer wavelengths (510 to 525 nm).

INTRODUCTION

Any aquatic environment tends to have a spectrally predictable light climate because of the way in which sunlight is modified by the water column and the presence of particles and dissolved substances specific to that environment (Kirk, 1983). Differences in spectral sensitivities of organisms from different environments can often be related to the light climates in which they live. In the current study we have obtained information on the spectral sensitivities of five marine decapod crustaceans using electroretinograms (ERGs). Two of these (*Paromola cuvieri* and *Chaceon* (*Geryon*) *affinis*) were deep-sea species and three (*Crangon allmani*, *Pandalus montagui* and *Nephrops norvegicus*) were coastal species. With the exception of *Chaceon affinis* (which has apposition eyes) these animals have superposition eyes in which light is reflected back through the rhabdoms by a tapetum (Gaten, 1998). Results from the study of these animals and from a review of data in the published literature show that spectral sensitivity appears to be strongly related to habitat.

Studies of spectral sensitivity in decapod crustacean eyes have used a variety of methods, none of which is completely satisfactory on its own. Investigations of spectral sensitivity through observations of behaviour show the true reaction of a species to a particular stimulus. Although there have been some elegant behavioural investigations into the spectral sensitivities of deep-sea crustaceans (Frank & Widder, 1992, 1994), interpreting the behaviour of an animal that has been removed from its habitat requires care; this is especially true for mesopelagic species which become disorientated when confronted with aquarium boundaries.

Spectrophotometry of extracted pigments has been used widely (Wald & Hubbard, 1957; Fernandez, 1973; Van Dover et al., 1989) although photopigments do not behave in the same way in solution as they do *in situ*. Differences of up to 20 nm in the peak sensitivity (λ_{Max}) have been reported (Bruno & Goldsmith, 1974). Microspectrophotometry (MSP) of intact rhabdoms is now preferred for assessing the spectral absorption of photoreceptors (Cronin & Frank, 1996; Kent, 1997; Cronin & Jinks, 2001). Although the MSP results give an accurate representation of spectral absorption characteristics of the rhodopsin within an eye, the measured absorbance spectrum of the photopigment may not reflect how it is utilized.

There have been many electrophysiological studies of spectral sensitivity in coastal decapods (Cummins et al., 1984; Lall & Cronin, 1987; Ziedins & Meyer-Rochow, 1990). Electrophysiological studies have the advantage that they provide information about responses in the receptor layer that take into account any optical filtering by the eye (Bryceson, 1986). However, like other non-behavioural methods, they may not indicate how a particular behaviour is affected by light.

Two hypotheses relating the spectral composition of light in the habitat and spectral sensitivity exist. The 'Sensitivity Hypothesis' suggests that an animal's visual pigment is matched to the spectral distribution of light in its habitat (Bayliss et al., 1936; Clarke, 1936). Alternatively the 'Contrast Hypothesis' suggests that visual pigments will be adapted to maximize the apparent contrast between an object of interest and its background (Lythgoe, 1968). In this case the pigment will be specifically adapted to respond maximally to light from a viewed object that is spectrally different from the background light.

The reasons suggested for differences in spectral sensitivity include the presence of gelbstoff in inland and coastal waters (Kirk, 1983), the greater complexity of the shallow water visual environment (Morin, 1983), and the presence of bioluminescence which can be an important source of light in the marine environment (Herring, 1983).

Studies of marine crustaceans have suggested that most species from shallow coastal waters have visual pigments with a λ_{Max} of around 500 nm whereas mesopelagic species have shorter wavelength-sensitive pigments (Kent, 1997).

The only benthic deep-sea species studied to date (*Geryon quinquedens*; Cronin & Forward, 1988) was found to have the shortest wavelength-sensitive pigment (λ_{Max} 473 nm) when compared to the range found in 27 semi-terrestrial and coastal species of crabs (λ_{Max} 483–515 nm). In addition, there is evidence for the presence of a violet/near ultraviolet receptor in many mesopelagic decapods (Frank & Case, 1988; Frank & Widder, 1992, 1994; Gaten et al., 1992; Cronin & Frank, 1996).

In the current study, an extensive review of other known decapod spectral sensitivities has been carried out and an attempt has been made to rationalize the relationship between spectral sensitivity and habitat.

MATERIALS AND METHODS

Baited traps were used to capture specimens of *Nephrops norvegicus* (L.) (Nephropidae) from Loch Torridon at 18–135 m and *Paromola cuvieri* (Risso) (Homolidae) and *Chaceon* (*Geryon*) *affinis* (A. Milne-Edwards & Bouvier) (Geryonidae) from 800 m depth on Rosemary Bank off the west coast of Scotland. To prevent light-induced damage to the eyes (Loew, 1976) the traps were not raised until surface light levels had dropped to less than 1.0 μmol m^{-2} s^{-1}. *Pandalus montagui* Leach (Pandalidae) and *Crangon allmani* Kinahan (Crangonidae) were supplied commercially. Adult specimens of each species were transported to the laboratory in light-tight containers and used as soon as practicable.

Specimens were prepared for ERG recordings under dim red light using a 600 nm filter. A small incision was made through the cornea on the dorsal part of the eye and sealed with petroleum jelly to prevent coagulation of the haemolymph. The extracellular silver electrode was inserted just below the cornea and the amplified responses recorded on a computer at a rate of one sample per 25 ms.

Light was supplied from a 75 W xenon arc lamp and light intensity was controlled using neutral density filters and directed at the eye via a silica light guide. The spectrum of light reaching the eye was limited using narrow pass band filters ranging from 360–600 nm λ_{Max} with a full width at half maximum (FWHM) of approximately 10 nm. Stimulus duration was controlled using an electronic shutter to give flashes of 0.1 s at 30 s intervals.

A V/Log I curve (response plotted against log light intensity) was generated at 500 nm and this was used to calculate the relative spectral sensitivity from the responses of the eye to isoquantal flashes at each wavelength. Dark-adapted animals were subjected to three flashes at each wavelength followed by a second V/Log I curve to check that the preparation had not deteriorated. The animals were then light adapted for 1 h using a green light-emitting diode (562 nm) at an intensity set at just below the mid-point of the response range revealed by the dark-adapted V/Log I curve. As reported by Johnson et al. (2000), when attempts were made to light adapt the deep-water species *Paromola cuvieri* and *Chaceon affinis* the eyes ceased to respond to any light stimuli.

The wavelength of peak response was determined after smoothing the normalized data using a three-point running average, which results in the peak being less affected by random noise (Kent, 1997). A rhodopsin spectral template was fitted using the method of Stavenga et al. (1993) based on the α absorption band of rhodopsin.

For a specific rhodopsin the proportion of light absorbed (absorptance) over distance (l) at a particular wavelength is given by:

$$F(l,\lambda) = 1 - e^{-kA(\lambda)l} \quad (1)$$

where k is the absorption coefficient at λ_{max} and $A(\lambda)$ is the absorbance spectrum of rhodopsin. Using this absorptance spectrum, the proportion of light at each wavelength absorbed by a photoreceptor of known length can be calculated (Warrant & Nilsson, 1997).

In many decapod species (Eguchi et al., 1973; Cummins & Goldsmith, 1981; Gaten et al., 1992) the rhabdom is partitioned into a distal rhabdom (absorbing at short-wavelengths) and a proximal rhabdom (absorbing at longer wavelengths). To model this for each species it was assumed that the violet receptor occupied the distal region of the rhabdom and that the proximal rhabdom absorbed light that had passed through the distal rhabdom. The rhodopsin template was fitted using the long-wavelength section of the data and the fit was then improved by the addition of a second shorter-wavelength template. For each species, approximate dimensions of the distal and proximal rhabdoms were measured from sections. The maximum absorption coefficient for decapod rhodopsins

Table 1. *Parameters of the spectral sensitivity data obtained from five decapod species by means of extracellular electrophysiological recordings. F-max corresponds to the spectral filter that elicited the maximum response. The 50% short and long points are the points of the spectral sensitivity curve where the response is 50% of the maximum. FWHM is the width of the spectral sensitivity curve in nm at the 50% maximum sensitivity point.*

Species	Adaptation	F-max	50% Short	50% Long	FWHM
C. allmani	Dark	538	449	570	121
	Light	519	463	567	104
P. montagui	Dark	519	448	566	118
	Light	511	452	566	114
N. norvegicus	Dark	519	463	564	101
	Light	519	437	570	133
P. cuvieri	Dark	460	405	516	111
C. affinis	Dark	467	356	531	175

https://doi.org/10.1017/S0025315402006203 Published online by Cambridge University Press

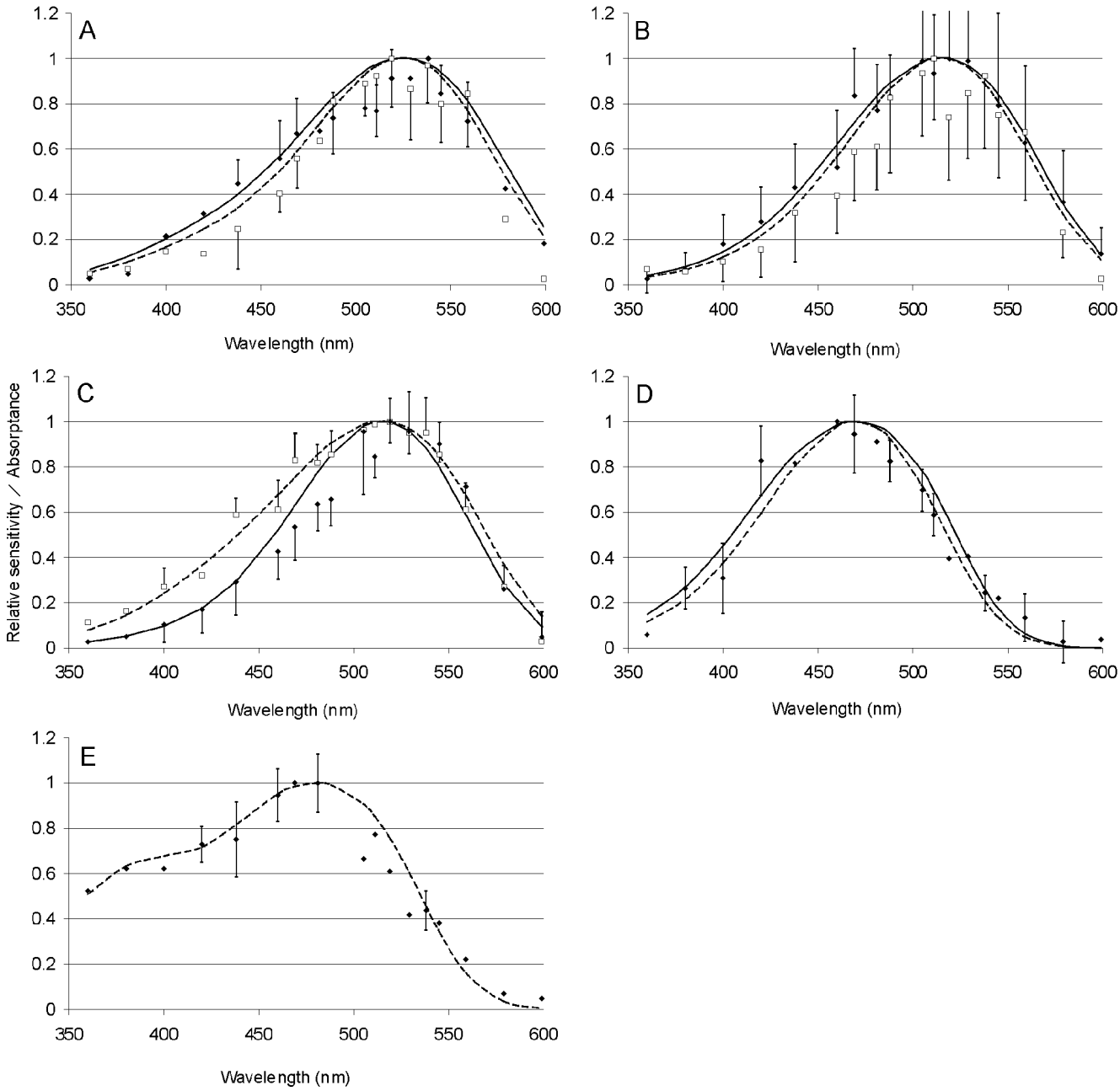

Figure 1. Relative sensitivity (from ERG measurements) and fitted absorptance spectra for five species of decapod. (A) *Crangon allmani*; (B) *Pandalus montagui*; (C) *Nephrops norvegicus*; (D) *Paromola cuvieri*; and (E) *Chaceon* (*Geryon*) *affinis*. In all cases dark-adapted data points are denoted by black diamonds and light-adapted points by open squares (unidirectional standard error bars are used on some graphs for clarity). Dotted lines are absorptance curves fitted using one pass through the rhabdom and solid lines show the effect of two passes through the rhabdom.

ranges between 0.003 and 0.01 (Kent, 1997; Frank & Widder, 1999). In the model, this value was set initially to 0.0067, that of *Homarus americanus* (Bruno et al., 1977) and the best fit was then achieved by sequential iteration of the two templates with respect to the absorption coefficient.

The modelled curve is based on the sum of the absorptance values at each wavelength calculated for distal and proximal rhabdoms. Total absorptance depends on whether the animal has a distal rhabdom and on whether it is dark adapted, in which case light will pass through the rhabdoms twice because of tapetal reflection.

RESULTS

Spectral sensitivity data for animals in the dark- and light-adapted states were obtained for *Crangon allmani* (3 preparations), *Pandalus montagui* (3) and *Nephrops norvegicus* (4). Only dark-adapted spectral sensitivity measurements were obtained for *Paromola cuvieri* (2 preparations) and *Chaceon affinis* (1). The three coastal species (*Crangon allmani*, *Pandalus montagui* and *N. norvegicus*) possess longer wavelength sensitivity than the two deep-sea species (*Paromola cuvieri* and *Chaceon affinis*) (Table 1).

https://doi.org/10.1017/S0025315402006203 Published online by Cambridge University Press

Table 2. *Variation in λ_{Max} by habitat in decapods as detailed in Appendix I.*

	Long-wavelength pigment			Short-wavelength pigment		
Habitat	N	Mean λ_{Max}	SD	N	Mean λ_{Max}	SD
Terrestrial	5	510	6.2	0	–	–
Freshwater	8	540	5.1	0	–	–
Estuarine	19	509	17.3	4	408	39.5
Coastal	23	519	16.9	5	432	36.2
Pelagic	41	505	8.9	6	408	12.4
Deep-sea	4	487	13.2	2	405	24.8

The ERG results are consistent with the presence of one or two rhodopsin based visual pigments. Using the rhodopsin absorbance templates of Stavenga et al. (1993) and measured rhabdom lengths, absorptance spectra were fitted to the data for all five species (Figure 1). The *Crangon allmani* ERG data can be fitted with an absorptance spectrum based on a rhodopsin template with a λ_{max} of 525 nm and an absorption coefficient (k) of 0.0067. The fit is enhanced by adding a second, short wavelength, pigment with a reduced absorption coefficient (λ_{max}=415 nm, k=0.003) (Figure 1A). The ERG data of *Pandalus montagui* showed a similar pattern to that of *C. allmani* but with a less pronounced short wavelength peak (Figure 1B). The best fit to this data was obtained using a single visual pigment (λ_{max}=515 nm, k=0.0067). Both of these species have spherically-symmetrical reflecting superposition eyes but there is no published data on the structure or absorbance properties of their rhabdoms.

In *N. norvegicus* there is enhanced short-wavelength sensitivity in light-adapted preparations thought to be due to the presence of a violet sensitive distal rhabdom. In the light-adapted state proximal shielding pigments cover all but the distal tip of the rhabdom, ensuring that all light passes through the distal rhabdom before reaching the proximal rhabdom (Shelton et al., 1986). The relative importance of the distal rhabdom is therefore enhanced. The absorptance spectrum fitted to the light-adapted ERG data is based on a short wavelength rhodopsin template (λ_{max}=425 nm, k=0.008) followed by one with a longer wavelength (λ_{max}=515 nm, k=0.005). When dark-adapted, the relative sensitivity to short wavelength light is reduced. This is thought to be due to the unique kidney-shaped eyes found in this species which results in the focusing of the superposition image at the base of the rhabdom layer, in contrast to spherically-symmetrical eyes where the point of focus is usually towards the distal end of the rhabdom. As the majority of the light will therefore enter the rhabdom without passing through the distal rhabdom, the best fit to the dark-adapted data is obtained using a single visual pigment (λ_{max}=515 nm, k=0.005) (Figure 1C).

Although the eye of *Paromola cuvieri* also uses reflecting superposition optics, it has an unusual rhabdom structure with the distal rhabdom located close to the crystalline cones (Gaten, 1998). Most incident light will be focused onto the proximal rhabdom without passing through the distal rhabdom so the absorptance spectra have been modelled (Figure 1D) using a single visual pigment (λ_{max}=470 nm, k=0.0067).

Chaceon affinis has an apposition eye with no tapetum so it was modelled using a single pass through the rhabdoms. The ERG data displayed a significant peak in the short wavelength arm (Figure 1E). The best fit to these data was obtained using two visual pigments (λ_{max}=480, k=0.0067; λ_{max}=380, k=0.014).

Further data on spectral sensitivities were obtained by carrying out an extensive literature search (Appendix I). A paired *t*-test comparing results obtained using both spectroscopic and electrophysiological methods for ten species suggests that for long wavelength pigments there is a significant difference ($P<0.004$, t=3.86, df=9) in observed spectral sensitivity; the mean difference between methods was 11.5 nm. Electrophysiological data were used where possible in the analysis by habitat, but where only spectrophotometric results were available the spectral sensitivity was adjusted up by 11.5 nm. The findings presented here and data from published studies of spectral sensitivity in decapods are classified by habitat (Table 2). The mean λ_{Max} of the long wavelength photopigments show significant variation by habitat ($P<0.001$, F=14.88, N=105) whereas there is no significant variation in the mean λ_{Max} of the short wavelength pigments (P=0.86, F=0.25, N=17). Most noticeable are the particularly long wavelength bias of freshwater species, as seen in mysids (Lindström & Nilsson, 1988), and the short wavelength bias of deep-water species (Table 2).

DISCUSSION

The findings here are in agreement with previous suggestions that coastal species generally have photoreceptive pigments more sensitive to longer wavelengths than deep water and pelagic species (Cronin, 1986; Partridge et al., 1992). The spectral sensitivity of an animal is based on the absorbance properties of rhodopsin, modified by the attenuation of light by the dioptric apparatus and the length and absorption coefficient of the rhabdom. When the resulting absorptance spectra were fitted to the ERG data, the curves presented for *Chaceon affinis* and *Crangon allmani* were found to be better explained by a model using two pigments whereas that of *Pandalus montagui* showed no evidence of a second pigment (Figure 1). Although they both have a distal rhabdom, *Paromola cuvieri* and *Nephrops norvegicus* (when dark adapted) both had absorptance spectra which fitted better when modelled as a single-pigment eye as the superposition of light rays occurred on the proximal rhabdom. The electrophysiological results presented here, together with those in Appendix I, suggest

https://doi.org/10.1017/S0025315402006203 Published online by Cambridge University Press

that possession of two photopigments is common in decapods.

Generally, dark-adapted absorptance spectra are broader due to the absorption of a large proportion of wavelengths close to λ_{max} during the first pass through the rhabdom followed by enhanced absorption of non-peak wavelengths following tapetal reflection. This is seen in all of the superposition eyes examined except for those of *N. norvegicus* in which the poorly-focused optics result in a reduced influence of the distal rhabdom when dark-adapted. The change in sensitivity to short wavelength light may also be influenced by the self-screening properties of the photopigments (Hariyama et al., 1986). There was no apparent change in λ_{max} during light or dark adaptation as found in crayfish (Bryceson, 1986).

In many decapods the properties of their long-wavelength pigments conform to the Sensitivity Hypothesis (Bayliss et al., 1936; Clarke, 1936). Shallow water species have greater sensitivity to the wavelengths that penetrate the yellow humic components (gelbstoff) of fresh and coastal waters while deep-sea species are most sensitive to the bluer wavelengths that penetrate clear oceanic water most efficiently. Conversely the observed values of the λ_{Max} of short wavelength pigments could indicate that these pigments conform to the Contrast Hypothesis (Lythgoe, 1968). This may be the cause of the restriction in the range of λ_{Max} of short wavelength pigments in pelagic species. Benthic species view complex visual environments, often with a high degree of spatial and spectral variation (Morin, 1983). However, in the pelagic realm light is generally either down-welling, in which case it will be centred around 475–490 nm depending on depth, or bioluminescent, in which case it will often be slightly bluer and have a broader or narrower spectrum than the down-welling light (Herring, 1983). An ideal strategy would be to possess an eye that can pick out silhouettes through a high degree of sensitivity to the prevailing light (long wavelength pigment) but also to pick out the slightly different spectrum of bioluminescence (short wavelength pigment). This strategy may explain the increase in the length of the short wavelength sensitive portion of rhabdoms from dorsal to ventral in some mesopelagic decapods (Gaten et al., 1992).

The authors gratefully acknowledge D. Bova and C.J. Chapman of SOAFD and the staff of the specimen supply department at Millport Marine Laboratory for providing light protected specimens.

REFERENCES

Bayliss, L.E., Lythgoe, J.N. & Tansley, K., 1936. Some forms of visual purple in sea fishes with a note on the visual cells of origin. *Proceedings of the Royal Society* B, **120**, 95–114.

Briggs, M.H., 1961. Visual pigments of grapsoid crabs. *Nature, London*, **190**, 784–786.

Bruno, M.S., Barnes, S.N. & Goldsmith, T.H., 1977. The visual pigment and visual cycle of the lobster, *Homarus*. *Journal of Comparative Physiology*, **120A**, 123–142.

Bruno, M.S. & Goldsmith, T.H., 1974. Rhodopsin of the blue crab *Callinectes*: evidence for absorption differences *in vitro* and *in vivo*. *Vision Research*, **14**, 653–658.

Bruno, M.S., Mote, M.I. & Goldsmith, T.H., 1973. Spectral absorption and sensitivity measurements in the single ommatidia of the green crab, *Carcinus*. *Journal of Comparative Physiology*, **82A**, 151–163.

Bryceson, K.P., 1986. The effect of screening pigment migration on spectral sensitivity in a crayfish reflecting superposition eye. *Journal of Experimental Biology*, **125**, 401–404.

Clarke, R.L., 1936. On the depths at which fishes can see. *Ecology*, **17**, 452–456.

Crandall, K.A. & Cronin, T.W., 1997. The molecular evolution of visual pigments of freshwater crayfishes (Decapoda: Cambaridae). *Journal of Molecular Evolution*, **45**, 524–534.

Cronin, T.W., 1986. Photoreception in marine invertebrates. *American Zoologist*, **26**, 403–415.

Cronin, T.W. & Forward, R.B., 1988. The visual pigments of crabs—I. Spectral characteristics. *Journal of Comparative Physiology*, **162A**, 463–478.

Cronin, T.W. & Frank, T.M., 1996. A short-wavelength photoreceptor class in a deep-sea shrimp. *Proceedings of the Royal Society* B, **263**, 861–865.

Cronin, T.W. & Goldsmith, T.H., 1982. Photosensitivity spectrum of crayfish rhodopsin measured using fluorescence of metarhodopsin. *Journal of General Physiology*, **84**, 63–81.

Cronin, T.W. & Jinks, R.N., 2001. Ontogeny of vision in marine crustaceans. *American Zoologist*, **41**, 1098–1107.

Cummins, D. & Goldsmith, T.H., 1981. Cellular identification of the violet receptor in the crayfish eye. *Journal of Comparative Physiology*, **142A**, 199–202.

Cummins, D.R., Chen, D.-M. & Goldsmith, T.H., 1984. Spectral sensitivity of the spiny lobster, *Panulirus argus*. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **166**, 269–276.

Eguchi, E., Waterman, T.H. & Akiyama, J., 1973. Localization of the violet and yellow receptor cells in the crayfish retinula. *Journal of General Physiology*, **62**, 355–374.

Fernandez, H.R., 1965. *A survey of the visual pigments of decapod Crustacea of South Florida*. PhD thesis, University of Miami.

Fernandez, H.R., 1973. Spectral sensitivity and visual pigment of the compound eye of the galatheid crab *Pleuroncodes planipes*. *Marine Biology*, **20**, 148–153.

Frank, T.M. & Case, J.F., 1988. Visual spectral sensitivities of bioluminescent deep-sea crustaceans. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **175**, 261–273.

Frank, T.M. & Widder, E.A., 1992. Comparative study of behavioural sensitivity thresholds to near-UV and blue-green light in deep-sea crustaceans. *Marine Biology*, **121**, 229–235.

Frank, T.M. & Widder, E.A., 1994. Evidence for behavioural sensitivity to near-UV light in the deep-sea crustacean *Systellaspis debilis*. *Marine Biology*, **118**, 279–284.

Frank, T.M. & Widder, E.A., 1999. Comparative study of the spectral sensitivities of mesopelagic crustaceans. *Journal of Comparative Physiology*, **185A**, 255–265.

Gaten, E., 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contributions to Zoology*, **67**, 223–235.

Gaten, E., Shelton, P.M.J. & Herring, P.J., 1992. Regional morphological variations in the compound eyes of certain mesopelagic shrimps in relation to their habitat. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 61–75.

Hamacher, H. & Stieve, H., 1984. Spectral properties of the rhodopsin system of the crayfish *Astacus leptodactylus*. *Photochemistry and Photobiology*, **39**, 379–390.

Hamacher, K.J. & Kohl, K.D., 1981. Spectroscopical studies of the *Astacus* visual pigment. *Biophysics of Structure and Mechanism*, **7**, 338.

Hariyama, T., Meyer-Rochow, V.B. & Eguchi, E., 1986. Diurnal changes in structure and function of the compound eye of *Ligia exotica* (Crustacea, Isopoda). *Journal of Experimental Biology*, **123**, 1–26.

Hays, D. & Goldsmith, T.H., 1969. Microspectrophotometry of the visual pigment of the spider crab *Libinia emarginata*. *Zeitschrift für Vergleichende Physiologie*, **65**, 218–232.

Herring, P.J., 1983. The spectral characteristics of luminous marine organisms. *Proceedings of the Royal Society* B, **220**, 183–217.

Hiller-Adams, P., Widder, E.A. & Case, J.F., 1988. The visual pigments of four deep-sea crustacean species. *Journal of Comparative Physiology*, **163A**, 63–72.

Johnson, M.L., Shelton, P.M.J. & Gaten, E., 2000. Temporal sensitivity in marine decapods from coastal and deep-sea habitats. *Marine Biology*, **136**, 243–248.

Johnson, M.L., Shelton, P.M.J., Herring, P.J. & Gardner, S., 1995. Spectral responses from the dorsal organ of a juvenile *Rimicaris exoculata* from the TAG hydrothermal vent. *BRIDGE Newsletter*, **8**, 38–42.

Kent, J., 1997. *The visual pigments of deep-sea crustaceans*. PhD thesis, University of Bristol.

Kirk, J.T.O., 1983. *Light and photosynthesis in aquatic ecosystems*. Cambridge: Cambridge University Press.

Lall, A.B. & Cronin, T.W., 1987. Spectral sensitivity of the compound eyes in the purple land crab, *Gecarcinus lateralis*. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **173**, 398–406.

Leggett, L.M.W., 1979. A retinal substrate for colour discrimination in crabs. *Journal of Comparative Physiology*, **133A**, 159–166.

Lindström, M. & Nilsson, H.L., 1988. Eye function of *Mysis relicta* Lovén (Crustacea) from two photic environments. Spectral sensitivity and light tolerance. *Journal of Experimental Marine Biology and Ecology*, **120**, 23–37.

Loew, E.R., 1976. Light and photoreceptor degeneration in the Norway lobster, *Nephrops norvegicus* L. *Proceedings of the Royal Society* B, **193**, 31–44.

Lythgoe, J.N., 1968. Visual pigments and visual range under water. *Vision Research*, **8**, 977–1012.

Martin, F.G. & Mote, M.I., 1982. Colour receptors in marine crustaceans: a second class of retinular cell in the compound eyes of *Callinectes* and *Carcinus*. *Journal of Comparative Physiology*, **145A**, 549–554.

Meyer-Rochow, V.B. & Tiang, K.M., 1984. The eye of *Jasus edwardsii* (Crustacea, Decapoda, Palinuridae). Electrophysiology, histology and behaviour. *Zoologica*, **45**, 1–61.

Minjuan, C. & Shujun, L., 1990. The spectral sensitivity of receptor system in the compound eye of *Penaeus penicillatus*. *Oceanologia et Limnologia Sinica*, **21**, 160–165.

Morin, J.G., 1983. Coastal bioluminescence: patterns and functions. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **33**, 787–817.

Partridge, J.C., Archer, S.N. & Van Oostrum, J., 1992. Single and multiple visual pigments in deep-sea fishes. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 113–130.

Scott, S. & Mote, M.I., 1974. Spectral sensitivity in some marine Crustacea. *Vision Research*, **14**, 659–663.

Shelton, P.M.J., Gaten, E. & Chapman, C.J., 1986. Accessory pigment distribution and migration in the compound eye of *Nephrops norvegicus* (L.) (Crustacea: Decapoda). *Journal of Experimental Marine Biology and Ecology*, **98**, 185–198.

Shukolyukov, S.A., Kalishevich, O.O., Polyanovskii, A.D. & Gribankin, F.G., 1985. Vision of the shore crab: spectral sensitivity of the eye and fine structure of the ommatidium. *Marine Biology (Vladivostok)*, **2**, 53–59.

Stowe, S., 1980. Spectral sensitivity and retinal pigment movement in the crab, *Leptograpsus variegatus*. *Journal of Experimental Biology*, **87**, 73–98.

Van Dover, C.L., Szuts, E.Z., Chamberlain, S.C. & Cann, J.R., 1989. A novel eye in the 'eyeless' shrimp from hydrothermal vents of the Mid-Atlantic Ridge. *Nature, London*, **337**, 458–460.

Wald, G. & Hubbard, R., 1957. Visual pigment of a decapod: the lobster. *Nature, London*, **180**, 278–280.

Wald, G. & Seldin, E.B., 1968. Spectral sensitivity of the common prawn, *Palaemonetes vulgaris*. *Journal of General Physiology*, **51**, 694–700.

Warrant, E.J. & Nilsson, D.-E., 1997. Absorption of white light in photoreceptors. *Vision Research*, **38**, 195–207.

Weiyun, Z. & Minjuan, C., 1990. Electrophysiological studies on the visual characteristics of *Portunus trituberculatus* (Miers). *Oceanologia et Limnologia Sinica*, **21**, 490–494.

Ziedins, I. & Meyer-Rochow, V.B., 1990. ERG-determined spectral and absolute sensitivities in relation to age and size in the halfcrab *Petrolisthes elongates* (Crustacea; Decapoda; Anomura). *Experimental Biology*, **48**, 319–328.

Submitted 6 March 2002. Accepted 29 August 2002.

Appendix I. *List of published λ_{Max} for photoreceptive pigments of decapods from different habitats. Where two pigments have been found, both are given. The abbreviations used for the methods of investigation are as follows: ERG—intercellular electrophysiology; EX—spectrophotometry of pigment extract; IC—intracellular electrophysiology; MSP—microspectrophotometry.*

Species name	Method	λ_{Max}	λ_{Max}	Source
Terrestrial				
Coenobita clypeatus	MSP		508	Cronin & Forward, 1988
Coenobita rugosa	MSP		491	Cronin & Forward, 1988
Gecarcinus lateralis	MSP		487	Cronin & Forward, 1988
Gecarcinus lateralis	ERG		510	Lall & Cronin, 1987
Uca pugilator	IC		508	Scott & Mote, 1974
Uca pugnax	IC		508	Scott & Mote, 1974
Freshwater				
Astacus fluviatilus	MSP		530	Hamacher & Kohl, 1981
Astacus leptodactylus	MSP		530	Hamacher & Stieve, 1984
Cambarellus schufeldtii	MSP		526	Crandall & Cronin, 1997
Cambarellus ludovicianus	MSP		529	Crandall & Cronin, 1997
Engaeus cunicularius	MSP		522	Crandall & Cronin, 1997
Oronectes rusticus	MSP		535	Cronin & Goldsmith, 1982
Procambarus clarkii	MSP		535	Cronin & Goldsmith, 1982
Procambarus milleri	MSP		522	Cronin & Goldsmith, 1982
Estuarine				
Callinectes sapidus	MSP		503	Cronin & Forward, 1988
Callinectes sapidus	IC	440	508	Martin & Mote, 1982
Carcinus maenas	MSP		508	Bruno et al., 1973
Carcinus maenas	IC	440	508	Martin & Mote, 1982
Clibanarius vittatus	MSP		510	Cronin & Forward, 1988
Euryoanopeus depressus	MSP		480	Cronin & Forward, 1988
Hemigrapsus edwardsii	EX		513	Briggs, 1961
Hemigrapsus sanguinensis	ERG	360	480	Shukolyukov et al., 1985
Leptograpsus variegatus	IC		484	Stowe, 1980
Libinia dubia	MSP		489	Cronin & Forward, 1988
Libinia emarginata	MSP		493	Hays & Goldsmith, 1969
Menippe mercenaria	MSP		494	Cronin & Forward, 1988
Pagurus longicarpus	MSP		515	Cronin & Forward, 1988
Palaemonetes paladosus	EX		539	Fernandez, 1965
Palaemonetes vulgaris	ERG	390	540	Wald & Seldin, 1968
Panopeus herbestii	MSP		493	Fernandez, 1973
Panopeus obesus	MSP		492	Cronin & Forward, 1988
Rhithropanopeus harrisii	MSP		495	Cronin & Forward, 1988
Sesarma cinereum	MSP		492	Cronin & Forward, 1988
Sesarma reticulatum	MSP		493	Cronin & Forward, 1988
Sesarma reticulatum	IC		508	Scott & Mote, 1974
Scylla serrata	MSP		490	Leggett, 1979
Coastal				
Arenaeus cribiarius	MSP		498	Cronin & Forward, 1988
Calappa flamea	MSP		486	Cronin & Forward, 1988
Callinectes ornatus	MSP		501	Cronin & Forward, 1988
Callinectes sapidus	MSP		504	Cronin & Jinks, 2001
Cancer irroratus	MSP		496	Cronin & Forward, 1988
Crangon allmani	ERG	415 ?	525	Present study
Dardanus fucosus	MSP		511	Cronin & Forward, 1988
Hepatus epheliticus	MSP		487	Cronin & Forward, 1988
Homarus americanus	MSP		515	Bruno et al., 1977
Homarus gammarus	MSP		515	Kent, 1997
Jasus edwardsii	ERG	472	536	Meyer-Rochow & Tiang, 1984
Nephrops norvegicus	MSP		498	Kent, 1997
Nephrops norvegicus	MSP		498	Loew, 1976
Nephrops norvegicus	ERG	425 ?	515	Present study
Ovipales stephensoni	MSP		505	Cronin & Forward, 1988
Pagurus pollicaris	MSP		515	Cronin & Forward, 1988
Palurinus argus	ERG	379	510	Cummins, et al., 1984
Pandalus montagui	ERG		515	Present study
Penaeus duororum	EX		516	Fernandez, 1965

continued

https://doi.org/10.1017/S0025315402006203 Published online by Cambridge University Press

Appendix I. *Continued.*

Species name	Method	λ_{Max}	λ_{Max}	Source
Penaeus penicillatus	ERG	480	570	Minjuan & Shujun, 1990
Petrochirus diogenes	MSP		508	Cronin & Forward, 1988
Petrolisthes elongates	ERG		536	Ziedins & Meyer-Rochow, 1990
Pilumnus sayi	MSP		489	Cronin & Forward, 1988
Portunus trituberculatus	ERG		513	Weiyun & Minjuan, 1990
Portunus spinimanis	MSP		483	Cronin & Forward, 1988
Pelagic				
Acanthephyra curtirostris	ERG		510	Frank & Case, 1988
Acanthephyra curtirostris	MSP		485	Hiller-Adams et al., 1988
Acanthephyra curtirostris	MSP		485	Kent, 1997
Acanthephyra microphthalma	MSP		482	Kent, 1997
Acanthephyra purpurea	MSP		492	Kent, 1997
Acanthephyra smithi	ERG		510	Frank & Case, 1988
Acanthephyra smithi	MSP		491	Hiller-Adams et al., 1988
Acanthephyra stylorostratis	MSP		489	Kent, 1997
Bentheogennema intermedia	MSP		494	Kent, 1997
Bentheogennema pasithea	MSP		500	Kent, 1997
Funchalia villosa	ERG		489	Frank & Widder, 1999
Gennadas sp.	MSP		495	Kent, 1997
Gennadas valens	MSP		495	Kent, 1997
Hymenodora frontalis	MSP		495	Kent, 1997
Hymenodora glacialis	MSP		500	Kent, 1997
Janicella spinicauda	ERG	400	500	Frank & Case, 1988
Meningodora miccyla	MSP		486	Kent, 1997
Meningodora vesca	MSP		487	Kent, 1997
Notostomus elegans	ERG		490	Frank & Case, 1988
Notostomus gibbosus	ERG		480	Frank & Case, 1988
Oplophorus gracilirostris	ERG	400	500	Frank & Case, 1988
Oplophorus spinosus	ERG	400	500	Frank & Case, 1988
Oplophorus spinosus	MSP		492	Kent, 1997
Parapasiphaea sulcatifrons	MSP		501	Kent, 1997
Pasiphaea chacei	MSP		509	Kent, 1997
Pasiphaea emarginata	MSP		497	Kent, 1997
Pasiphaea multidentata	ERG		497	Frank & Widder, 1999
Petalidium suspirosum	MSP		501	Kent, 1997
Pleuroncodes planipes	EX		523	Fernandez, 1973
Plesionika martia	MSP		499	Kent, 1997
Plesiopenaeus armatus	MSP		493	Kent, 1997
Sergestes arcticus	ERG		495	Frank & Widder, 1999
Sergestes corniculum	ERG		500	Frank & Widder, 1999
Sergestes curvatus	MSP		493	Kent, 1997
Sergestes similis	MSP		495	Kent, 1997
Sergestes tenuiremis	MSP		495	Hiller-Adams et al., 1988
Sergia grandis	ERG		500	Frank & Widder, 1999
Sergia maximus	MSP		495	Kent, 1997
Sergia phorcus	MSP		495	Kent, 1997
Sergia robustus	MSP		496	Kent, 1997
Sergia splendens	MSP		497	Kent, 1997
Stylopandalus richardi	MSP		491	Kent, 1997
Systellaspis braueri	MSP	411	500	Kent, 1997
Systellaspis cristata	MSP	414	498	Kent, 1997
Systellaspis debilis	MSP	400	498	Cronin & Frank, 1996
Systellaspis debilis	ERG	400	500	Frank & Case, 1988
Systellaspis debilis	MSP		493	Hiller-Adams et al., 1988
Systellaspis debilis	MSP	417	497	Kent, 1997
Deep benthic				
Bythograea thermydron	MSP		489	Cronin & Jinks, 2001
Chaceon (Geryon) affinis	ERG	380 ?	480	Present study
Geryon quinquendens	MSP		473	Cronin & Forward, 1988
Paromola cuvieri	ERG	?	470	Present study
Rimicaris exoculata	ERG		500	Johnson et al., 1995
Rimicaris exoculata	EX		500	Van Dover et al., 1989

https://doi.org/10.1017/S0025315402006203 Published online by Cambridge University Press