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# Crustacean Larvae – Vision in the Plankton

**Thomas W. Cronin[1,*],**
**Michael J. Bok[†],**
**and**
**Chan Lin[*]**

[*]Department of Biological Sciences
University of Maryland Baltimore County
Baltimore, MD 21250

[†]Department of Biology
Lund Vision Group
Lund University
223 62 Lund, Sweden

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[1]Email: cronin@umbc.edu

**Synopsis** We review the visual systems of crustacean larvae, concentrating on the compound eyes of decapod and stomatopod larvae as well as the functional and behavioral aspects of their vision. Larval compound eyes of these macrurans are all built on fundamentally the same optical plan, the transparent apposition eye, which is eminently suitable for modification into the abundantly diverse optical systems of the adults. Many of these eyes contain a layer of reflective structures overlying the retina that produces a counterilluminating eyeshine, so they are unique in being camouflaged both by their transparency and by their reflection of light spectrally similar to background light to conceal the opaque retina. Besides the pair of compound eyes, at least some crustacean larvae have a non-imaging photoreceptor system based on a naupliar eye and possibly other frontal eyes. Larval compound-eye photoreceptors send axons to a large and well-developed optic lobe consisting of a series of neuropils that are similar to those of adult crustaceans and insects, implying sophisticated analysis of visual stimuli. The visual system fosters a number of advanced and flexible behaviors that permit crustacean larvae to survive extended periods in the plankton and allows them to reach acceptable adult habitats, within which to metamorphose.

## Introduction

Marine crustacean larvae face challenging visual tasks in the plankton, quite different from those the adult must deal with. Typically much smaller than the subsequent adult, with tiny eyes and a far simpler nervous system, they nevertheless must succeed in finding food (generally animal prey), avoiding predators, and finding an appropriate environment in which to metamorphose and settle into successful adult lives. This demands effective vision coupled to a high-functioning neural analytical system to generate sophisticated responses to visual stimuli. The challenges are particularly severe if adults transition from the pelagic larval habitat to a benthic one. Such a change not only introduces new tasks very unlike those of the larva, but frequently it also offers very different lighting conditions and visual scenes. Of course, adult crustaceans have famously complex behavior, sometimes involving sophisticated means of locating, recognizing, and – on occasion ambushing – their food, as well as very elaborate mating displays and associated mating behavior.

Vision in crustacean larvae has not been reviewed for some time (e.g. Cronin et al.1995; Cronin and Jinks 2001), so the time is ripe for another look at this question. Marine crustaceans are taxonomically diverse, with equally variant eye designs (Cronin 1986; Cronin and Porter 2008; Fincham 1980; Land 1984), but unfortunately the larval eye designs are not described for all taxa. Certainly, the most elaborate eyes are the compound eyes of larval barnacles (at least, in the cyprid stage; Hallberg and Elofsson 1983), euphausiids, decapods, and stomatopods. Here we will restrict the discussion primarily to the compound eyes of decapod and stomatopod crustacean larvae. They are the most elaborate types and have been most investigated. Our review will cover the structure and optics of these eyes as well as their neuroanatomy and functional roles in larval life.

## Crustacean larval eye structure and optics

In their overall features, larval compound eyes of euphausiids, decapods, and stomatopods (as well as the eyes of juvenile mysids, which lack a larval stage) are remarkably similar despite the enormous diversity of adult types into which they develop. Nilsson (1983) and Nilsson et al. (1986) showed that the relatively simple optical system typical of such larval eyes is essentially preadapted for remodeling into the full diversity of adult eye designs (see Cronin 1986; Cronin and Porter 2008). Larval eyes consist of a nearly spherical array of ommatidia with a compact retina, visible due to its dark screening pigment, in the center of the sphere. The number of ommatidia varies with developmental stage and species, reaching several hundred in late-stage larvae of many species. Each photoreceptive rhabdom receives light that has entered through the single optical system of the same ommatidium, so the eyes are of apposition compound design. However, because the retina is so compact, most of the eye consists of the essentially transparent outer corneal layer overlying the equally clear crystalline cones. Consequently, in Nilsson's classification system nearly all larval compound eyes are termed "transparent apposition eyes" (Nilsson 1989, 1996). As the name implies, the eyes are virtually transparent, a critical advantage to larvae that increases their invisibility in the featureless illumination of their pelagic environments (Nilsson 1996). But they still have the black nodule of their miniscule retinas to contend with (Fig. 1D,G), and larvae use special means to conceal even this.

Since each rhabdom in a transparent apposition eye is ideally stimulated by light entering only a single facet, it must be shielded from off-axis light entering through other facets. Similarly, it must be protected from light entering the eye from other locations and from light scattered within the retina itself or shed by other rhabdoms. Hence, the photoreceptors of each ommatidium are usually wrapped with a coating of black screening pigment. In a few species,

some of the screening pigment may be yellow (Jutte et al. 1998), since this absorbs the blue light that stimulates those species' photopigments. The pigment screen is easily visible when the larva is backlit (as in Fig. 1D). However, in the open sea the larva is usually seen against a background of scattered spacelight while being simultaneously illuminated by downwelling light from other directions. Larval eyes frequently contain a layer of structures overlying the photoreceptor layer that effectively reflect and scatter this downwelling light, creating a blue, green, or gold eyeshine at the location of the retina (Feller and Cronin 2014; Jutte et al. 1998). This is easily seen in Fig. 1C,F, and G as a patch of bright color in the center of the eye.

The eyeshine has the potential to replace the light that was absorbed by the retina, reducing its visibility against the background light. Feller and Cronin (2014) investigated this possibility using several approaches. Larvae were examined in the underwater environment by being mounted on very fine rods and photographed from the full hemisphere of view below them against natural background light. Analysis of the resulting photographs made it clear that larval eyeshine decreased retinal contrast very effectively, on average by more than 75%. Significantly, the spectral properties of the eyeshine were also measured and found to be similar to those of the background, nullifying the potential for detection of the larvae using any spectral offset (Feller and Cronin 2014). Uniquely, therefore, crustacean larvae may combine overall transparency with controlled reflection of light from the retinal center of the eyes to make themselves in essence perfectly invisible in an open, three-dimensional world that literally offers nowhere to hide.

## Visual pigments of crustacean larvae

Individual rhabdoms in crustacean larval retinas can be examined for their visual pigment

content by standard methods of microspectrophotometry. Somewhat surprisingly, only two decapod species, both crabs, have so far had their larval visual pigments described. The megalopa (the postlarval stage, which follows several zoeal stages) was examined in the estuarine species *Callinectes sapidus* (Cronin and Jinks 2001). The postlarval visual pigment had identical spectral absorption to the adult's, with a spectral maximum ($\lambda_{max}$) at 504 nm. This is not much of a surprise, since the megalopa settles in waters that will subsequently be occupied by the adult, and one would expect its vision to be similar. It would be interesting to know if the preceding zoeal stages differ from the later megalopa, since they inhabit coastal pelagic waters, which are generally clearer and bluer than the estuarine waters favored by megalopae and adult blue crabs. Fortunately, the visual pigments of several life stages are known in the other, far more exotic, decapod species: the hydrothermal vent crab *Bythograea thermydron*. Here, visual pigment descriptions exist for a zoeal stage, the megalopa, and the adult (Jinks et al. 2002). Zoea larvae are pelagic, and while their living depths are unknown, their visual pigment has a $\lambda_{max}$ at 447 nm, not unreasonable for a creature inhabiting moderate depths in clear oceanic waters. Adults of the same species inhabit hydrothermal vents. Their very simplified compound eyes have a "naked retina" with no optics to speak of and a disorganized sheet of hypertrophied rhabdoms (Jinks et al. 2002). The visual pigment peaks at 489 nm, which could be adaptive for viewing the light emitted from hot-water vents (Van Dover et al. 1989). The megalopa, transitional between zoea and adult, is thought to descend through the water column and attempt to locate vent sites near which to metamorphose; its rhodopsin peaks at 479 nm, between the zoeal and adult maxima.

In contrast to decapods, absorbance spectra of the visual pigments of numerous larval stomatopod species are available (Cronin et al. 1995; Cronin and Jinks 2001; Feller and Cronin

2016; Feller et al. 2015; Jutte et al. 1998). Stomatopod adults have a superabundance of visual pigments – up to sixteen photoreceptor classes may exist in a single highly complex retina (Bok et al. 2014, 2015; Cronin et al. 1993, 2014; Cronin and Marshall 2004). Of course, with their much simpler eyes, larvae would be expected to have only a single photoreceptor class in main rhabdoms. Indeed, this has been the consistent finding.

Feller and Cronin (2016) examined the question of adaptation of visual sensitivity to environment by comparing the visual pigments of a diverse selection of stomatopod larvae, all collected in clear nearshore waters off Lizard Island Research Station near Australia's Great Barrier Reef (Fig. 2). Somewhat unexpectedly, considering that they were all from the same location, there was considerable variation in their spectral absorbance, with $\lambda_{max}$ ranging from 439 to 504 nm. There were two rather distinct spectral ranges of visual pigment absorbances, one with peaks near 450 nm and the second near to 500 nm (Fig. 2). In fact, the shorter-wavelength results were mainly obtained from larvae that were collected while still in early zoeal stages (stomatopods may pass through 11 or more stages before metamorphosing to the juvenile), but the 500-nm group mostly reflected larvae obtained just prior to metamorphosis. At this point, it is unknown whether this reflects an ontogeny of visual sensitivity within only the zoeal sequence, or some other cause of variation in visual pigment spectral placement. It is noteworthy that larvae of *Squilla empusa*, collected in greener estuarine waters in North Carolina, USA, had visual pigments with the longest-wavelength $\lambda_{max}$ yet measured, 509 nm (Fig. 2, Cronin and Jinks 2001). Another significant finding is that, in general, larval visual absorbance spectra do not correspond to any of the members of the diverse assortment in the subsequent adult, a strong indication that there is a subset of specialized larval pigments (see Table 1 in Feller and Cronin 2016).

Visual pigments throughout animals are based on a genome-encoded opsin protein coupled to a retinoid chromophore. In adult stomatopods, the chromophore appears always to be retinal$_1$ (Goldsmith and Cronin 1993), so any diversity in $\lambda_{max}$ is solely effected by changes in the sequence of the opsin. Given their complex photoreceptor sets, many opsins should be expressed in adult stomatopod retinas – up to perhaps 16 different ones. In actuality, though, the expressed number of opsins far exceeds this number, reaching possibly several dozen different sequences (Porter et al. 2009, 2013). While the explanation of this extreme overduplication is unclear, it would be helpful to know (a) if any of these adult types are expressed in the larval retina within the same species, and (b) whether or not there is more than one larval opsin expressed. These questions are only beginning to be addressed, but preliminary results suggest that at least some opsins are apparently restricted to larval stages and that there may be many opsins coexpressed in larval retinas, to some extent mirroring the adult situation (M.L. Porter, personal communication). It will be very interesting to see how this story develops.

In stomatopods, but not decapods, one reason that the larvae might have a distinct opsin set is that the larval retina is not remodeled into the adult type. Instead, an entirely new adult-type ommatidial array, including a separate retina, develops adjacent to the larval retina in the later zoeal larval stages (Cronin et al. 1995; Feller et al. 2015; Williams et al. 1985). In contrast to the simple, spherical array of rhabdoms in larvae, the developing adult retina has the full midband structure with accompanying intrarhabdomal filters (Cronin et al. 1995, 2014) and an overlying optical set containing adult-type ultraviolet filters (Bok et al. 2014, 2015). The adult retina is visible in final-stage *Lysiosquillina maculata* larvae (Fig. 1C) as a reddish mass anterior to the larval retina, revealed by its eyeshine, and in the last-stage *Squilla empusa* larva (Fig. 1F) as a dim grayish region also anterior to the eyeshine of the larval retina. This new retina

becomes photosensitive while still in its early appearance (Feller et al. 2015). Following metamorphosis it rapidly displaces the larval retina, which subsequently degenerates. Another fascinating feature of this developmental sequence is that the adult retina is associated with a novel sequence of visual neuropils that will also replace the larval set. This is described in the next section of the paper.

Setting aside stomatopods, in mysids, euphausiids, and decapods the adult retina continues as an expansion of the larval ommatidial set (see Cronin and Jinks 2001 for a brief review). This does not preclude the expression of successive sets of visual proteins (including opsins), and this research question deserves attention using both molecular genetic and spectral approaches. The sequence of visual pigments seen in the developmental stages of *B. thermydron* (Jinks et al. 2002) hints that visual pigment replacement could be fairly common, at least in decapods.

## Structure and development of the optic lobes of crustacean larvae

Beneath the crustacean larval and adult compound eyes, visual information from photoreceptor cells is relayed to the central brain through a series of visual neuropils in the optic lobes. In crustaceans, these optic lobes are generally present within the eyestalks, and in larvae can sometimes be visualized through the transparent cuticle (Fig. 1F). Fossil records and neural cladistic analyses resolve an ancestral pancrustacean ground pattern consisting of four visual neuropils that typify the optic lobe organization of extant malacostracan crustaceans and adult insects (Ma et al. 2012; Strausfeld and Andrew 2011; Strausfeld et al. 2016). These include the lamina (also termed the lamina ganglionaris), medulla (medulla externa), lobula (medulla interna), and lobula plate (visual tectum). Each neuropil is organized into small columnar

subunits, each of which receives inputs from neurons that are associated with a single ommatidium in the eye. Thus, a retinotopic arrangement is preserved throughout the optic lobe. In addition, two axonal chiasmata exist in the anteroposterior plane (Fig. 3C,E, and F), one between the lamina and medulla and the other between the medulla and lobula, whereas the lobula plate receives uncrossed axons from the medulla and lobula (Strausfeld 2005).

The pattern of neurogenesis and visual neuropil formation has been studied in several decopod crustaceans (Harzsch et al. 1999; Harzsch and Dawirs 1996). From embryonic through larval into adult stages, three band-shaped proliferation zones (PZ1-3) were constantly found to give rise to the new addition of ommatidia (PZ1), lamina and medulla (PZ2), and lobula and lobula plate (PZ3 and possibly other scattered neuroblasts in lateral protocerebrum). This continuous adding process in decapods is consistent with what is seen in hemimetaboulous insects (Anderson 1978; Harzsch et al. 1999; Harzsch and Dawirs 1996). The larval-megalopal-adult metamorphoses typical of marine decapods do not appear to greatly alter the general organization of their optic lobes (Fig. 3A-C).

In stomatopods, however, the formation of adult compound eyes and visual neuropils follows a distinctly different developmental scheme. During the pelagic larval stages, each larval optic lobe is equipped with a deeply curved medulla and a pronounced lobula beneath the lamina (Fig. 3D). The lobula plate is diminutive, a situation that is seen in many malacostracans (Strausfeld 2005). As noted earlier, terminal-stage stomatopod larvae are equipped with unusual double-retina eyes (Fig. 1 C,F), and beneath those eyes, an entirely new set of adult visual neuropils, including a new adult lamina, medulla, and lobula, develops adjacent to the larval ones (Fig. 3E,F). After larval-adult metamorphosis, the larval eye and its visual neuropils completely degenerate and are replaced by the adult system. This transition is comparable to what occurs in

holometabolous insects, where the adult compound eyes and the four underlying visual neuropils form *de novo* from specialized eye-antennal imaginal discs and replace the larval visual system after metamorphosis (Fischbach and Hiesinger 2008; Lin and Strausfeld 2013; Sbita et al. 2007).

## Larval naupliar eyes

In addition to the compound eyes, most (perhaps all) crustacean larvae have frontal eyes, often joined in a group of three to build a medial naupliar eye. The transparent cuticles of these larvae, and particularly of stomatopod zoea larvae, make these eyes very easily visualized on the ventral surface of the anterior brain (Fig. 1F). Crustaceans commonly have various configurations of frontal eyes in this region centered around an ocellus composed of three pigment cup photoreceptors, termed the tripartite or naupliar eye, and with their axons projecting to the protocerebrum (reviewed in Elofsson 2006; see also Fischer and Scholtz 2010). These relatively simple photoreceptive organs are probably involved in orientation or other rudimentary visual tasks, and may also be important in circadian timing. For instance, a pigmented, medial frontal naupliar eye stands out in terminal-stage larvae of the squilloid stomatopod *Alima pacifica* (Fig. 5A). Viewed in coronal section, the frontal eye of *A. pacifica* is located ventrally in a projecting cuticular structure known as the "bec ocellaire", below the rostrum and anterior to the dorsal margin of the brain (Fig. 4B). This positioning is consistent with that seen in other malacostracan crustaceans (Elofsson 1965).

When viewed in the transmission electron microscope, ultra-thin (50-70 nm) coronal and horizontal sections of the *A. pacifica* frontal eye reveal that it is indeed composed of three pigment cup cells, into which several rhabdomeric photoreceptors project microvilli (Figs. 4C,D). Two of the pigment cup ocelli face laterally while the third is directed dorsally. This is

consistent with the broad structural features of frontal eyes previously reported in the larvae of *Lysiosquilla occulta* and *Squilla mantis* (Jacques 1976). The naupliar eye persists into adulthood in stomatopods and has been examined in detail in *Squilla mantis, Pseudosquilla ciliata*, and *Neogonodactylus oerstedii* (Elofsson (1965). Since most crustacean adults possess up to seven frontal eyes, it will be interesting to discover whether or not additional, less conspicuous frontal eye types are associated with the tripartite naupliar eye. Learning the details of the fine structure and neural innervation of the frontal photoreceptive organs in larvae of stomatopod and decapod crustaceans, their photoreceptor and visual pigment complements, and their functions awaits further research.

## Functions of larval visual systems

Larval crustaceans are highly adapted to their habitats – they are not just simple versions of the adults hanging around in the plankton waiting to metamorphose. Nearly all marine invertebrates, as well as most marine fishes, begin life as larvae, though they are rare among freshwater members of the same taxa. Having a larval stage allows the adults to disperse their young to new, sometimes even ephemeral, habitats – a benefit that is particularly relevant to benthic marine crustaceans. These species frequently send larvae great distances in ocean currents along coasts and between estuaries, and in some cases their larvae even cross oceans (Scheltema 1975, 1988). Even when larvae are transported quite short distances, for example within a single estuary, their behavior governs their success in reaching appropriate habitats for settlement and metamorphosis (Cronin 1982). To succeed in (and just to survive) the very challenging tasks of navigating oceans, or even estuaries, crustacean larvae are blessed with abundant sensory and behavioral resources. As suggested by the presence of their elegant compound eyes, vision ranks among their most important senses (Cronin and Feller 2014).

One of the most important of larval behaviors is their ability to maintain an appropriate depth. Larvae are challenged by a series of predators, and their safest refuge is an environment that is dark enough to make visual predation difficult. An equally important task is to prevent themselves from being transported far from suitable habitats, or at least to have the ability to find their way to such habitats when ready to metamorphose. Larvae are expert long-distance travelers, using currents in the ocean, along shorelines, or within estuaries to ride to locations where they metamorphose (Cronin 1982; Epifanio and Garvine, 2001; Scheltema 1988). This requires depth choices that change over development, so regulation of depth is a primary responsibility of larval vision. Perhaps the most dramatic behavior under visual control is diel vertical migration (Forward 2009, Forward et al. 1984), a rhythmic sequence during which larvae swim to shallower waters during the night and retreat to depth during the day.

Anyone who has used a flashlight underwater, or even just shined a bright light beam into the ocean, knows that all sorts of plankton swim towards the light, often engulfing it in a cloud of tiny milling creatures. This positive phototaxis has been used to characterize spectral responses of larval crustaceans (Fig. 5A), and the general finding is that retinal visual pigment absorbance spectra predict phototactic sensitivity (Forward et al. 1984; Forward and Cronin 1979). Thus, one might wonder how positive phototaxis can possibly produce a migration pattern in which larvae descend during the brightly-lit day? The answer to this questions hinges on the structure of the light field creating the stimulus. Highly directional light, like a flashlight beam, evokes a photopositive behavior. Downwelling light underwater, on the other hand, is diffuse, with a characteristic broad angular light distribution. When light with this distribution is used in laboratory experiments, a normal diel migratory pattern can be evoked (Forward et al. 1984). During larval transport, the photoresponses that govern this pattern are continuously modified by

internal developmental and nutritional changes within larvae as well as by environmental changes in salinity, temperature, turbulence, and probably many other local stimuli that affect vertical position-keeping via negative-feedback mechanisms (Cronin 1982; Forward 2009). Light exerts a secondary influence on vertical migration behavior by regulating the timing of endogenous rhythms of migratory swimming (Cronin and Forward 1979, 1983), possibly via frontal eye photoreceptors.

Vertical migration furthers larval transport and is a passive mechanism for avoiding visual predators, but crustacean larvae also have active photoresponses for predator evasion. In particular there is the shadow response, a rapid induction of negative phototaxis by an incremental decrease in light intensity. Such a stimulus would be created by the overhead presence of a fish or even a gelatinous predator (Forward 1977). Ctenophores in particular exert heavy predation pressure on larvae; despite their transparency, they produce a decrease in irradiance beneath them sufficient to produce a full-blown shadow response. Shadow responses are enhanced by the presence of chemicals characteristic of predators (called kairomones), exemplified by the exudates of ctenophores (Fig. 5B) or mucus from fish (Cohen and Forward 2003; Charpentier and Cohen 2015). In fact, the presence of chemicals produced by fish directly alters visual structure and sensitivity in the eye of some larval crab species, further amplifying their tendency to produce shadow responses (Charpentier and Cohen 2015).

Larval visual responses, doubtless in combination with responses to many other stimuli such as chemical mixtures, not only bring larvae to habitats suitable for metamorphosis - in some cases they even dictate larval settlement choices. Barnacles in their settlement stage, the cyprid larva, have a pair of rather simple compound eyes with no more than a dozen ommatidia (Hallberg and Elofsson 1983). Both the planktonic earlier larval stages and the sessile, benthic

adults have much simpler naupliar eyes, so the presence of this relatively advanced eye in only the cyprid suggests a role in settlement behavior. Indeed, Matsumura and Qian (2014) reported that cyprid larvae of the barnacle *Balanus amphitrite* use red fluorescence from adult barnacle shells as a cue to recognize a proper settling substrate, choosing to settle on red surfaces over other colors. The brightness of the substrate does not appear to affect their settlement choice, implying that they are relying on a barnacle-specific spectral emittance to guide their choices. A role for vision in settlement has not been investigated in other crustacean larvae, however.

Somewhat surprisingly, even though vision is implicated in larval responses that avoid predation, select appropriate transport mechanisms, and even choose settlement habitats, there is currently no established role of vision in larval feeding behavior. Larvae do feed more effectively during the day than at night (Cronin and Forward 1980), though this does not prove that they are feeding visually. All crustacean larvae with compound eyes have the full neural complement of analytical networks associated with their retinas, as was discussed earlier. In Fig. 1F it can be seen that the visual neuropils within a single eyestalk can be larger in volume than the central brain (cerebral ganglion) below them, certainly implying excellent visual capabilities. Furthermore, the compound eyes of this stomatopod larva are placed at the ends of long stalks. All this is circumstantial evidence that form vision is very important to at least some crustacean larvae, and that it probably is involved in larval predatory behavior. It seems that crustacean larvae are competent, flexible little beings, with an array of visual behaviors scarcely inferior to those of the adults they are destined to become.

## Summary and conclusions

Throughout this review, we have emphasized the truly wonderful sophistication of the visual

systems of many crustacean larvae. Their miniscule compound eyes are served by a well-developed series of neuronal processing centers that can actually be larger in volume than the cerebral ganglion (central brain), and the eyes have exotic optical components to reduce their visibility in natural waters. Larvae of different species have diverse visual pigments in the photoreceptive rhabdoms of their compound eyes, and there is some evidence that the pigments can change over development – even in species where the adults have only a single middle-wavelength class of photoreceptors. In stomatopods, the larval visual pigments are apparently distinct from any of those in the famously complex eyes of adults of the same species. Stomatopods also have a unique and very unusual developmental sequence in which the entire visual system within the compound eye moves over to a retina served by a new set of visual neuropils at the time of metamorphosis. How this entirely new neural system becomes functionally integrated into the central analysis of vision is difficult to understand.

Crustacean larvae may develop quickly, minimally within just a few days, or they may persist in the plankton for extended periods. Larvae of some species are found in plankton tows made in the open ocean, far from the habitats where any source population could exist. These events suggest that some species may have larval lives of many weeks, or even months, and that larvae may even travel between continents (or even oceans). Adults of at least one stomatopod species, *Gonodactylaceus falcatus*, have been collected in the Red Sea, in the Indopacific, and in waters of the Hawaiian archipelago. The vent crab, *Bythograea thermydron*, exists along the vents of the East Pacific Rise and the Galapagos Rift, a distribution made possible only by larval dispersal among isolated sites. Living for long durations in the plankton demands effective survival abilities, including high-quality visual adaptations and sophisticated behavior that includes responses to a variety of visual inputs. Larval behavior is complicated and

flexible, demonstrating the quality of their vision. It is important to remember that crustacean larvae can be quite large, even exceeding the sizes of many adult insects and with commensurately large nervous systems, so they could well have sensory abilities rivaling those of adult arthropods.

Besides their compound eyes, crustacean larvae have frontal eyes including at a minimum a ventral naupliar eye. The behavioral role of this sensor, and its integration into the central nervous system, are still being worked out. Another area of intense interest is the nature of the visual pigments of both the compound eyes and the frontal eyes, and their changes with development. The basics of larval predator-avoidance behavior is understood (at least in the case of shadow responses), but how vision plays a role in complex activities such as prey capture remains unknown. The truly fearsome prey-capture appendages of stomatopod larvae (see Fig. 1A) would appear to demand visual control for their effective use, for instance. At present, we are just beginning to appreciate just how fascinating these creatures can be.

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## Figure Captions

**Figure 1.** Examples of crustacean larvae, showing their eyes. A) Scanning electron micrograph of a late-stage larva of the stomatopod *Odontodactylus brevirostris*. Note the well-developed compound eye and the large and very impressive raptorial appendages hanging below the body. The larva is about 5 mm long. B) Newly-hatched larva of the stomatopod *Lysiosquillina maculata* next to the eyes of the adult of the same species. Each miniature larval eye will metamorphose and grow into an adult eye, typically about 1 cm tall. These early larvae are about 1.5 mm long. (Photo by R.L. Caldwell). C) Terminal larval stage of *L. maculata*, showing the double retina in each of the compound eyes (the larval retina is the shiny gold region). Note the change in size and form from the first-stage larva in B. This animal is about 2 cm in overall length. (Photo by R.L. Caldwell). D) Third-stage zoea of the crab *Rhithropanopeus harrisii*. Note the obvious contrast of the dark retina against the directional beam of the microscope lamp, a situation in which eyeshine is not produced. The larva is about 4 mm long from tip of rostral spine to tip of abdomen. E) Scanning electron micrograph of the zoea larva of an unknown crab species. The compound eye is ~200 μm in diameter. F) A ventral view of a final-stage larva (zoea IX) of *Squilla empusa*, showing the long stalked eyes, the visual neuropils visible through the eyestalks, the double retinas (the greenish shiny region is the larval retina), and the larval brain. The arrow indicates the frontal (naupliar) eye. The two compound eyes are separated by ~5 mm. G) Eye of an early-stage larva of *Chorisquilla sp*., lit with incident light to show its blue eyeshine.

**Figure 2.** Wavelengths of maximum absorbance of visual pigments in single rhabdoms of various species of larval stomatopods collected near Lizard Island, Australia (data from *Squilla*

*empusa*, marked with an asterisk, were taken from larvae collected at the Duke Marine Laboratory, North Carolina). Each point is a measurement from a single rhabdom; each median is indicated by a single line, with the outlining box showing the interquartile range. Circled points indicate outliers. Modified from Feller and Cronin (2016).

**Figure 3.** Osmium-ethyl gallate stained preparations showing the optic lobe organization of the larval brachyuran decapod *Dyspanopeus sayi* (A-C) and of stomatopods *Pullosquilla* sp. (D) and *Alima pacifica* (E, F). In the decapod optic lobe, visual neuropils including the lamina (La), medulla (Me), and lobula (Lo) are not subject to drastic modification between zoeal (A), megalopal (B, C) and adult stages. D) In early-stage *Pullosquilla* larval optic lobes, the medulla (Me) is deeply curved, and this image shows its dorsal and ventral components above a pronounced lobula (Lo). E, F) Two successive sagittal sections of a terminal larval stage *A. pacifica* showing the double-retina eye (LrRt and AdRt) containing an entirely new set of adult visual neuropils, including the new adult lamina (AdLa), medulla (AdMe), and lobula (AdLo) developing adjacent to the larval lamina (LrLa), medulla (LrMe), and lobula (LrLo). The lobula plate neuropil is diminutive in these species and is not shown here. A, B, D are frontal sections and C, E, F are sagittal sections. Axonal chiasmata (arrows) can be seen in images in the sagittal sectioning plane. All scale bars indicate 100 μm.

**Figure 4.** Frontal (naupliar) eye of terminal stage *Alima pacifica* larvae. A) Pigmented naupliar eye of *A. pacifica* viewed through the ventral surface of the head. B) Coronal thin section (2 μm) through the head of an *A. pacifica* larva. C) Transmission electron micrograph of a coronal section through the frontal eye (TEM was carried out according to the protocol published in Bok

et al. 2016). D) Diagrammatic representation of a coronal section through the tripartite frontal eye. Scale bars: B, 50 μm; C, 10 μm.

**Figure 5.** A) Phototaxis of early-stage larvae of the crab *Rhithropanopeus harrisii* to various wavelengths of light, showing spectral sensitivity peaks at 500 nm and ~400 nm. B) Descent behavior by these larvae (both negative phototaxis and passive sinking) when stimulated by decreases in light intensity of the percentages indicated. Note that when in water containing exudates of ctenophores, the behavior is initiated with much small decrements in light intensity. Modified from Forward (2009).