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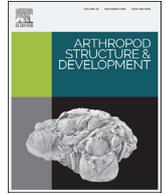
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Review article

Visual metamorphoses in insects and malacostracans: Transitions between an aquatic and terrestrial life

Alice Chou ^{a,*}, Chan Lin ^{a,b}, Thomas W. Cronin ^a^a Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250, USA^b Department of Invertebrate Zoology, Smithsonian National Museum of Natural History, Washington, DC, 20560, USA

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ABSTRACT

Arthropods operate in an outrageous diversity of environments. From the deep sea to dense tropical forests, to wide open arctic tundra, they have colonized almost every possible habitat. Within these environments, the presence of light is nearly ubiquitous, varying in intensity, wavelength, and polarization. Light provides critical information about the environment, such as time of day or where food sources may be located. Animals take advantage of this prevalent and informative cue to make behavioral choices. However, the types of choices animals face depend greatly on their environments and needs at any given time. In particular, animals that undergo metamorphosis, with arthropods being the prime example, experience dramatic changes in both behavior and ecology, which in turn may require altering the structure and function of sensory systems such as vision. Amphibiotic organisms maintain aquatic lifestyles as juveniles before transitioning to terrestrial lifestyles as adults. However, light behaves differently in water than in air, resulting in distinct aquatic and terrestrial optical environments. Visual changes in response to these optical differences can occur on multiple levels, from corneal structure down to neural organization. In this review, we summarize examples of alterations in the visual systems of amphibiotic larval and adult insects and malacostracan crustaceans, specifically those attributed to environmental differences between metamorphic phases.

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1. Introduction

The value of vision for mobile animals cannot be understated, as it allows them to detect objects and navigate in complex environments. The majority of natural light on earth originates from the sun. Despite this singular source, optical environments vary significantly on both temporal and spatial scales (Cronin et al., 2014). Beyond providing information about the cyclical temporal events of night and day, light cues also inform organisms about surrounding conspecifics and other animals, location, and motion.

Throughout their life histories, animals can exist in diverse habitats, each with its own photic properties. How are visual systems adapted to these different environments? How do they cope with environmental variations? In particular, arthropods that metamorphose are under intense selective pressure, favoring sensory systems that can accommodate their dramatic alterations in behavior and ecology. This is especially true for amphibiotic arthropods, who spend consecutive life stages in water and air, places

in which light behaves very differently. Visual systems that were once dedicated to larval behavior must either be replaced or modified to allow for a successful adult existence. What levels of visual remodeling occur in arthropods that metamorphose between aquatic and terrestrial lifestyles? These questions have broad implications for understanding sensory adaptations, as well as eye evolution and development.

Although vision research on different stages of development in any single species is relatively scarce, existing studies confirm many fascinating transitions between different eye types within individual organisms and thus encoded in single genomes. In this paper, we discuss literature on aerial and aquatic visual adaptations in amphibiotic insects and crustaceans in order of increasing complexity: from optical anatomy, to functional changes in polarization, spatial and spectral vision, and ultimately to the neural centers where visual information is processed.

2. Light, photoreception, and eyes

Light interacts with the environment both as particles and as waves. It may be absorbed, reflected, refracted, or scattered (Johnsen, 2012). Each particle, or photon, is characterized by its

* Corresponding author.

E-mail address: achou2@umbc.edu (A. Chou).

wavelength (λ); for vision, the relevant wavelengths range from the UV (~350 nm) to the far red (750 nm). When viewing an object underwater, one can expect contrast to be significantly reduced compared to viewing the same object in the air. This is because light is filtered and attenuated in water due to absorption by water molecules and/or dissolved organic materials and to scattering from suspended particles. The absorption of light is wavelength-dependent, resulting in varying spectral distribution across depths and types of water. For example, oceanic waters are often a deep blue, whereas freshwater bodies tend to be yellowish. Furthermore, the surface of water in nature is rarely perfectly calm. Surface disturbances can introduce inconsistent, flickering illumination that adds an element of unpredictability for visually guided aquatic animals (Cronin et al., 2014).

Fundamentally, photoreception occurs when a photon is absorbed by a visual pigment molecule (which is comprised of an opsin protein and a chromophore) in a specialized cell (a photoreceptor). The activated visual pigment then triggers a downstream avalanche of molecular signals which ultimately results in neural signals that leave the eye and are relayed to higher order visual processing center (Yau and Hardie, 2009). However, the sense of vision is vastly more complex than this biochemical cascade and is adapted in part by the designs of the visual organs in which the photoreceptors usually exist.

In general, three different types of photoreceptive organs are involved in vision in arthropods, with individuals possessing one or two types at any given time. The most conspicuous and widespread of the three is the pair of paired, multifaceted compound eyes (Fig. 1) (Cronin, 1986). Each facet of a compound eye is the surface of a single optical unit called an ommatidium. A

single ommatidium is comprised of an optical structure, usually consisting of a corneal lens and a crystalline cone, atop a bundle of photoreceptor cells surrounded by pigment cells. Visual pigments function in a microvillar region of the photoreceptor, called the rhabdomere. Together, the rhabdomeres within a single ommatidium form the photosensitive rhabdom. Compound eyes are divided into several subtypes, with the apposition type being the simplest. In apposition eyes, a single facet provides light only to a single rhabdom, whereas in superposition eyes a rhabdom may receive light from many hundreds of corneal lenses (Horridge, 1972; Exner, 1989; Nilsson, 1989; Cronin et al., 2014).

The two other kinds of visual organs found in many insects and malacostracans are ocelli and stemmata, both of which only contain a single focusing element (as opposed to the many facets of compound eyes). Most often found in triplicate, ocelli are located dorsally on the head of many adult insects (Goodman, 1981). Although they are underfocused and do not likely form detailed images, ocelli can provide basic information about changes in light intensity or polarization, which contributes to sophisticated functions like maintaining flight stability or detection of horizontal features like the horizon (Stange and Howard, 1979; Stange, 1981; Taylor, 1981; Stange et al., 2002; Berry et al., 2007). On the other hand, stemmata are simple eyes clustered on the side of holometabolous (see next section) insect larval heads that possess similar cellular organization to single ommatidia of compound eyes. Their many variations and functions, including color and motion vision, are beyond the scope of this review (Gilbert, 1994; Buschbeck, 2014). Due to the depth and breadth of the literature available, we will focus primarily on compound eyes and the metamorphic changes they may undergo.

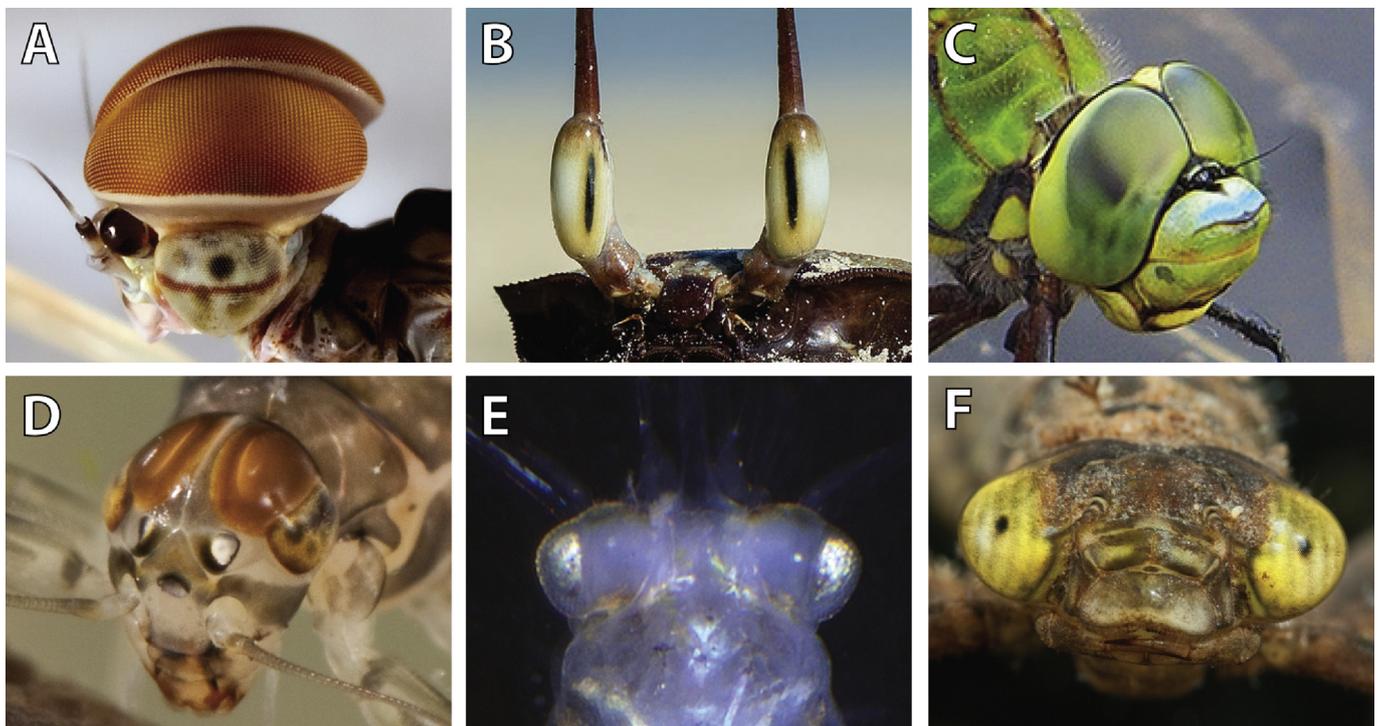


Fig. 1. Compound eyes of adult (A–C) and juvenile (D–F) amphibiotic arthropods. (A, D) The eyes of male mayflies in the family Baetidae. Adult males possess a second tubular pair of compound eyes that are oriented dorsally for overhead detection of female conspecifics. These specialized eyes begin developing in nymphal stages (Zimmer, 1897). (B, E) Adult eyes of the ghost crab *Ocypode ceratophthalma* and typical larval crustacean compound eyes, shown here in the larval mud crab *Dyspanopeus sayi*. Adult crabs are terrestrial, inhabiting flat habitats such as beaches or mud flats, and possess stalked eyes with regions of high vertical acuity, whereas their larvae possess the apposition compound eyes common to most marine crustacean larvae (see text) (Zeil et al., 1986; Cronin and Jinks, 2001). (C, F) The eyes of Aeschnid dragonfly adults and nymphs. In every case, the adult is aerial, whereas the larvae are aquatic. Images adapted from David Reed (A), Jan Hamrsky (D, F) and Wikimedia Commons (B, C).

3. Arthropod metamorphoses

3.1. Insect metamorphosis

Metamorphosis has long captured curiosity as a stunning life history event in which animals go through dramatic transformations during development. The discrete life stages seen in metamorphic animals often occupy different ecological niches and possess effective adaptations to permit specific behaviors, such as feeding, dispersal, or reproduction. Caterpillars, for example, are a far cry from their elegant adult lepidopteran counterparts, but are perfectly adapted for feeding on foliage, while the subsequent adult will generally feed on flowers. Three categories of metamorphosis exist in insects. The ancestral trait is ametaboly, in which little or no difference is seen between juvenile and adult forms. While still common in basal insects, it is not considered in this review. However, the evolution of flight in the Devonian catalyzed the appearance of hemimetaboly, which then led to holometaboly (Belles, 2019).

Hemimetaboly, also known as incomplete metamorphosis, is a life history that includes three stages: egg, nymph, and adult. Nymphs, the immature stages of hemimetabolous species, generally resemble wingless adults and often live in the same habitats as adults (Truman, 2019). However, insects in the orders Odonata (dragonflies and damselflies) and Ephemeroptera (mayflies) are exceptions. They are the sole living orders of Palaeoptera, an ancestral group of winged insects that is sister to the more recent Neoptera (Hovmöller, 2002). Unlike the majority of hemimetabolous insects known today, the nymphal stages are very distinct from the adults and live in aquatic environments (Truman and Riddiford, 2002). Due to the visual prowess of many adult hemimetabolous insects, odonates in particular, they are subjects of great interest to visual ecologists. Nymphs hatch with well-developed compound eyes, and some species add anterior ommatidial rows as they develop (Fig. 1) (Lerum, 1968; Liu and Friedrich, 2004). In some extreme cases of visual adaptations, such as in aeschnid dragonflies, entire regions of the adult compound eyes are generated during the final transition from nymph to full maturity (Sakamoto et al., 1998).

First seen in the Permian, holometabolous insects form a monophyletic group whose development is characterized by the presence of a larval stage with little to no resemblance to the adult form and an essentially immobile, non-feeding transitional stage known as the pupa (Wheeler, 2001; Truman, 2019). This developmental innovation enables adults and larvae to specialize in different adaptive behaviors, and to exploit different habitats and food sources. As briefly described earlier, holometabolous insect larvae possess stemmata that are thought to be evolutionarily derived from compound eyes. Stemmatal diversity is vast, and ranges from severe reductions to sophisticated image-forming single-chamber eyes (Buschbeck, 2014).

The evolution of hemi- and holometaboly occurred after insects colonized terrestrial environments. However, several groups either retained aquatic larvae, like the palaeopterans described earlier, or made their way back to the water through secondary adaptations; although there is debate as to whether an aquatic lifestyle in larvae is ancestral (Pritchard et al., 1993; Toms, 2007; Lancaster and Downes, 2013). Ultimately, regardless of origin, morphological and behavioral changes require adjusting sensory capabilities to best serve biological needs. For amphibiotic animals, which transition between aquatic and terrestrial environments, the radical change in light environment and the

importance of vision to many species makes visual adaptations especially relevant.

3.2. Malacostracan crustacean development

Development in malacostracan crustaceans, the paraphyletic group from which insects are derived, is comparable to ametaboly or hemimetaboly in that the basic body plan is most commonly produced embryonically (Osorio et al., 1995; Giribet et al., 2001; Regier et al., 2005; Edgecombe, 2010; Schwentner et al., 2017). However, the immature stages of Crustacea often bear little or no resemblance to the mature stages. The number of immature stages, all of which will be referred to broadly here as larvae, varies widely among species and groups. Most malacostracan larvae are planktonic and spend a significant portion of those life stages in a mid-water environment. During that time, they engage in such visually directed tasks as eating, avoiding predators, and orientation behaviors such as diel vertical migration. After the planktonic stage, environmental cues stimulate settlement, molting, and a transition to a benthic or nektonic – and occasionally terrestrial – existence as juveniles and adults (Anger, 2006). Marine crustacean larvae generally share a common eye plan: a spherical, apposition type compound eye with a condensed retina (Fig. 1E) (Nilsson, 1983; Cronin and Jinks, 2001; Cronin et al., 2017).

Although most crustaceans are aquatic, several groups have evolved to become either semi-terrestrial or terrestrial as adults, emerging onto land after the final larval stage. Many of these amphibiotic crustaceans have developed aerial visual and olfactory systems (Greenaway, 2002; Hyatt, 1975, 1974; Krång et al., 2012; Ping et al., 2015; Stensmyr et al., 2005). Perhaps the most conspicuous and well-studied terrestrial crustaceans are the land crabs, especially those species that inhabit shorelines, marshes, or mangrove swamps. Interestingly, land crabs adapted to the terrestrial environment in two different ways, and can be functionally categorized by the pathway they took to land (Bliss, 1979). One group adapted straight from the sea, via the littoral zone. Notable examples include the families Ocypodidae, which includes fiddler crabs and ghost crabs, Grapsidae, the shore crabs, and Coenobitidae, comprised of the terrestrial hermit crabs and robber crabs. Other land crabs became terrestrial after their adaptation to freshwater via estuaries, such as some species in the superfamily Potamoidea. Due to limitations in osmotic regulation, freshwater land crabs usually complete development to a juvenile form of the adult within the egg—most species hatch from eggs as miniaturized adults (Anger, 1995; Lutz, 1969). Leaving the sea presents significant challenges in respiration, metabolism, and biomechanics, not to mention the numerous differences in photic environments like those detailed earlier in this review. Separate saltwater and freshwater trajectories to land may have even influenced eye design, but this intriguing hypothesis has, to the best of our knowledge, not yet been investigated.

4. Adaptive visual events in amphibiotic arthropods

4.1. Corneal nipple arrays

In air, light both reflects and refracts at the surface of eyes due to the change in refractive index. In vertebrate camera-type eyes, such as those of humans, reflections from the cornea are easily seen as Purkinje images. For arthropods, whose compound eyes have many facet lenses from which light can be reflected, this phenomenon can be severely detrimental. Not only is there a decreased total

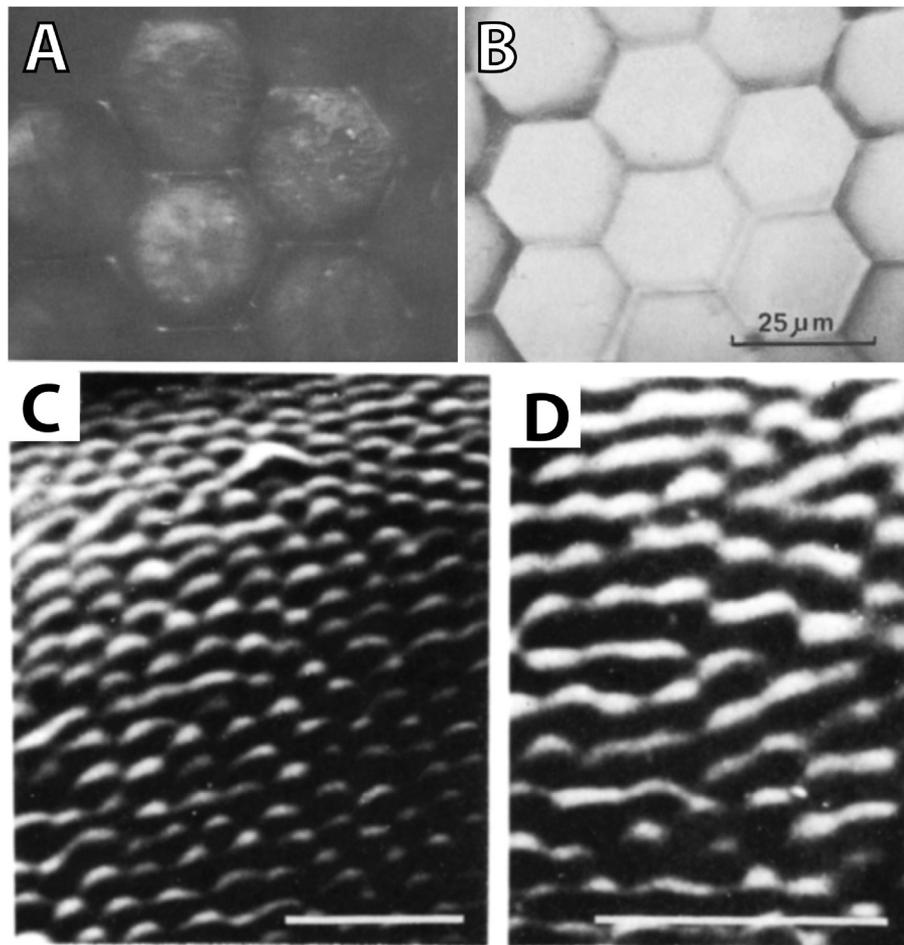


Fig. 2. Surface structure of eyes with and without corneal nipple arrays. (A,B) A comparison of light reflected from a moth eye surface (A) with corneal nipples and on a grasshopper eye surface (B) with no nipples and a smooth surface, adapted from Miller (1979). Scale bar applies to both (A) and (B). (C, D) Scanning electron microscopy of single facets in the central (C) and peripheral (D) compound eye regions of the mayfly *Cloeon* sp. Scale bars = 1 μ m. Adapted from Gupta et al. (1989).

amount of light that reaches the retina, but reflections may have negative impacts on animals for whom camouflage is essential (Johnsen, 2012). Much like a flashlight shining off a window at night, reflections can reveal the presence of something otherwise unseen.

First discovered in moths in 1962, corneal nipple arrays form a transitional optical surface between the surface of the eye and its surrounding medium (Bernhard and Miller, 1962; Miller, 1979). Similar nanoprotuberances have since been reported on the transparent wings of cicadas, butterflies, and moths, as well as on the appendages of deep sea amphipods (Yoshida et al., 1996; Siddique et al., 2015; Bagge et al., 2016; Morikawa et al., 2016). Eyes and other structures with nipple arrays are covered with a dense carpet of protuberances, usually about 150 nm–250 nm in length (Bernhard et al., 1970). These dimensions are shorter than the wavelengths of visible light, and result in a gradual change in refractive index that greatly reduces reflection (Fig. 2).

However, the refractive index of water (1.3) is distinctly greater than the refractive index of air (1.0), and thus is close to the refractive index of most corneas. This suggests that aerial insects might have more need for corneal nipple arrays than aquatic insects, as light is more likely to be reflected from eye surfaces in the air. Early studies in dragonflies found no corneal modifications between larval and adult eyes. Notably, the refractive index of both larval and adult dragonfly corneas is about 1.4. This value is

between that of fully terrestrial insects (1.3), such as Diptera and Hymenoptera, and that of the marine decapod crustaceans (1.5) (Goldsmith, 1964; Mazokhin-Porshniakov, 1969; Minelli and Pavan, 1974). In contrast, scanning electron microscopy studies reveal differences in corneal ultrastructure between developmental stages in the mayfly *Cloeon* sp. The penultimate pre-adult stage, the subimago, is terrestrial and was found to have nipples of varying lengths covering the external surface of the cornea (Fig. 2C, D). However, the facet surfaces of compound eyes in the aquatic early instars to mature nymphs are entirely smooth (Dey, 2007; Gupta et al., 1989).

Although the functional significance of this finding is unresolved, there are several possible explanations. Mayfly nymphs are important prey for a wide range of aquatic predators. They spend significant time on solid surfaces, such as submerged rocks and logs, where their corneal reflections would be similar to reflections from objects and surfaces in the surrounding environment, and thus not a salient signal for predators. Nipple arrays may simply not be ecologically relevant for mayfly nymphs. On the other hand, corneal nipple arrays offer a modicum of concealment for subimago mayflies during the yearly mass emergence. These visual adaptations would increase light transmission to adult retinas, likely allowing them to better spot potential mates or enemies (Brodskiy, 1973). Notably, nanoprotuberances have biological functions beyond enhancing vision. Ordered cuticular micro- and

nanostructures are strongly hydrophobic and have been demonstrated to have enhanced anti-wetting properties, an ability which would be meaningless and likely detrimental in an aquatic setting (Watson et al., 2017).

4.2. Polarization vision

Light from natural sources (e.g. the sun and moon) is unpolarized, meaning that the photons' electric field vectors (*e*-vectors) exist on randomized axes. However, if the *e*-vectors are oriented in a single plane, the light is considered polarized. Polarized light in nature is abundant and is most often created by the scattering of sunlight in air or water or by reflection from shiny surfaces, such as water surfaces or surfaces of plants and animals (Cronin and Marshall, 2011; Johnsen, 2012; Cronin et al., 2014). Most of it is partially polarized, meaning that some fraction of the photons are oriented in parallel; this fraction is referred to as the degree of polarization. In the air, Rayleigh scattering produces a distinctive and predictable band of polarized light across the sky that is most apparent at dawn and dusk.

Polarization sensitivity is useful for the execution of several complex behaviors, including detection of bodies of water in habitat-finding, intraspecific signaling between conspecifics, and navigation and orientation (Waterman, 1981; Horváth, 1995; Cronin et al., 2003a, 2003b; Kriska et al., 2009; Homberg et al., 2011; Dacke and Jundi, 2018). This ability to 'see' polarized light depends on the overall orientation of visual pigments in photoreceptors. Chromophores are dichroic; they are more likely to absorb photons with an *e*-vector parallel to their linear orientation. Because chromophore molecules are aligned with microvilli, the linear orientation of microvilli in rhabdoms allows individual photoreceptors to be intrinsically sensitive to light with certain *e*-vector orientations (Goldsmith and Wehner, 1977). Many insects actually remove this natural property by twisting their rhabdoms in order to better employ their color vision (Wehner and Bernard, 1993). Some insects, especially those who depend on the overhead sky polarization pattern to orient, restrict polarization vision to a dorsal rim area in compound eyes with specialized ommatidia for determining angle, degree, and intensity of polarization (Labhart and Meyer, 1999; Homberg et al., 2011).

In water, light during the day primarily arrives from overhead sunlight. Scattering by water molecules, dissolved organic matter, and suspended particles results in a significant decrease in contrast of the surrounding scenery. However, this light is predominantly polarized in the horizontal direction, so the use of a vertically-tuned polarization receptor in aquatic eyes can enhance object detection (Cronin et al., 2003b; Cronin and Marshall, 2011).

Unfortunately, studies on polarization vision in insect larvae, especially those which are aquatic, are limited. Whether or not all larvae even possess polarization vision is unclear, but polarotactic ability has been demonstrated in a diverse range of insect and crustacean larvae (Sullivan and Wellington, 1953; Meyer-Rochow, 1974; Doane and Leonard, 1975; Via and Forward, 1975; Waterman, 1981; Gilbert, 1994). Electrophysiological and anatomical studies in larval diving beetle eyes indicate high polarization sensitivity in multiple photoreceptors (Stowasser and Buschbeck, 2012). However, adult and nymphal dragonflies are the only amphibiotic insects shown to use polarization sensitivity for different functions in their respective habitats (Fig. 1C, F). Adult dragonflies, as well as other aerial insects like mayflies, use polarization vision in part to detect large bodies of water for mating and oviposition, to such a degree that they will maladaptively be attracted to road surfaces, cars, and oil slicks (Horváth et al., 1998; Kriska et al., 2009). Conversely, optomotor experiments suggest that larval odonates likely use polarization vision to improve visual

contrast in the water. When presented with naturalistic light fields scattering horizontally polarized light, nymphs track visual gratings more closely than they track the same gratings viewed through a non-polarized light-scattering field (Sharkey et al., 2015). Presumably, this ability serves the predacious nature of dragonfly nymphs by helping them to detect prey in turbid water.

Polarization vision is well described in many malacostracan crustaceans, including in terrestrial species such as fiddler crabs in the genus *Uca* (How et al., 2012). Although there are relatively few studies on terrestrial crustacean larvae, polarotactic ability has been documented in the larvae of the intertidal decapod *Rhithropanopeus harrisi* (Via and Forward, 1975). More studies are necessary to understand if and how polarization vision might change during terrestrial crustacean development.

4.3. Spatial vision

In addition to having adequate sensitivity, image-forming photoreception is characterized by the ability to resolve spatially defined features in the environment, or spatial vision. Spatial vision enables animals to determine directionality of light, and depends on the angular width of light that reaches each photosensitive unit, which in the case of compound eyes is an ommatidium (Land and Nilsson, 2002). Thus, the resolution with which an arthropod with apposition compound eyes sees is first and foremost determined by the angular spacing of their ommatidia, or inter-ommatidial angle (Horridge, 1978). The smaller this value is, the higher the spatial resolution, and vice versa. It can be affected by facet size and/or the curvature of the eye surface, both of which can vary greatly within a single eye (Land, 1997; Cronin et al., 2014). Many compound eyes have specialized regions of higher resolution (similar to mammalian foveas), called acute zones, to better discern ecologically relevant parts of the environment.

Adult and juvenile dragonflies are both voracious visual predators, albeit with drastically different predation strategies. Generally, aeshnid dragonfly nymphs are ambush hunters: only when prey pass in front of their eyes do nymphs strike. Their acute zones view a region of binocular overlap which occurs just short of maximum strike distance, about 9 mm (Sherk, 1977). As they molt through consecutive instars, more ommatidia are added along the anterior border (Sherk, 1978a). Unlike their juvenile forms, many aeshnid adults employ a hawk-like hunting strategy in which they fly above water or vegetation actively looking for prey. In those species, their acute zones face anteriorly (Sherk, 1978b). Furthermore, some dragonfly species also possess additional dorsally-directed acute zones that enable them to spy prey overhead (Labhart and Nilsson, 1995). Because most species that hawk retain the majority of nymphal ommatidia, the ommatidial design is compromised in order to serve different functions in different light environments and developmental stages (Sherk, 1978b). However, the addition of new anterior ommatidia during development gradually changes ommatidial arrangements such that the visual requirements for the terrestrial, flying adults are satisfied (Sherk, 1978c). Ultimately, the larval binocular vision used for close-range vision is abandoned in favor of greater monocular resolution in each eye for far-range vision (Sherk, 1978b). Behavioral adaptations for close-range hunting and long-range hawking in aquatic and terrestrial environments, respectively, likely drove the visual specializations.

Crabs inhabiting flat beaches or mud-flats, such as the ocypodids, possess conspicuous, stalked eyes optically [or "spatially"] tuned to the geometry of their terrestrial surroundings (Fig. 1B). Nearly all structures of interest to these animals lie in a single plane below the horizon. Around the equator of their tall and narrow eyes is a region where the vertical inter-ommatidial angles have values only a quarter of those of the horizontal ommatidia. This narrow

band of high vertical acuity enables detection of predators or conspecifics on the horizon (Zeil et al., 1986; Zeil and Hemmi, 2006). However, shore crabs that live in more complex visual environments, such as rocky intertidal zones, lack these horizontally specialized acute zones (Zeil et al., 1989).

Unfortunately, few physiological or behavioral studies exist on the vision of the immature counterparts of the terrestrial crustaceans described above. Generally, larval crustacean eyes are spherical and possess no structural specializations. Most crustacean larvae are pelagic; the water columns in which they reside would not have the defined horizon seen in terrestrial environments. Studies in wholly aquatic malacostracans such as rock lobsters, mantis shrimps, and hydrothermal vent crabs suggest that crustacean eyes can change quite significantly between larval and adult stages: both structurally, via visual pigment expression or optical design, and even at the level of neural organization (Cronin et al., 1995; Jinks et al., 2002; Lin and Cronin, 2018; Meyer-Rochow, 1975). Although little is actually known about the visual capabilities of larval terrestrial crustaceans, we can reasonably hypothesize that, given the broad similarity in ecology across marine crustacean larvae and in the terrestrial specializations of adults, their eyes undergo dramatic changes in structure and function.

4.4. Opsin expression

Although light in any given environment can be highly variable; spectral distributions, like the polarization pattern in the sky, are relatively predictable at a given time and place. On a clear sunny day, almost anyone would call the sky blue — short-wavelength dominant. Later when the sun sets, the western sky is awash in light that is more long-wavelength dominant; or what humans would perceive as reds, pinks, and oranges. The presence of light of different wavelengths accounts for broad spectral variation across environments. Because species must respond to the light present in their habitats, many visual systems are tuned to the ambient spectra they experience (Lythgoe, 1979). Spectral tuning is a common strategy, whereby eyes are tuned to maximize photon capture and therefore sensitivity; alternatively, they may be tuned to optimize contrast of objects against a background (Cronin et al., 2014). Photoreceptors fall into different spectral classes due to their expression of specific visual pigments. The wavelength of maximum absorption (λ_{max}) of a visual pigment is determined by the opsin's specific amino acid residues and/or the specific chromophore that is associated with the protein. Co-expression of multiple opsins has been reported in horseshoe crabs and other arthropods (as well as some vertebrates), which could contribute to even more flexible tuning of photoreceptors (Arikawa et al., 2003; Dalton et al., 2015; Battelle et al., 2016; Valdez-Lopez et al., 2018; Porter et al., 2020). Photoreceptor types in retinas can range from a single class to over a dozen, and their spatial distribution is often organized in an ecologically relevant manner.

In true dragonfly (Anisoptera) eyes, for example, opsins are regionally expressed. Adult compound eyes of the dragonfly *Sympetrum* are functionally and morphologically divided into dorsal and ventral regions (Labhart and Nilsson, 1995). The dorsally directed region is dominated by short-wavelength photoreceptors, whereas long-wavelength photoreceptors are expressed in the ventral region (Futahashi et al., 2015). This differential dorso-ventral expression corresponds to the surrounding spectral environment. Light from above and in aquatic environments trends towards short wavelengths, where light from below is primarily long-wavelength. Whether dragonfly nymphs similarly possess regional opsin expression is unknown. However, they express fewer visual opsin genes than adult dragonflies, all of which are distinct from adult opsins (Futahashi et al., 2015).

Opsin expression in some mayfly families also changes throughout development, particularly in those whose visual systems are notably sexually dimorphic. Male mayflies in the genus *Atalophlebia* possess a striking second set of dorsal compound eyes with high sensitivity to UV light that develop during the nymph stage (Zimmer, 1897; Horridge and McLean, 1978). These tubular, superposition eyes are located dorsal to the ventral apposition eyes and are likely used to spot females against a crepuscular sky (Horridge, 1976). Genetic analyses of the species *Cloeon dipterum*, in which males also possess a second pair of dorsal compound eyes, indicate that a UV opsin and a blue opsin are highly upregulated in males compared to females. Significantly, these opsins first appear in late stage nymphs and subsequent stages, likely in preparation for a terrestrial existence as adults (Almudi et al., 2020). In both dragonflies and mayflies, opsin expression is likely spatiotemporally regulated. Not only is there regional differentiation in the adults, but opsin expression is adapted to respective nymphal and adult habitats. Whether opsin expression changes throughout development in malacostracan crustaceans is still poorly understood.

5. Neurobiological implications

Given the diversity of eyes described in this review, arthropod nervous systems must accommodate the numerous morphological, behavioral, and ecological changes that accompany metamorphosis. What then, are the implications for neural organization when it is tasked with controlling what are essentially two different animals? We know that in some arthropod species, such as *Manduca sexta*, most larval sensory neurons degenerate during metamorphosis and are entirely replaced by adult neurons (Matsumoto and Hildebrand, 1981). In others, larval neurons undergo synaptic reorganization to serve the needs of adults (Levine and Truman, 1982). What of the visual system? Beneath the compound eyes of adult insects and malacostracans is a series of dedicated neuropils in the optic lobes which includes the lamina, medulla, lobula, and lobula plate. These neuropils maintain a retinotopic organization through small columnar subunits which correlate with individual ommatidia (Strausfeld, 2005, 2012). Similarities in the development of the optic neuropils in hemimetabolous insects and decapod malacostracans are considerable, involving three proliferation zones which, during development, continuously give rise to new cells in the retina, lamina and medulla, and lobula and lobula plate (Anderson, 1978; Harzsch et al., 1999; Cronin et al., 2017). Although it is generally assumed that optic lobe organization in hemimetabolous arthropods remains relatively unchanged during metamorphosis (Fig. 3A and B), whether there are neural modifications that correspond to visual specializations in adults, such as the dorso-ventral differentiation in dragonfly eyes or the acute equatorial zone in land crab eyes, awaits further investigation.

Perhaps the most unusual known example of optic lobe metamorphosis is found in the whirligig beetle *Dineutus sublineatus*. Adult whirligig beetles live at the interface of air and water, spending their lives on the surfaces of ponds and streams. They are unique in their possession of two pairs of compound eyes: one aerial and one aquatic, each with its own lamina, medulla, and partially fused lobula (Fig. 3C). Like most adult insect eyes, the lower aquatic eyes are equipped with a pair of lobula plates, but no lobula plates exist in conjunction with the upper aerial eyes (Lin and Strausfeld, 2013). Developmental studies show that the missing upper lobula plates actually develop precociously in the subaquatic larval stage, where they are used to detect prey movement during ambush hunting with the larval stemmata system (Fig. 3D; Lin and Strausfeld, 2013). During pupal metamorphosis, the larval stemmata and the underlying stemmata neural circuitry

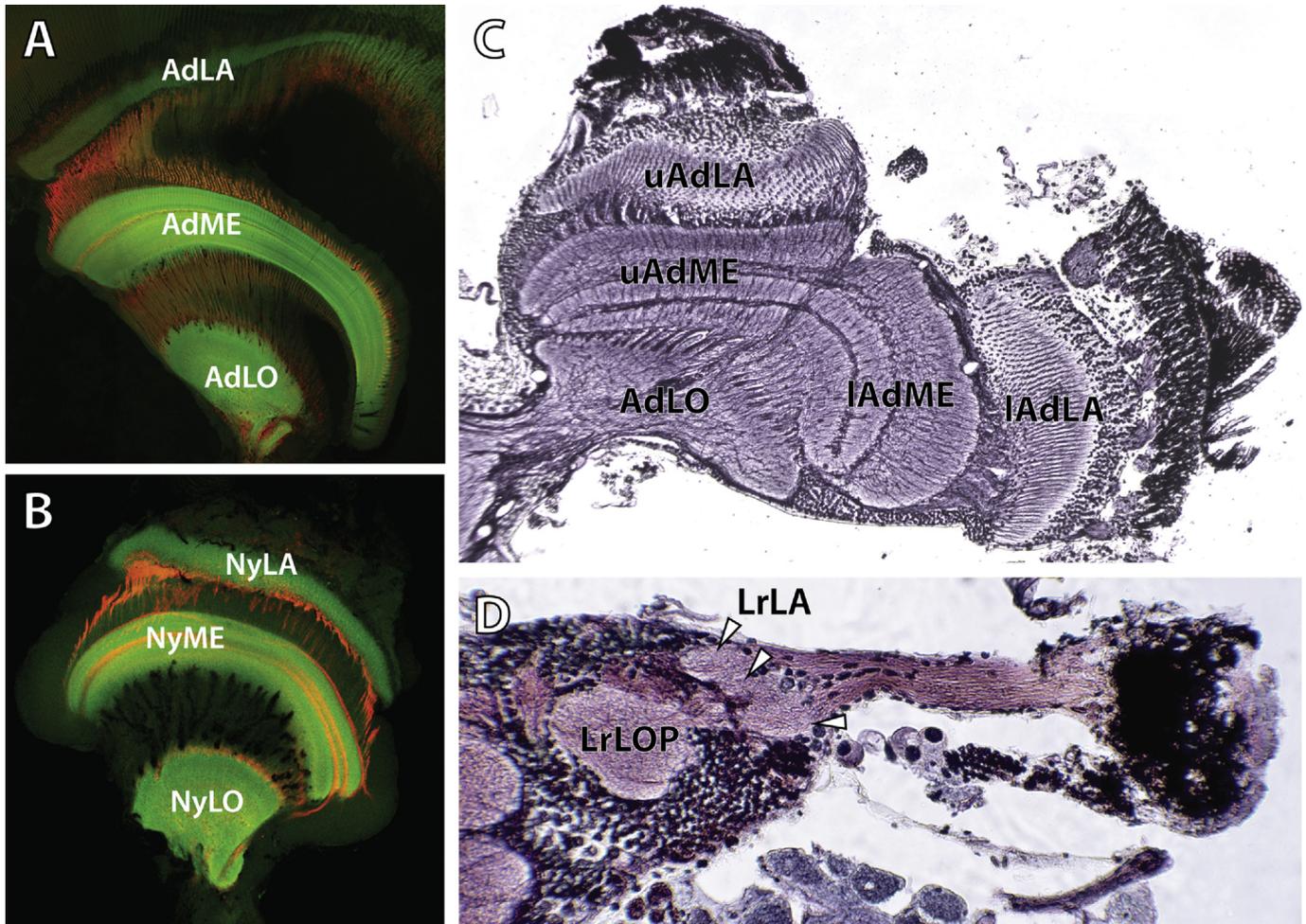


Fig. 3. Comparisons of optic neuropil development between the hemimetabolous dragonfly *Pantala flavescens* (A, B) and the holometabolous whirligig beetle *Dineutus sublineatus* (C, D). (A, B) Optic neuropils in a dragonfly adult (A) and nymph (B) immunostained with antibodies raised against synapsin (green) and α -tubulin (red). Adults retain the same set of lamina (AdLA), medulla (AdME), and lobula (AdLO), as in the developing nymphs (nymph lamina, NyLA; nymph medulla, NyME; nymph lobula, NyLO). (C, D) Reduced silver-stained optic neuropils in adult (C) and larval (D) whirligig beetles. Adult whirligig beetles possess a pair of upper aerial eyes and lower aquatic eyes, each with its own lamina and medulla (upper adult lamina, uAdLA; upper adult medulla, uAdME; lower adult lamina, lAdLA; lower adult medulla, lAdME). They also have a partially fused lobula (AdLO) and a small lobula plate posterior to the lobula (not shown here) that is associated with the lower aquatic eyes alone (Lin and Strausfeld, 2013). (D) Larval whirligig beetles possess a different set of three lamina neuropils (LrLA, triangles) associated with the three dorsal-most stemmata and a precocious lobula plate (LrLOP), likely used for the detection of overhead prey movement (Lin and Strausfeld, 2013).

degenerate, along with the precocious lobula plates. The newly emerged adult beetle thus possesses only smaller lobula plates associated with the lower aquatic eyes (Lin and Strausfeld, 2013). Whirligig beetles demonstrate that the same set of visual circuitry can be adapted for different functional roles, e.g. motion detection for prey capture in larvae, and locomotion stabilization in adults (Lin and Strausfeld, 2013). Ultimately, similar studies could provide insights into aerial and aquatic neurobiological adaptations in amphibiotic arthropods.

Although most malacostracan optic neuropils, such as those of the mud crab *Dyspanopeus sayi*, are not subject to drastic modification between larval and adult stages (Cronin et al., 2017), one known example of optic neuropil transformation during crustacean metamorphosis is found in mantis shrimps (Malacostraca: Stomatopoda). Stomatopod crustaceans are aquatic predatory malacostracans that have highly specialized compound eyes as adults, but typical larval crustacean compound eyes when immature. During the final larval stage, the larval eyes and larval optic lobes

disintegrate while a new set of adult optic neuropils is created to serve the adult eyes (Lin and Cronin, 2018). In this regard, their visual metamorphosis resembles that seen in holometabolous insects, in which the adult compound eyes and optic lobes replace the larval visual system after metamorphosis (Green et al., 1993; Meinertzhagen and Hanson, 1993; Sbita et al., 2007; Fischbach and Heisinger, 2008; Lin and Strausfeld, 2013). However, holometabolous insects typically possess stemmata as larvae and, if present, greatly reduced optic lobes (Gilbert, 1994). In the fruit fly *Drosophila melanogaster*, for example, larvae exist entirely within fruit. Their stemmata consist of just 12 photoreceptors that contribute to simple phototactic behaviors and circadian entrainment (Keene and Sprecher, 2012). These stemmatal photoreceptor axons project to a small stalk-like optic neuropil where they synapse onto lateral clock neurons and the neuronal precursors to the adult optic lobes (Tix et al., 1989; Sprecher et al., 2011). In contrast, the highly-mobile, aquatic larvae of chaoborid and culicid Diptera are reported to exhibit visually-mediated predator avoidance

behaviors. These behaviors are presumably driven by their peramorphic (adult-like) compound eyes whose ommatidia project onto a relatively sophisticated peramorphic lamina and medulla (Melzer and Paulus, 1990, 1991; Gilbert, 1994). The development of larval visual systems and optic neuropils therefore appears to be dependent upon the visual demands of that life stage and may vary among taxa.

6. Summary and conclusions

Throughout this review, we have focused on literature on the visual ecologies of amphibiotic insects and malacostracan crustaceans, and elaborated on the extensive developmentally distinct features of visual systems using several examples. The tasks animals face throughout their life histories vary greatly; and thus, so can the sensory systems that guide their behaviors. The ecological niches of aquatic larvae and terrestrial adults differ significantly with regard to the visual world, particularly in polarization, intensity, spectral distribution of light, and in the behavioral requirements demanded of their visual systems. These distinctions are often reflected in the structures and functions of their eye designs. Overcoming the constraints and costs imposed by metamorphosis, animals adapt their visual systems to best suit their current life stage. As a consequence of the dearth of work on amphibiotic insects and crustaceans, most of the studies considered in this review focus on Odonata, Ephemeroptera, and Malacostraca. We hope that this initial assessment of the field will encourage sensory ecologists to explore visual metamorphoses further.

Author statement

A.C. reviewed the literature. A.C. and C.L. wrote the manuscript and A.C., C.L. and T.W.C. edited and revised the manuscript.

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