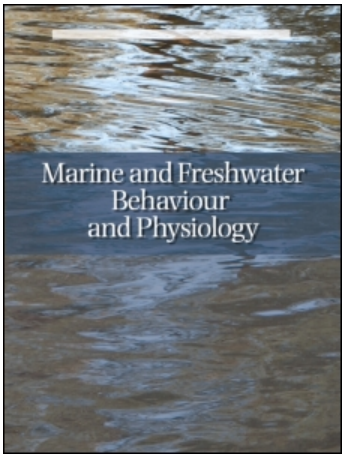

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COMPOUND EYES AND OCULAR PIGMENTS OF CRUSTACEAN LARVAE (STOMATOPODA AND DECAPODA, BRACHYURA)

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KEY WORDS: larvae, compound eyes, stomatopod, crab, visual pigment, metamorphosis

Larvae of decapod and stomatopod crustaceans possess paired compound eyes not unlike those of adult crustaceans. However, the visual demands of larval and adult life differ considerably. Furthermore, the eyes of adult stomatopods appear to be far more specialized than those of the larvae. We examined eyes of several stomatopod species just before and after larval metamorphosis. At this time, the entire larval retina is joined by a new, adult-type retinal array which gradually replaces the remnants of the larval retina. The new retina of the postlarva is anatomically similar to that of the full-grown adult, and has virtually identical assemblages of intrarhabdomal filters. We determined the photopigments of *Gonodactylus aloha*, the only species for which we were able to obtain both larval and adult specimens, using microspectrophotometry. The single middle-wavelength larval rhodopsin (λ_{max}= 499 nm) disappears at metamorphosis; none of the 10 classes of adult rhodopsins has λ_{max} between 473 and 510 nm. This metamorphic change of visual pigment does not occur in a comparison species of decapod crustacean, the blue crab *Callinectes sapidus*. Here, rhodopsins both of the megalops larva and the adult had λ_{max} at 503–504 nm. The difference between these two species can be explained by the varying ecological requirements of their larvae and adults, and more study of visual pigments in retinas of larval and adult crustaceans is warranted.

INTRODUCTION

Metamorphosis is a common event in the development of marine animals. As changes take place in the body plan, habitat, and mode of life, sensory organs like the eye are altered as well. Metamorphosis generally leads to an enlarged eye, and may include more subtle changes in eye location, optical design, neural wiring, and photoreceptor complement. Some amphibians and fish change the chromophore of visual pigments at this time (reviewed in Bridges, 1972; Lythgoe, 1979). For example, metamorphosis is accompanied by the expression of a new suite of visual pigments in the rods and cones of winter flounder (Evans *et al.*, 1993), white sturgeon (Loew and Sillman, 1993), and probably other species of fish as well (Carlisle and Denton,

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1959; Munz and McFarland, 1973). In other fish species, additional cone types come and go as development proceeds (Bowmaker and Kunz, 1987; Shand, 1988; Shand *et al.*, 1993; Hawryshyn *et al.*, 1989; Wood and Partridge, 1993). In all of these cases, the changes are due both to the increasing complexity of the visual apparatus and to the changing ecological requirements faced as individuals mature.

In most marine crustaceans, the planktonic larvae share a common eye plan, in which a transparent compound eye with a condensed, central retina forms an apposition image (Fincham, 1980; Nilsson, 1983; Cronin, 1986). Changes that occur at metamorphosis may leave the eye largely unchanged, as in many crabs, or may lead to a quite different adult design, often with fundamentally different operating principles (see Meyer-Rochow, 1975; Nilsson *et al.*, 1986; Douglass and Forward, 1989).

The stomatopod crustaceans offer a particularly interesting case, because the compound eyes of adult stomatopod crustaceans are extremely unusual. They contain a midband of several rows of ommatidia separating extended dorsal and ventral ommatidial regions (Exner, 1891; Horridge, 1978; Cronin, 1986; Marshall, 1988). Specializations of adult eyes can include the presence of up to 4 different classes of intrarhabdomal filters, division of some main rhabdoms into distinct tiers, and the partitioning of at least 11 different rhodopsins among the various photoreceptor types (Marshall, 1988; Cronin and Marshall, 1989a, 1989b; Marshall *et al.*, 1991a, 1991b; Cronin *et al.*, 1993, 1994a, 1994b, 1994c). Yet the compound eyes of stomatopod larvae resemble those of other crustacean meroplankton, showing none of the adult specializations. The larval eye is round, not divided, and is mainly transparent with a glittering green iridescence. The transition to the adult triple eye form occurs in a single step at metamorphosis to the postlarva (Provenzano and Manning, 1978; Morgan and Provenzano, 1979; Greenwood and Williams, 1984; Williams *et al.*, 1985).

We wished to examine the changes that occur in eyes of larval crustaceans when they metamorphose to the juvenile stage and to compare changes in the visual pigment composition during metamorphosis of stomatopods to what takes place in more typical decapod crustaceans. Accordingly, we examined several species of stomatopods at the time of metamorphosis, as well as a brachyuran crab. Our findings show that physiological changes in stomatopods are as extravagant as the anatomical events, while the crab, in contrast, exhibits a basic physiological and anatomical conservatism.

METHODS

Animals

All larvae were collected at night in the wild and identified to the lowest possible taxonomic level. Few descriptions of stomatopod larvae exist, so we were not always able to identify them beyond genus. Final stage larvae of *Alima sp.* and *Haptosquilla sp.* (probably *H. trispinosa*; adults of this species are locally abundant) were collected near the Lizard Island Research Station (Queensland, Australia) using dipnets with a hand light, while those of *Lysiosquilla sulcata* and postlarvae of *Pseudosquilla ciliata* were similarly collected near the Richard B. Gump South Pacific Biological Research Station (Moorea, French Polynesia). *Gonodactylus aloha* larvae were collected using a light-trap, pump, and plankton net from the docks of the Hawaii Institute of Marine Biology (Kaneohe, Hawaii, USA), and megalopa larvae of

Callinectes sapidus were taken by plankton tow near the Duke University Marine Laboratory (North Carolina, USA). Adult *Gonodactylus aloha* were collected from coral rubble in Kaneohe Bay, Hawaii, USA.

Stomatopod larvae in the final pelagic stage tend to molt to the postlarva almost immediately after collection. Larvae of *Alima sp.* and *Haptosquilla sp.* were preserved as soon as possible after collection, but *Haptosquilla* larvae molted to postlarvae during sorting and were preserved as such. These species were fixed and prepared by standard histological techniques for light microscopy (Marshall *et al.*, 1991a). Larvae of *L. sulcata* also molted to postlarvae shortly after collection, and *P. ciliata* had already molted in the plankton. *G. aloha* larvae were collected when in the first pelagic stage, while *C. sapidus* were collected as megalopae; neither species molted before examination. All these species were maintained on a diet of small zooplankton and transported to Baltimore for microspectrophotometry (MSP) and scanning electron microscopy (SEM) within days of collection. Adult *G. aloha* were fed adult *Artemia salina* and frozen shrimp and were examined by MSP a few weeks after collection.

MICROSPECTROPHOTOMETRY

We used MSP to characterize the intrarhabdomal filters, photostable pigments, and visual pigments of the various species. When examining visual pigments, animals were first dark-adapted for several days and all procedures were carried out in the dark or in dim red light. Our techniques are fully described elsewhere (Cronin and Marshall, 1989a; Cronin *et al.*, 1994a). Briefly, live larvae were quick-frozen using cryogenic spray and sectioned in a cryostat (–25°C to –30°C) at thicknesses of 8 to 14 μm. Sections of the larval compound eyes were mounted in Marine Crustacean Ringers (Cavenaugh, 1956) for scanning of visual pigments or photostable pigments other than intrarhabdomal filters; filters were examined in mineral oil medium to reduce scattering (see Cronin *et al.*, 1994a). Scans were carried out from 400 to 700 nm at 1-nm intervals. To measure absorption spectra of rhodopsins, some sections were mounted in Ringers containing 2.5% glutaraldehyde to enhance the rate of photobleaching. Scans were taken of the fully dark-adapted material and again after 2 to 5 minutes of photobleaching with bright white light. The difference between the two sets of scans was taken as the absorption spectrum of the photobleachable rhodopsin. Each class of rhodopsin was characterized by first averaging at least 5 individual photobleaches, and then matching the average photobleach to template spectra provided by Gary D. Bernard (Bernard, 1987), using a least-squares procedure (see Cronin and Marshall, 1989a). In some cases the photobleach treatment generated a product absorbing at short wavelengths; since the fit to the template was tested on the visual pigment's long-wavelength absorption limb, these distortions had only minor effect on the analysis.

SCANNING ELECTRON MICROSCOPY

Material was prepared for SEM by fixing in 2.5% glutaraldehyde in seawater, drying through an ethanol series, and extracting the ethanol using hexamethyldisilazane (HMDS). Due to their very flexible exoskeletons, many of our specimens became distorted during drying. They were subsequently examined in a JEOL JSM-35CF scanning electron microscope.

TERMINOLOGY

We use our standard terminology for describing compound eyes of stomatopod crustaceans (Cronin *et al.*, 1994c). The dorsal and ventral regions of the eye, with extended fields of view, are termed the "peripheral retina", while the rows of the midband region are numbered from dorsal to ventral; thus, Row 1 is the most dorsal. The photoreceptor tiers of the main rhabdom and intrarhabdomal filters nearer the cornea are distal, while those nearer the basement membrane are proximal.

RESULTS AND DISCUSSION

Development of the Adult Retina in Stomatopods

As noted earlier, stomatopod larval compound eyes change at metamorphosis from a unitary (as exemplified by *Gonodactylus aloha* in Figure 1A) to the characteristic adult triple form with a specialized midband region. Midbands of squilloid stomatopods (e.g. *Squilla, Alima*), have only 2 ommatidial rows, while lysiosquilloids (e.g. *Heterosquilla, Lysiosquilla*) and gonodactyloids (e.g. *Haptosquilla* and *Gonodactylus*) have 6 highly specialized rows of ommatidia in their midbands. We examined eyes and retinas in final pelagic larval stages of the squilloid species *Alima sp.* and in newly molted postlarvae of the gonodactyloid *Haptosquilla sp.* to learn more about the changeover from the larval retinal type to both adult types.

The duplication of the retina is visible even from outside the larval eye in *Alima,* with the larval retina residing laterally and ventrally, and the future adult retina placed dorsal to it. (In the other species we examined, the future adult retina is not externally obvious before metamorphosis). In sections of the larval eye, both arrays of rhabdoms are well organized (Figure 1B). The early adult-type retina already reveals the 2-row midband and the severe skewing of other ommatidia adjacent to it (see Schiff *et al.*, 1986, Marshall and Land, 1993).

Almost half of the retina of the newly molted postlarva of *Haptosquilla* is still the larval type (Figure 1C, 1D), even though the overall form of the eye resembles the adult type (see photographs of the similar eye of *Heterosquilla tricarinata* in Williams *et al.*, 1985). The juvenile retina includes all the structural specializations of the adult form, including the intrarhabdomal filters, tiering of main rhabdoms in Rows 1 to 4, and mutually orthogonal rhabdomeres of retinular cell 8 in Rows 5 and 6 (Figure 1D).

Beneath the level of the retina, axons of the new adult photoreceptors lead to a newly developed lamina and medulla externa. These initially share the medulla interna with the larval retina, ultimately monopolizing it as the larval eye degenerates in the first postlarval stage (see also Williams *et al.*, 1985).

INTRARHABDOMAL FILTERS OF JUVENILE AND ADULT EYES

Among the most distinctive features of stomatopod eyes with 6-row midbands is the presence of intrarhabdomal filters (plugs of strongly colored photostable pigments) placed between the tiers of rhabdoms in Rows 2 and 3. The filters function to tune spectral sensitivities of the underlying photosensitive regions of the rhabdom. Their precise effect is determined by their dimensions as well as the absorption spectra and densities of the pigments they contain.

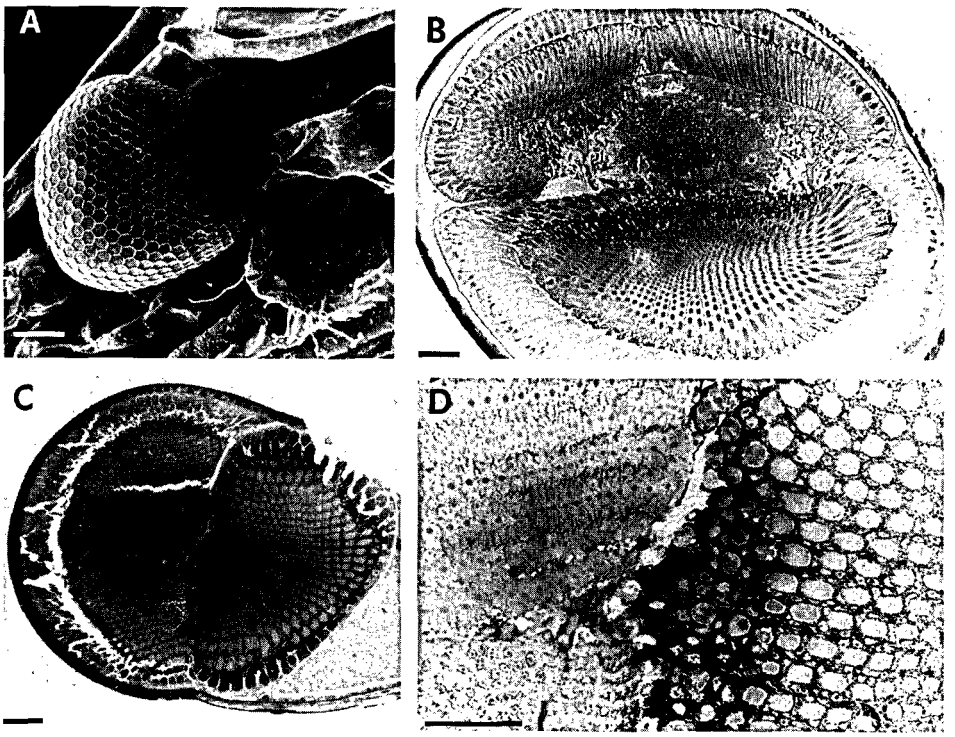

Figure 1 Eyes of larval and postlarval stomatopod crustaceans. All scale bars represent 100 μm. **A.** *Gonodactylus aloha,* scanning electron micrograph of first pelagic larval stage. Note the spherical compound eye composed of hexagonally arranged ommatidia, with no midband region or other regional specialization apparent. **B.** *Alima sp.,*; section of retina of final pelagic larval stage. The retina is already doubled, with the new adult retina (top of panel) placed adjacent to the larval retina. The adult retina shows typical squilloid features, including a two-row midband region, with skewed ommatidia adjacent to it. **C.** and **D.** *Haptosquilla (trispinosa?*); section of postlarval retina. The larval retina remains as an array of large rhabdoms adacent to the new adult-type retina. All standard features of the gonodactyloid type of retina exist in this first postlarval stage, including a specialized 6-row midband region, tiered photoreceptors in midbands Rows 1 through 4, intrarhabdomal filters in Rows 2 and 3, and modified 8th retinular cells in midband Rows 5 and 6.

Since postlarval eyes are so much smaller and more transparent than adult eyes, we wished to learn whether they contain different filters than the adults. Accordingly, we examined postlarvae of a lysiosquilloid species (*Lysios quilla sulcata*) and a gonodactyloid species (*Pseudosquilla ciliata)* for comparison with adults of the same species. Postlarval intrarhabdomal filters were essentially identical to those of the adults, in optical density as well as number and spectral types of classes (Figure 2; see also Cronin *et al.*, 1994a). The only postlarval example that differed in any way from the corresponding filter class of the adult was the distal filter in Row 2 of *L. sulcata*: in the postlarvae the spectrum had a broader, flattopped appearance compared to the adult (Figure 2, top). The difference probably reflects the cellular environment within which the filter is packaged, as the postlarval filter's spectrum

resembles numerous examples of Row 2 distal filters in other stomatopod species (Cronin *et al.*, 1994a). In the small eyes of juvenile stomatopods, spectral tuning of the photoreceptors in postlarvae probably differs from the precise, narrow spectral functions of the adult retina (see, for example, Cronin and Marshall, 1989a, 1989b; Cronin *et al.*, 1993, 1994b).

Pigments of Larval Compound Eyes

During the summer of 1994 we were fortunate to obtain living specimens of larval *Gonodactylus* in the first pelagic stage. Only 2 species of *Gonodactylus* could have produced these larvae: *G. aloha* (may be *G. falcatus*, see Manning and Reaka (1981), Kinzie (1984); the larvae are described by R. Kinzie, unpublished) and *G. hendersoni* (larvae undescribed). We identified the larvae we collected as *G. aloha* due to the

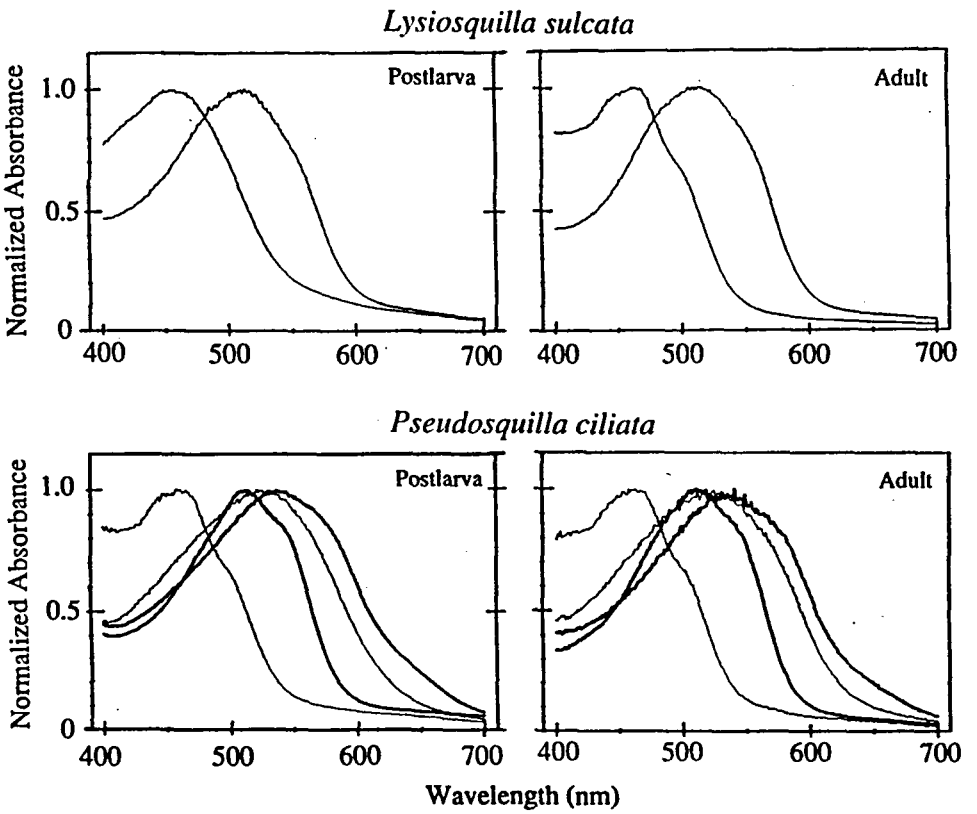

Figure 2 Normalized absorption spectra for the intrarhabdomal filters of postlarvae and adults of a lysiosquilloid (*Lysiosquilla sulcata*) and of a gonodactyloid (*Pseudosquilla ciliata*) species of stomatopod. Distal filters are plotted with thin lines (*L. sulcata* has only distal filters); the spectrum for the distal filter of Row 2 always lies to the left of that for Row 3. Proximal filters are plotted with thick lines for *P. ciliata*; again, Row 2 lies to the left of Row 3. Note that spectra of filters in postlarval retinas are very similar or identical to corresponding filters of adult retinas.

following observations: (1) They could be captured almost at will throughout the summer, from at least late June to mid August. *G. aloha* is known to reproduce throughout the year (R. Kinzie, pers. comm). (2) They were the same size as 1st-pelagic-stage *G. aloha* larvae (4.5 mm; see Provenzano and Manning, 1978) and resembled Kinzie's drawings of the species. (3) *G.aloha* is by far the more abundant species as an adult; in our experience it outnumbers *G. hendersoni* by roughly 2 orders of magnitude. It is also much larger than *G. hendersoni*, and would be expected to produce far more larvae. Nevertheless, since we did not rear the larvae to metamorphosis it remains possible (though very unlikely) that they were misidentified.

These larvae did not molt to later stages during the short time required to transport them to Baltimore, and thus offered us the opportunity to examine ocular pigments in cryosections of fresh-frozen larval eyes. We also obtained adults of the same species and were able to compare all visual pigments of the adult retina to those of conspecific larvae. In order to examine visual pigments in another species of crustacean larva for which the adult pigment is known, we also collected megalopa larvae of the blue crab *Callinectes sapidus*.

Pigments of Larval Stomatopod Eyes

Photostable pigments. Spectra were obtained from 3 types of photostable pigment in the larval compound eye (Figure 3A). Like the compound eyes of many other crustacean larvae, larval *G. aloha* eyes shine with an iridescent green color in direct illumination, resembling the green shiny color often seen in eyes of adult squilloid species. The color is produced by a yellowish pigment present in a layered structure that adds a blue structural tint to produce the overall impression of green iridescence (Marshall *et al.*, 1991b). The absorption spectrum of the responsible pigment (Figure 3A, thin line) is almost identical to the reflecting pigment of adult *Squilla empusa* (Cronin *et al.*, 1993). Adult *G. aloha* eyes do not have this green sheen, but do have a thin layer of this reflecting pigment overlying the retina (see also Marshall *et al.*, 1991b).

Larval *G. aloha* larvae have no intrarhabdomal filters in their retinas, but have at least 2 other stable pigments that must interact with incoming light. One is the typical ommochrome screening pigment found in virtually all crustacean eyes (Figure 3A, dotted line), much like the ommochromes of other stomatopods (Cronin and Marshall, 1989a; Marshall *et al.*, 1991b). Also present are masses of a bright orange pigment, in droplets (Figure 3A, dark line), which is similar to the orange pigment in oil droplets in eyes of the squilloid *Cloridopsis dubia* (Cronin *et al.*, 1993). The screening pigment protects photoreceptors from stimulation by laterally incident light. Similarly, the orange pigment, located at the back of the retina, blocks stimulatory light from reaching the bluegreen-sensitive larval rhodopsin (see below) from behind.

Visual Pigment. We found the same visual pigment in all photoreceptors we examined in cryosections of the larval eye (Figure 3B). Difference spectra for photobleaching were well fit by a template spectrum of λ_{max} 499 nm. The data of Figure 3B represent an average of 6 photobleaches of fresh-frozen material; similar data were obtained from eyes of another specimen that were lightly fixed in glutaraldehyde-containing Marine Crustacean Ringer's before sectioning. The close fit to the rhodopsin template indicates that, as in adults (Goldsmith and Cronin,

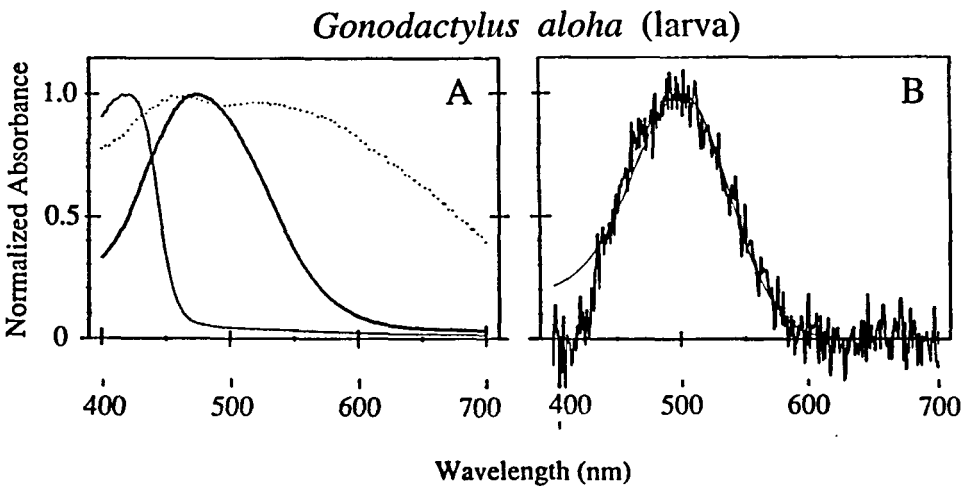

Figure 3 *Gonodactylus aloha.* Normalized absorption spectra of pigments in eyes of first pelagic stage larvae. **A.** Photostable pigments. Dotted trace: ommochrome lateral screening pigment. Thin trace: green reflecting pigment (average of 5 scans). Thick trace: Orange pigment at base of retina (average of 4 scans). **B.** Photobleach spectrum of the visual pigment (average of 5 bleaches of unfixed material), plotted in the thick trace. The thin trace is the spectrum of the best-fit template, with λ_{max} of 499 nm.

1993) the chromophore of the larval visual pigment is retinal$_1$, making the pigment a true rhodopsin.

We speculated that the larval rhodopsin would also occur in one of the adult photoreceptor classes, most likely that of the peripheral retina. Accordingly, we surveyed all of the rhodopsins in main rhabdoms of adult *G. aloha*, a total of 10 classes (2 each in the tiered Rows 1 through 4, one in Rows 5 and 6, and another in the periphery). Results are given in Figure 4. The adult rhodopsins are distributed in a fashion now known to be typical of stomatopods with 6-row midbands (Cronin and Marshall, 1989a, 1989b; Cronin *et al.*, 1993, 1994b, 1994c). Each of the 4 tiered, dorsal rows is devoted to a section of the spectrum; from shortest to longest wavelengths they are ordered Row 1, Row 4, Row 2, and Row 3, with the proximal tier always containing a rhodopsin absorbing at longer wavelengths than the distal tier. Rows 5 and 6, and the periphery, have middle-wavelength rhodopsins suitable for achromatic analysis of form, motion, and polarization. Interestingly, in many cases the specific absorption maximum differs from what would be found in corresponding photoreceptors of the congener *Gonodactylus oerstedii* (Cronin and Marshall, 1989a); similar discrepancies were noted in two species of *Odontodactylus* (Cronin *et al.*, 1993). Such variation among closely related species, living in similar habitats, implies that evolutionary rates for rhodopsins can be extremely rapid.

Nevertheless, none of these diverse visual pigments in the adults corresponded to that of the larva. Larval rhodopsin λ_{max} is near 499 nm; the visual pigments placed nearest to this in the adults are at 510 nm (peripheral retina) and 473 nm (Row 4, proximal tier). We used identical techniques to examine rhodopsins in the larvae and adult, and we have previously estimated that differences in λ_{max} greater than

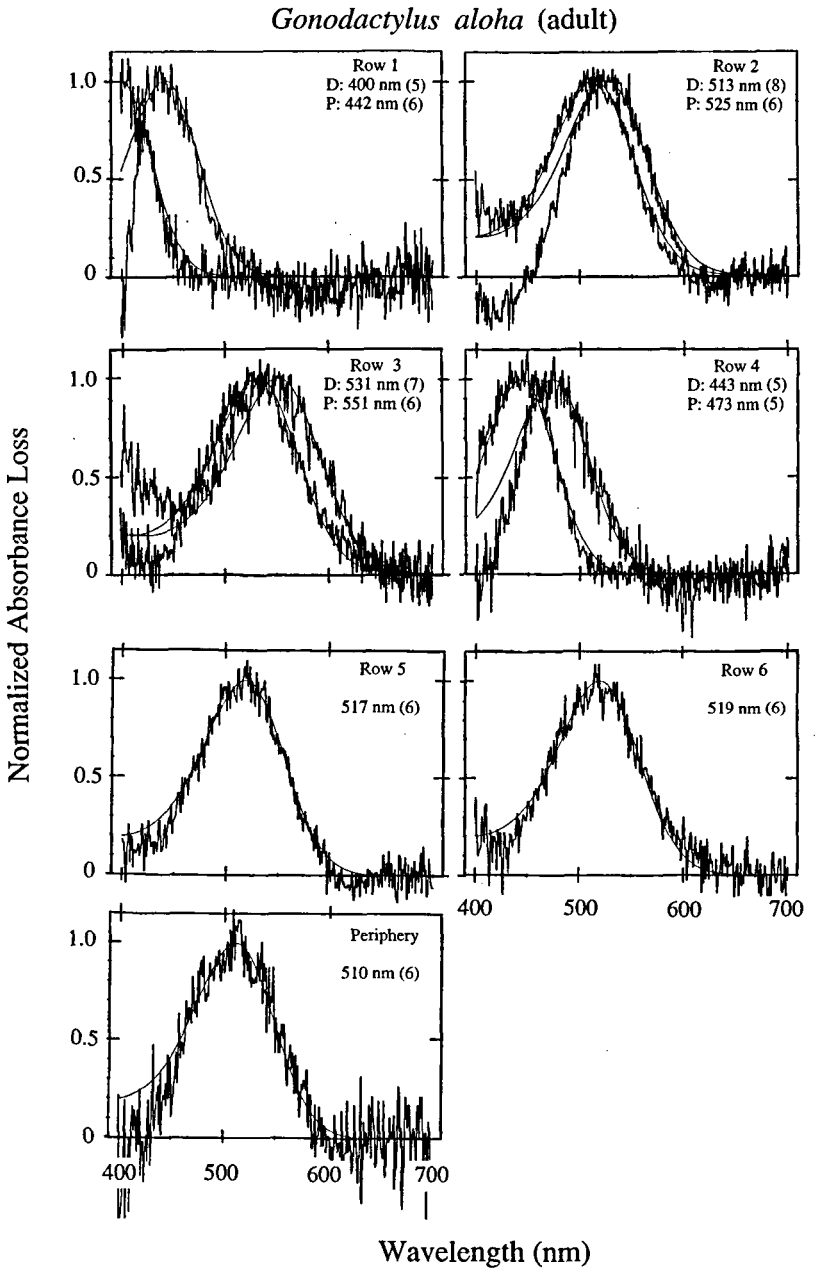

Figure 4 *Gonodactylus aloha*. Normalized, average spectra for photobleaching of visual pigments in all retinal regions below the level of the rhabdomere of the 8th retinular cell. Mean absorbance change from 651 to 700 is set to 0 in each case. Thick, jagged traces represent data, thin, smooth traces represent the best-fit template spectrum (see text). Retinal locations of measurements are given in each panel; the number of bleaches averaged is given in parentheses as well as the λ_{max} of the template spectrum producing the best match. D: distal tier, P: proximal tier.

10 nm are sufficient to distinguish separate rhodopsin classes (Cronin *et al.*, 1993). A 499-nm rhodopsin is unlikely to exist elsewhere in the adult retina, since the only photoreceptor classes we did not census were the rhabdomeres of 8th retinular cells, known to be ultraviolet photoreceptors (Cronin *et al.*, 1994d. It is not known if similar ultraviolet receptors exist in larvae, but anatomically normal R8 cells occur in the larval retina of *Alima*). Further, the difference is unlikely to represent a change in chromophore. The absorption spectrum resembles the rhodopsin template and is at a very short wavelength for a porphyropsin; also, no stomatopod species is known to use any chromophore other than retinal$_1$ (Goldsmith and Cronin, 1993). Therefore, our data strongly suggest that the visual pigment of the larva is replaced at metamorphosis. Although changes like these are well documented in marine fishes, this is the first example known to us of possible changes in visual pigments at metamorphosis in any invertebrate. The larval rhodopsin perhaps represents the common case for midwater plankton, wh.ile the adult (and postlarval) retina is specialized for polychromatic diurnal vision in clear, shallow water.

Visual Pigments of Larval Crab Eyes

The discovery of a possible change in visual pigment complement at metamorphosis in a stomatopod species led us to question whether such changes may be routine in crustaceans. We therefore obtained megalopae (final stage larvae, see Costlow and Bookhout, 1959) of blue crabs *Callinectes sapidus* as a comparison species. Brachyuran crabs are particularly suitable as study subjects since they tend to be very conservative in their use of rhodopsins. Among 18 species of shallow-water brachyurans we have surveyed, each species has a single rhodopsin class, with λ_{max} in the range from 491 nm to 506 nm (Cronin and Forward, 1988). *C. sapidus* rhodospin sits at 503 nm. If visual pigment absorption changes by even a few nm at metamorphosis in crabs, it should be detectable.

Our results show that *C. sapidus* megalopae have a single visual pigment with λ_{max} at 504 nm (Figure 5). This is within one nm of what we found in *C. sapidus* adults (Figure 5, see Cronin and Forward, 1988), and very similar to Bruno and Goldsmith's (1974) earlier analysis of this species, where λ_{max} was at 500 nm. It also corresponds well to the blue-green behavioral sensitivity maximum found throughout crab and other crustacean larvae (Forward and Cronin, 1979; see review of Forward and Douglas, 1989). Spectrally, at least, there is no change in retinal visual function when the megalopa eventually reaches the adult stage. In a species where both the larvae and the adults inhabit waters throughout estuaries, changes in visual sensitivity are probably unnecessary in any case.

CONCLUSIONS

The dramatic change in the external shape of the eyes of larval stomatopods is reflected by a number of alterations in its internal features as well. The larval eye may be viewed as belonging to a generalized crustacean type, with a green reflecting pigment on its surface, colored oil droplets, and a single middle-wavelength rhodopsin (λ_{max} near 500 nm) with the main rhabdoms. Thus, crustacean larval photoreceptors functionally resemble rod photoreceptors of fish larvae, and, like them are probably

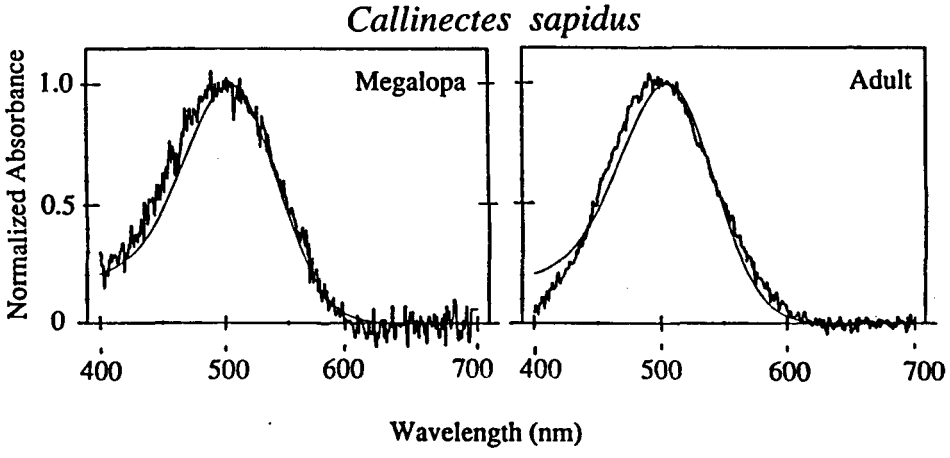

Figure 5 *Callinectes sapidus.* Normalized, average spectra for photobleaching of visual pigments of megalopa larvae (n = 6 bleaches, unfixed rhabdoms) and adults (n = 12 bleaches, lightly fixed rhabdoms; from Cronin and Forward (1988)). Average change in absorbance from 651 to 700 nm is set to 0 in each case. The jagged trace represents the average data, while the smooth trace represents a template spectrum of λ_{max} 504 nm.

specialized for maximum sensitivity in coastal or pelagic waters at twilight (see Munz and McFarland, 1977; Forward and Douglass, 1989). At metamorphosis, a new retina, with its own lamina and medulla externa, takes over and the remaining larval retina quickly degenerates. The new, juvenile retina is a miniature version of the adult's, with multiple photoreceptor classes, specialized 8th retinular cells, tiered photoreceptors, intrarhobdomal filters, and (probably) a new ensemble of visual pigments.

The change in visual pigment expression does not occur in the only other species we examined, a brachuryan crab, so generalizations are not possible. A reasonable working hypothesis is that as planktonic larvae, all crustaceans have a middle-wavelength rhodopsin throughout the retina. Adult crustaceans that possess only one rhodopsin class in their main rhabdoms will probably express the same rhodopsin as the larvae, but crustaceans with a diversity of visual pigments may have a special larval rhodopsin. This hypothesis will no doubt face critical testing in the next few years.

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