

Variation in Stomatopod (*Gonodactylus smithii*) Color Signal Design Associated with Organismal Condition and Depth

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Key Words

Stomatopod · Signal design · Color vision ·
Gonodactylus smithii · Crustacean · Invertebrate

Abstract

In interactions, many tropical stomatopod species display conspicuous colored body spots that can communicate information about the sender's state (e.g., sex, aggressiveness, etc.). Species inhabiting a variety of depths experience large differences in illumination spectrum and intensity due to filtering of light by water and its constituents. Stomatopod spectral sensitivity is known to vary phenotypically with changes in light environment (associated with depth) that potentially affects the detection of color signals. Animals collected at different depths also have different body coloration. This study examines how spectral differences in colored body spots vary with organismal condition and models the effects of changing body coloration, light environment, and spectral sensitivity on the detection of color signals in a gonodactyloid species, *Gonodactylus smithii*. Of the seven conspicuous color spots that were measured in *G. smithii*, three had spectral differences that correlated with sex, aggression, and female reproductive state. A model of color detection in *G. smithii* indicates that longer-wavelength spectral content was affected most by varying body coloration and light conditions. Most color signals were perceived similarly both by shallow- and by deep-adapt-

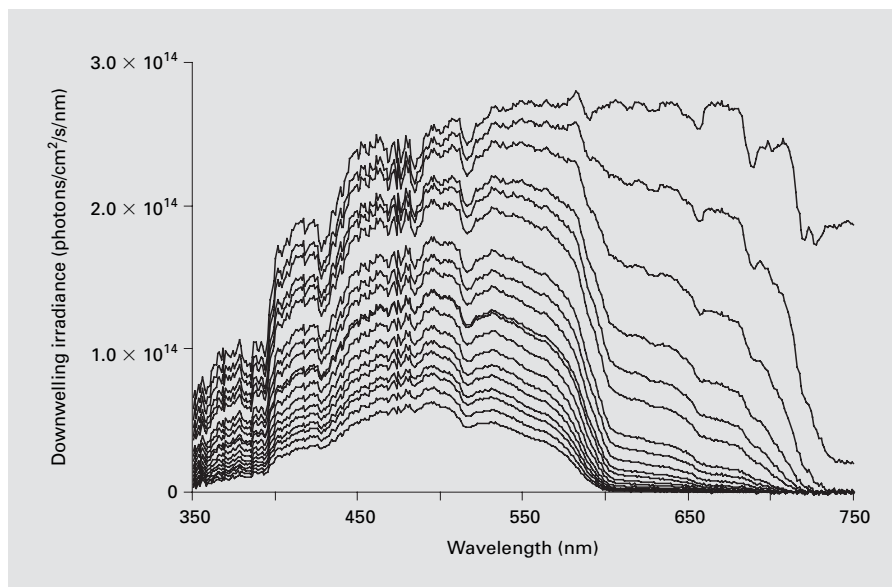
ed photoreceptor sets over a range of depths (1–13 m). Eye spot ('meral spot') color detection also was invariant over the same depth range in shallow- and deep-adapted, long-wavelength receptors, but deep-adapted receptors continued to maintain a consistent detection of these spots down to 18 meters. These results suggest that meral spot coloration may have evolved as a constant signal when viewed by conspecifics from various depths.

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Introduction

Many animals use color signals to communicate information such as sex, level of aggression, or overall health. Excluding bioluminescence, color signals utilize colored body parts that are externally illuminated. Spectral properties of color signals are influenced by the reflectance spectrum of the body part as well as the illuminating light's spectral content. The reddish hue of a sunset or the bluish underwater marine environment are examples of spectral variation in natural illumination due to optical modification by the transmission medium that can significantly affect the detection of color signals [McFarland and Munz, 1975; Hailman, 1977; Loew and McFarland, 1990]. In heterogeneous light environments (such as under a plant canopy), colored body parts displayed in areas that are directly lit from above, rather than shaded, are

Fig. 1. Downwelling irradiance measured at Cobia Hole near Lizard Island, Australia in July 2002 on a clear, sunny day near noon. Each trace represents the irradiance at 1-meter intervals from the surface (top trace) down to the bottom depth of 18 m (bottom trace).



often more easily seen by conspecifics [Endler, 1991; Endler and Thèry, 1996; Gamble et al., 2003; Heindl and Winkler, 2003].

Although color signals have little or no relevance to animals with only one or two photoreceptor classes, species with three, four, or more classes often employ colored body parts for intraspecific signaling – familiar examples include fishes, birds, and butterflies [see Endler, 1990, 1991]. The stomatopod crustaceans, or mantis shrimps, have at least eight color classes of photoreceptors, giving them true color vision; they can distinguish targets based on chromatic content alone [Marshall et al., 1996]. These animals widely use color signals for both intraspecific and interspecific communication [Caldwell and Dingle, 1975; Chiao et al., 2000]. Their color-vision systems are based on eight photoreceptor classes located in 4 rows of ommatidia within a specialized region of the compound eye termed the midband, each row incorporating tiered photoreceptor types (fig. 1). Each photoreceptor class in one tier of one ommatidial row has a spectrally unique maximal sensitivity (or lambda max) and responds over a narrow spectral band. This narrow spectral tuning not only confers the potential for excellent color discrimination, but it also may lead to unusually good constancy in color detection regardless of changing light spectrum [Osorio et al., 1997]. The color constancy is a consequence of the ability of each receptor class to adapt independently to the spectrum of downwelling light in a given habitat [see Osorio et al., 1997 for a theoretical study of this ability in stomatopods]. Within the compound eye, the second and

third ommatidial rows in the midband have intrarhabdomal filters within the photoreceptor tiers that modify the light reaching the underlying photoreceptors [Marshall et al., 1991; Cronin et al., 1994a].

In addition to the potential for color constancy, conspecific stomatopods inhabiting different depth (and therefore light) environments have different color sensitivities that are physiologically adaptive [Cronin et al., 1994b, 2000]. Marine waters only a few meters deep can severely limit the overall intensity and also reduce the spectral content of downwelling irradiance, absorbing over 75% of long-wavelength (>600 nm) light within 5 m (fig. 2). Stomatopods residing in deep-water habitats have receptor classes that are short-wavelength shifted relative to conspecifics in broad-spectrum, shallow-water conditions [Cronin and Caldwell, 2002]. This aspect of the stomatopod color vision system adaptively varies in some species that inhabit a wide depth range (>20 m) and involves strongly-colored filters that overlie longer-wavelength classes of photoreceptors [Cronin et al., 2001; Cheroske et al., 2003]. Spectral and physical changes in the filters ‘tune’ the spectral content and total amount of the light reaching the photoreceptor below. The flexible color vision system of mantis shrimps might enhance the reception of color-coded information during behavioral displays under different lighting conditions [Chiao et al., 2000].

Most stomatopod species with the complex color vision system described above utilize intricate behavioral displays during intraspecific interactions either as resi-

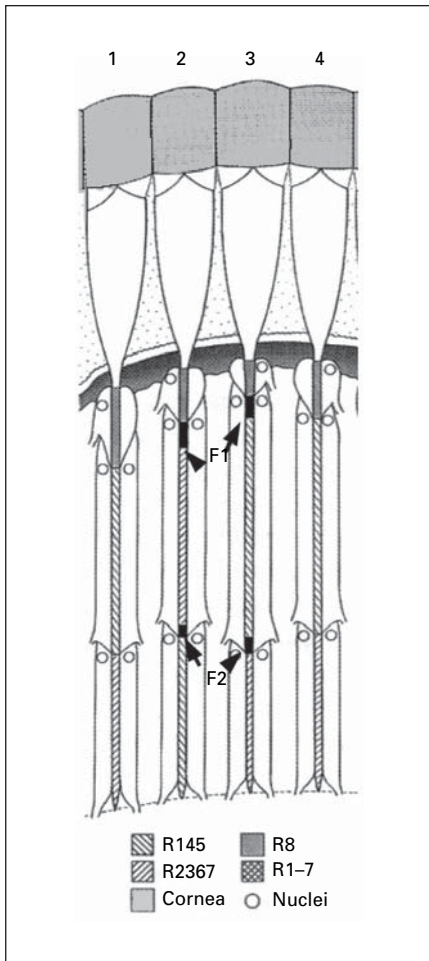


Fig. 2. Diagram of 4 of 6 rows within the ommatidial midband in *Gonodactylus smithii* showing the cornea, crystalline cones, rhabdoms and intrarhabdomal filters. Crystalline cones are represented by the clear, paraboloid structures below the cornea. Represented nuclei (circles) are of the reticular cells in each tier. Abbreviations: 1–4 = row number in the ommatidial midband; F1 = distal intrarhabdomal filters; F2 = proximal intrarhabdomal filters; R145 = rhabdom created by the 1st, 4th and 5th reticular cells; R2367 = rhabdom created by the 2nd, 3rd, 6th, and 7th reticular cells. R8 = rhabdomere of the 8th reticular cell. [Modified from Chiao et al., 2000.]

dents in their domiciles in the coral substratum or while exposed outside of the cavity [Dingle and Caldwell, 1969; Caldwell and Dingle, 1975; Marshall et al., 1991, 1996]. Many of the displays involve conspicuously colored body parts that can transmit information about sex or level of aggression. The colors of these signals are species-specific, but there is variation in coloration both between and within molting cycles according to varying environmental conditions such as light [AGC, TWC, and Roy

Caldwell, pers. obs.] and could also indicate physiological state.

Communication using color signals might reduce the risk of potentially deadly physical contests. A common posture is called the ‘meral spread,’ in which a particularly prominent eye spot (or meral spot) on the medial side of each raptorial appendage is displayed (fig. 3). The color of the meral spot in different species has been correlated with species aggressiveness [Caldwell and Dingle, 1976; Osorio et al., 1997]. During the meral spread, all the maxillipeds are extended towards the substrate and held statically. During sexual interactions, maxillipeds are quickly moved in circular motions or ‘whirling’ that might be a visual display or used as a means to increase conveyance of chemical signals. Pleopod and telson coloration are displayed when stomatopods perform a behavior known as the ‘telson curl,’ during which the abdomen is flexed, bringing the telson in front of the animal (fig. 3). In this posture, the telson is used as a shield against raptorial strikes of an aggressor while allowing the ‘curled’ animal to deliver strikes over the telson. Because stomatopods can change depth habitats when searching for new domiciles in the coral substratum or a potential mate, color signals may be used in a variety of light environments. If the flexible color signaling system of stomatopods coevolved with the complex color vision system, biologically important body colors should be very visually prominent to the visual systems of conspecifics.

To investigate color signal visibility in stomatopods, we used an Indo-Pacific species, *Gonodactylus smithii*, that is found commonly at depths <1 m but also occasionally down to 20 m or more. We utilized a previously established chromaticity model [Chiao et al., 2000; Cronin et al., 1994a] to quantify the detection of different colored body parts in deep and shallow habitats. When evaluating color signaling systems, it is paramount to assess objectively each component of the system in order to characterize how signals would be perceived in relevant viewing organisms [Endler, 1990; Bennett et al., 1994]. The chromaticity model of Chiao et al. [2000] is based on the hypothesis that color content is processed initially through multiple dichromatic channels and uses calculated spectral sensitivity functions for *G. smithii* and other closely related species, irradiance spectra, and spectral reflectance measurements from various body spots potentially used for signaling. In this study, we assessed the reflectance spectra of various body parts of *G. smithii* collected in <1 m and >15 m. Spectral sensitivities of Row 1–4 photoreceptor tiers (below the distal R8 ultraviolet receptors) were calculated for animals residing in these two

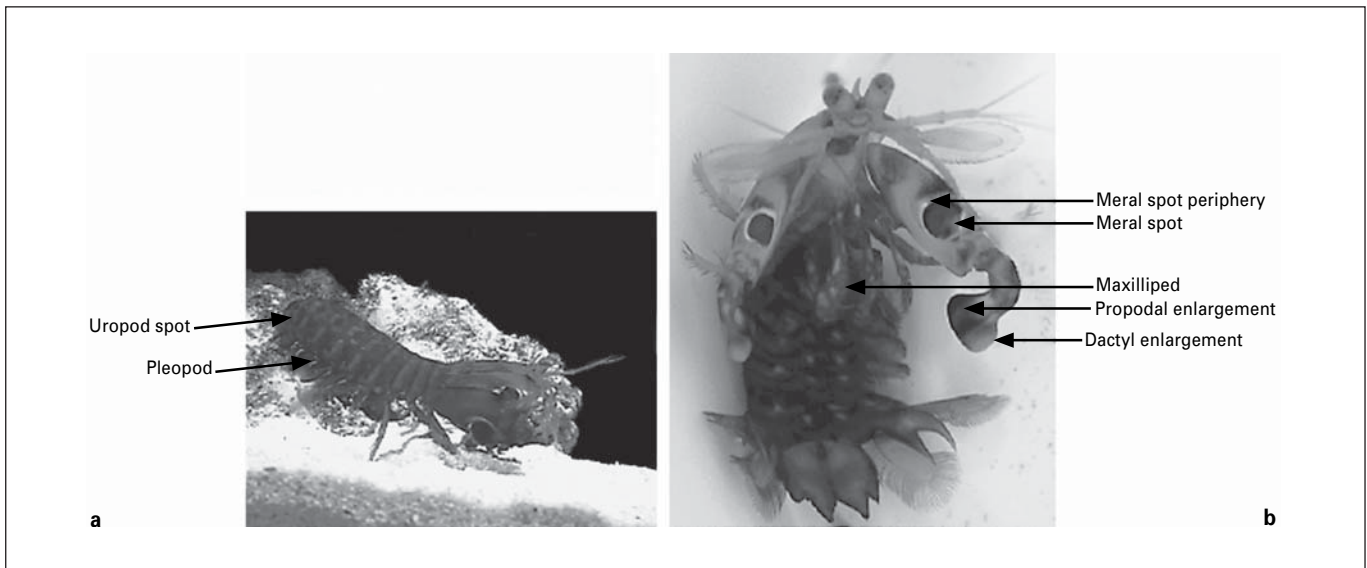


Fig. 3. Schematic showing various colored body spots on *G. smithii*. **a** Longitudinal view. **b** Anterior view of an animal exhibiting a ‘telson curl’.

depth habitats. We also measured downwelling irradiance at the depths inhabited by *G. smithii*. These three sets of measurements were then included in the model to estimate how various body spots might be detected by stomatopods in different depth habitats. We hypothesized that: 1) color markings vary according to sex and physiological state (i.e. reproductive stage, or aggressiveness) and 2) the combined changes in spectral sensitivity and body coloration associated with depth in this species produces color signals that are highly visible and spectrally modified or ‘tuned’ for improved function in their respective environments.

Materials and Methods

Animals and Experimental Preparation

Gonodactylus smithii were collected at 18 m depth near Heron Island (Queensland, Australia) in January 2000 and at shallow (<1 m) and deep (15 m) sites near Lizard Island (Queensland, Australia) during July 2002. All animals were maintained in marine aquaria at approximately 25°C and were fed fresh fish every other day. Shortly after collection, animals were sexed and total length measured. Females were assessed for cement gland development, as late-stage reproductive females about to lay eggs have obvious, opaque cement glands observable through the ventral integument of the thoracic segments.

To assess the color of body spots on *G. smithii*, animals were quick frozen to reduce body movement and kept moist during color measurements. Reflectance spectra were taken using a low-power microscope fitted with a photographic head in conjunction with

an Ocean Optics (Dunedin, FL) USB2000 spectroradiometer. A fiber optic cable ran from the spectroradiometer into the photographic head so that a relatively small (approx. 1 mm²) area of color reflectance could be measured. Illumination (400–750 nm) used for measurements was from a fiber-optic light source referenced to a 99% diffuse white reflectance standard. Animals were evaluated for potentially important color signaling areas based on perceived signal conspicuousness from both color and body position relative to areas known to be used in behavioral repertoires. Colored body parts measured were the meral spot center and periphery, maxilliped, dactyl enlargement, propodal enlargement, lateral edge of the pleopod, and the proximal portion of the uropod (fig. 3). The posterior carapace also was used as a measure of overall body coloration.

A subsample of the animals collected intertidally (n = 8 males, 4 females, and 4 late-stage reproductive females) were employed in intrasexual behavioral trials in a laboratory setting. During these assays in 5-liter aquaria, one individual occupied an artificial burrow (section of PVC pipe) and another size-matched adult was introduced at the opposite end of the tank as an intruder. All interactions were recorded on video during a 20-minute trial and responses categorized and analyzed. Interactions of both contestants were classified as either offensive or defensive. Offensive, but non-contacting, actions included approach, antennular flicking, meral spread, telson push (pushing the telson into the domicile of the resident), and lunge. Offensive contacts included grab (grasping the body of another using maxillipeds), stab (extension of the dactyl and piercing another), and strike (hitting another with the dactyl closed). Defensive actions were avoid and telson curl. The total number of all reactions also was recorded for each animal.

Measurement of Underwater Downwelling Irradiance

During August 2002, we measured downwelling irradiance (350–750 nm) at 1-meter intervals from the surface down to the

bottom (18 m) at Cobia Hole adjacent to Lizard Island, near or in *G. smithii* habitat. Measurements were taken near midday on a nearly cloudless day using an Ocean Optics USB2000 spectrometer connected to a 25-m-long, 400- μm diameter, fiberoptic cable with cosine-correcting head. Using SCUBA, one of us (AGC) maintained the head of the fiber vertically by reference to an attached leveling device and ascended at 1-meter intervals using a depth gauge. Data were collected on a computer by the other author (TWC) in a boat anchored above. At each depth, spectral irradiance measurements (photons/cm²/s/nm) were taken continuously for approximately 45 s and later averaged.

Computation of Photoreceptor Sensitivities in Row 1–4 of the Midband

For shallow water *G. smithii*, we used the spectral sensitivity functions calculated by Chiao et al. [2000]. No deep-water individuals of this species that we collected were suitable for microspectrophotometric measurements of filter absorbance spectra in the third ommatidial row; although small remnants of these filters were visible in sectioned material, these could not be measured. However, habitat-specific filter types are similar for a great diversity of gonodactyloid stomatopods [see Cronin et al., 1994a, 2002], and the filter remnants had the color appearance of typical deep-water types from other species. We therefore estimated spectral sensitivity functions for deep-water *G. smithii* using intrarhabdomal filter data from a sympatric, related species that inhabits a similar depth range, *Gonodactylellus affinis* [Cronin and Caldwell, 2002; Cronin et al., 2002].

Calculation of Stomatopod Color Signals in Row 1–4 Photoreceptors

Chromaticity values were calculated according to Chiao et al. [2000]. In brief, we calculated the quantum catch (Q) of each photoreceptor class according to:

$$Q = \frac{\sum I(\lambda)R(\lambda)S(\lambda)}{\sum I(\lambda)S(\lambda)} \quad (1)$$

where $I(\lambda)$ is the irradiance at 1 m or 18 m depth at wavelength λ , $S(\lambda)$ is the spectral sensitivity of the photoreceptor, and $R(\lambda)$ is the measured reflectance spectrum of each body part. These products are summed from 400 to 750 nm. Photoreceptors were considered to be adapted to overall illumination levels using an adaptation similar to that originally proposed by von Kries [1905], whereby each photoreceptor quantum catch was divided by the summed product of the illumination and sensitivity function. In stomatopods, the axons leading from the proximal and distal photoreceptor tiers in the same row project into the same laminar cartridge [Kleinlogel et al., 2003]. Accordingly, the first processing of color contrast may occur at the laminar level. The chromaticity (C) of color signals as perceived by photoreceptor pairs in each row of Rows 1–4 therefore was calculated as the difference in responses between the distal and proximal tier (fig. 1). Intensity-response functions of photoreceptors can be mathematically complex, but receptors typically encode intensity logarithmically, and modeling of receptor functions commonly employs log-transformed data [see Chiao et al., 2000; Siddiqi et al., 2004; Vorobyev et al., 1998]. Thus:

$$C = \log Q_{\text{distal}} - \log Q_{\text{proximal}} \quad (2)$$

Chromaticities of shallow-collected animals were statistically compared using individual t tests with a Bonferroni correction ac-

ording to the number of comparisons [Sokal and Rohlf, 1995]. For comparisons of sexual chromaticity differences, independent t tests were used. In models where we used the same animals viewed under different conditions, we used pairwise t test comparisons. All statistical analyses were performed using the Simple Interactive Statistical Analysis web resources [Uitenbroek, 1997].

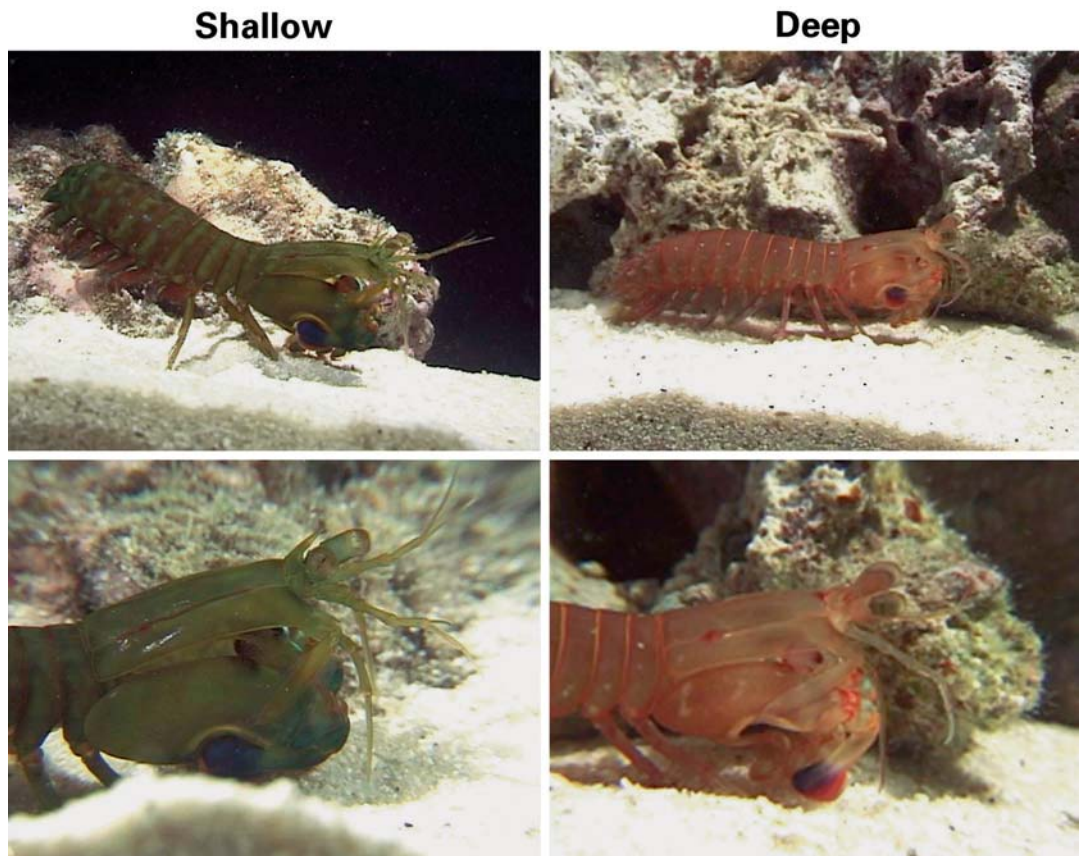
Results

Twenty-six adult *G. smithii* [mean total length (\pm SD) = 62.3 (\pm 4.7) mm] were collected intertidally; 14 were male, 8 were female, and 4 more were late-stage reproductive females with visibly developed cement glands. Our deep collections yielded 4 juvenile (<20 mm) *G. smithii* and 1 adult (47 mm) female. Because juveniles have variable coloration, only the adult was used for spectral analyses. Collection of stomatopods at depth is difficult, as it involves collecting coral rubble using SCUBA, then breaking apart this rubble at the surface to extricate stomatopods that may still be residing in cavities. Except for very common species, few individuals are collected this way. Due to the inherent inefficiency of the collection technique and limitations associated with diving, obtaining deep-living stomatopods remains a challenge.

Using results from the subset of stomatopods that performed in behavioral assays, we calculated an aggressive index for each animal by dividing the number of aggressive contacts by the total number of behavioral responses recorded for that animal. We excluded 2 animals (both females) as non-responsive because they had low total numbers of responses (<10) during behavioral trials. For the remaining stomatopods ($n = 14$), the range of percent aggressive contacts for all animals ranged from 0–40% of all recorded responses. Seven animals were considered aggressive ($n = 4$ males, 2 females, and 1 late-stage reproductive female), and 7 animals were non-aggressive ($n = 3$ males, 2 females, and 2 late-stage reproductive females). On average (SD), aggressive contacts constituted 31.2% (7.0%) of all acts in aggressive animals and only 6.6% (6.4%) in non-aggressive animals.

Underwater Downwelling Irradiance Measurements

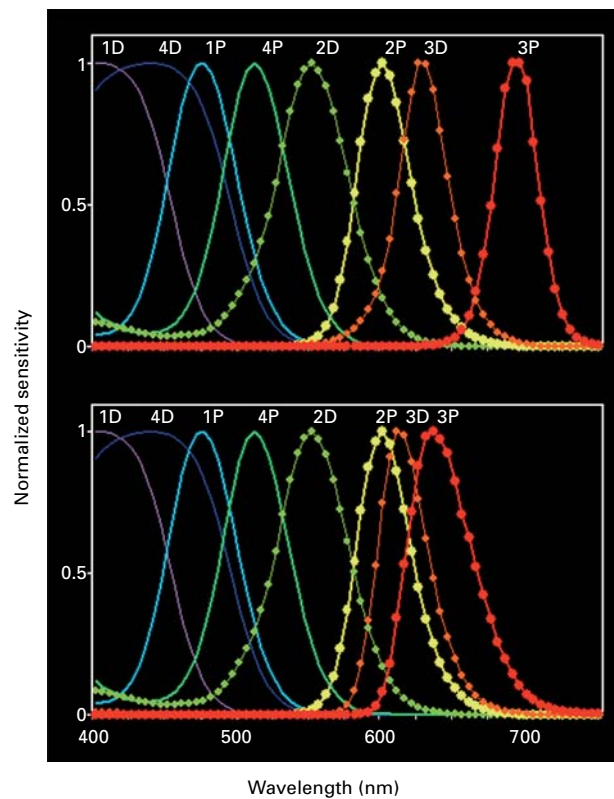
Similar to previous measurements of underwater illumination in tropical marine waters [McFarland and Munz, 1975; Loew and McFarland, 1990], our measurements show that overall intensity in *G. smithii* habitats decreases with depth, and wavelengths >600 nm are increasingly absorbed relative to other wavelengths, producing a dimmer and bluer light environment at depth (fig. 2).



4

Fig. 4. Representative *G. smithii* collected in shallow (<1 m) and deep (18 m) habitats near Lizard Island, Queensland, Australia. The shallow-collected animal is a 73-mm male and the deep-collected animal is a 53-mm female.

Fig. 5. Calculated spectral sensitivities for shallow-adapted (top panel) and deep-adapted (bottom panel) photoreceptors in Rows 1–4 of the ommatidial midband of *Gonodactylus smithii*. Numbers denote ommatidial Row in the midband and letters denote proximal (P) or distal (D) photoreceptor tier. Traces with dots denote photoreceptors with overlying intrarhabdomal filters.



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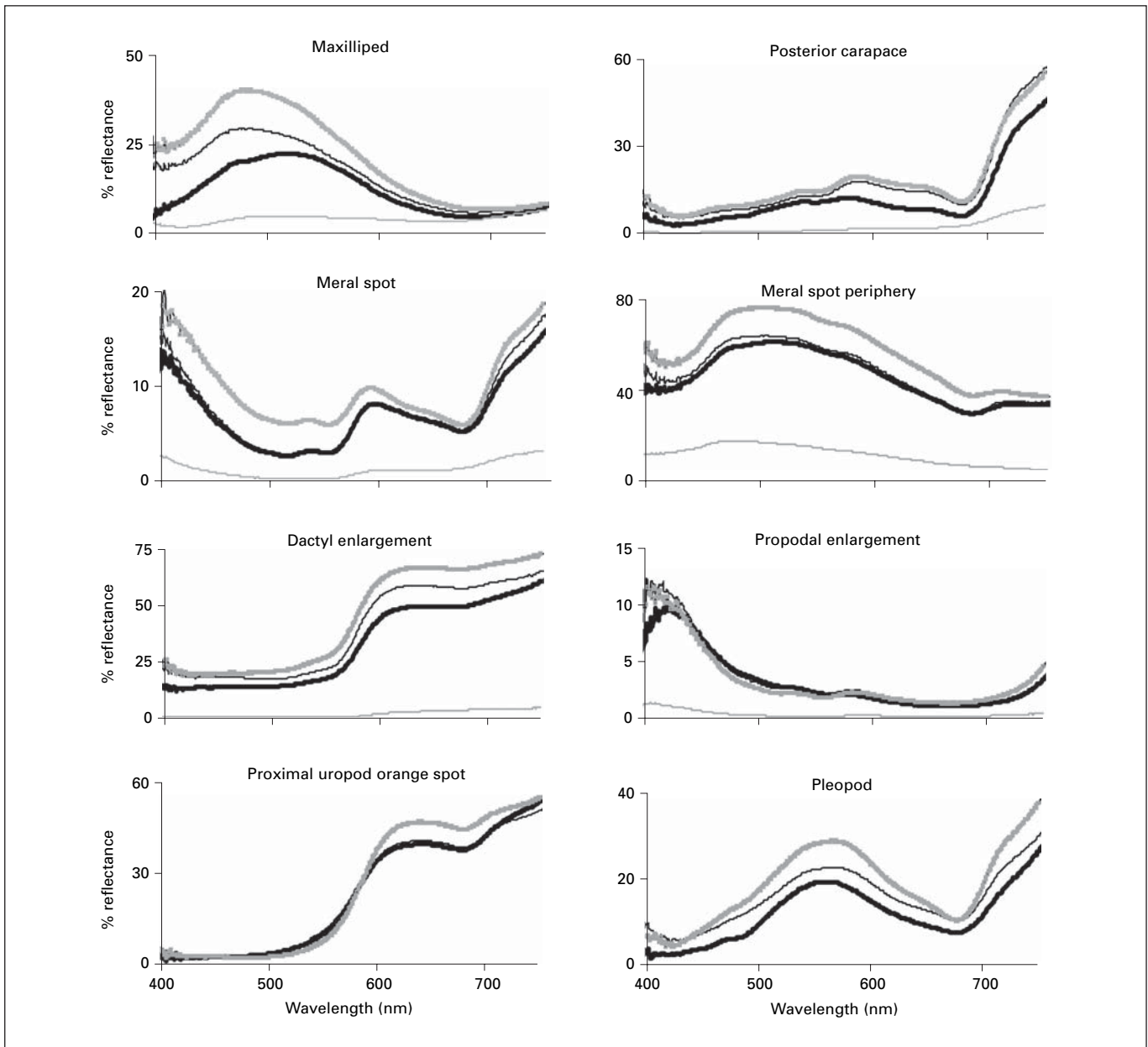


Fig. 6. Reflectance spectra of 8 different body parts in *G. smithii*. Comparisons are among late-stage reproductive females collected shallow (thick grey line, $n = 4$), females collected shallow (thin black line, $n = 8$), males collected shallow (thick black line, $n = 14$) and one female collected in deep water (grey line, $n = 1$). Each curve represents an average of all animals within a group (excluding the one deep-collected female). No measurements of pleopod or uropod scale reflectance were made for the deep animal.

Spectral Sensitivities of G. smithii in Different Depth Habitats

We used data from field-collected shallow-water *G. smithii* and a related deep-collected species (*Gonodactylellus affinis*) to generate spectral sensitivities for shallow and deep-living *G. smithii*. As described above, no

filter material suitable for microspectrophotometric scanning was obtained from deep-living *G. smithii*, so we used filter data from *Gonodactylellus affinis* from identical habitats to compute the required spectral sensitivities in photoreceptors of the third ommatidial row. Computed spectral sensitivities of the 8 photoreceptor classes of

shallow-adapted *G. smithii* have maxima ranging from 400 to 695 nm (fig. 6). Due to spectral changes in the Row 3 filters in deep-living individuals, distal Row 3 receptors are estimated to be short-wavelength shifted by approximately 15 nm relative to shallow-adapted animals. The spectral sensitivity of the proximal Row 3 tier is blue-shifted further (~55 nm) due to changes in filtering both by overlying intrarhabdomal filters and by the distal Row 3 tier.

Detection of Stomatopod Color Signals in Rows 1–4

Comparison of Sexual Coloration in Same Environment. In general, for all shallow-living *G. smithii* we collected, ‘posterior carapace’ and ‘meral spot periphery’ produced low chromaticity values in all receptor pairs (fig. 6, 7). The pink dactyl enlargement’s reflectance was well-placed spectrally to generate high chromaticity values only in Row 2. Reflectances from pleopods and propodal enlargements produced highest chromaticity in the short-wavelength Rows 1 and 4. Those of meral spots produced large chromaticities in Rows 1, 2 and 4. Despite their apparent bluish-white appearance to humans, maxilliped reflectances generated relatively larger chromaticity values in the longer wavelength receptors (Rows 2 and 3). The spectrum from the orange spot on the proximal uropod produced the largest single chromaticity value of all body parts measured (approximately 1.0 in Row 2).

Upon comparing the chromaticity values of body parts of males and females, particular body colors were found to vary sexually (fig. 7). Posterior carapace coloration produced statistically insignificant different chromaticities in all receptor pairs, whereas the maxillipeds were sexually different in their chromaticity values for the short-wavelength receptor pairs (Rows 1 and 4). Late-stage reproductive females differed from males and other females in the Row 2 chromaticity of the uropod orange spot (fig. 7). Females with well-developed cement glands and males had similar chromaticities for meral spot and pleopod reflectances, but these were significantly different from corresponding values for other females (Rows 1 and 4, fig. 7).

Comparison of Aggressive Coloration in the Same Light Environment. In general, reflectances from aggressive animals were brighter (i.e., higher percent reflectance) compared to non-aggressive animals (fig. 8). However, chromaticity values for these spectra from aggressive and non-aggressive *G. smithii* were significantly different only for pleopod coloration in Row 2 chromaticities (fig. 9). The difference in pleopod chromaticity was primarily due to an approximate 20-nm spectral shift in the short-wavelength peak of the reflectance spectrum

between the two groups, with the more aggressive group being long-wavelength shifted.

Physiologically-Adapted G. smithii Color Signaling Systems in Different Depth Environments

To compare *G. smithii* color communication in different light environments, we evaluated how variation in the three components of color signaling (spectral reflectance, spectral sensitivity, and illumination) affected the detection of colors in these animals. We hypothesized that color-signaling systems in *G. smithii* are adapted to their local environment (i.e., shallow vs. deep), so that color signals perceived in the native light environment of deep or shallow-living individuals would produce comparable chromaticity values in Row 1–4 receptor pairs. Furthermore, we predicted that changing any one of the components would generate dissimilar chromaticities and alter the modeled detection of color signals. First, we will make some initial general comparisons of color signals in animals physiologically adapted to their local light conditions. Further modeling comparisons regarding variation in each of the 3 components involved in color signal detection will focus only on the group of shallow-collected animals.

To begin, we compared the chromaticities of body coloration in shallow-adapted animals as normally seen by these same animals (e.g., shallow body coloration, shallow irradiance, shallow sensitivities) with deep-adapted animals seen by deep-living animals (e.g., deep body coloration, deep illumination, deep sensitivities) (fig. 8). Because we only have reflectance data for one deep-collected adult *G. smithii*, comparative differences between shallow and deep coloration should be interpreted with caution. To human vision, *G. smithii* from deeper habitats appear noticeably different in overall body coloration compared to those collected intertidally (fig. 4). Commonly, juveniles and adults collected from deeper water appear reddish whereas shallow-water animals are mottled dark green or olive. This increase in long-wavelength reflectance was seen in the different color signaling areas as well (fig. 6). Consequently, most large chromaticity differences between shallow-living and deep-living animals occurred in the long-wavelength Row 3 receptors. Chromaticities perceived by the other 3 receptor pairs were similar for all body markings except the maxillipeds. Reflectance spectra from maxillipeds from the deep-living individual produced high chromaticity values in the Rows 1 and 4 receptors and low values in Row 2 and 3 receptors, whereas those from shallow maxillipeds produced the opposite pattern of stimulation: low Row 1 and 4 values and high Row 2 and 3 values.

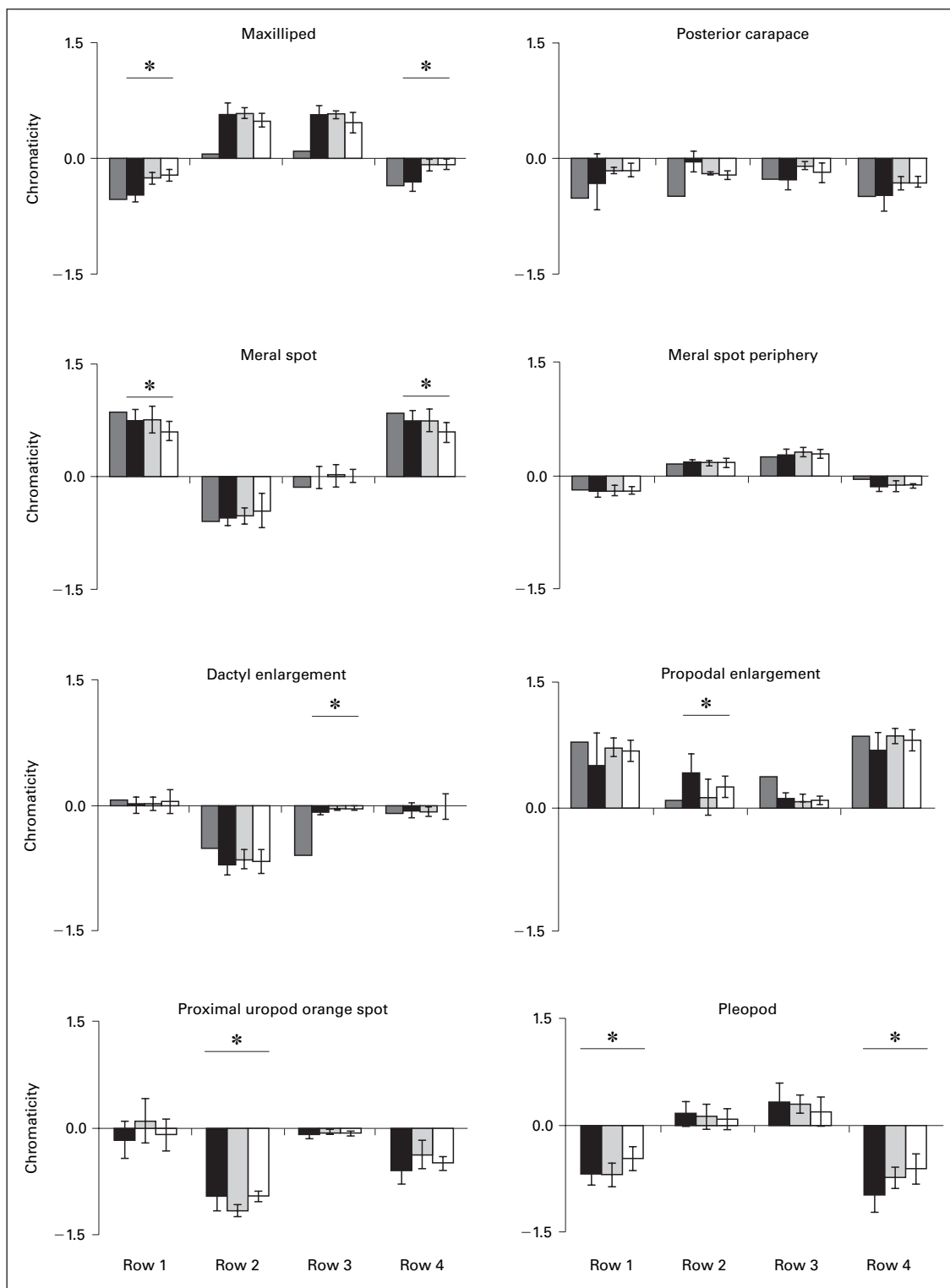


Fig. 7. Chromaticity values of various colored body spots on *G. smithii* as perceived by the midband ommatidial Rows 1–4. Comparisons are between deep-adapted females (deep sensitivity, deep body coloration = grey bars; $n = 1$) and shallow-adapted females (shallow sensitivity, shallow body coloration = white bars; $n = 8$) as

seen in their respective environments. Additionally, shallow females are compared with late-stage reproductive shallow females (hatched white bars; $n = 4$) under shallow (1 m) illumination. All data are means \pm 1 SD. Significant pairwise statistical comparisons are denoted by an asterisk.

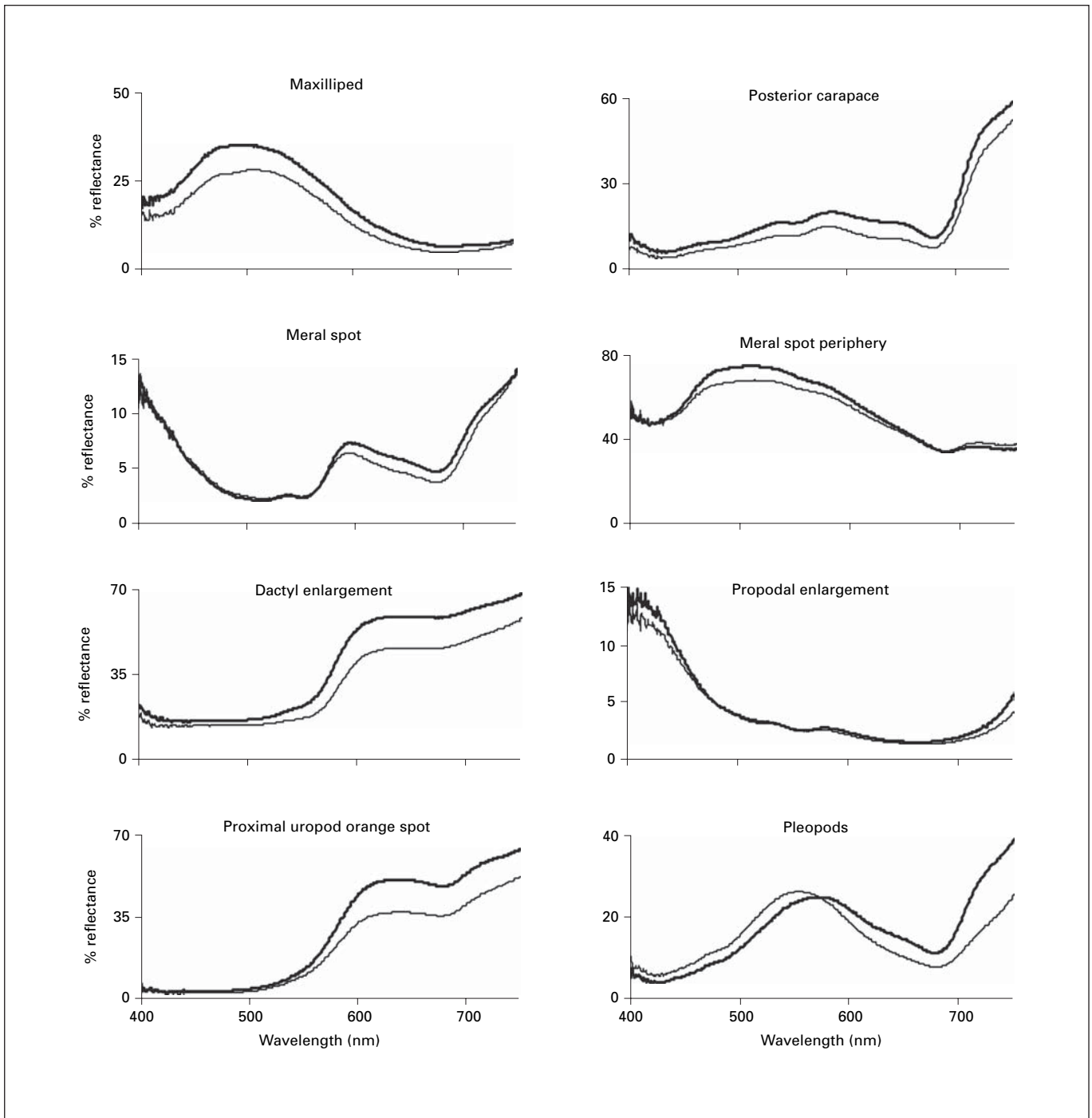


Fig. 8. Reflectance spectra of 8 different body parts in *G. smithii*. Comparisons are of non-aggressive (thin black line, $n = 7$), and aggressive (thick black line, $n = 7$) animals as assessed during intrasexual laboratory trials. See text for group classifying criteria. Each curve represents an average of all animals within a group.

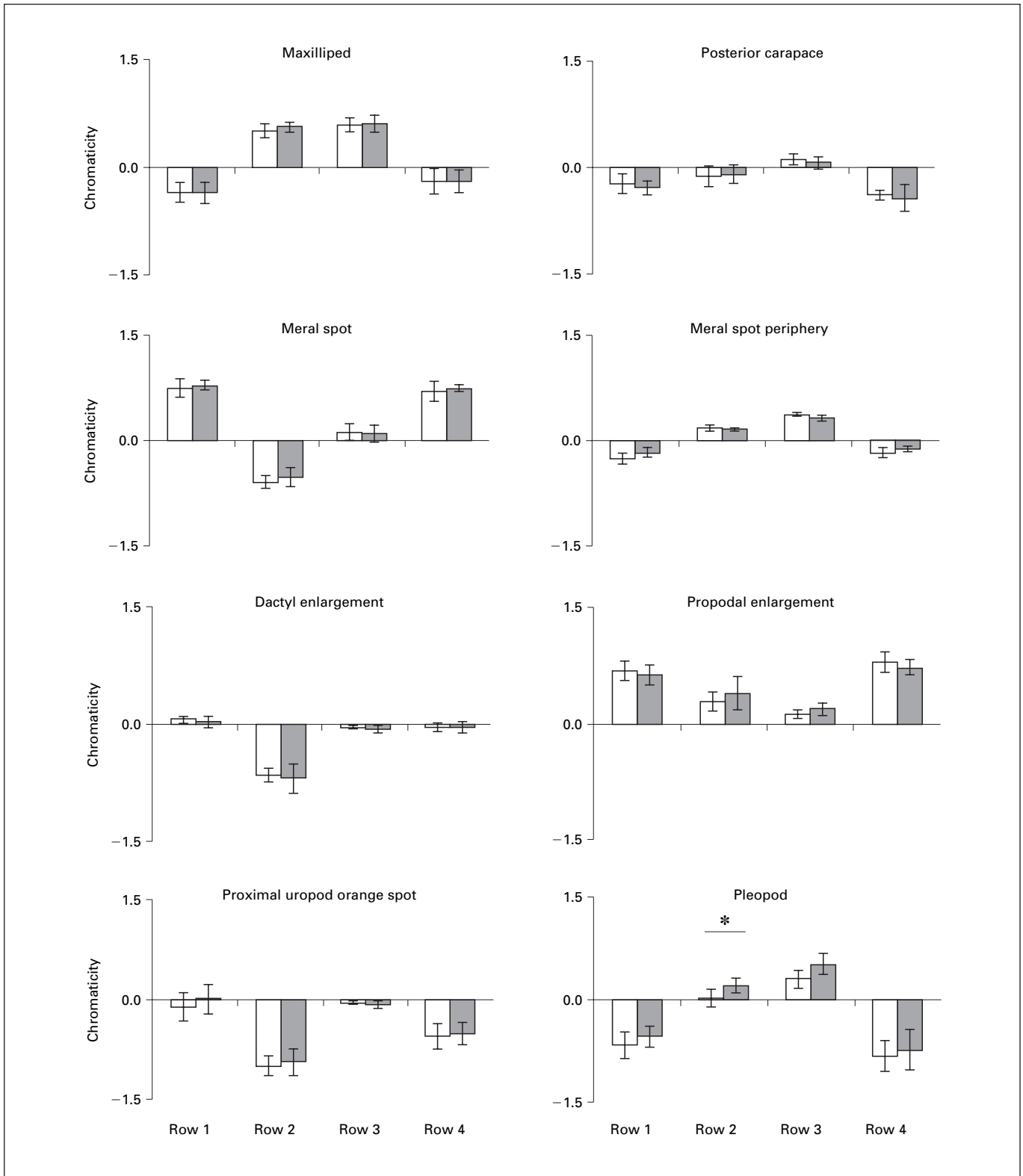


Fig. 9. Chromaticity values of various colored body spots in aggressive versus non-aggressive *G. smithii* as perceived by the midband ommatidial Rows 1 through 4. White bars denote aggressive ani-

mals ($n = 7$) and white-hatched bars denote non-aggressive animals ($n = 7$). All data are means ± 1 SD. Significant pairwise statistical comparisons are denoted by an asterisk.

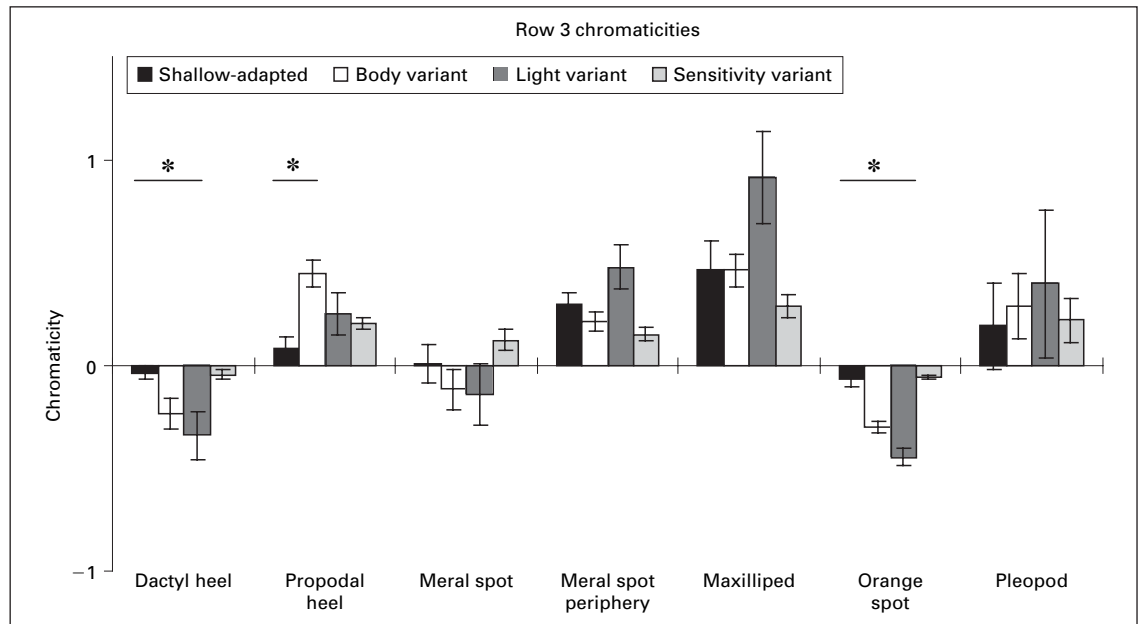


Fig. 10. Mean chromaticity values for various color signaling areas in female *G. smithii* ($n = 8$) as perceived in Row 3 photoreceptors. This figure shows the effect of changing the 3 components involved in Row 3 color signal detection (spectral reflectance, illumination and spectral sensitivity) in *G. smithii*. All models use the spectral reflectance data from intertidal animals. Black bars denote the model of an intertidal animal that is physiologically-adapted (shallow body coloration and spectral sensitivity) in its native light environment. White bars represent a model of an animal with typical

coloration of an intertidal animal viewed by a deep-adapted Row 3 receptors under deep (18 m) illumination. White-hatched bars represent a model of an animal with typical intertidal coloration viewed with shallow-adapted Row 3 receptors but under deep (18 m) illumination. Grey bars denote a model of an animal with typical intertidal coloration viewed with a deep-adapted Row 3 channel under its natural shallow (<1 m) illumination. All data are means \pm 1 SD. Significant pairwise statistical comparisons are denoted by an asterisk.

Effects of Changing Model Components on G. smithii Color Signals

We contrasted the effects of changing body coloration, light environment and spectral sensitivity on chromaticity values by comparing an intertidal animal that was spectrally adapted in both sensitivity and body coloration in its native light environment to other hypothetical variants with one of the three signaling components changed. By creating such a hypothetical color signaling system, we were able to visualize how each component separately affects color signal detection. As seen previously, chromaticities perceived in Rows 1, 2, and 4 were similar for both deep and shallow color morphs, each in its 'own' lighting environment (excluding spectra for the maxillipeds), so we present these data for the Row 3 receptor pairs only (fig. 10). Changes in the body coloration or the illumination both created significantly different Row 3 chromaticity values for the reflectances from the dactyl enlargement (or heel) and the uropod orange spot. The chromaticities for color of the propodal heel were significantly affected in the body color variants only.

Interestingly, the short-wavelength-shifted Row 3 sensitivity set ('sensitivity variant' representative of deeper, subtidal animals often generated similar chromaticities for body markings which had elevated long-wavelength spectral reflectances (dactyl heel, meral spot, orange spot; fig. 10). To examine the performance of spectrally-tuned sensitivity functions of Row 3 when assessing red or orange body markings, we calculated chromaticity values for these markings as illuminated in water over all depths for which we had irradiance measurements (1–18 m). The analysis focused on those body spots that had relatively high long-wavelength reflectance values (dactyl enlargement, uropod orange spot, and meral spot), as these should be the color signals most affected by the spectral changes in illumination occurring with increasing depth (fig. 11). In dactyl enlargement and uropod orange spot coloration, variations in illumination slightly changed the magnitude of the chromaticity, but not the sign (i.e., which tier in a row was more stimulated). Detection of these two spots by shallow- and deep-adapted Row 3 channels was similar from 1 to 13 m. In contrast, chang-

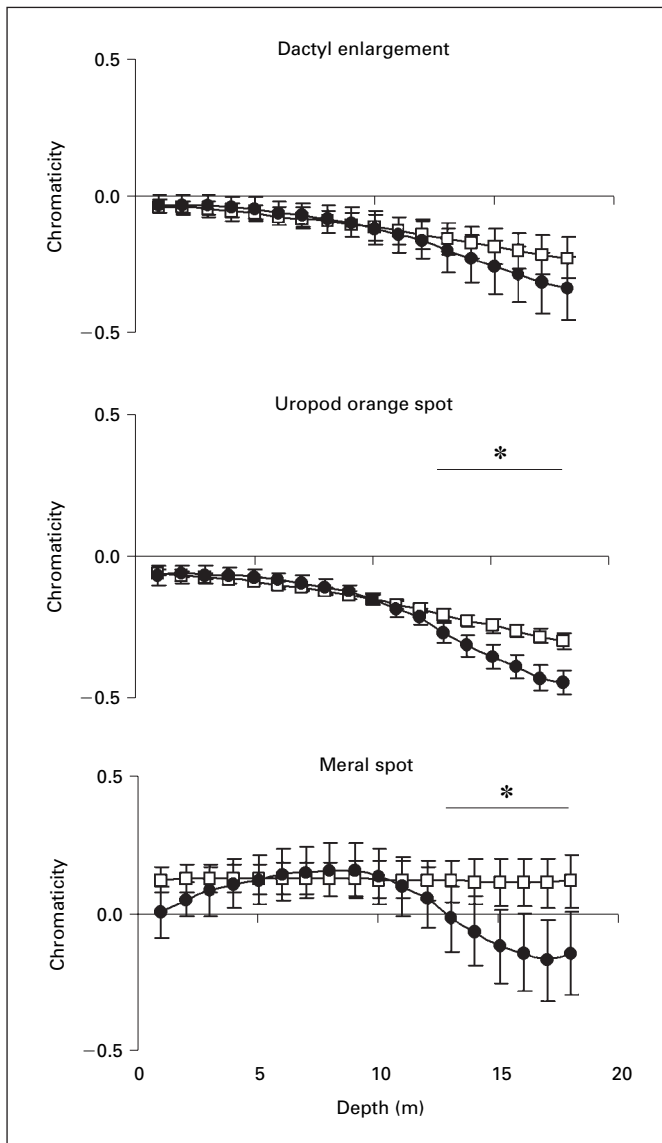


Fig. 11. Chromaticities for 3 body spots in shallow-colored females as viewed by deep-adapted (filled circles) and shallow-adapted (open squares) Row 3 photoreceptors at depths (1–18 m), irradiance spectra from figure 1. All data are means \pm 1 SD. Significant pairwise statistical comparisons between the chromaticity values of deep- and shallow-adapted Row 3 receptors at each depth are denoted by an asterisk.

es in illumination severely affected the detection of meral spots, depending on which Row 3 sensitivity pair (e.g., shallow- or deep-adapted) was chosen. Meral spot chromaticity values from shallow-water reflectance types, as perceived in shallow-adapted Row 3 receptors, varied over 200% (–0.171–0.158) and changed sign as light changed with depth. In contrast, chromaticities for the

same shallow-type meral spots as viewed by deep-adapted Row 3 receptors varied less than 15% (0.109–0.125) with no sign reversal. At depths of 1–13 m, meral spot detection (again, using reflectance from shallow-type animals) in shallow- and deep-adapted Row 3 receptors was similar, but at greater depths (14–18 m) only the deep-adapted Row 3 receptor types maintained a consistent detection of meral spot long-wavelength coloration.

Discussion

The complex color vision system described here and in previous work is generally found in stomatopods of the superfamilies Gonodactyloidea and Lysiosquilloidea that inhabit the clear, marine waters of tropical environments [Harling, 2000]. The species used in this work, *Gonodactylus smithii*, is representative of other ‘smasher’ gonodactyloids with raptorial appendages that have enlarged, highly-calcified dactyl heels that are used for hammering at hard-shelled prey. These armaments also are frequently employed during intraspecific and interspecific contests for resources [Caldwell and Dingle, 1975; Caldwell, 1987]. Most ‘smasher’ mantis shrimp species also have conspicuously colored body spots that are displayed during interactions. It has been hypothesized that these colors might be used as signals to communicate information such as sex or species identification and that the stomatopod color vision system should be able to discriminate these colors in a variety of environments [Caldwell and Dingle, 1976; Hazlett, 1979; Chiao et al., 2000].

According to our analysis, *Gonodactylus smithii* could present information about sex, aggressiveness and reproductive state in colored body parts used in behavioral displays, and these spectral differences should be discernable to other stomatopods with complex color vision. *Gonodactylus smithii* are sexually dichromatic in maxilliped coloration (fig. 6). Maxillipeds are used for signaling during several types of interactions in stomatopods [Dingle, 1969; Dingle and Caldwell, 1969]. Late-stage reproductive females with developed cement glands had uropod orange spots that produced generally greater chromaticity values than did these spots in males or other females. This color indicator of reproductive stage could be critical information for male viewers. In *G. smithii*, well-developed cement glands indicate that a female is about to lay eggs regardless of whether the eggs are fertilized or not. By displaying the colored uropods during such behaviors as the ‘defensive curl’ [where the telson is curled underneath and in front of the cephalo-

thorax, fig. 2, see Caldwell and Dingle, 1976], females may convey their willingness to mate and thereby increase their chance for reproductive success. Another seemingly conspicuous body part, the pink dactyl enlargement or heel, had relatively higher long wavelength reflectances for late-stage reproductive females. However, these differences in overall reflectance did not actually lead to changes in chromaticity in the long-wavelength color channels (Rows 2 and 3). This result stresses the importance of evaluating how colors are seen by potential viewers to examine the biological importance of the color signals [Bennett et al., 1994].

By combining our spectral analyses with intrasexual behavioral assays, we were able to correlate aggressiveness with spectral changes in specific colored body parts. In general, aggressive animals were more brightly colored (i.e., they appear to have higher overall reflectances) in overall body coloration as well as in particular body regions (fig. 9). According to our model, aggressive animals could be spectrally discerned from non-aggressive animals in the coloration of the pleopods using Row 2 receptors (fig. 9). Pleopod spectral reflectance is long-wavelength shifted by approximately 20 nm in aggressive animals compared to non-aggressive animals. There are many examples of aggressive visual displays in both vertebrates and invertebrates [Dingle, 1969; Dingle and Caldwell, 1969; Bradbury and Vehrencamp, 1998]. By visually communicating an indicator of willingness to fight, costly physical contests may be circumvented. Previous behavioral work demonstrates that stomatopods commonly use motion and postural signals in threat displays [Dingle and Caldwell, 1969; Adams and Caldwell, 1990; Bennett et al., 1994]. Body coloration has been correlated with aggression among different gonodactylid species [Caldwell and Dingle, 1976], but our work shows that individual stomatopods might use the color (and potentially brightness also) of specific body parts to communicate a proclivity for violent attacks as well.

The detection of color signals depends on the spectral properties of the target, the illumination, and the 'eye of the beholder'. In species such as *G. smithii* that occur over a wide range of lighting conditions, maintaining signal constancy can be a problem. The colors of the adult female *G. smithii* we collected at a depth of 14 m generally produced larger chromaticity values in the Row 1–4 photoreceptors (when viewed in their natural setting) than did those of animals collected intertidally. Maxillipeds of shallow and deep animals had quite different patterns of chromaticity among photoreceptor classes. Shallow-colored, female maxillipeds generated large chromaticities in the short-

wavelength channels (Rows 1 and 4), whereas the maxillipeds from our deep-collected, adult female created larger chromaticities in the long-wavelength channels (Rows 2 and 3, fig. 5). We have consistently captured *G. smithii* at depths greater than 10 m over many years of collecting at sites on the Great Barrier Reef and, in all cases, the overall body coloration appears red. In opposition to our hypothesis that color signal components should vary adaptively with depth, the coloration of signaling areas in animals residing in deeper habitats does not seem to be effective at maintaining a consistent visual signal that mimics a comparable signal in animals from shallow water. At this time, we only have spectral measurements from one animal and need more samples to examine the spectral properties of color signaling areas in these deep populations.

By varying the illumination in our analysis, we found that in 3 of the 4 hypothetical color receptor pairs of *G. smithii*, variable light environments associated with different depths affected the detection of stomatopod body spots minimally. For Rows 1, 2, and 4, chromaticity values remained similar over the depth range from 1 to 18 m (fig. 2). However, the long-wavelength receptor pair (Row 3) was affected more by the spectral variation in illumination, no doubt because light >600 nm is preferentially absorbed in coastal waters.

Presumably, the phenotypic plasticity evidenced in Row 3 spectral sensitivity functions (associated with changes in the intrarhabdomal filters found therein) could produce a relatively constant detection of long-wavelength color content. Obviously, matching spectral sensitivity to light environment benefits all color-vision functions in stomatopods, not just color signaling. But color signals (such as the shallow-type meral spots) that stimulate these receptors similarly in their differently spectrally-adapted states would maintain an aspect of signal constancy important in communication. An earlier analysis of vision in this species led to the hypothesis that the meral spot may be well-tuned to the Row 3 photoreceptors [Chiao et al., 2000]. From 1 to 13 m, meral spot chromaticities are similar for shallow- and deep-adapted Row 3 receptors. In deeper environments, signal detection varies in the shallow-adapted Row 3 channel. Deep-adapted Row 3 photoreceptors are almost invariant in their detection of meral spot coloration across all depths. Thus, meral spot coloration might have evolved as a constant signal in this species when viewed by conspecifics from any habitat depth.

In summary, using a multiple dichromatic model developed by Chiao et al. [2000], we assessed how variation in body coloration, illumination, and visual spectral sensitivity associated with changing depth can affect color

signal detection in a gonodactyloid stomatopod, *Gonodactylus smithii*. We determined that particular *G. smithii* colors can be used as indicators of sex, sexual condition, and aggressiveness. Particular colored body parts such as the uropod orange spots seemed tuned to specific photoreceptor classes and could be very distinctive color signals in a spectrally diverse environment. Variation in illumination over a wide depth range (1–18 m) mostly affected the detection of color signals in the Row 3 color receptors in this species. The adaptive spectral changes in Row 3 filters that occur with changing depth undoubtedly increase the effective reception of long-wavelength color content in different light environments. The color of the behaviorally important meral spot might have evolved as

a color signal that can be identified readily by other stomatopods in any habitat.

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