

PHOTORECEPTION IN THE PLANKTONIC LARVAE OF TWO SPECIES OF *PULLOSQUILLA*, A LYSIOSQUILLOID STOMATOPOD CRUSTACEAN

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Summary

Optical microscopy, electron microscopy and microspectrophotometry were used to characterize pigments in the eyes of planktonic larvae of two species of the lysiosquilloid stomatopod *Pullosquilla*, *P. litoralis* and *P. thomassini*, which live sympatrically in French Polynesia. In contrast to the adult retina, which contains a diverse assortment of visual pigments in the main rhabdoms, the principal photoreceptors throughout the larval eyes of both species were found to contain a single rhodopsin with an absorption maximum (λ_{\max}) close to 446 nm. The expression of this visual pigment may survive metamorphosis, since several adult rhodopsins occur at a similar spectral position. The retinas of these planktonic larvae also contain a novel yellow photostable pigment,

which is arrayed in a regular pattern at the distal margin of the larval retina. The absorption spectrum of this pigment is well matched to the larval rhodopsin, suggesting that it acts to screen the rhabdoms from stray light. By replacing opaque, black screening pigment, the transparent yellow pigment may act together with a blue iridescent layer in the larval retina to reduce the visual contrast of the larval eye against downwelling and sidewelling light, while simultaneously acting as a retinal screen.

Key words: *Pullosquilla litoralis*, *Pullosquilla thomassini*, stomatopod, visual pigment, compound eye, crustacean, larva, zooplankton, photoreception.

Introduction

In most cases, metamorphosis involves a change in both lifestyle and habitat, whether it be from planktonic zoea to benthic crab, aquatic tadpole to terrestrial bullfrog or aquatic nymph to aerial dragonfly. The changes that occur in the physiology, morphology and behavior of an animal during the transition from larva to adult often include a massive overhaul of the visual system. The ontogeny of the visual system of metamorphosing marine animals generally leads to eye enlargement and may produce changes in eye location, visual pigment array, eye structure and neural wiring. Modifications to the visual system are not simply made in response to habitat and lifestyle changes, but rather prepare animals in advance for their new environments.

In the marine environment, many species of fish have eyes that undergo dramatic transformations at the biochemical, physiological and anatomical levels (Evans and Fernald, 1990). In one example, the eel (*Anguilla anguilla*) develops new visual pigment assortments during the transformation from leptocephalus larvae to elver to adult eel (Wood *et al.* 1992). In fact, the visual pigments of fish commonly change in species that make a transition to different depths and feeding behavior at metamorphosis (e.g. Bowmaker and Kunz, 1987; Shand, 1993).

Marine invertebrates that metamorphose often undergo even more striking alterations to their visual systems. For instance, the planktonic larvae of most marine crustaceans have transparent compound eyes which form apposition images (Nilsson, 1983; Cronin, 1986; Cronin *et al.* 1995). These may be radically transformed when the adult eye forms, although the degree of change varies among species (Nilsson *et al.* 1986; Douglass and Forward, 1989). However, these changes have been fully documented only rarely. In particular, the differences in the visual systems of larval and adult stomatopod crustaceans (mantis shrimps) have been studied in just a few species (Provenzano and Manning, 1978; Morgan and Provenzano, 1979; Greenwood and Williams, 1984; Cronin *et al.* 1995), and most work addresses the external structural changes that take place during larval development and metamorphosis. Cronin *et al.* (1995) made the first attempt to analyze the visual pigments within both the adult and larval forms of the same stomatopod species, *Gonodactylaceus* (formerly *Gonodactylus*) *aloha*. Adults and first pelagic instar larvae were examined using scanning electron microscopy and microspectrophotometry. The results suggested that the single visual pigment present in *G.*

aloha larvae disappears at metamorphosis and is replaced by ten classes of adult rhodopsin. Moreover, the characteristic complex features of adult stomatopod eyes, such as the division into dorsal and ventral hemispheres of ommatidia separated by a six-row midband and the presence of photostable intrarhabdomal filters, are not present in the early larval eye. Other stomatopod species available as postlarvae were also analyzed and were found to display eye structure, and presumably photopigment arrays, analogous to those of conspecific adults (Cronin *et al.* 1995). Thus, the major ocular reorganization occurs at the metamorphic molt from larva to postlarva.

The goal of the research reported here was to learn more about the visual systems of larval crustaceans, particularly stomatopod larvae, and to compare these results with those found in conspecific adults. Larvae of both *Pullosquilla litoralis* and *P. thomassini* were available through a captive breeding program (Jutte, 1997), and the visual systems of adult *P. litoralis* and *P. thomassini* were the subject of recent characterization (Jutte *et al.* 1998). The results of this work on larval stomatopods provide new insights into the changes that take place during the ontogeny of the crustacean eye.

Materials and methods

Animal collection and husbandry

Adult *Pullosquilla litoralis* (Michel and Manning, 1971) and *P. thomassini* (Manning, 1978) were collected at the University of California at Berkeley's Richard B. Gump South Pacific Biological Station in Moorea, French Polynesia. Collecting trips were made in May 1995, September–November 1995 and March–April 1996. Animals were returned to UC Berkeley, where they were paired. Pairs of both species were maintained in the laboratory in a captive breeding program (Jutte, 1997). Larvae used in this work were removed from parental containers with an eyedropper and placed in artificial sea water. Animals were fed 1-day-old brine shrimp nauplii (*Artemia salina*, San Francisco Bay strain) and provided with new artificial sea water daily. Larvae were maintained in fluorescent lighting on a 12h:12h light:dark schedule in addition to natural indirect sunlight. *Pullosquilla* larvae remain planktonic for over a month, going through more than six instars (Jutte, 1997).

Larvae from ten clutches were transported to the University of Maryland, Baltimore County, where their eyes were examined in detail in July–August 1996. Larval clutches varied in hatching dates from 11 July to 17 July 1996. Animals were maintained in fluorescent lighting on a 12h:12h light:dark schedule and were otherwise maintained as at UC Berkeley. Specimens used for analysis were 15 days old or younger (approximately third larval instar).

Microspectrophotometry

Larvae used for analysis (*P. litoralis*, $N=5$; *P. thomassini*, $N=4$) were dark-adapted for at least 24 h before preparation, and all procedures were carried out in the dark or in dim red light. Because of the small size of *Pullosquilla* larvae (body

length approximately 1.7 mm), entire larvae were placed on cryosection stubs, eyes upwards, and flash-frozen with cryogenic spray. Preparations were sectioned at 14 μm in a cryostat (-30°C) and collected on coverslips. Sections prepared for microspectrophotometry of visual pigments were viewed only with dim red light. The sections were mounted between coverslips within a ring of silicone grease in pH 7.5 marine crustacean Ringer's solution (Cavanaugh, 1956) containing 2.5 % glutaraldehyde. Sections prepared for analysis of the photostable pigment and for observations of eye structure were mounted in mineral oil medium to reduce light scattering (see Cronin *et al.* 1994).

The single-beam instrument and procedures used previously to study stomatopod visual pigments were employed in this study (see Cronin and Marshall, 1989; Cronin *et al.* 1993; Jutte *et al.* 1998). A circular, linearly polarized beam, 1.5 μm in diameter, was placed within the pigmented areas. Absorbance values were computed by comparing the amount of light passing through the pigmented material with the amount of light measured when the beam was placed in a clear area of the preparation. To reveal the presence of photopigments, scans were taken of fully dark-adapted material and again after 2 min of photobleaching with bright white light (crustacean visual pigments photobleach rapidly in the presence of glutaraldehyde; see Goldsmith, 1978). The difference between the photobleached spectrum and the dark-adapted spectrum was taken to be that of the photobleachable rhodopsin.

Spectral analysis of visual pigments

Any difference spectra showing irregular bleaches or no change from the dark-adapted state were omitted from analysis. Spectra that suggested the presence of a photobleachable rhodopsin were averaged, and any net baseline shift was stripped by setting the mean absorption from 651 to 700 nm equal to zero. The mean difference spectrum for photobleaching was then matched to template spectra derived by Palacios *et al.* (1996). A least-squares procedure was used to fit the template spectra to averaged difference spectra (see Cronin and Marshall, 1989). Each curve was tested against templates of λ_{max} from 400 to 600 nm at 1 nm intervals. The curve was first normalized to the mean of the five data points nearest to the λ_{max} being tested. The best fit was defined as that producing the least sum of squares of deviations from 25 nm below the wavelength of maximum of absorption (or 400 nm, whichever was greater) to 75 nm above the maximum (for further details, see Cronin and Marshall, 1989).

Electron microscopy

Material was prepared by fixing whole larvae in 2.5 % glutaraldehyde in cacodylate buffer. Specimens were post-fixed in 1 % osmium tetroxide in cacodylate buffer, embedded following standard procedures, and sections were stained with uranyl acetate and lead citrate, and examined with a Zeiss EM10CA electron microscope.

Results

Each *Pullosquilla* larval eye is round, undivided and approximately 0.5 mm in diameter (Fig. 1A). In life, the eye appears to be mainly transparent except for a dark compact mass visible at the center of the eye (which often appears a striking iridescent blue on its surface, as seen in Fig. 1), representing the location of the retina.

The small size of the retina is emphasized in cryosections. At the outer margins of the retina, sections reveal a regular array consisting of clearer regions representing rhabdoms and reticular cells together with dark granules of screening pigment, alternating with masses of a bright yellow pigment (Fig. 1B). The yellow pigment is located superficially over the entire surface of the retina, but is confined to the distal region, where it is found only between rhabdoms and never within them. Electron micrographs of the larval eye (Fig. 2) reveal that the yellow pigment is packaged in large vesicles located

within the reticular cells, outside the rhabdom, near the top of the retina. *P. litoralis* and *P. thomassini* larval eyes have the same pattern of distribution of the yellow pigment. Microspectrophotometry shows that the absorbance spectra of yellow pigment in the eyes of both larval *Pullosquilla* species are similar, being smooth and featureless, mainly transparent at long wavelengths and peaking in absorbance in the region of 450 nm (Fig. 3). The pigment absorbs light strongly, reaching a mean peak absorbance of approximately $0.15 \mu\text{m}^{-1}$ (see legend to Fig. 3). A red pigment was also observed in the larval eyes, located near the basement membrane. This pigment

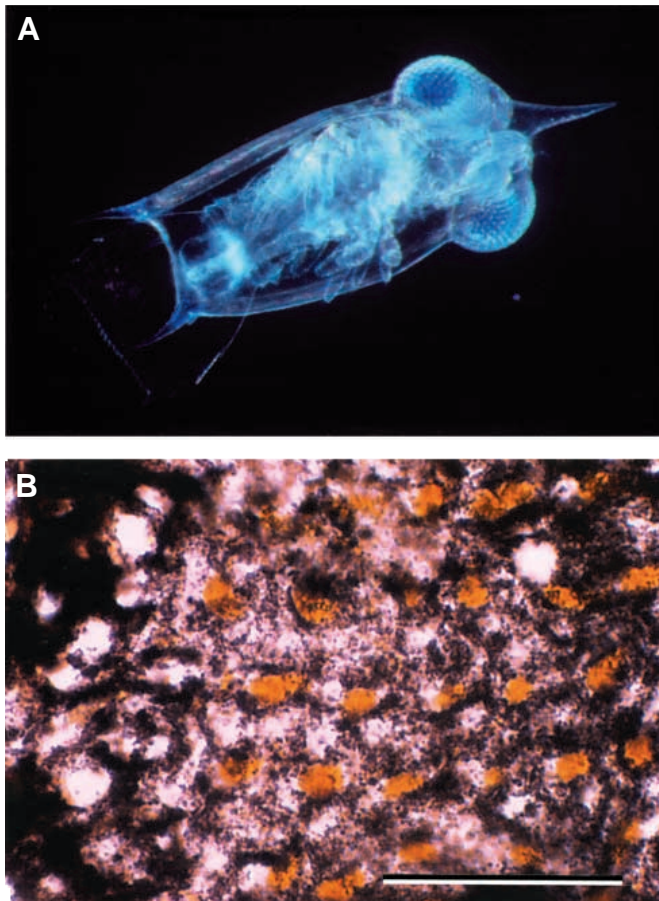


Fig. 1. (A) A view of a living larva of *Pullosquilla litoralis*. This individual is 4 days old (second larval instar) and is approximately 3 mm in length. Note the blue iridescence at the margin of the retina. (B) A true-color image of a cryosection (14 μm thick) from the larval eye of *P. thomassini* (8 days post-hatch). This section was taken just inside the distal margin of the retina. Note the pattern of yellow pigment interspersed regularly among the transparent regions of rhabdoms and reticular cells containing dark screening pigment. Scale bar, 100 μm .

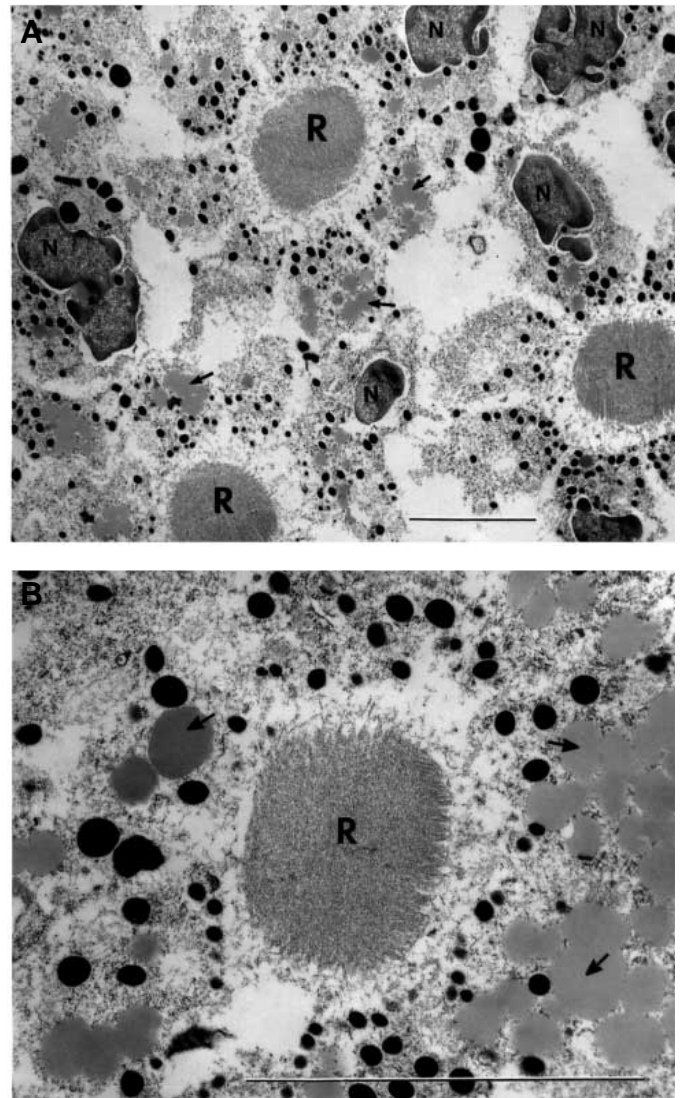


Fig. 2. (A,B) Electron micrographs of the larval retina of *Pullosquilla litoralis* stained with lead citrate and uranyl acetate (compare with Fig. 1B). The yellow pigment (arrows) is visualized as homogeneous gray blobs in several reticular cells, arrayed about the central rhabdom (R), in which the microvilli that contain the visual pigment are visible. Black granules of reticular cell pigment are also apparent. In A, obtained at lower power, several reticular cell nuclei (N) are visible, showing that the section is taken near the distal tips of the reticular cells. Scale bars, 5 μm .

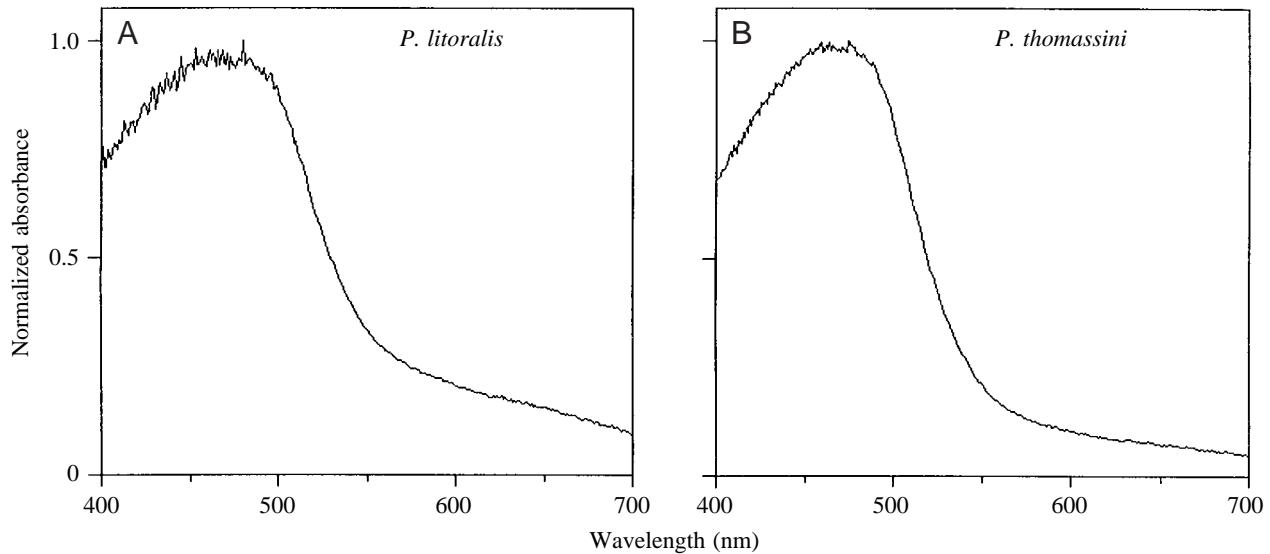


Fig. 3. Normalized absorbance spectra of the photostable yellow pigment in the distal larval retina of *Pullosquilla litoralis* (A) and *P. thomassini* (B). The plotted curves are averages of four (*P. litoralis*) and five (*P. thomassini*) single scans. The curves are very similar except for the residual absorbance in the long-wavelength tail, which varies among individual scans depending upon beam placement and the quality of the section. The spectra were normalized to maximum absorbances of 2.18 (*P. litoralis*) and 1.82 (*P. thomassini*). If the scanned pigments occupied the full thickness of the section ($14\mu\text{m}$), this corresponds to specific absorbances at the peak of $0.155\mu\text{m}^{-1}$ for *P. litoralis* and $0.131\mu\text{m}^{-1}$ for *P. thomassini*.

degraded quickly in light, was not in the pathway of light entering the retina through the cornea and was not analyzed further.

Twenty successful measurements were made of the visual pigments in the larval photoreceptors. In both species, all scans produced similar spectral shapes, showing that each has a single photoreceptor class throughout its main retina, where rhabdoms are formed from the fused rhabdomeres of reticular cells 1–7 (Fig. 4). Mean difference spectra for photobleaching

of *P. litoralis* scans were well fitted by a rhodopsin template spectrum of $\lambda_{\text{max}}=446\text{ nm}$ and for *P. thomassini* by a template spectrum of $\lambda_{\text{max}}=447\text{ nm}$. When the scans were analyzed individually for best fit, the following results were obtained: *P. litoralis*, $N=14$, $\lambda_{\text{max}}=446.71\pm 8.27\text{ nm}$; *P. thomassini*, $N=6$, $\lambda_{\text{max}}=442.33\pm 15.70\text{ nm}$ (means \pm s.d.). These results are not statistically different (Student's t -test, $P\approx 0.4$), suggesting that the both species possessed the same photopigment. In both species, fits to the rhodopsin template were far better (Palacios

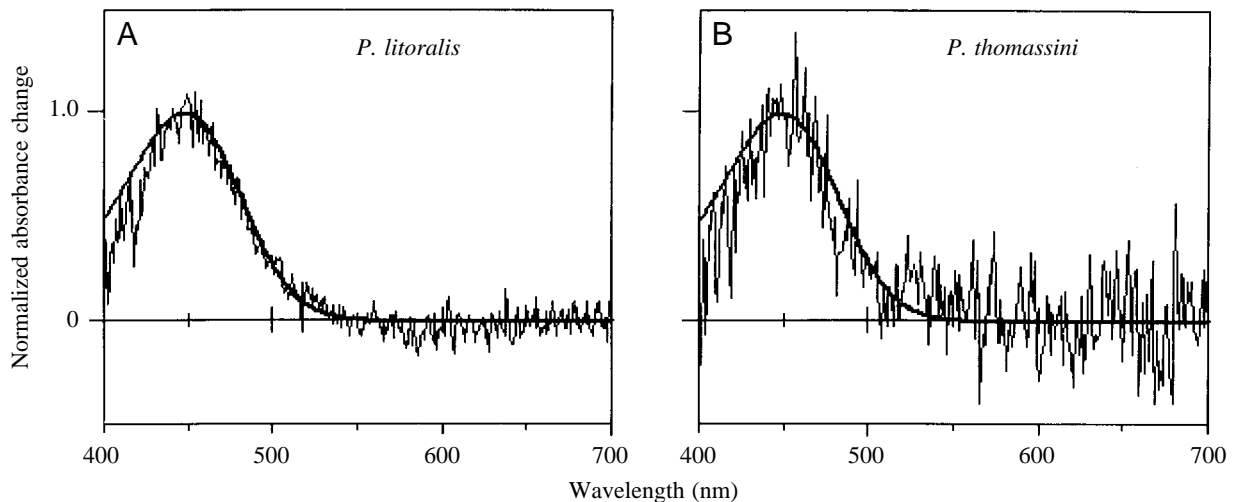


Fig. 4. Normalized, average spectra for photobleaching of visual pigments in the larval retinas of *Pullosquilla litoralis* (A) and *P. thomassini* (B). The mean absorbance change from 651 to 700 nm is set to zero in each curve. The smooth, dark trace is the best-fit template spectrum, determined as described in the text; *P. litoralis*, $\lambda_{\text{max}}=446\text{ nm}$; *P. thomassini*, $\lambda_{\text{max}}=447\text{ nm}$. The number of individual photobleaches included in each average is 14 for *P. litoralis* and six for *P. thomassini*.

et al. 1996) than those to the porphyropsin template (Stavenga *et al.* 1993); the sum of squared deviations from the best porphyropsin fit was 2.86 (*P. thomassini*) to 7.63 (*P. litoralis*) times as great as that from the best rhodopsin fit.

Discussion

Larval eyes of *P. litoralis* and *P. thomassini* have a different optical organization and possibly a different visual pigment from those of conspecific adults. They thus pass through a developmental sequence analogous to that of *Gonodactylaceus aloha*, the only other stomatopod larval/adult system studied to date. Moreover, *Pullosquilla* have an unusual yellow pigment, distributed in a regular geometrical array in their eyes, that has not been reported previously in larval or adult stomatopods.

The yellow pigment of larval Pullosquilla eyes

While similar orderly arrays of colored pigment have not been noted before in eyes of larval crustaceans, nor indeed in those of any other zooplankton, analogous colored structures are common in animal eyes. In fact, yellow- and orange-colored pigments are well-documented in both vertebrate and invertebrate eyes (e.g. Walls and Judd, 1933; Muntz, 1972; Marshall *et al.* 1991b; Stavenga, 1992).

As in other animals with yellow ocular pigments, the yellow material in *Pullosquilla* larval eyes is probably a carotenoid. The shape and spectral location of its absorbance curve are consistent with this possibility (Vetter *et al.* 1971), and the intrarhabdomal filters in adult stomatopod eyes are made of these substances (Cronin *et al.* 1994). While the shape of the absorbance spectrum of the larval pigment is not identical to that of any adult filter pigment, it is very reminiscent of the yellow pigment incorporated into distal filters in the second ommatidial row of the midband (Cronin *et al.* 1994). However, this similarity to the adult pigments does not reflect identical functions in the larva and adult. In larvae, the pigment is positioned in the eye in such a way that incident light does not pass through it on the direct path to the rhabdom: the pigment is found only between rhabdoms and never within them (Fig. 1B). At best, it will exert a minor influence on the tuning of photoreceptor spectral sensitivity.

The larval pigment is not only in a different location from that of an adult intrarhabdomal filter, it is also packaged differently. The larval pigment is found in large vesicles within the actual reticular cells (Fig. 2), while the adult intrarhabdomal filters are found in tiny vesicles located where rhabdomal microvilli would normally occur (Marshall *et al.* 1991b). Such differences suggest that these structures share neither a common origin nor a common function. It remains possible, however, that these larval pigments could be cellular precursors to adult intrarhabdomal filters. Another intriguing possibility is that they represent a potential pigmentary ancestor to the intrarhabdomal filters of adult stomatopods.

The location of the pigment around, or adjacent to, the rhabdom is characteristic of a screening pigment. Black

screening pigments in the eyes of arthropods isolate photoreceptors into discrete units, effectively trapping unwanted or off-axis light that would otherwise excite the photoreceptors (Autrum, 1981; Marshall *et al.* 1991a). Colored pigments, in contrast, are not normally effective for light trapping. Such pigments are present in many insects, including butterflies (Ribi, 1979; Arikawa and Stavenga, 1997), digger wasps (Ribi, 1978), drone honeybees (Stavenga, 1992), dragonflies (Labhart and Nilsson, 1995), fruit flies (Strother and Superdock, 1972) and fireflies (Lall *et al.* 1988). In crustaceans, they occur in all known stomatopod retinas (Marshall *et al.* 1991b) and are found in decapods such as the crab *Leptograpsus variegatus* (Stowe, 1980). Such colored screening pigments act as spectrally tuned filters that reduce glare, prevent the deterioration of spatial acuity, sharpen spectral sensitivity or intensify spectral contrast to optimize vision in a particular photic environment (Lall *et al.* 1988; Cronin and Marshall, 1989; Stavenga, 1992). Larval *Pullosquilla* are therefore rather unusual in employing colorful, transparent pigments as a blocking screen.

A major concern for planktonic animals is the minimization of their visibility in silhouette against the underwater light field. Midwater animals often go to great lengths to reduce their silhouette, commonly by becoming flat and silvery like a mirror, by producing bioluminescent counterillumination or by being as transparent as possible (for a review, see Nilsson, 1996). Small plankton, such as crustacean larvae, generally use transparency for camouflage. In such an animal, the black pigments of the eye are almost always the body part most difficult to conceal. For best function, the photoreceptors must absorb light from the appropriate direction only, and both the absorption and screening require appropriate light-absorbing pigments (see Nilsson, 1996).

Pullosquilla larvae are themselves transparent over most of their bodies (see Fig. 1). Partially replacing black, opaque screening pigments with transparent yellow pigments may assist this transparency by reducing the contrast between the eye and the rest of the body. While light from most directions is predominantly blue or blue-green in planktonic habitats, downwelling light in shallow water contains the full spectral range typically present in air (McFarland and Munz, 1975; Lythgoe, 1979). The yellow pigment, arrayed in a regular pattern just at the distal margin of the retina, absorbs only light to which the photopigment is sensitive, passing the longer wavelengths of downwelling light and reducing the visibility of the eyes to upward-looking predators. In addition, the blue iridescence of the eyes replaces the light absorbed by the retina and yellow screen, further helping to camouflage the animals from predators swimming at the same depth. The relatively narrow absorption spectrum of the yellow pigment, complemented by the blue iridescence, could make these larval eyes virtually invisible in the midwater environment. Systems such as these may be common in zooplankton and would have been missed in earlier work simply because most histology is performed on fixed and stained specimens, from which the natural coloration has been lost.

The yellow pigment may play a second role in the eye. The thermally stable metarhodopsins of arthropods tend to absorb maximally at approximately 500 nm (see Stavenga, 1992). In the retina of *Pullosquilla* larvae, they would therefore absorb in a spectral range well above that of the short-wavelength rhodopsins. The light transmitted by the yellow pigment could flood the inner retina, reconvert the metarhodopsin to rhodopsin and maintaining maximum photosensitivity. The colored screening pigments of insect eyes commonly play such a role in vision (Stavenga, 1992).

Visual pigments of Pullosquilla larvae

The spectra of larval *Pullosquilla* visual pigments are far more similar to rhodopsin than to porphyropsin templates, suggesting that the chromophore of the larval visual pigment is retinal. If so, like the adult visual pigments (Goldsmith and Cronin, 1993), those of *Pullosquilla* larvae are probably rhodopsins. As in other fully marine animals, both fish and invertebrates, there is no evidence of chromophore replacement at the time of metamorphosis. The similarity between the absorption spectra of the visual pigments within the larval *P. littoralis* and *P. thomassini* eyes suggests that the two species may actually have the same larval visual pigment, based on similar or identical opsin molecules.

In *G. aloha*, the single larval visual pigment seems to be replaced at metamorphosis with a new suite of adult visual pigments. On the basis of spectral similarity, however, *Pullosquilla* larval visual pigments may be incorporated into one or more receptor classes of the adult eye, although there is sufficient uncertainty in the data to make this a tentative conclusion only (see Jutte *et al.* 1998). Further studies with larger sample sizes of both adult and larval retinal scans, or using molecular genetic analyses, are required before a conclusion may be drawn on the fate of larval visual pigments in these species. In adult stomatopods, the peripheral retina forms the array that samples the visual field spatially (Marshall and Land, 1993). Since the larvae possess a single visual pigment in all rhabdoms, one might predict that it would be similar to the rhodopsins of the adult peripheral retina. In fact, the larval pigment is more like the peripheral rhodopsin of *P. thomassini* (adult λ_{\max} =467 nm) than that of *P. littoralis* (λ_{\max} =509 nm). *P. thomassini* is the deeper-living species as an adult, occurring to depths of at least 37 m. If planktonic larvae are spread throughout a range of depths in dynamic coastal waters, this may partially explain the spectral location of the larval pigment. In addition, for optimal screening, the visual pigment must have an absorption spectrum similar to that of the yellow pigment, necessitating a rhodopsin absorbing maximally in the blue. Nevertheless, the visual pigment of these larvae has an unusually short spectral placement, and it will be interesting to learn more about the visual pigments of coastal and open-ocean marine larvae and other shallow-water zooplankton.

In conclusion, the eyes of *P. littoralis* and *P. thomassini* go through striking changes during ontogeny. Not only do they change externally in color and design during the transition

from larva to adult, but there are less obvious, and equally significant, internal changes as well. The larval eyes contain an unusual array of a stable yellow pigment, not seen in adults, that probably acts as a retinal screen and may also reduce larval visibility in the plankton. Unlike the only previously studied larval/adult stomatopod system, the *Pullosquilla* larval visual pigment may continue to be expressed in some photoreceptor classes of the adult retina. Despite their rather different adult environments, the larvae of these species of *Pullosquilla* appear to be adapted to live in identical photic worlds during their planktonic development.

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