

Adaptive color vision in *Pullosquilla litoralis* (Stomatopoda, Lysiosquilloidea) associated with spectral and intensity changes in light environment

Alexander G. Cheroske^{1,*}, Thomas W. Cronin¹ and Roy L. Caldwell²

¹Department of Biological Sciences, University of Maryland, Baltimore County, Baltimore, MD 21250, USA and

²Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

*Author for correspondence (e-mail: cheroske@umbc.edu)

Accepted 17 October 2002

Summary

Some stomatopod crustacean species that inhabit a range of habitat depths have color vision systems that adapt to changes in ambient light conditions. To date, this change in retinal function has been demonstrated in species within the superfamily Gonodactyloidea in response to varying the spectral range of light. Intrarhabdomal filters in certain ommatidia within the specialized midband of the eye change spectrally, modifying the sensitivity of underlying photoreceptors to match the spectrum of available light. In the present study, we utilized *Pullosquilla litoralis*, a member of the superfamily Lysiosquilloidea that also has a wide depth range. Individuals were placed within one of three light treatments: (1) full-spectrum, high-intensity 'white' light, (2) narrow-spectrum 'blue' light and (3) full-spectrum, reduced-intensity 'gray' light. After 3 months, the

intrarhabdomal filters in Row 3 ommatidia of the midband in blue- and gray-light-treated animals were short-wavelength shifted by 10–20 nm compared with homologous filters in animals in white-light treatments. These spectral changes increase the relative sensitivity of associated photoreceptors in animals that inhabit environments where light spectral range or intensity is reduced. The adaptable color vision system of stomatopods may allow animals to make the best use of the ambient light occurring at their habitat regardless of depth. The major controlling element of the plasticity in lysiosquilloid stomatopod color vision appears to be light intensity rather than spectral distribution.

Key words: mantis shrimp, *Pullosquilla litoralis*, visual ecology, filter pigments, phenotypic plasticity, color vision.

Introduction

When evaluating vision in marine habitats, it is important to consider the effects of the aquatic medium on the light environment. In shallow waters (<5 m), the spectral quality of downwelling light is broad and the intensity is high (Lythgoe, 1990; McFarland and Munz, 1975). With increasing depth, the ambient light becomes more limited (Jerlov, 1976). Decreased light spectral range and overall quantity can arise from the scattering and absorptive properties of water as well as from associated constituents such as organic compounds, particles or plankton. In tropical environments, while overall water clarity is often increased compared with other coastal marine environments, the attenuation of downwelling light still creates a spectrally narrower and blue-shifted light environment for those animals living at depths greater than approximately 10 m (McFarland and Munz, 1975).

Stomatopod crustaceans, including species in the superfamilies Gonodactyloidea and Lysiosquilloidea, commonly reside in these tropical waters. Most species are active diurnally when light intensities are highest, but some become most active at crepuscular periods, perhaps because of decreased fish predator densities at these times (Dominguez

and Reaka, 1988; Jutte et al., 1998). Additionally, members of both superfamilies have specialized apposition compound eyes that include a central midband composed of six rows of large faceted ommatidia (Harling, 2000; Manning et al., 1984; Marshall, 1988). A total of 10 spectral classes of photoreceptors operating at wavelengths of >400 nm exists in this midband area (Cronin and Marshall, 1989b; Marshall et al., 1994), plus four or more additional ultraviolet classes (Cronin et al., 1994d; Marshall and Oberwinkler, 1999). Within the ommatidial midband, Rows 1–4 are believed to be responsible for color vision in both gonodactyloid and lysiosquilloid stomatopods (Cronin et al., 1993, 1994c; Marshall et al., 1996). Below the level of the 8th reticular cell, these four rows are tiered, with distal tiers acting as long-pass filters for the proximal tiers below (Cronin and Marshall, 1989a,b; Marshall et al., 1991). In Rows 2 and 3, stomatopods of the family Gonodactyloidea have two sets of intrarhabdomal filters placed between junctions of the tiers. These filters serve to narrow the sensitivity of the underlying photoreceptor and aid in producing the wide range of spectral sensitivities typical for these animals (Cronin et al., 1994a). The narrowly tuned

classes of photoreceptors in these rows trade quantity (reduction in photon catch) for increased spectral coverage (Cronin and Marshall, 1989a,b; Cronin et al., 1993, 1994c). Having a series of narrowly tuned photoreceptors may also serve to create color constancy in heterogeneous light environments (Osorio et al., 1997).

The visual systems of various mantis shrimp species living in the same depth range have similar structure and sensitivity and seem well suited to the variation of light conditions that they encounter (Cronin et al., 1994b, 1996, 2000). While photopigments remain constant in any given species, intrarhabdomal filters of conspecifics of some stomatopod species from different depth environments are not only spectrally different but are also of different lengths and optical densities (Cronin et al., 2002; Cronin and Caldwell, 2002). Filter differences vary adaptively with depth and permit individuals occupying different photic environments to make full use of the ambient spectrum of light in each habitat. Cronin et al. (2001) established that light treatments in the laboratory that replicated the spectral features of shallow- or deep-water light environments in nature could cause spectral shifts of intrarhabdomal filters in a gonodactyloid stomatopod species (*Haptosquilla trispinosa*) that occupies a rather large depth range (0–30 m) with correspondingly diverse photic conditions. Young animals raised in each type of light environment generated filters that were effectively ‘tuned’ to utilize the full spectrum of available light. The phenotypic plasticity evidenced in this species may be representative of many stomatopods that have large depth ranges (Cronin et al., 2002; Cronin and Caldwell, 2002).

Mantis shrimp in the superfamily Lysiosquilloidea reside in tropical coastal environments similar to those of gonodactyloids, but lysiosquilloid species burrow within coral sediments rather than residing in hard substrata like most gonodactyloids. Many members of this superfamily also inhabit wide depth ranges and experience a variety of light environments. Much like gonodactyloid stomatopod retinas, the retinas of lysiosquilloids contain two intrarhabdomal filters in Row 2 ommatidia but, unlike gonodactyloids, they only have one filter in Row 3 photoreceptors (Cronin et al., 1993, 1994a).

The research we report here expands upon two different aspects of the previous work on the adaptable stomatopod color

vision system. First, all work done thus far has been conducted with animals within one superfamily (Gonodactyloidea). If the flexible color vision system evidenced is generally adaptable to ambient light conditions, the corresponding changes in intrarhabdomal filters could occur in all mantis shrimp species with color vision that inhabit diverse depths, including lysiosquilloids. Second, to date, stomatopod filter modification has been examined with regard to spectral changes in light. If the mechanism of filter change involves a response to a reduction in stimulus to certain photoreceptor classes, as proposed by Cronin and Caldwell (2002), then an overall reduction in light intensity across all wavelengths may initiate similar retinal changes.

Materials and methods

Focal species

Pullosquilla litoralis Michel and Manning 1971 is a small (<20 mm) species within the superfamily Lysiosquilloidea. These stomatopods live as monogamous pairs within U-shaped burrows in the sand and can occur at depths from <1 m to >30 m (Jutte, 1997). *P. litoralis* has both a proximal and distal filter in each ommatidium of Row 2 that sequentially filter the light entering these ommatidia (Jutte et al., 1998). The distal filter appears yellow, while the proximal filter appears orange. Row 3 possesses only a filter class in the distal position, which commonly appears red.

In March 2001, animals were collected as planktonic larvae in a lagoon in Rangiroa in the Tuamotus atolls, French Polynesia and kept in the dark for two days during transport back to the marine aquarium facility at the University of California, Berkeley where they were then maintained in containers with artificial seawater.

Experimental treatments

Upon arrival at the University of California, Berkeley, stomatopods were placed randomly into one of three light treatments: (1) a broad-spectrum white-light treatment, (2) a narrow-spectrum blue-light treatment or (3) a reduced-intensity, broad-spectrum light treatment. Irradiance spectra of these treatments are provided in Fig. 1. Animals were maintained individually within 250 ml plastic containers.

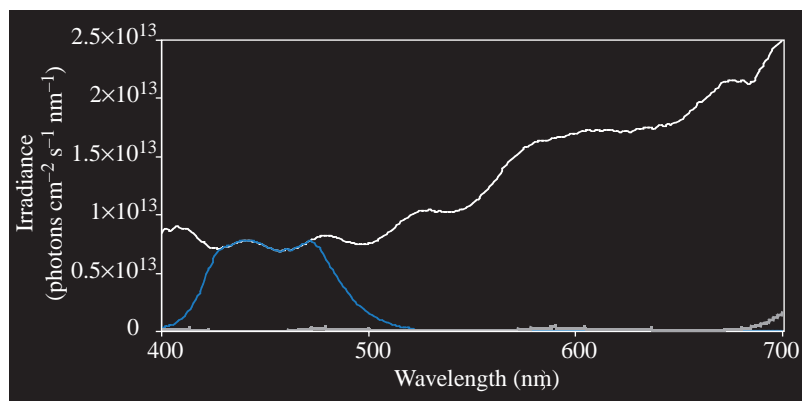


Fig. 1. Irradiance spectra of experimental light treatments ($N=5$ animals per treatment). The white line represents full-spectrum, high-intensity ‘white’ light, the blue line represents the narrow-spectrum ‘blue’ light and the gray line represents the reduced-intensity full-spectrum light treatment. The gray line is calculated from the full-spectrum irradiance and the absorbance of the four layers of 50% neutral density filter material.

White lighting was from GE Aqua-Rays tubes (General Electric, Cleveland, OH, USA) as well as indirect ambient light from a nearby window. Animals in the reduced-intensity treatment were subjected to the same lighting conditions as the white-light treatment but were placed in a sealed Styrofoam container with a 10 cm×17.5 cm window in the lid. The window was covered with four layers of 50% neutral-density filter material so that light reaching the animal containers was full spectrum but reduced intensity (<10% irradiance intensity of the full-spectrum treatment; Fig. 1). Blue-light-treated animals were housed in similar 250 ml plastic containers that were placed in a separate room where lighting was only from GE Aqua-Blue fluorescent tubes (General Electric, Cleveland, OH, USA) filtered with a blue plastic filter material that selectively attenuated wavelengths of light of <430 nm and >480 nm (Fig. 1). Illumination in all three light treatments was measured using an Ocean Optics spectrometer (Dunedin, FL, USA). Three times each week, the water in all experimental containers was changed and animals were fed brine shrimp. In reduced-intensity-light-treated animals, water changes occurred after sunset in dimly lit conditions. All animals were maintained on a 12 h:12 h light:dark photoperiod.

After 11 weeks (June 2001), all treated animals ($N=5$ per treatment) were shipped to the laboratory at the University of Maryland, Baltimore County for microspectrophotometry. In brief, our procedures were as follows (see Cronin and Marshall, 1989a; Cronin et al., 1994a). Eyes from freshly sacrificed, sexually mature stomatopods were sectioned at 14 μm at -30°C in a cryostat. Sections were mounted in mineral oil between two coverslips and placed on a microscope stage. A monochromatic, circular beam, 1.5 μm in diameter, was first placed in a clear region of the slide and varied at 1 nm intervals from 400 nm to 700 nm for a reference scan. The sample was then moved so that the beam passed through an intrarhabdomal filter, and an absorbance curve was generated. Between three and five replicate scans of each filter type, each from a different filter, were taken per individual, and the absorbance curves were averaged within filter types over all animals within a treatment.

Environmental radiometry

Downwelling irradiance was measured from 410 nm to 694 nm using a MER-1015 scanning

spectroradiometer (Biospherical Instruments, San Diego, CA, USA) with an attached cosine collector. Data were taken in typical *Pullosquilla* habitat at Cook's Bay near the University of California's Gump Marine Station, Moorea, French Polynesia at approximately noon on a clear, sunny day during August 1991. Spectral data were collected at 1 m depth intervals from 1 m to 22 m by a SCUBA diver positioning the spectroradiometer in midwater (Cronin et al., 1994c).

Spectral sensitivity model

Within the specialized ommatidial midband in *P. littoralis*, ommatidial Rows 1–4 contain two tiered photoreceptors, each with a spectrally different photopigment, for a total of eight classes below the level of the 8th reticular cells (Jutte et al., 1998). Using previously published photopigment absorption data for *P. littoralis* (at peak densities of 0.008 per μm), together with known rhabdom lengths and diameters (see Jutte et al., 1998), we generated sensitivity curves for all eight receptor classes (see Cronin et al., 1994d, 2002b for further

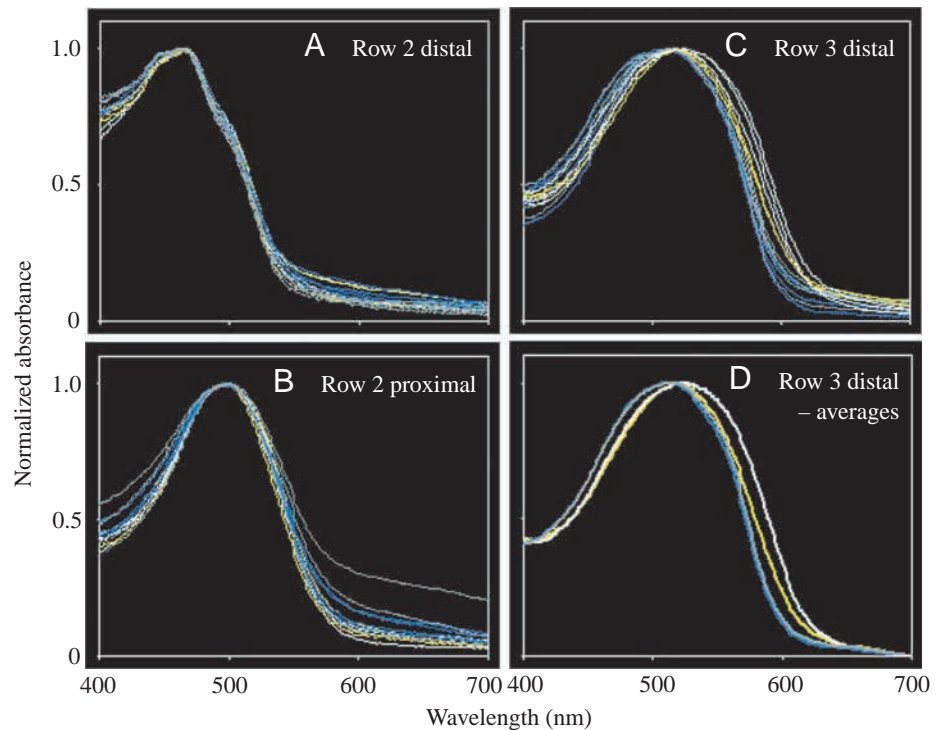


Fig. 2. Absorbance spectra for *Pullosquilla littoralis* intrarhabdomal filters from each of the three light treatments. Each spectrum is normalized to its peak. (A) Row 2 distal filters, (B) Row 2 proximal filters, (C) Row 3 distal filters. In A–C, each trace represents an average for an individual animal. The color of the trace represents the light treatment that the animal inhabited: blue represents the narrow-spectrum, short-wavelength treatment; gray represents the reduced-intensity, full-spectrum treatment; and white represents the high-intensity, full-spectrum treatment. The yellow traces represent animals from the white treatment that developed a shorter wavelength class of Row 3 filter. Variance in baselines among curves is due to differences in the quality of the scans. (D) Means of the three spectral classes of Row 3 receptors from the light treatments. Each curve represents the mean of all animals within a treatment with a particular Row 3 filter class [the blue line represents blue light ($N=4$), the gray line represents reduced-intensity light ($N=5$), the white line represents long-wavelength filter class from white light ($N=3$), and the yellow line represents shorter-wavelength filter class from white light ($N=2$)]. All curves have baselines normalized to zero to facilitate comparison.

details on sensitivity modeling) in both white- and blue- or gray-treated animals. These models also assume absorbances of overlying optics and R8 rhabdomeric cells to be exclusively in the ultraviolet (<400 nm; Cronin et al., 1994d). Because stomatopod photopigments in individual receptor classes do not appear to vary within a species (Cronin et al., 2000), and Row 2 filters also do not change, sensitivities in receptors of Rows 1, 2 and 4 are computed to be the same in all animals.

Results

Filter absorbances

Our measurements found no variation in proximal and distal

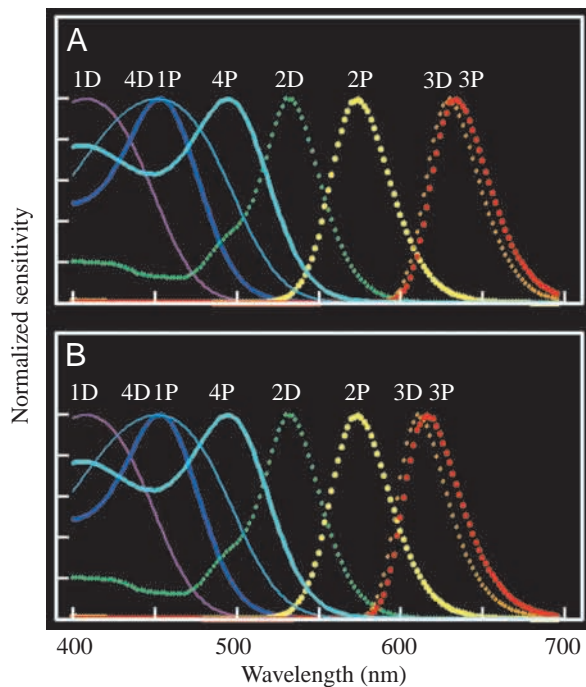


Fig. 3. Calculated sensitivity spectra for the tiered photoreceptors in the four midband ommatidial rows of *Pullosquilla litoralis* from experimental light treatments. (A) Sensitivities for white-light-treated animals. (B) Sensitivities for blue- or gray-light-treated animals. All spectra are normalized to their peak. Rows with intrarhabdomal filters (Rows 2 and 3) are plotted as broken lines, while others (Rows 1 and 4) are plotted as solid lines. The number above each curve denotes the row; D, distal; P, proximal.

Row 2 filters among light treatments (Fig. 2A,B). While scan quality varied, spectral positions of each class of Row 2 filters were indistinguishable regardless of treatment and we were unable to discern filter optical density differences among treatments. The Row 3 distal filters varied spectrally among treatments (Fig. 2C), but the optical densities of the filter classes were again similar among treatments. Blue- and gray-light-treated animals had distal Row 3 filters that had a sharp long-wavelength attenuation with a 50% absorbance point on the long wavelength limb of the curve at approximately 570 nm, while high-intensity, full-spectrum-light-treated animals had Row 3 filters that were spectrally shifted approximately 10–20 nm to longer wavelengths (Fig. 2D). Within the white-light-treated animals, two classes were found: one long-wavelength class with a 50% absorbance point at approximately 590 nm ($N=3$ animals) and another class with its 50% absorbance point at approximately 580 nm ($N=2$ animals; see Fig. 2D). The longer-wavelength class in white-light-treated animals is similar to those Row 3 filters previously found in shallow-water *P. litoralis*, while the Row 3 filters from blue- or gray-light-treated animals were similar to those found in *Pullosquilla thomassini* residing in deeper habitats (Jutte et al., 1998). Regardless, both classes of Row 3 filters within the white-light-treated animals always absorbed light in a spectral range more than 10 nm longer than did those found in narrow-spectrum ('blue') or reduced-intensity ('gray') treatments.

Spectral sensitivity models

Row 3 sensitivities change between white- and blue- or gray-light-treated animals due to the spectral shift in the distal Row 3 filter (Fig. 3). The adaptable Row 3 filters change the sensitivity functions of both underlying Row 3 photoreceptors, moving the sensitivity maxima of receptors in reduced-light-treated animals to wavelengths 20 nm shorter compared with homologous receptor classes of white-light-treated animals. In the proximal tier, the sensitivity maximum of the photoreceptor changes from 635 nm to 615 nm, while in distal receptors, the sensitivity maximum shifts from 630 nm to 610 nm in full-intensity white-light-treated and reduced-light-treated animals, respectively.

We measured downwelling irradiance spectra at 1 m intervals (from the water surface to 22 m) throughout the depth range of habitats occupied by *P. litoralis*. Knowing these, and

Table 1. Calculated sensitivity and percent photon capture at the sensitivity maximum of Row 3 ommatidial tiers in *Pullosquilla litoralis* from different light treatments

Receptor class	Full-spectrum, high-intensity treatment		Narrow-spectrum, reduced-intensity treatment		Ratio Deep:shallow
	Sensitivity λ max (nm)	% Photons absorbed	Sensitivity λ max (nm)	% Photons absorbed	
Row 3 distal tier	630	0.4	610	1.5	3.75
Row 3 proximal tier	635	1.0	615	2.9	2.90

Calculations for percentage photons absorbed combine spectral data at depths of 1 m and 20 m with spectral sensitivity functions for each of the photoreceptors in Row 3. Ratios presented in the last column are the quotient of percentage photons absorbed by a deep-adapted Row 3 receptor by percentage photons absorbed in a shallow-adapted Row 3 receptor of the same tier.

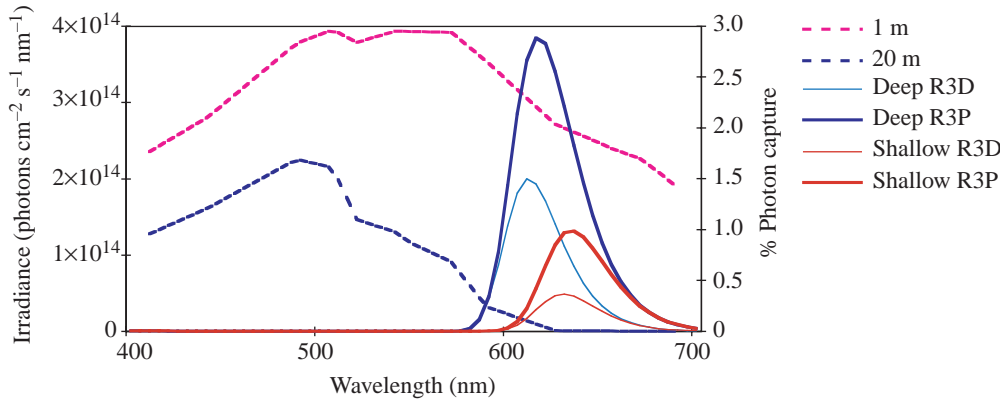


Fig. 4. Comparison of the spectrum of downwelling irradiance in two depth environments of *Pullosquilla littoralis* with the calculated percentage photon capture rate for animals with Row 3 receptors adapted to shallow and deep light environments. Downwelling irradiance spectra were measured in waters off Moorea, French Polynesia. R3D, Row 3 distal tier; R3P, Row 3 proximal tier.

using our modeled spectral sensitivity functions for the Row 3 photoreceptors (Fig. 3), we estimate that in a stomatopod living in a shallow water environment (depth=1 m), approximately 0.4% of the photons arriving at the receptor tip are absorbed in the distal photoreceptor of Row 3 and 1.0% are absorbed in the proximal tier (Table 1). Correspondingly, an animal residing in deeper habitats (depth=20 m) but utilizing adapted Row 3 filters could absorb 1.5% of the photons entering the ommatidium in the distal photoreceptor and 2.9% in the proximal tier. Photon capture proportions for ‘deep’ animals are higher in the Row 3 photoreceptors despite the overall decrease in irradiant spectral bandwidth at the depth used in the calculations, due to the increased overlap between Row 3 spectral functions and the ambient irradiance spectra in deeper water environments (Fig. 4). While the short-wavelength shift in Row 3 filters of ‘deep’ animals does confer a relatively greater photon capture rate to Row 3 photoreceptors, the reduced light intensity and spectral range found at 20 m depth (for example) still reduce overall capture rates of these photoreceptors in ‘deep’ animals to <17% of Row 3 receptors in shallow animals living in the bright light conditions occurring at 1 m depth (ratio of deep:shallow photon capture rates are 16% and 9% in adapted distal and proximal Row 3 receptors, respectively).

Discussion

Stomatopod color vision systems provide excellent examples of the adaptability of animal sensory systems to their environmental conditions. In most animals with varying spectral receptor classes, changes occur either on evolutionary time scales (Carleton and Kocher, 2001; Cronin et al., 1996; Hope et al., 1997; Hunt et al., 1996; Lythgoe et al., 1994; McDonald and Hawryshyn, 1995; Morris et al., 1993) or concurrent with overall ontogenetic changes in physiology (Beaudet and

Hawryshyn, 1999; Cronin and Jinks, 2002; Marshall et al., 1999; Shand, 1993; Shand et al., 1999). Visual changes resulting from chromophore replacement also occur in adult animals in response to changes in temperature and diurnal light (Cronin and Hariyama, 2002; Saszik and Bilotta, 1999; Suzuki et al., 1985; Tsin and Beatty, 1977). To date, there is only one vertebrate species in which direct adaptation to spectral or intensity changes in light stimuli has been thoroughly studied.

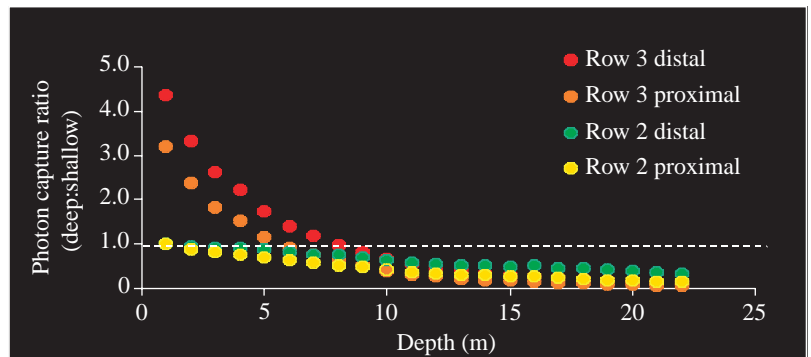


Fig. 5. Ratio of photoreceptor photon capture rates in ‘deep-adapted’ and ‘shallow-adapted’ photoreceptors in *Pullosquilla littoralis*. Values are calculated from spectral sensitivity functions for photoreceptors in Rows 2 and 3 combined with measured downwelling irradiances in various depth environments (see text for details). The broken line on the y-axis at a ratio of 1.0 indicates a level at which photon capture rates between deep and shallow animals would be the same. Row 3 photoreceptor calculations are ratios of a ‘deep’ photoreceptor with a short-wavelength shifted distal filter compared with a ‘shallow’ photoreceptor with a long-wavelength distal filter, each capturing photons of the available light at 1 m intervals from 1 m to 22 m depth. All Row 2 comparisons are photon capture rates of each photoreceptor at 1–22 m relative to capture rates at 1 m depth. Row 2 calculations are also a ratio of photon capture rates but, as the proximal and distal filter in this row did not vary, changes in photon capture ratios show the effects of decreasing light intensity and spectral range with increasing depth only. By contrasting the photon capture rates of Row 2 receptors and Row 3 receptors, the significant increase in photoreceptor sensitivity due to the adaptable intrarhabdomal filters in Row 3 is evident. In depths of 1–7 m, the adaptable distal filters in Row 3 increase the photon capture rate of underlying photoreceptors as much as fourfold, overcoming the actual decrease in illumination with increasing depth. Thus, capture rates for ‘deep’ photoreceptors at 6–8 m are equivalent to those of ‘shallow’ receptors operating at a depth of 1 m.

When reared in experimental light treatments differing in intensity and spectral bandwidth, the cichlid fish *Aequidens pulcher* develops modified cone photoreceptor morphology (outer segment lengths) and frequency distributions of cone types (Kröger et al., 1999; Wagner and Kröger, 2000) as well as changes in connectivity and spectral response in some horizontal cells (Braun et al., 1997; Kröger et al., 2001). The retinal changes in the cichlid confer an overall spectral sensitivity shift. While studies of the influence of light environment on visual system development are currently very limited, it is reasonable to expect that other fishes, or vertebrates in general, may evidence similar retinal responses when developing in different light environments. Stomatopod crustaceans, on the other hand, are the only animals known to spectrally 'tune' individual photoreceptor classes in an adaptive way using a flexible system of filters. Furthermore, we have preliminary evidence that such tuning can occur at any time during an individual's life following metamorphosis.

The lysiosquilloid *Pullosquilla litoralis* was previously reported to inhabit only tropical waters less than 2 m deep (Jutte, 1997) but, more recently, we have observed *P. litoralis* in habitats from 1 m to 30 m. Accordingly, the wide depth range that these animals inhabit has a similarly broad range of light conditions. As these animals have planktonic larval stages, the quality of light that any individual may occupy after metamorphosis may not be predictable. Also, if *P. litoralis* is mobile as an adult, it may encounter variable light environments throughout its life. Therefore, in *P. litoralis*, the possession of tuneable color vision enables effective sensory function in the different photic conditions of its range of habitats.

Previous to this work, only stomatopods within the superfamily Gonodactyloidea have evidenced these tuneable Row 3 filters (Cronin and Caldwell, 2002; Cronin et al., 2001). Cronin and Caldwell (2002) showed that spectral and structural changes in intrarhabdomal filters of three gonodactyloid species could alleviate the effects of the reduced spectral range of light available in deeper habitats. Typically, narrow-spectrum, deep-water animals developed blue-shifted filters that were also anatomically shorter than those collected in shallow water. We have shown that direct adaptation to surrounding photic conditions also occurs in the lysiosquilloid species *P. litoralis*. We used our measured spectral changes in Row 3 filters to construct photoreceptor sensitivity spectra for deep- and shallow-adapted animals (Fig. 3), which were then used to estimate photon capture rates in the environmental lighting conditions at variable depths. When comparing photon capture rates of Row 3 receptors at 1 m depth with the red-shifted (shallow) filters to capture rates of receptors with blue-shifted (deep) distal filters at various depths and light environments, it is clear that the deep-adapted Row 3 photoreceptors have a greater level of stimulation in natural light down to at least 5–7 m depth (Fig. 5). At greater depths, the reduction in ambient light intensity and spectral range overwhelms the benefit of the increased photon capture rate associated with the tuneable filter. Because of the absorptive

properties of water, even at shallow depths there are relatively few photons available at the long wavelengths at which the Row 3 photoreceptors operate. The situation becomes much worse at greater depth; in this case, the spectral properties of the adaptable distal filters are insufficient to offset the effects of the greatly decreased light levels. It is possible that at intermediate depths within the range of *P. litoralis* (e.g. 5–15 m), a reduction in filter length can increase photon capture efficiency to ameliorate the decreased illumination to some extent. At this time, our model is conservative in its predictions on depth variation in the function of the adaptable color vision system of *P. litoralis*.

The type of filter that was formed in the distal, Row 3 position varied among our light treatments. Within the white-light-treated animals, two longer-wavelength classes of filters were present. While the longest class (50% absorbance at 590 nm) is typical for shallow *P. litoralis* (Jutte et al., 1998), the other class (50% absorbance at 580 nm) was slightly blue-shifted. This type may be an intermediate or mixed type that is still adapting to the light environment after 11 weeks. If this is the case, adaptation to bright environments may require a longer period of time. The reduced spectral range (blue) and reduced intensity (gray) treatments produced animals with homogeneous short-wavelength shifted Row 3 filters with 50% absorbance at 570 nm. From these results, it is apparent that the mechanism controlling the spectral shift occurring in stomatopod Row 3 intrarhabdomal filters is not wavelength dependent (implying some interaction among photoreceptors) but arises simply from a reduced intensity of light stimulus in single photoreceptors.

The mechanism of filter change remains unknown. Hypothesized to be constructed of fused carotenoprotein vesicles, intrarhabdomal filters are created by the surrounding reticular cells of the photoreceptor (Cronin et al., 1994a; Marshall, 1988; Marshall et al., 1991). The data from the present work seem to support the hypothesis put forth by Cronin and Caldwell (2002) that spectral changes in intrarhabdomal filters may arise from feedback between the photoreceptive and synthetic machinery of the Row 3 photoreceptors. Variation in intracellular calcium levels associated with light and dark adaptation may control or initiate the filter changes observed in both gonodactyloid and lysiosquilloid stomatopod retinas. If this is the case, one would predict that individual ommatidia may respond differentially, depending on each one's levels of light or dark adaptation.

We thank two anonymous reviewers for valuable comments on this manuscript.

References

- Beaudet, L. and Hawryshyn, C. W. (1999). Ecological aspects of vertebrate visual ontogeny. In *Adaptive Mechanisms in the Ecology of Vision* (ed. S. Vallerga), pp. 413–438. Dordrecht: Kluwer Academic Publishers.
- Braun, S. C., Kröger, R. H. H. and Wagner, H.-J. (1997). Connectivity patterns of cone horizontal cells in blue acara (*Aequidens pulcher*, Cichlidae) reared in different light regimes. *Neurosci. Lett.* **235**, 145–148.

- Carleton, K. L. and Kocher, T. D.** (2001). Cone opsin genes of African cichlid fishes: tuning spectral sensitivity by differential gene expression. *Mol. Biol. Evol.* **18**, 1540-1550.
- Cronin, T., Caldwell, R. and Erdmann, M.** (2002). Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. I. Visual pigments. *J. Comp. Physiol. A* **188**, 179-186.
- Cronin, T. W. and Caldwell, R. L.** (2002). Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. II. Filter pigments. *J. Comp. Physiol. A* **188**, 187-197.
- Cronin, T. W., Caldwell, R. L. and Marshall, N. J.** (2001). Tunable colour vision in a mantis shrimp. *Nature* **411**, 547-548.
- Cronin, T. W. and Hariyama, T.** (2002). Spectral sensitivity in crustacean eyes. In *The Crustacean Nervous System* (ed. K. Wiese), pp. 499-511. Berlin: Springer.
- Cronin, T. W. and Jinks, R. N.** (2002). Ontogeny of vision in marine crustaceans. *Am. Zool.* **41**, 1098-1107.
- Cronin, T. W. and Marshall, N. J.** (1989a). Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. *J. Comp. Physiol. A* **166**, 261-275.
- Cronin, T. W. and Marshall, N. J.** (1989b). A retina with at least ten spectral types of photoreceptors in a mantis shrimp. *Nature* **339**, 137-140.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L.** (1993). Photoreceptor spectral diversity in the retinas of squilloid and lysiosquilloid stomatopod crustaceans. *J. Comp. Physiol. A* **172**, 339-350.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L.** (1994a). The intrarhabdomal filters in the retinas of mantis shrimps. *Vision Res.* **34**, 279-291.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L.** (1994b). The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). *J. Comp. Physiol. A* **174**, 607-619.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L.** (1996). Visual pigment diversity in two genera of mantis shrimps implies rapid evolution (Crustacea; Stomatopoda). *J. Comp. Physiol. A* **179**, 371-384.
- Cronin, T. W., Marshall, N. J. and Caldwell, R. L.** (2000). Spectral tuning and the visual ecology of mantis shrimps. *Phil. Trans. R. Soc. Lond. B* **355**, 1263-1267.
- Cronin, T. W., Marshall, N. J., Caldwell, R. L. and Shashar, N.** (1994c). Specialization of retinal function in the compound eyes of mantis shrimps. *Vision Res.* **34**, 2639-2656.
- Cronin, T. W., Marshall, N. J., Quinn, C. A. and King, C. A.** (1994d). Ultraviolet photoreception in mantis shrimp. *Vision Res.* **34**, 1443-1452.
- Dominguez, J. H. and Reaka, M. L.** (1988). Temporal activity patterns in reef-dwelling stomatopods: a test of alternative hypotheses. *J. Exp. Mar. Biol. Ecol.* **117**, 47-69.
- Harling, C.** (2000). Reexamination of eye design in the classification of stomatopod crustaceans. *J. Crust. Biol.* **20**, 172-185.
- Hope, A., Partridge, J. C., Dulai, K. S. and Hunt, D. M.** (1997). Mechanisms of wavelength tuning in the rod opsins of deep-sea fishes. *Proc. R. Soc. Lond. B* **264**, 155-163.
- Hunt, D. M., Fitzgibbon, J., Slobodyanyuk, S. J. and Bowmaker, J. K.** (1996). Spectral tuning and molecular evolution of rod visual pigments in the species flock of cottoid fish in Lake Baikal. *Vision Res.* **36**, 1217-1224.
- Jerlov, N. G.** (1976). *Marine Optics*. Amsterdam: Elsevier.
- Jutte, P. A.** (1997). The ecology, behavior, and visual systems of *Pullosquilla littoralis* and *P. thomassini*, two monogamous species of stomatopod crustacean. In *Integrative Biology*. PhD thesis, University of California at Berkeley. 248p.
- Jutte, P. A., Cronin, T. W. and Caldwell, R. L.** (1998). Vision in two sympatric species of *Pullosquilla* (Stomatopoda, Lysiosquilloidea) living in different depth ranges. *Mar. Fresh. Behav. Physiol.* **31**, 231-250.
- Kröger, R. H. H., Bowmaker, J. K. and Wagner, H.-J.** (1999). Morphological changes in the retina of *Aequidens pulcher* (Cichlidae) after rearing in monochromatic light. *Vision Res.* **39**, 2441-2448.
- Kröger, R. H. H., Braun, S. C. and Wagner, H.-J.** (2001). Rearing in different photic and chromatic environments modifies spectral responses of cone horizontal cells in adult fish retina. *Vis. Neurosci.* **18**, 857-864.
- Lythgoe, J. N.** (1990). *The Ecology of Vision*. Oxford: Clarendon Press.
- Lythgoe, J. N., Muntz, W. R. A., Partridge, J. C., Shand, J. and Williams, D. M.** (1994). The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *J. Comp. Physiol. A* **174**, 461-467.
- Manning, R. B., Schiff, H. and Abbott, B. C.** (1984). Eye structure and the classification of stomatopod crustacea. *Zool. scripta* **13**, 41-44.
- Marshall, N. J.** (1988). A unique colour and polarization vision system in mantis shrimps. *Nature* **333**, 557-560.
- Marshall, N. J., Jones, J. P. and Cronin, T. W.** (1996). Behavioural evidence for colour vision in stomatopod crustaceans. *J. Comp. Physiol. A* **179**, 473-481.
- Marshall, N. J., Kent, J. and Cronin, T. W.** (1999). Visual adaptations in crustaceans: spectral diversity in diverse habitats. In *Adaptive Mechanisms in the Ecology of Vision* (ed. S. Vallergera), pp. 285-328. Dordrecht: Kluwer Academic Publishers.
- Marshall, N. J., Land, M. F. and Cronin, T. W.** (1994). The 'six-eyed' stomatopod. *Endeavour* **18**, 17-26.
- Marshall, N. J., Land, M. F., King, C. A. and Cronin, T. W.** (1991). The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour pigments in the eyes of stomatopod crustaceans: Polychromatic vision by serial and lateral filtering. *Phil. Trans. R. Soc. Lond. B* **334**, 57-84.
- Marshall, N. J. and Oberwinkler, J.** (1999). The colourful world of the mantis shrimp. *Nature* **401**, 873-874.
- McDonald, C. G. and Hawryshyn, C. W.** (1995). Intraspecific variation of spectral sensitivity in threespine stickleback (*Gasterosteus aculeatus*) from different photic regimes. *J. Comp. Physiol. A* **176**, 255-260.
- McFarland, W. N. and Munz, F. W.** (1975). Part II: The photic environment of clear tropical seas during the day. *Vision Res.* **15**, 1063-1070.
- Morris, A., Bowmaker, J. K. and Hunt, D. M.** (1993). The molecular basis of a spectral shift in the rhodopsins of two species of squid from different photic environments. *Proc. R. Soc. Lond. B* **254**, 233-240.
- Osoerio, D., Marshall, N. J. and Cronin, T. W.** (1997). Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vision Res.* **37**, 3299-3309.
- Saszik, S. and Bilotta, J.** (1999). The effects of temperature on the dark-adapted spectral sensitivity function of the adult zebrafish. *Vision Res.* **39**, 1051-1058.
- Shand, J.** (1993). Changes in the spectral absorption of cone visual pigments during the settlement of the goatfish *Upeneus tragula*: the loss of red sensitivity as a benthic existence begins. *J. Comp. Physiol. A* **173**, 116-121.
- Shand, J., Archer, M. A. and Collin, S. P.** (1999). Ontogenetic changes in the retinal photoreceptor mosaic in a fish, the black bream, *Acanthopagrus butcheri*. *J. Comp. Neurol.* **412**, 203-217.
- Suzuki, T., Arikawa, K. and Eguchi, E.** (1985). The effects of light and temperature on the rhodopsin-porphyrin visual system of the crayfish, *Procambarus clarkii*. *Zool. Sci.* **2**, 455-461.
- Tsin, A. T. C. and Beatty, D. D.** (1977). Visual pigments changes in rainbow trout in response to temperature. *Science* **195**, 1358-1359.
- Wagner, H.-J. and Kröger, R. H. H.** (2000). Effects of long-term spectral deprivation on the morphological organization of the outer retina of the blue acara (*Aequidens pulcher*). *Phil. Trans. R. Soc. Lond. B* **355**, 1249-1252.