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RESEARCH ARTICLE

Physiological and behavioral evidence for multiple spectral channels in the larval stomatopod visual system

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ABSTRACT

Larval stomatopods have generally been described as having a typical larval crustacean compound eye, which lacks the visual pigment diversity and morphological specializations of the well-studied stomatopod adult eye. However, recent work has suggested that larval stomatopod eyes are more complex than previously described. In this study, we provide physiological and behavioral evidence of at least three distinct photoreceptor classes in three species of larval stomatopods: *Gonodactylellus* n. sp., *Gonodactylaceus falcatus* and *Pullosquilla* n. sp. First, electroretinogram recordings were used to measure the spectral sensitivity of each species. Evidence for at least three spectral classes were identified in each: an ultraviolet, peaking at 340–376 nm; a short-wavelength blue, peaking at 455–464 nm; and a long-wavelength orange, peaking at 576–602 nm. Next, the behavioral response to light was investigated. We found that each species demonstrated positive phototactic responses to monochromatic stimuli across the UV–visible spectrum. In wavelength preference trials, distinct preferences among species were identified when different colored light stimuli were presented simultaneously. All species displayed a strong response to the UV stimulus, as well as responses to blue and orange stimuli, although at different response strengths, but no response to green. The results of this study demonstrate that larval stomatopods not only have multiple physiologically active spectral classes but they also display clear and distinct responses to wavelengths across the spectrum. We propose that the spectral classes demonstrated in each are related to visually guided ecological tasks of the larvae, which may differ between species.

KEY WORDS: Vision, Electroretinogram, Phototaxis, Stomatopod, Larvae

INTRODUCTION

Benthic adult stomatopod crustaceans are known for having the most complex visual system in the animal kingdom, with each eye split into three distinct regions that host up to 16 morphologically distinct photoreceptor types (Marshall et al., 1991, 2007). The adults have unparalleled visual pigment diversity and polarization sensitivity within these photoreceptors, providing up to 12 distinct spectral classes for color vision (Bok et al., 2018; Cronin et al., 2014; Thoen et al., 2017). While these unique specializations have long been studied in adult stomatopod visual systems, there have been comparatively few studies of the visual systems of pelagic larval stomatopods (Cronin and Jinks, 2001; Feller, 2014, 2013; Morgan and Goy, 1987). Similarly to other malacostracan crustacean larvae, during the planktonic pelagic phase, stomatopod larvae differ from adults in both ecological tasks and the light environment they inhabit. As visual system form and function tend to reflect the light environment and ecological need of a given organism or stage of life history (Cronin et al., 2017), we expect these different visual needs to be reflected in the larval visual system physiology and behavior (Cronin and Jinks, 2001; Feller and Cronin, 2014).

It is common for malacostracan crustacean larvae to have fundamental shifts in their visual systems between larvae and adults because of their different ecological needs. Most often the adult visual system is built upon the larval, adding complexity to existing structures (Cronin et al., 2017). However, probably because of the extreme difference in complexity between the stomatopod larval and adult visual systems, when larval stomatopods metamorphose, the larval retina and all associated neural connections are fully replaced by newly developed adult structures (Feller et al., 2015; Jutte et al., 1998; Lin and Cronin, 2018). This means that larval stomatopod visual systems are physiologically and morphologically distinct from the adults, and therefore must be considered separately. Like other malacostracan crustacean larval compound eyes, stomatopod larvae have been described to have a uniform and nearly spherical apposition compound eye hosting a single type of photoreceptor with a peak sensitivity between 450 and 500 nm (Cronin and Jinks, 2001; Feller and Cronin, 2016; Jutte et al., 1998). However, more recent studies question the uniformity of the larval stomatopod visual system (Feller et al., 2019; McDonald et al., 2022). In one family of larval stomatopods, the Nannosquillidae, a long-wavelength intrarhabdomal structural reflector (ISR) was recently identified that is hypothesized to increase the larval visual system sensitivity to long wavelengths in the ventral portion of the retina (Feller et al., 2019). In addition, physiological UV sensitivity – and the opsins that drive that sensitivity – were recently described in one species of larval stomatopod, *Neogonodactylus oerstedii* (McDonald et al., 2022), and we now hypothesize that UV sensitivity is likely to be widespread in larval stomatopods. This is supported by recent work investigating opsin expression, showing that larvae not only have middle wavelength (i.e. blue-sensitive) visual opsins, but also UV- and long-wavelength-sensitive opsins (Palecanda, 2022).

We hypothesized that larval stomatopod eyes have multiple physiologically active and behaviorally relevant spectral classes. In this study, we test this using both physiological spectral sensitivity measurements and behavioral wavelength responses. These trials were completed on three species of larval stomatopods encompassing two out of the three main stomatopod superfamilies: *Gonodactylaceus falcatus*, *Gonodactylellus* n. sp. and *Pullosquilla* n. sp. (Fig. 1). For each species, electroretinogram (ERG) recordings

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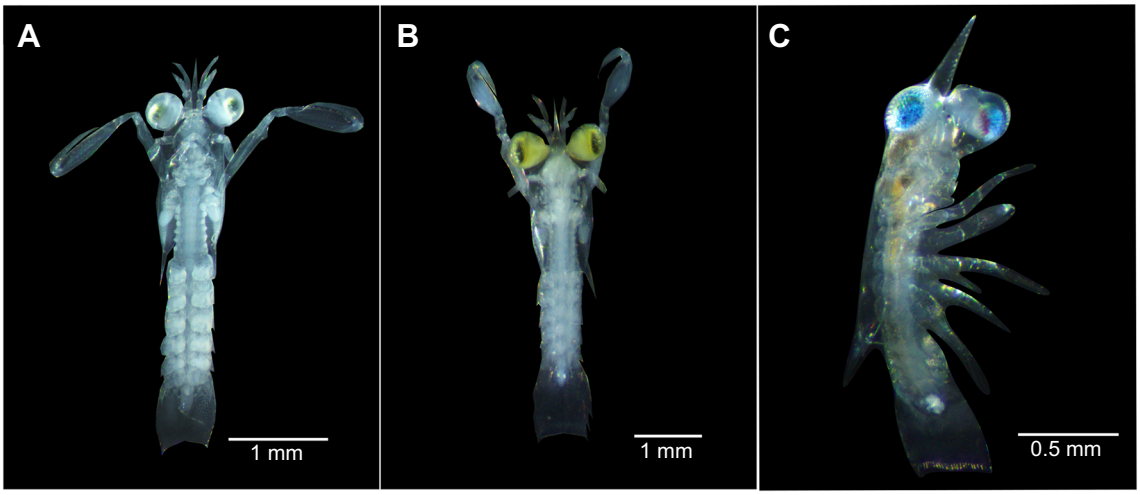

Fig. 1. Images of the three larval stomatopod species used for electrophysiological and behavioral trials. (A) *Gonodactylaceus falcatus*, (B) *Gonodactylellus* n. sp. and (C) *Pullosquilla* n. sp. with approximate scale bars. All larvae used were 3–4 mm in size. Images taken by M.S.M.

were completed under a series of light adaptations to allow us to isolate and model spectral sensitivities. Additionally, innate color-driven behaviors were tested, as color is an important signal in many natural habitats and behavior is driven by any given organism's perception of and subsequent response to different wavelengths of light (Kelber et al., 2003; Song and Lee, 2018; van der Kooi et al., 2021). Behavioral phototaxis was measured across the ultraviolet-visible (UV–vis) spectrum, to test how larvae respond to single color cues and determine how physiological measurements translate into wavelength-guided behavior (Cohen et al., 2010; Forward, 1987; Forward and Cronin, 1979). Finally, wavelength preference tests were completed on the larvae, as these are often used to understand innate color-driven behaviors or response to different colors without prior training (Bascuñán et al., 2009; Kawamura et al., 2010; Kawamura et al., 2016; Mason et al., 2011). This study provides a comprehensive assessment of sensitivities of larval stomatopods and determined that larval stomatopods have at least three spectral classes of photoreceptors that are sensitive in the UV, short-wavelength and long-wavelength portions of the spectrum. These photoreceptor classes are both behaviorally and physiologically relevant in animals previously understood to have monochromatic vision.

MATERIALS AND METHODS

Larval collection and rearing

Three species were used in this study: *Gonodactylaceus falcatus* (Forskål 1775), *Gonodactylellus* n. sp. and *Pullosquilla* n. sp. (Fig. 1). There are seven stomatopod superfamilies currently accepted but over 80% of the currently described species reside in the three main superfamilies: Gonodactyloidea, Lysiosquilloidea and Squilloidea (Porter et al., 2010; Van Der Wal et al., 2017). The species used in this study are in the superfamilies Gonodactyloidea (*Gonodactylellus* n. sp. and *G. falcatus*) and Lysiosquilloidea (*Pullosquilla* n. sp.). Most of the animals were collected as egg clutches and hatched in the laboratory. Egg masses were collected from both Wailupe Beach Park and the Kaneohe Bay Sandbar on Oahu, Hawai'i. Upon collection, eggs were taken to the University of Hawai'i at Mānoa where they were placed in 1 litre containers of seawater supplied from the Waikīkī Aquarium (~30 psu) and left on a table rocker (Benchmark Scientific BR1000, Sayreville, NJ, USA) under a full spectrum lamp (WILLS 165 W aquarium light) on a 12 h:12 h light:dark cycle until hatching. Upon hatching, larvae were moved off the table rocker and placed in 1 litre beakers at ambient temperature with daily water changes under the same lamp and light cycle. During larval development, animals were supplied daily with a diet of fresh hatched *Artemia* nauplii. Trials were completed on larvae when they reached positively phototactic pelagic stages.

For behavioral experiments, *G. falcatus* larvae were collected at night from the Makai Research Pier in Waimanalo, O'ahu, using underwater flashlights and dipnets. Stomatopod larvae were then visually sorted from the rest of the plankton. Upon collection these larvae were maintained under the same conditions as the other species, with a 12 h:12 h light:dark cycle, daily water changes, and a diet of fresh hatched *Artemia* nauplii for up to 1 week prior to testing.

DNA barcoding of wild-caught samples

To verify samples of *G. falcatus*, a subset of 25 individuals were randomly pulled from multiple collection periods at Makai Pier for cytochrome oxidase I (COI) barcoding. DNA was extracted from each individual larva using a DNeasy Kit (Qiagen, Hilden, DE, USA), following the manufacturer's protocols, and then a polymerase chain reaction (PCR) protocol was used to amplify the COI mitochondrial gene. Each 20 µl PCR reaction was composed of Phire Hot Start Taq (Thermo Fisher Scientific, Waltham, MA, USA), 5–10 ng of DNA and 0.5 µl of 1× forward and reverse primers. The cycling parameters used consisted of a single two-minute incubation at 94°C; 40 cycles of 20 s 94°C denaturing, 10 s 46°C annealing and 1 min 65°C elongation; and a final elongation at 65°C for 7 min. PCR success was verified using gel electrophoresis and samples were cleaned with EXO-SAP-IT (Thermo Fisher Scientific, Waltham, MA, USA) if successful. Successfully amplified samples were sent to the Advanced Studies in Genomics, Proteomics, and Bioinformatics facility at the University of Hawai'i at Mānoa for Sanger sequencing. Upon sequencing, samples were assembled in Geneious and run through NCBI's Basic Local Alignment Tool (BLAST) to verify species. All samples returned a hit with *G. falcatus* with less than 3% divergence. Each individual was then aligned to a curated list of stomatopod references sequences (Steck et al., 2022) and placed in a Neighbor Joining Tree with a Tamura–Nei distance model for additional species verification.

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Electrophysiology

ERG recording system

Extracellular electroretinogram (ERG) recordings, representing the summed response of a group of photoreceptors to a light stimulus, were used to determine the peak sensitivities of the larval visual system. During experimentation, larval stomatopods were immobilized with cyanoacrylate gel adhesive (Loctite, Rocky Hill, CT, USA) on a plastic head of a pin and suspended in a static room temperature bath (~25°C) of seawater within a light-tight Faraday cage. The recording electrode (75 µm standard fine metal microelectrode; FHC, Bowdoin, ME, USA) was placed subcorneally in one eye of the larva. A second comparable reference electrode was placed in the seawater bath, which was grounded with an AgCl-coated wire to the Faraday cage. During experimentation, the differential AC signals were amplified, with a high-pass frequency of 1 Hz and a low-pass frequency of 0.3 kHz, (Model 3000 AC/DC, Model 3000 Regular Head Stage; A-M systems, Sequim, WA, USA) and recorded through a data acquisition system (PowerLab 4/26, ADInstruments, Colorado Springs, CO, USA) before being digitized and stored for later analysis (LabChart, ADInstruments).

Light stimulus

Monochromatic light stimuli were provided by a xenon arc lamp (Spectral Products AST-XE-175-BF, Putnam, CT, USA) filtered through a hot mirror (Edmund Optics, Barrington, NJ, USA), a series of fused-silica neutral density filters (Thorlabs, Newton, NJ, USA) for intensity control and narrow bandpass filters [10 nm full width at half maximum (FWHM), Thorlabs] for spectral control. Irradiance at each wavelength and neutral density filter combination was measured by handheld spectroradiometer with a cosine corrector (StellarNet Inc., Tampa, FL, USA). A light stimulus duration of 75 ms was provided by a computer-controlled electromagnetic shutter, and there was a minimum of 1 min interval between experimental flashes (Uniblitz D122, Vincent Associates, Rochester, NY, USA). The light was conveyed to the animal through one branch of a bifurcated liquid light guide (Newport 76846, Irvine, CA, USA). The second branch of the light guide led to an accessory lamp (HL-2000, Ocean Optics, Orlando, FL, USA) that was used to provide illumination for specimen preparation, as well as chromatic adaptations (described below). The light guide emitted a large enough circle of light to stimulate the whole eye of the specimen with both the monochromatic stimulus and the adapting light.

Spectral sensitivity experiments

Prior to experimentation, animals were dark adapted for a minimum of 30 min until a consistent amplitude of response to a dim test flash was achieved. The intensity and wavelength of the test flash differed between preparations owing to individual sensitivity and adaptation, but the same flash was used throughout a given experiment to ensure adaptation was maintained. If a test flash response shifted throughout an experiment, the animal was discarded from the study, as this means the baseline response of the animal changed and comparison between wavelengths would no longer be consistent. ERGs were measured under both dark and chromatic adaptations. Chromatic adaptations apply continuous light to the eye in a restricted waveband in order to continually photoactivate the eye in particular portions of the spectrum, which allows any secondary peaks to be visualized (Cohen et al., 2010; Goldsmith, 1986). While the primary photoreceptor response was expected to be 450–500 nm (Feller and Cronin, 2016), we hypothesized at minimum two additional sensitivity peaks with responses in the UV (~300–400 nm) and middle–long wavelengths (~500–600 nm) based on opsin expression (Palecanda, 2022). Therefore, three different chromatic adaptions were completed with the goal of uncovering secondary UV or middle–long-wavelength peaks. Adaptations were completed by filtering the accessory light with colored glass filters, then directing this light onto the eye via the second branch of the bifurcated light guide. Four different light adaptations were used: (1) full dark, referred to as 'dark adaptation'; (2) a constant broadband UV–blue light referred to as 'blue adaptation' (BG5 315–445 nm, Thorlabs); (3) a constant yellow light, referred to as 'yellow adaptation' (GG495 long-pass filter, Schott glass, Mainz, Germany); and (4) a constant orange light, referred to as 'orange adaptation' (OG570 long-pass filter, Thorlabs) (Fig. S1). For each type of adaptation, responses were recorded from 350–650 nm at 30 nm increments using the criterion response method (e.g. Cohen and Frank, 2006), with the exception of the Yellow adaptation which was completed at 20 nm increments from 340 to 500 nm in an attempt to clearly differentiate any potential UV peaks. Responses for each adaptation were plotted as the normalized reciprocal of the irradiance required to meet the criterion (typically 30 µV) at each wavelength.

Statistical analysis

Results of each adaptation were plotted as the average of response at each wavelength ±s.e.m. The results were then modeled to find the best fit λ_{max} for each of the adaptations. The model evaluated the fit of the Govardovskii visual pigment template (Govardovskii et al., 2000) from 330 to 660 nm at 1 nm steps, drawn from the R package PAVO (https://CRAN.R-project.org/package=pavo; Maia et al., 2019). The model ran through all possible iterations of λ_{max}, which were then ranked using Akaike's information criterion (AIC_c) (Akaike, 1974) to determine the visual pigment that best fit the data at each adaptation. We conducted this analysis for all species under all adaptations.

In order to determine if the amplitude of response at peak sensitivities were affected by adaptation, ratio responses were calculated (Cohen and Frank, 2006; Cohen et al., 2010). Two ratio responses were calculated for each species. To test if the there was a significant increase in long-wavelength responses under any adaptive state, ratios were constructed by dividing the long-wavelength responses (590–620 nm) by the blue responses (440–470 nm) (orange:blue ratios). To determine if there was an increase in UV response in any adaptive state, ratios were constructed by dividing the UV responses (350–380 nm) by the Blue responses (440–470 nm) (UV:blue ratios) and compared within species using one-way analysis of variance (ANOVA) tests with Tukey *post hoc* tests. If the responses changed significantly by adaptive state, this provides support for multiple photoreceptor spectral classes.

Behavioral response spectrum

Phototaxis apparatus

Behavioral response spectrum trials were run in a horizontal UV-transmissive acrylic trough (L×W×H, 410×100×120 mm; UV Trans Cast Acrylic, Professional Plastics, Pasadena, CA, USA). The trough was divided into 5 equal sections through slides attached to an upper lid, designed to move vertically in unison (Fig. S2A). Monochromatic light stimuli were used from 350 to 650 nm at 30 nm increments and created through use of a xenon arc lamp (Spectral Products, AST-XE-175-BF) filtered through a hot mirror (Edmund Optics) and laser line filters (10 nm FWHM, Thorlabs).

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The light was provided to the animal through a liquid light guide (Newport 76846) that was applied to one end of the chamber along the horizontal axis (Fig. S2A).

All wavelengths were matched to an equal quantal intensity for each trial. To determine what intensity was best to test for each species, preliminary trials were run for each species to determine the light intensity that evoked a significant but not maximal phototactic response (Cohen et al., 2010) at the dominant wavelength of each animal identified through spectral sensitivity experiments. Matched quantal intensity at each wavelength was completed with fused silica neutral density filters (Thorlabs) and measured with a handheld spectroradiometer (StellarNet Inc.). The intensity that evoked a significant response varied between species, and therefore the intensity used for trials varied between species. For *Gonodactylaceus* falcatus and *Gonodactylellus* n. sp., trials were run at 1×10^{14} photons cm^{-2} s^{-1}. For *Pullosquilla* n. sp., trials were run at 1×10^{13} photons cm^{-2} s^{-1}.

Phototaxis experimental trials

Experiments were conducted in a dark room. Prior to testing, animals were dark adapted for a minimum of 30 min. A single trial consisted of 5–10 animals on a single wavelength of light. Prior to experimentation, animals were transferred to the experimental chamber with the aid of a red headlamp (>600 nm). The group of animals were placed in the middle section of the chamber, which was filled with 30 psu seawater at ambient temperature. Animals were further adapted for a minimum of 10 min within the testing chamber itself. At the onset of the trial, the light was turned on and partitions were removed in unison allowing the animals to freely swim for 45 s. The partitions were then replaced and the number of individuals in each chamber was counted. A response was considered positive when the larvae moved to the chamber closest to the light source and was considered a non-positive response if the animal ended the trial in any other chamber.

Statistical analysis

A full set of wavelengths was needed to complete one experimental round. A minimum of 5 experimental rounds of each wavelength were completed for each species. For each round, wavelengths were presented in a randomized order. The same clutch of larvae was used for each round. However, owing to limitations of clutch size, to complete a full experimental round, animals were occasionally used in a second wavelength trial. If animals were used for a second wavelength trial, we ensured that there was a minimum of 1 h between trials and animals were dark adapted again prior to further experimentation. The results of the trials were tested with a binomial generalized linear model in R (https://www.r-project.org/) followed by a Dunnett's contrast test to compare the response at each wavelength to the control (Hothorn et al., 2008).

Behavioral wavelength preference

Wavelength preference apparatus

Wavelength preference was tested by presenting larvae simultaneously with five different colors of LED lights: UV (LED375E, 10 nm FWHM), blue (LED465E, 25 nm FWHM), green (LED525E, 25 nm FWHM), orange (LED591E, 20 nm FWHM) (all from Thorlabs, Newton, NJ, USA) and a control consisting of an LED light that was not turned on. The light stimuli presented during the wavelength preference trials were chosen to fit within the measured physiological spectral sensitivity peaks from each species (e.g. UV, blue and orange). While physiological measurements found no evidence of a distinct physiological peak in the green portion of the spectrum, larvae still exhibited a strong positive response to green light in our behavior response trials (see below), so a green stimulus was included in preference testing. The LED lights were controlled through a solderless breadboard (Arduino, Somerville, MA, USA), with lights wired in series to a 9 V battery. The light output was adjusted through a series of resistors, which allowed us to match the total quantal output of each stimulus light. The irradiance output was measured with a handheld spectroradiometer (StellarRad, StellarNet Inc.) and all lights were adjusted to a total output of ∼50 W m^{-2} (Fig. S3). We chose to match the total quantal output of each light, as the commercially available LED lights in the desired ranges had different FWHM. The wires to power each LED were sealed with clear silicone to keep them watertight (Loctite, Rocky Hill, CT, USA) and encased with black heat-shrink tubing for a consistent visual cue between wires. A cylindrical experimental chamber was used for experiments (25.4 cm diameter, 15.24 cm high; Azar Displays, Kingston, PA, USA). Light stimuli were placed at equal intervals, approximately every 5 cm around the top of the experimental chamber and extended 2 cm into the water (Fig. S2B).

Wavelength preference behavioral trials

Prior to each trial, larvae were dark adapted for a minimum of 30 min. All trials were completed in the dark. At the onset of the trial, larvae were placed in groups of 5 in the center of the experimental chamber. The lights were then simultaneously turned on and larvae were allowed to freely swim for 15 s. At the end of 15 s, larvae at each light stimulus were counted by two observers. A response was considered positive if a larva approached and remained on the LED stimulus at the end of the trial. In our observations, larvae would typically swim from the center and pick a stimulus within 5–10 s of trial onset and typically remained on the chosen light until the end of the trial. Approaches were not considered as positive responses if the larvae did not remain on the stimulus.

Statistical analysis

Trials were replicated 40–50 times for each species. Owing to limitations in the amount of larvae we were able to obtain, some larvae were tested twice. If two sets of trials were run on the same day, there was a minimum of 1 h between trials and larvae were re-dark adapted during this time. Preferences were then analyzed with a zero inflated Poisson distribution (Zeileis et al., 2008) and compared using a Tukey contrast test (Lenth, 2016). The results were plotted as the mean percent positive approach ±s.e.m. for each stimulus, with letters to denote significant differences between groups (α=0.05).

Table 1. Modeled λ_{max} for each of the species used in this study at each of the adapting lights

Species	Adaptation	AIC_c	λ_{max} (nm)
Gonodactylaceus falcatus	Dark	−19.01	460
	Blue	−2.95	581
	Yellow	−21.74	340
	Orange	−30.38	457
Gonodactylellus n. sp.	Dark	−18.66	455
	Blue	−30.48	578
	Yellow	−20.82	376
	Orange	−26.59	462
Pullosquilla n. sp.	Dark	−3.29	597
	Yellow	−5.07	353
	Orange	−19.85	468

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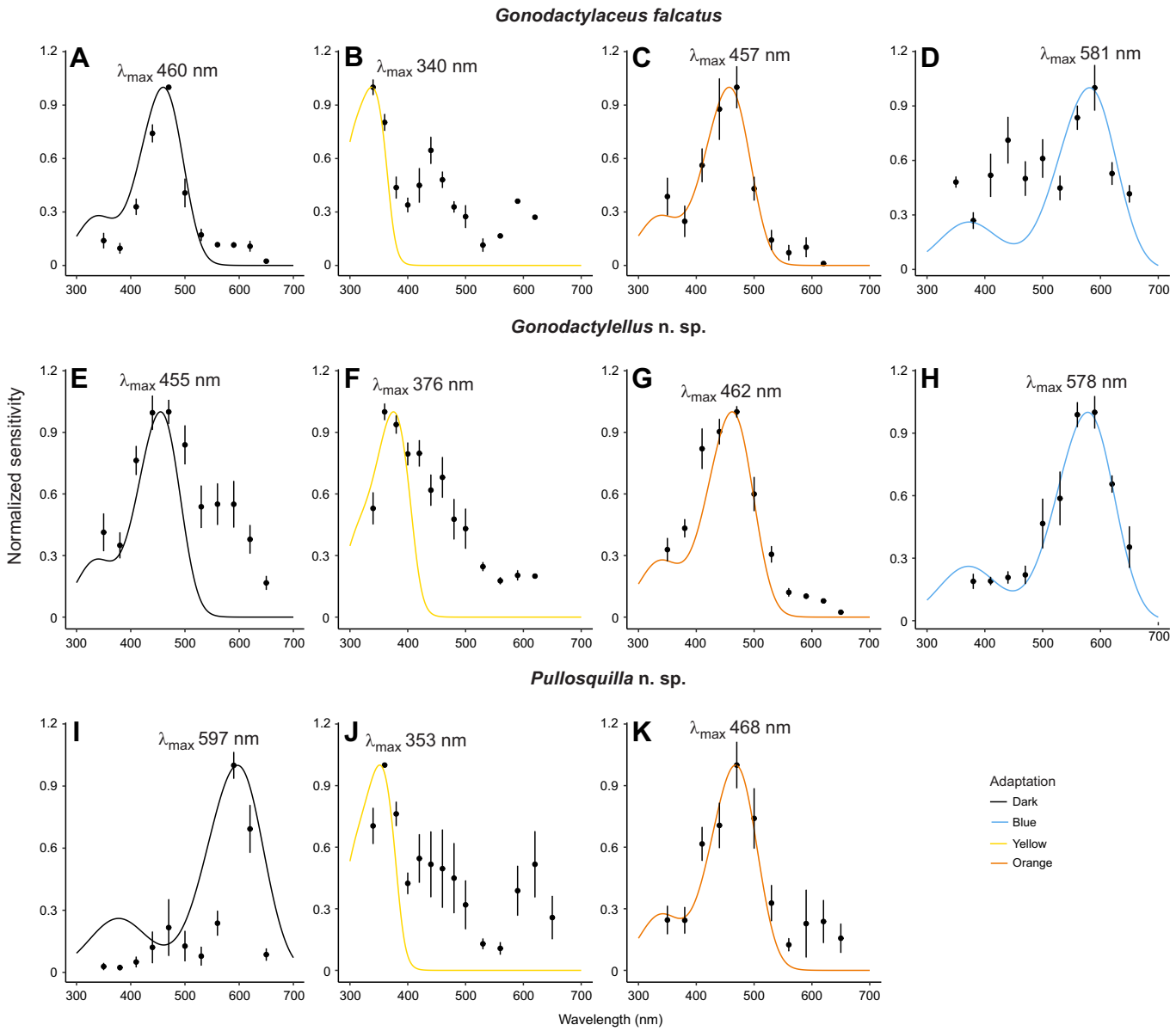

Fig. 2. Spectral sensitivity curves with best fit λ_{max} for each of the three species tested. Data for each adaptation in each species is plotted as the average of the normalized response required to elicit the criteria response±s.e.m., with the best model fit overlaid as a solid line. The responses of *Gonodactylaceus falcatus* under (A) dark adaptation (n=5), (B) yellow adaptation (n=8), (C) orange adaptation (n=5) and (d) blue adaptation (n=7). Responses of *Gonodactylellus* n. sp. under (E) dark adaptation (n=9), (F) yellow adaptation (n=7), (G) orange adaptation (n=6) and (H) blue adaptation (n=6), are displayed. Response of *Pullosquilla* n. sp. under (I) dark adaptation (n=7), (J) yellow adaptation (n=6) and (K) orange adaptation (n=6); the blue adaptation was omitted because of the dominant orange peak under dark adaptation.

RESULTS

Electrophysiology

Three spectral peaks were identified in each of the species using ERG recordings and chromatic adaptations (Fig. 2). While the best-fit modeled peak sensitivities varied between species (Table 1), each species followed a similar pattern with distinct UV, blue and orange peaks (Fig. 2). Under dark adaptation, the two Gonodactyloid species, *G. falcatus* and *Gonodactylellus* n. sp. had blue spectral peaks modeled at 460 nm (Fig. 2A) and 455 nm (Fig. 2E), respectively. A UV peak was seen in both species under the yellow adaptation, with *G. falcatus* modeled at 340 nm (Fig. 2B) and *Gonodactylellus* n. sp. at 376 nm (Fig. 2F). Under blue adaptation, a long-wavelength peak was seen in these two species, with *G. falcatus* measured at 581 nm (Fig. 2D) and *Gonodactylellus* n. sp. at 578 nm (Fig. 2H). We did not see any significant difference in peak sensitivity between the dark and orange adaptations, with both of these species maintaining a peak sensitivity between 455 and 465 nm under the chromatic adaptation (Fig. 2C,G). The slight differences seen in peak sensitivity between dark and orange adaptations were attributed to the relatively broad wavelength steps used for measurements and model fit.

Under dark adaptation, the Lysiosquilloid species *Pullosquilla* n. sp. had a dominant long-wavelength peak measured at 597 nm (Fig. 2I) and, like the Gonodactyloid larvae, had a UV peak at 353 nm under yellow adaptation (Fig. 2J). Under orange adaptation, a blue peak sensitivity was also identified at 468 nm (Fig. 2K). Owing to the dominant long-wavelength sensitivity exhibited under dark adaptation, blue chromatic adaptations were not completed in this species.

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Response ratios were constructed to test for differences in peak sensitivity among adaptations, (Fig. 3). For orange:blue response ratios, in species that had a blue-dominant eye under dark adaptation we expected the orange response to significantly increase compared to the blue response under the blue chromatic adaptation. This was seen in both *G. falcatus* (Fig. 3A) and *Gonodactylellus* n. sp. (Fig. 3B). For *Pullosquilla* n. sp., which had a dominant response in the long wavelength under dark adaptation and a blue peak resolved under chromatic adaptation, we observed a higher orange response under dark adaptation and a significantly lower response under orange chromatic adaptation (Fig. 3C). UV:blue response ratios were also constructed for each species to test if there was a significant increase in the UV response compared with the blue under any adaptation. For each of the three species, the UV peak was resolved using the yellow adaptation; the response ratios correspondingly showed a significant increase in UV: blue under yellow adaptation compared with the dark adaptation (Fig. 3D–F).

Behavioral response spectrum

In the behavioral phototaxis trials, all three species of larval stomatopods demonstrated an inherent positive phototaxis to monochromatic light across the majority of the UV–vis spectrum tested (i.e. 350–650 nm), with decreasing responses to longer wavelengths (Fig. 4). The first species tested, *G. falcatus*, displayed a significant response at each wavelength tested from 350 to 620 nm (Fig. 4A). *Gonodactylellus* n. sp. displayed positive phototaxis from 350 to 620 nm but did not have a significant response at 650 nm (Fig. 4B). Finally, *Pullosquilla* n. sp. displayed the strongest positive responses from 350 to 590 nm (Fig. 4C).

Wavelength preference

During wavelength preference tests, larval stomatopods typically responded to the suspended LED stimuli within 5–10 s of exposure by swimming straight towards the chosen stimulus. Larvae were placed in the center of the arena at a distance of approximately 10 cm from any stimuli at the onset of the trial, and a rapid direction choice was observed when the stimuli were turned on. This indicates they were able to detect and find a stimulus from a distance at least 25 times their body length of approximately 2.5–4 mm. Larvae would then interact with the light by continually bumping the light, swimming in tight circles around the chosen light, or hovering in position directly below or adjacent to the light.

Gonodactylceus falcatus larvae displayed the highest preference for UV light, compared with every other stimulus (Fig. 5A). Additionally, *G. falcatus*. larvae showed a significant preference for both the blue and orange stimuli compared with the control, although these were both significantly lower preferences than the UV response (Fig. 5A). No preference was shown for the green stimulus. The same trends were observed in *Gonodactylellus* n. sp. with the highest response to the UV stimulus, and a significant preference for blue and orange over the control (Fig. 5B). Again, no preference was shown for the green stimulus. *Pullosquilla* n. sp. displayed the highest responses to the UV, orange and blue stimuli, showing a significant preference over the control and green stimuli (Fig. 5C).

DISCUSSION

In this study, we investigated the capabilities of larval stomatopod visual systems using physiological and behavioral techniques.

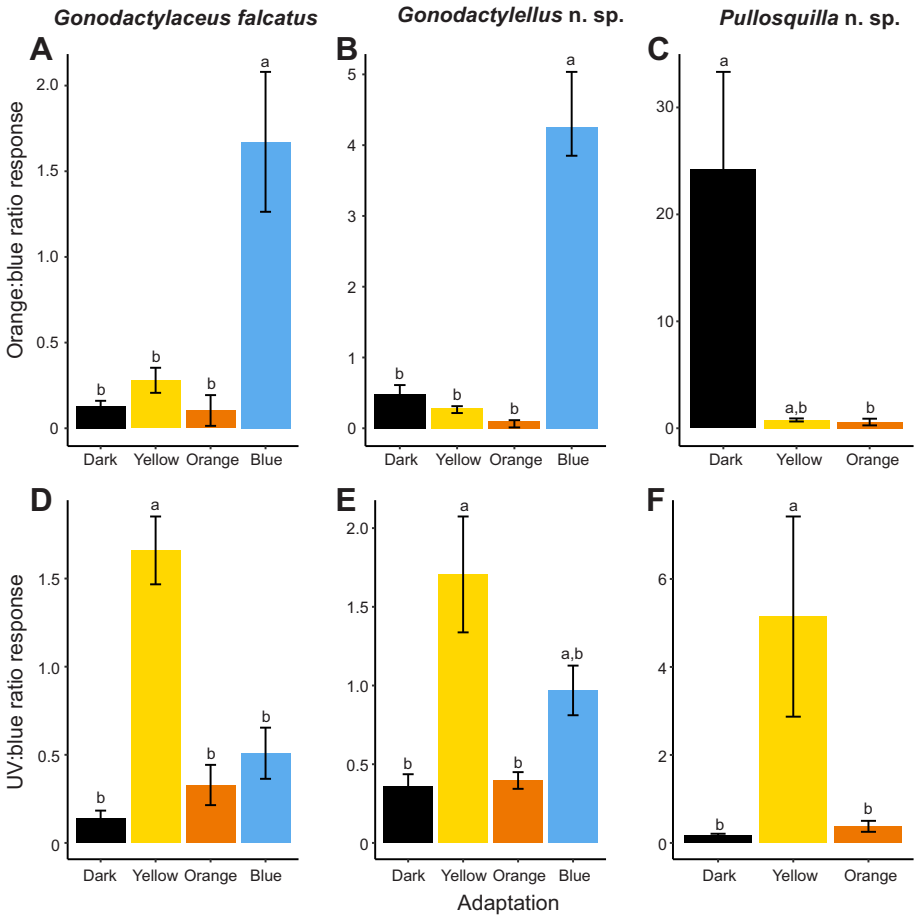

Fig. 3. Comparative ratio responses for each adaptive state for each species studied. Orange:blue (A–C) and UV:blue (D–F) adaptations plotted as means±s.e.m. A one-way ANOVA with a Tukey *post hoc* test was run for each ratio and each species; letters indicate significant differences between ratios of each adaptation state (α=0.05). Ratios were constructed using the ERG amplitudes in the UV (350–380 nm), blue (440–470 nm) and orange (590–620 nm) adaptations.

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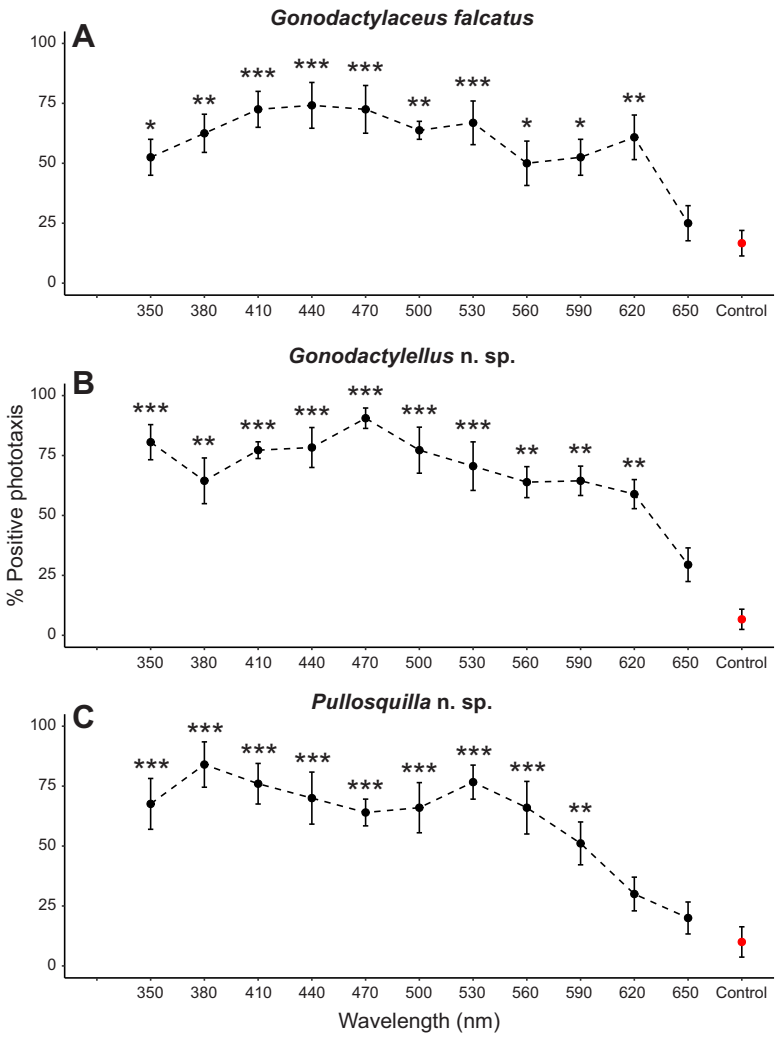

Fig. 4. Positive phototaxis upon stimulation with different wavelengths of light for each of three species tested. Percentage positive phototaxis upon stimulation with different wavelengths of light (solid black circles) as well as the dark control (solid red circle) plotted as mean±s.e.m. *Gonodactylaceus falcatus* (n=8) and *Gonodactylellus* n. sp. (n=6) trials were completed at 1×10^{14} photons m^{-2} s^{-1} and *Pullosquilla* n. sp. (n=6) were completed at 3×10^{13} photons m^{-2} s^{-1}. Wavelengths evoking a mean response significantly greater than the control level were tested using a general linear model with a binomial distribution compared through a Dunnett's contrast. Significance is denoted using asterisks (*P<0.05, **P<0.01, ***P<0.001).

Larvae were thought to have a single blue–green spectral class; however, we provide compelling new evidence for at least three distinct physiological spectral classes in each species studied, which represent two of the three main stomatopod superfamilies. These results were modeled from spectral sensitivity measurements under various chromatic adaptations (Fig. 2), and we verified that different spectral channels were being used through ratio response tests, which provide statistical evidence that the modeled peaks under different adaptations were significantly different (Fig. 3). We also show that this physiological sensitivity translates to behavior. In phototaxis trials, we found that larvae maintained strong positive phototaxis across the majority of the UV–vis spectrum (Fig. 4), with especially high responses in the UV–blue portion of the spectrum. There was a significant but decreasing response in the longer wavelengths and some species-specific differences in where positive responses tailed off (Fig. 4). To investigate the role of behavioral wavelength-driven responses further, preference tests were used. *Gonodactylaceus falcatus* and *Gonodactylellus* n.sp. displayed the strongest preference to UV light over every other stimulus when simultaneously presented with stimuli within the measured behavioral and physiological ranges (Fig. 5A,B). *Pullosquilla* n. sp. also showed a strong preference for the UV stimulus but with an equally strong response to the blue and orange stimuli (Fig. 5C), consistent with the demonstrated dominant long-wavelength sensitivity seen in ERG trials (Fig. 2I). These results are among the first to demonstrate multi-spectral responses in larval stomatopod crustaceans. Previous opsin expression studies have suggested that larval stomatopods have this capability, documenting multiple UV (McDonald et al., 2022), short-wavelength and long-wavelength opsins (Palecanda, 2022). Notably, in this study, we demonstrate that these opsins translate into the physiology and behavior of the larval stomatopod.

All three species studied had a blue spectral sensitivity peak, which was expected based on previous studies of both opsin expression (McDonald et al., 2022) and MSP data from multiple larval stomatopod species (Feller and Cronin, 2016). The modeled blue sensitivity peaks also match the expectation for an animal living in shallow to moderate depths in clear oceanic waters (Cronin et al., 2017) and the strong response in phototaxis trials in all three species supports this sensitivity. Dominant blue spectral sensitivity (450–500 nm) is the most common strategy in pelagic organisms, not just for crustacean larvae (Cronin and Jinks, 2001; Cronin et al., 2017) but also for other animals, including large pelagic predators such as sharks (Hart, 2020; Hart et al., 2011). This is hypothesized to be because the open ocean environment is a relatively uniform and predictable photo-environment, so multiple spectral peaks are not always necessary (Marshall et al., 2015). The primary behavioral tasks of crustacean larvae are typically orientation in the water column, vertical migration and avoidance of predators, and previous studies predict that blue sensitivity is all that is needed to

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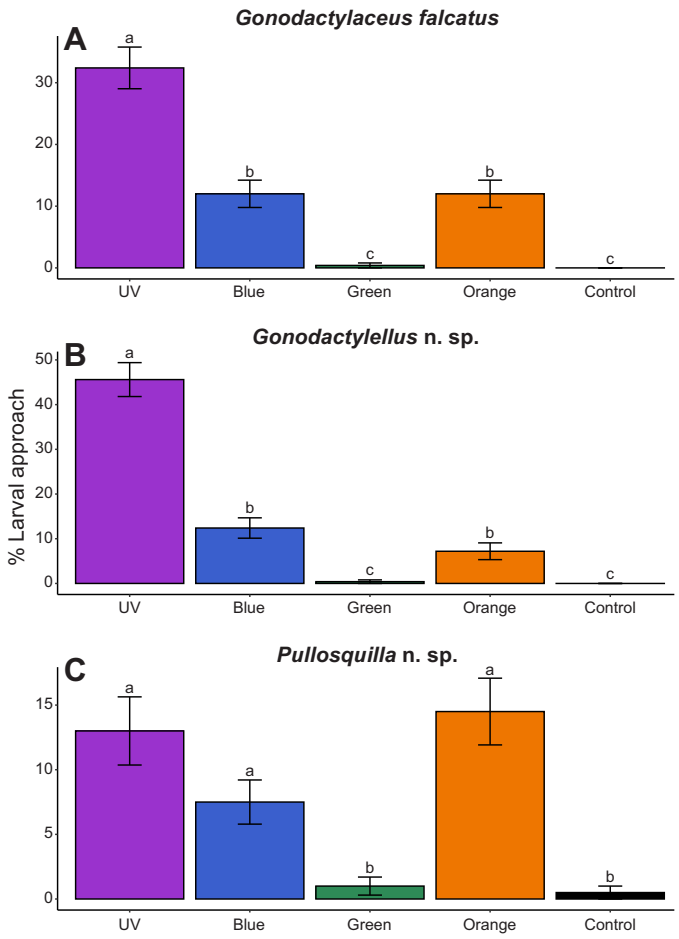

Fig. 5. Larval approach to each light stimulus for each of three species tested. (A) *Gonodactylaceus falcatus* (*n*=50), (B) *Gonodactylellus* n. sp. (*n*=50) and (C) *Pullosquilla* n. sp. (*n*=40). Results are plotted as the mean ±s.e.m. Letters indicate significant differences between stimulus choice (zero inflated Poisson regression with Tukey contrast, α=0.05).

orient in their environment for this suite of tasks (Cronin and Jinks, 2001; Cronin et al., 2017; Forward et al., 1984). However, this may not be the case in larval stomatopods based on our results, as the three species have multiple spectral peaks (Fig. 2) and multiple distinct wavelength preferences, not just to blue (Fig. 5). A leading hypothesis for oceanic animals with multiple peak sensitivities in their visual systems, which could apply here to stomatopod larvae, is that one photoreceptor peak is used to match the background environment (e.g. blue), while secondary and tertiary sensitivity peaks (e.g. UV) are used to offset the contrast of other animals against the background for discrimination (Marshall et al., 2015).

UV sensitivity was observed – both physiologically and behaviorally – in all three species in this study. While broadband UV sensitivity has been reported previously in larvae from the stomatopod *Neogonodactylus oerstedii* (McDonald et al., 2022), this is the first study to characterize distinct UV receptor classes in a larval stomatopod eye. We found a surprisingly broad range in the modeled UV peaks, with a span of 36 nm between peaks among species. This could be for a variety of reasons, including model fit of the data. However, this could also suggest that larval stomatopods have a relatively wide range in UV peak sensitivities that could correspond to differences in either visual tasks or ecologies, such as depth distribution, as is seen in adults (Cheroske et al., 2003, 2009). Alternatively, earlier work has suggested that larval stomatopods have the potential for multiple UV peak sensitivities based on multiple opsin classes (McDonald et al., 2022). It is possible that multiple UV peaks are present in each species, resulting in the broad range observed. Further work is needed to determine if there are multiple peak sensitivities in the UV range in any of these species.

Additionally, further studies are needed to understand the ecological role that UV light plays for larval stomatopods. All three species showed a strong attraction response to UV stimuli in both behavioral trials. This is contrary to many other planktonic organisms, which tend to display a strong aversion to UV light (Boeing et al., 2004; Guggiana-Nilo and Engert, 2016; Leech and Johnsen, 2002), potentially to avoid the damaging effect UV light can have on biological tissues (Schuch and Menck, 2010). There are multiple hypotheses that larval stomatopods may be using UV vision. The attraction to UV displayed by stomatopod larvae could indicate a preference for shallow waters which are enriched in UV wavelengths (Frank and Widder, 1996, 2002), which may indicate larval stomatopods remain in shallow water during the day, rather than vertically migrating as has been previously hypothesized (Feller, 2013). Another hypothesis is that UV vision is being used for more efficient feeding. UV vision in marine environments is hypothesized to assist in prey detection by increasing the contrast of objects against the relatively uniform background of the open ocean (Browman et al., 1994; Johnsen and Widder, 2001; Losey et al., 1999; Siebeck and Marshall, 2007). A recent study found that light availability affects prey consumption in larvae, and there was some suggestion that UV light may play a role in prey consumption (McDonald and Porter, 2023). While more studies are needed, particularly on transparent prey, it is possible that UV vision is being used for effective prey detection in larval stomatopods.

We have also now documented long-wavelength sensitivity in larval stomatopods; indeed, one of very few reports of long-wavelength sensitivity in any larval crustacean. While *G. falcatus* and *Gonodactylellus* n. sp., both had a long-wavelength sensitivity peak that was recovered under Blue chromatic adaptation (Fig. 2D,H), we found that *Pullosquilla* n. sp. had a dominant long-wavelength peak under dark adaption (Fig. 2I). This was predicted, as *Pullosquilla* n. sp. has a long-wavelength intrarhabdomal structural reflector (ISR) that is hypothesized to increase long-wavelength sensitivity in the larval eye (Feller et al., 2019; McDonald et al., 2023). Nannosquillidae, the family in which *Pullosquilla* n. sp resides, is currently the only known family of stomatopods with such a filter. This filter acts as both a narrowband reflector and a transmissive spectral filter, which acts to preferentially allow certain wavelengths through while reflecting long-wavelength light back onto the distal portion of the photoreceptor, allowing this portion of the photoreceptor to have an increased quantal catch of long-wavelength photons (Feller et al., 2019). While spectral reflectance of the filter has been previously measured in three species (Feller et al., 2019), here we show that the ISR filter is increasing physiological sensitivity in the long-wavelength portions of the spectrum. This is significant, because *Pullosquilla* n. sp., and likely other Nannosquillidae larvae, are increasing their long-wavelength sensitivity in ways the other species are not. This hypothesis is likewise supported by behavioral observations, as *Pullosquilla* n. sp. displayed a significantly higher preference for the orange stimuli (Fig. 5C) in innate preference trials that was not observed in the other two species. While *G. falcatus* and *Gonodactylellus* n. sp. also had long-wavelength-sensitive peaks, they do not have an ISR or any other additional retinal tiering of the main rhabdom (McDonald et al., 2023), and do not appear to display either the dominant physiological sensitivity or strong behavioral attraction to orange stimuli seen in *Pullosquilla* n. sp.

Currently, we are unsure of the ecological purpose of the heightened physiological and behavioral long-wavelength sensitivity observed in *Pullosquilla* n. sp. One hypothesis is that Nannosquillidae larvae are using the ISR to increase sensitivity to bioluminescent prey at night (Feller et al., 2019), using this filter to increase the quantal catch of the short flashes of light. Further studies are needed to test this hypothesis.

Overall, we provide compelling evidence for at least three spectral channels in larval stomatopod crustaceans. Additionally, there is a chance there are further spectral channels that were not identified with the current methods. Studies on the opsins in larval stomatopods found that there are multiple opsins in each of the spectral classes studied, including at least three UV opsins currently identified in one species of larval stomatopod (McDonald et al., 2022). This means there is the potential for multiple UV spectral classes, as well as short wavelength and long wavelength based on larval opsin transcripts (Palecanda, 2022). As extracellular recordings were used in this study, which take the sum of a group of photoreceptors, it is possible that there are more spectral classes that were missed with the current methods. Future studies may consider more precise methods using single-cell recordings to further test if there are more spectral channels than the three that were observed here. Additionally, further work needs to be done to understand how larvae are processing these peaks beyond the retina level. While ERG recordings are an effective method of investigating the visual sensitivity at the photoreceptor level that takes into account any filtering in the eye not measured other methods (e.g. microspectrophotometry), it is unclear how the larvae are processing these colors further downstream. While many animals, including humans, use opponent processing to establish color vision (Kelber, 2016; Kelber and Osorio, 2010), it is currently hypothesized that adult mantis shrimp may handle the processing of colors in a different way, although this is still being studied (Streets et al., 2022; Thoen et al., 2014, 2017). However, because larval stomatopods have not only a separate retina, but separate neural connections to the brain (Lin and Cronin, 2018), we do not currently know how larval processing occurs. If larval stomatopods do have color vision, there is a chance that they are completing a different type of processing from the adults and could be using a more 'standard' opponent processing model for true color vision during their early life history. While color vision was not tested in this study, we do show that the larvae have distinct wavelength-driven attraction. Future trials will need to determine how color is being processed by the larvae and to establish behavioral tests to determine if they are using true color vision. In this study, all tests were completed under controlled laboratory conditions and therefore do not represent complex natural light environments. Future studies investigating preferences in natural light environments will be important to understand ecological implications.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.S.M.; Methodology: J.H.C.; Validation: J.H.C.; Investigation: M.S.M.; Writing - original draft: M.S.M.; Writing - review & editing: J.H.C., M.L.P.; Supervision: M.L.P.; Funding acquisition: M.S.M., M.L.P.

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Data availability
All relevant data can be found within the article and its supplementary information.

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