

**Adaptive signalling behaviour in stomatopods under varying light conditions**

ALEXANDER G. CHEROSKE<sup>1\*</sup>, THOMAS W. CRONIN<sup>1</sup>, MARY F. DURHAM, & ROY L. CALDWELL<sup>2</sup>

<sup>1</sup>*Department of Biological Sciences, University of Maryland, Baltimore County  
Baltimore, MD 21250, U. S. A.*

<sup>2</sup>*Department of Integrative Biology, University of California, Berkeley, CA 94720,  
U. S. A.*

\*Corresponding author (Current contact information: Life Science Department, Mesa Community College, 7110 E. McKellips Road, Mesa, AZ 85207; email: drcheroske@gmail.com; phone: 480-654-7303; fax: 480-654-7372)

Keywords: marine, crustacean, mantis shrimp, color, communication, vision

## ABSTRACT

Stomatopod crustaceans (mantis shrimp) are aggressive benthic marine predators with extraordinary color vision. When communicating with conspecifics, many stomatopods display conspicuously colored body areas, often in combination with other types of signals such as motion and chemical cues. Some species occupy wide depth ranges (>30 m), where changing light conditions can influence color perception. To test the potential effects of differing ambient light on signalling behaviour, stomatopods (*Gonodactylus smithii*) interacted with conspecifics in aquaria, under full-spectrum, high-intensity light or light restricted in either spectrum or intensity. During intra- and intersexual trials in full-spectrum, high-intensity light, animals performed more aggressive acts using colored body parts (meral spread, lunge, strike). Stomatopods used significantly more antennular flicking, and performed aggressive acts at reduced distances under restricted light conditions. To compare the use of antennules in visual and chemical communication, additional experiments showed more antennular flicking in response to chemical stimuli from food or conspecifics compared to seawater controls. This response ceased immediately after ablation of antennular chemoreceptors but returned to pre-treatment levels after 5 days of recovery. These findings suggest that stomatopods can vary their use of signals during conspecific interactions under different photic conditions. These inducible, plastic behavioral responses can potentially improve signal transfer in varying light environments.

## Introduction

The phrase “as different as day and night” is used in reference to diurnal light changes, but photic variability occurs at much finer temporal and spatial scales as well. Changes in ambient light intensity and spectrum can be caused by variation in solar angle, atmospheric conditions and overlying structures such as plant canopies (Cummings and Partridge, 2001; Endler, 1991; Fleishman et al., 1997; Hailman, 1977; 1979; Thèry, 2001). Aquatic communities are affected by these and additional factors that modify illumination underwater (Loew and McFarland, 1990; Lythgoe, 1990). Passing waves can alter light intensity in the water column on small temporal and spatial scales (McFarland and Loew, 1983). The water and its constituents (such as dissolved organic matter or phytoplankton) also absorb light, so that even the clearest tropical waters absorb downwelling light (McFarland and Munz, 1975). With increasing depth, the ambient light becomes dimmer and bluer until approximately 1000 meters, where the intensity of downwelling light in even the clearest waters becomes insufficient for vision (Denton, 1990).

Many aquatic organisms use behavioral displays that incorporate color to communicate during interactions. Research with aquatic vertebrates is dominated by studies of poeciliid guppies (Endler, 1991; Gamble et al., 2003; Guevara-Fiore et al., 2009; Reynolds et al., 1993; Rodd et al., 2002), and examples from other colorful fish also exist (Boughman, 2001; Fuller, 2002; McLennan, 1994; Rowe et al., 2004). Data on signalling in aquatic invertebrates are severely lacking by comparison. Ostracods in the genus *Vargula* use bioluminescent flashes of light to communicate to conspecifics in

midwater environments (Morin and Cohen, 1991). Color signalling in fiddler crabs, genus *Uca*, has a significant role in identifying other species and potential mates (Detto, 2007; Detto et al., 2006; Forward et al., 1988; Zeil and Hofmann, 2001).

Mantis shrimp in the superfamily Gonodactyloidea use ritualized displays of colorful body parts including eye-spots on the medial surface of the meral segments of the second maxillipeds, termed “meral spots,” as well as other colored areas of the maxillipeds, the pleopods, and telson (Figure 1; Adams and Caldwell, 1990; Caldwell, 1987; Caldwell and Dingle, 1976). These displays may transmit information about willingness to fight or notify potential mates of quality or sexual receptivity (Cheroske and Cronin, 2005). The evolution of these color signals may have been facilitated by the complex stomatopod color vision system (Chiao *et al.*, 2000). Many gonodactylid stomatopod species occur over a wide range of depths from shallow intertidal down to greater than 50 meters, so their light environment varies significantly (Cronin et al., 2002; Cronin et al., 1994a; Cronin et al., 2000). Variation in illumination intensity or spectral composition can obscure visual signals and affect the perception of reflected animal coloration (Endler, 1991; Hailman, 1979). Under visually limited conditions, many animals utilize other communication behaviours either in addition to or instead of visual signals (Hailman, 1979; Hebets and Papaj, 2005; Ord and Stamps, 2008; Rypstra et al., 2009; Salmon and Astsaides, 1968). This paper describes research to assess the effects of changing light environment and chemical cues on the behaviour of conspecific receivers in a gonodactylid stomatopod species. While stomatopods use various conspicuously colored body parts during interactions, other visual signals may come from the movement

of other less conspicuously colored body parts such as the antennules. Under restricted light conditions, these animals may change their signalling behaviour to maintain effective communication, using different types of visual signalling or switch to chemical signals. Since antennae and antennules also are used for chemoreception, our experiments test their use in reaction to chemical stimuli and then observe their use during behavioural trials interacting with other individuals under different light conditions. This work serves to demonstrate the plastic signalling behaviours of stomatopods that may occur according to the variable photic environment in which these animals live.

## **Methods**

### ***Focal species***

*Gonodactylus smithii* is a medium-sized species of mantis shrimp (~ 60 mm at maturity; maximum total length of 95 mm) that commonly resides in tropical Pacific littoral zones but also has been found at depths greater than 20 meters. Individuals of *Gonodactylus smithii* were collected intertidally on Coconut Reef flat on the eastern side of Lizard Island, on the Great Barrier Reef of Australia, during the summers of 2002, 2003 and 2006. Animals were maintained in containers in a laboratory under fluorescent and natural lighting from a nearby window. Natural seawater in the containers was changed daily, and animals were fed fresh fish biweekly.

### ***Behavioral assays***

#### ***Animal interactions.***

Interactions between animals took place during July 2002, August 2003 and June 2006. Assays were conducted with adult animals (> 50 mm) at Lizard Island Research Station, Australia. All experiments were performed in an enclosed indoor laboratory under full-spectrum (white), reduced intensity white, or reduced spectrum (blue) fluorescent lighting (Figure 2A). These two light treatments were very coarse approximations of the photic variation associated with depth as measured in waters near collection sites for *G. smithii* (Figure 2B). Longer wavelengths (> 550 nm) in the blue light treatment were removed using plastic filter material (Lee Filters, HT 172) placed around a blue fluorescent tube. Reduced intensity lighting was produced by covering full-spectrum fluorescent tubes with 3 layers of standard fiberglass window screening that allowed approximately 20% light transmission. While many stomatopods are known to have multiple ultraviolet receptors (Cronin et al., 1994b), the work on behaviourally relevant colored body spots on *G. smithii* conducted previously by two of the authors (AGC and TWC) focused only on wavelengths between 400 and 750 nm. To remain consistent with previous work and limit the introduction of additional factors associated with unknown ultraviolet signals, these experiments also were conducted with a similar spectral range. During assays, animals were housed in 4-liter aquaria with a 1.5 cm diameter polyvinyl chloride (PVC) pipe as a domicile. The domicile was placed adjacent to the front glass with one end abutted to the side of the aquarium to provide only one entrance to the tube. This position ensured that all interactions took place with the animal facing out and facilitated clear video images of interactions for later analysis. Animals were size-matched (within  $\pm 2$  mm body length, = < 5% difference) in all trials, as body length differences as little as 10% can affect fight outcomes (Adams and Caldwell, 1990; Caldwell and Dingle, 1979).

Experiments were conducted to assess the effect of sex (intrasexual and intersexual interactions) and light (white and blue) on behaviors between individuals. During intrasexual trials, one animal of each matched pair ( $n = 5$  trials in each light treatment) was assigned randomly to be the “resident” and was allowed to acclimate to the aquarium and domicile overnight before a trial. For intersexual trials, residents ( $n = 8$  trials per light treatment) were all female, as males commonly look actively for receptive females in their native habitats. To begin a trial, the “intruder” was introduced to the opposite end of the tank from the resident in the domicile. All interactions were video recorded for a 20-minute period. Previous studies of stomatopod behaviour have shown that most relevant interactions occur within the first 20 minutes, and in size-matched contests, dominance by one animal is usually established within 10-20 minutes (Dingle, 1969; Dingle and Caldwell, 1969). Interactions of both contestants were classified as neutral, offensive or defensive. Offensive actions included: approach, antennular flicking, meral spread, telson push (pushing the telson into the domicile of the resident), lunge, grab (grasping the body of another using maxillipeds), strike (hitting another with the dactyl closed), and stab (extension of the dactyl and piercing another) (Dingle, 1969; Dingle and Caldwell, 1969). Defensive actions included avoid and telson curl (flexion of the abdomen that brings the telson underneath and in front of the animal). Additionally, whether the resident retained or vacated the domicile was recorded. Response variables were number of aggressive contacts (including grab, strike and stab), number of antennular flicking bouts, and number of meral spreads. For each of the three response variables, the mean percent of each variable ( $\#$  of specific response/total  $\#$  of responses)

was calculated for each treatment, and results were compared using a two-way, fixed factor ANOVA using light and sex as main effects with a significance level of  $p < 0.05$  (S-Plus statistical software). Animals that were relatively unresponsive ( $< 9$  total responses/trial) were excluded from analyses to reduce bias in calculated performance percentages due to low total responses. The distances at which antennular flicking and meral spreads occurred were estimated to the nearest centimeter, and these data were compared using a t-test with an assumed significance level of  $p < 0.05$  (S-Plus statistical software).

Additional size-matched, additional intrasexual interactions (n=22) took place under laboratory conditions described previously but comparing behaviors in full-intensity and reduced-intensity white fluorescent light to both visual and chemical cues. After reviewing results from our earlier experiments, we modified experimental protocols for visual stimuli in three ways. First, we conducted experiments under high or low intensity light conditions (Figure 2A) without spectral modification to avoid confounding effects of intensity and spectral modifications of light environment. Second, interacting animals were separated by a clear panel of plexiglass to ensure that the animals could not harm each other. Lastly, we modified our assay periods. We recorded 90 seconds of ambient activity before the introduction of an intruder or chemical stimulant and then 90 seconds after the test period ended. These data allowed us to compare a baseline of activity by each animal prior to an experimental treatment in order to show that any behaviors observed after treatment were in response to the treatment and not due to an “overly active” animal. Resident response categories were recorded as before, but “grab”

was changed to “attempted grab” since the animals were could not touch one another due to the plexiglass partition. Because the responses of the same animals were used in both light treatments, we used a Wilcoxon pairwise comparison at  $p < 0.05$  for these data.

#### *Chemical stimuli.*

To establish a context of behaviours of *G. smithii*'s use of antennules, a subset of animals used in the 2006 intrasexual interactions was used in experiments testing their responses to various chemicals introduced into the surrounding water. Chemicals introduced were 1) water from a 100 ml container with seawater with approximately  $0.5 \text{ mm}^3$  of fish suspended in it for 3 minutes, 2) seawater from a 300 ml container that housed a size-matched conspecific for 24 hours, and 3) seawater with no odorant added. Following the 90 second “pre-treatment” period, one ml of one of the experimental solutions was introduced via a 3 ml syringe and the behavioral responses that occurred in the following 90 seconds were recorded. The 1 ml solution was administered from above the surface of the water over the domicile at an approximately constant rate by removing the plunger from the syringe and allowing the fluid to drain until gone. The order of odour presentation was random. Data were analyzed using a Wilcoxon signed rank test at  $p < 0.05$  for paired data and Friedman's test at  $p < 0.05$  for comparing more than 2 treatments.

To show that stomatopod antennular behaviors in the above experiments were due to responses to chemical and not mechanical stimuli, we ablated *G. smithii* antennules and then again recorded their responses to the three chemical treatments. In

stomatopods, ablation of chemoreceptive sensillae on the antennules with freshwater has been suggested to be effective for approximately one week at which time the ability to respond to chemical stimuli returns (RLC). Individual *G. smithii* that had already completed a full round of chemical stimuli were ablated and then retested the next day. During ablation, individuals had all their antennae, and antennules entirely submerged in distilled water for 1 minute. Afterwards, they were given 5 days to recover and were tested again to the same chemical stimuli. Data were analyzed using a Wilcoxon signed rank test at  $p < 0.05$ .

## **Results**

Our behavioral experiments were conducted to determine if stomatopods of the species *Gonodactylus smithii* changed their signalling behaviors according to different light conditions. We compared behavioral responses during intra/intersexual encounters under unrestricted and restricted light conditions. We conducted further experiments to explore the use of antennules as structures involved in both visual and chemical signalling. We also included a comparison of 90 seconds of pre/post experimental treatment activity to exclude the possibility that behaviors recorded were an “overly active” animal rather than in response to the treatment. In all cases, we found no significant differences in behaviour between the treatments in the pre-experimental observation period.

### ***Animal interactions***

#### ***Intrasexual assays.***

No significant effect of light or sex on aggressive contacts was observed in 2002-03 intrasexual assays. However, *G. smithii* performed significantly more antennular flicking in blue light than in white ( $F_{1,23} = 4.34, p < 0.05$ , Figure 3). There were no significant sexual differences in antennular flicking. The relative frequency of meral spreads performed did not vary significantly according to sex or light but the performance distance for meral spreads was reduced in blue light compared to white (Welch Modified t-Test:  $t_{25} = -2.43, p < 0.05$ , Figure 4).

*Intersexual assays.*

In intersexual assays, there again was no significant effect of light or sex on aggressive contacts (Figure 3). As in the intrasexual trials, antennular flicking occurred more in the blue light than white ( $F_{1,8} = 5.41, p < 0.05$ ), but there was no effect of sex. There was no significantly differential use of meral spreads according to either factor (Light:  $F_{1,9} = 3.55, p < 0.10$ ; Sex:  $F_{1,9} = 0.98, p < 0.35$ ). Performance distances of meral spreads were reduced significantly in blue light relative to white (Welch Modified t-test:  $t_{26} = -2.44, p < 0.05$ , Figure 4).

***Additional intrasexual assays.***

*Visual stimuli.* During 2006, residents performed more aggressive acts (meral spreads, strikes, attempted grabs) when viewing a conspecific under full intensity light conditions when compared to low intensity treatments (Wilcoxon test:  $W = 18, z_{15} = -2.521, p < 0.05$ , Figure 5). When in reduced intensity light, significantly more antennular flicking occurred relative to full intensity light (Wilcoxon test:  $W = 60, z_{15} = -2.215, p < 0.05$ , Figure 5).

*Chemical stimuli.*

Animals exposed to a 1 ml water sample taken from a container with suspended food or a conspecific, exhibited significantly more antennular flicks compared to a seawater control (Friedman's test:  $X^2 = 11.63$ ,  $df = 2$ ,  $n = 15$ ,  $p < 0.005$ , Figure 6). Flicking behaviors included unilateral and bilateral movement of the antennules at various angles.

*Ablation experiments.*

Immediately after treating the antennae and antennules with freshwater, flicking in the presence of either test odorant was significantly reduced compared to untreated response levels to both odorants (Wilcoxon tests. Conspecific:  $W = 60$ ,  $z_{15} = -2.045$ ,  $p < 0.05$ ; food:  $W = 115.5$ ,  $z_{21} = -3.007$ ,  $p < 0.005$ , Figure 7). After 5 days of recovery, animals once again responded to both odorants and at levels unchanged from pre-ablation results (Wilcoxon tests. conspecific:  $W = 14$ ,  $z_7 = -2.366$ ,  $p < 0.05$ ; food:  $W = 10.5$ ,  $z_6 = -1.992$ ,  $p < 0.05$ , Figure 7). No significant differences were detected for seawater controls in the pre-ablation versus post-ablation (Wilcoxon = 18,  $z_8 = -1.12$ ,  $p < 0.13$ ) or post-ablation versus recovered conditions (Wilcoxon = 3,  $z_3 = 0$ ,  $p < 0.50$ ).

**Discussion**

Many animals perform signals in specific environments that increase the conspicuousness of the signal. In particular, photic conditions influence the timing and type of display used by birds and fishes (Endler, 1991; Fuller, 2002; Gamble et al., 2003; Heindl and Winkler, 2003; Long and Rosenqvist, 1998; McNaught and Owens, 2002; Reynolds et

al., 1993). Few previous examples of variation in signalling tactics with environment exist for marine animals or for invertebrates in general (Acquistapace et al., 2002; Hazlett et al., 2007; Hebets, 2005; Hebets, 2008; Hebets and Papaj, 2005; VanderSal and Hebets, 2007). In our experiments, *G. smithii* used different types of signals in different light environments. Animals performed significantly more aggressive behaviors including meral spreads, grabs, and strikes, in high-intensity light compared to light conditions with reduced intensity. The reduction in light across a broad spectrum may have limited the stimulation of many of *G. smithii* photoreceptor types possibly making the discernment of an intruder more difficult and thereby reducing their willingness to engage in aggressive actions. In a visually limited environment, where light intensity is relatively low and/or the spectrum is truncated, color or pattern signals would be potentially unreliable. However, by using other types of signals such as antennular flicking or by performing signals closer to viewing conspecifics, *G. smithii* could increase signal transfer efficiency in restricted light conditions.

In fact, we did find that signalling tactics in *G. smithii* varied according to light environment, potentially increasing successful information transmission and reception. Antennular flicking was used significantly more in light conditions where either intensity or spectral range was reduced during both intersexual and intrasexual interactions (Figures 2, 4). This behaviour may enhance communication in several ways. In stomatopods, antennular flicking can be used as an aggressive visual signal (Dingle, 1969; Dingle and Caldwell, 1969). Visual displays often involve a component of movement that works to increase conspicuousness and draw the attention of the intended

receiver, and in vertebrates, motion signals are often used prior to other visual signals (Fleishman, 1988; Hailman and Dzelzkalns, 1974; Peters and Evans, 2003; Taylor et al., 2000), perhaps as an alerting mechanism (Ord and Stamps, 2008). In stomatopods, antennular flicking (itself a signal of aggression) is often used with other aggressive acts such as meral spreads and strikes with the raptorial appendage, so it may have several roles as a motion signal. Upon seeing another stomatopod, an individual will often display a lateral spread of antennules then quickly bring the antennules together in a medial sweep. If a meral spread follows, the antennules continue to be held spread laterally as part of the aggressive display (Figure 1).

While movements of the antennules in stomatopods occur during visual signalling, such movements also play roles in chemoreception. Stomatopods can recognize conspecifics using chemical cues alone (Caldwell, 1979). In this study, we saw significantly more antennular flicking in response to seawater containing chemicals from a conspecific or fish than to control seawater lacking such chemicals. We also verified that this response is absent when chemoreception is eliminated. The increased use of antennular flicking in normal animals under restricted light treatments (spectrum and/or intensity) may indicate that *G. smithii* use multimodal signals, and introduce other signalling modalities when visual signals may be compromised or to increase signal transfer as seen in other invertebrates (Hebets, 2005; Hebets, 2008; Hebets and Papaj, 2005; Rypstra et al., 2009). Quick movements of antennules reduce boundary layers around the sensory structures and facilitate delivery of chemical compounds (Mead *et al.*, 1999) but as described above, such movements also may be used as an achromatic

motion signal or as a mechanical means of communication. Other invertebrates, such as fiddler crabs (Genus *Uca*) and jumping spiders (Salticidae), have been shown to use non-visual signalling systems under visually restricted conditions (Jackson, 1977; Salmon, 1967; Salmon and Astsaides, 1968; VanderSal and Hebets, 2007).

Changes in light environment also affected the distance at which *G. smithii* displayed visual signals. Display distances were reduced in blue compared to white light in both sets of experiments that examined conspecific interactions: meral spreads were performed closer to conspecific viewers under blue-light conditions in both intrasexual and intersexual assays (Figure 4). Waters around Lizard Island where these animals were collected preferentially absorb long-wavelength and ultraviolet light (Figure 1B, Cheroske and Cronin, 2005), so *G. smithii* may commonly encounter spectral variations in light environment similar to those of our experiments. Similarly, natural light intensities vary with depth, weather, and time of day. By performing signals closer to conspecifics when light becomes limited, *G. smithii* may minimize the risk of wasting extra energy on repeated signals. Similarly, guppies also reduce courting distances under low light intensities in lentic environments (Long and Rosenqvist, 1998).

Our work suggests that mantis shrimps place less reliance on color signalling in low light environments. In such conditions, alternative signalling methods were recruited. Our results illustrate the importance of environment in signalling behaviour and suggest that invertebrates can be excellent subjects for studies of visual communication.

**Acknowledgements**

We thank Justin Marshall, Kylie Jennings, and Short Chiou for help collecting animals, data and lively discussions. We also thank the directors and staff of Lizard Island Research Station for facilitating our field work and two anonymous reviewers for their constructive comments. Brian Bradley, Karen Osborne and Zhen Li offered statistical advice. Lastly, we thank the tireless efforts of the editor for his part in the publishing of this work. This research was funded partially by NSF grant (IBN-0235820) to TWC and Sigma Xi Grants-in-Aid to AGC.

## References

- Acquistapace P, Aquiloni L, Hazlett BA, Gherardi F, 2002. Multimodal communication in crayfish: sex recognition during mate search by male *Austropotamobius pallipes*. *Can. J. Zool.* 80:2041-2045.
- Adams ES, Caldwell RL, 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behavior* 39:706-716.
- Boughman JW, 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 411:944-946.
- Caldwell RL, 1979. Cavity occupation and defensive behavior in the stomatopod *Gonodactylus festai*: evidence for chemically mediated individual recognition. *Anim Behav* 27:194-201.
- Caldwell RL, 1987. Assessment strategies in stomatopods. *Bulletin of Marine Science* 41:135-150.
- Caldwell RL, Dingle H, 1976. Stomatopods. *Scientific American* 234:80-89.
- Caldwell RL, Dingle H, 1979. The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. *Behaviour* 69:255-264.
- Cheroske AG, Cronin TW, 2005. Variation in stomatopod (*Gonodactylus smithii*) color signal design associated with organismal condition and depth. *Brain, Behavior and Evolution* 66:99-113.
- Chiao CC, Cronin TW, Marshall NJ, 2000. Eye design and color signaling in a stomatopod crustacean, *Gonodactylus smithii*. *Brain Behav Evol* 56:107-122.
- Cronin TW, Caldwell RL, Erdmann MV, 2002. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. I. Visual pigments. *J Comp Physiol A* 188:179-186.
- Cronin TW, Marshall NJ, Caldwell RL, 1994a. The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). *J. Comp Physol. A* 174:607-619.
- Cronin TW, Marshall NJ, Caldwell RL, 2000. Spectral tuning and the visual ecology of mantis shrimps. *Phil Trans R Soc Lond B* 355:1263-1267.
- Cronin TW, Marshall NJ, Quinn CA, King CA, 1994b. Ultraviolet photoreception in mantis shrimp. *Vision Res.* 34:1443-1452.
- Cummings ME, Partridge JC, 2001. Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. *J Comp Physiol A* 187:875-889.
- Denton EJ, 1990. Light and vision at depths greater than 200 meters. In: *Light and life in the sea* (Maddock L, ed). Cambridge: Cambridge University Press; 357.
- Detto T, 2007. The fiddler crab *Uca mjoebergi* uses colour vision for mate choice. *Proc. R. Soc. Lond. B* 274:2785-2790.
- Detto T, Backwell P, Hemmi JM, Zeil J, 2006. Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proc. R. Soc. Lond. B* 273:1661-1666.
- Dingle H, 1969. A statistical and information analysis of aggressive communication in the mantis shrimp *Gonodactylus bredini* Manning. *Anim Behav* 17:561-575.
- Dingle H, Caldwell R, 1969. The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Behaviour* 33:115-136.

- Endler JA, 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Res* 31:587-608.
- Fleishman LJ, 1988. Sensory influences on physical design of a visual display. *Anim Behav* 36:1420-1424.
- Fleishman LJ, Bowman M, Saunders D, Miller WE, Rury MJ, Loew ER, 1997. The visual ecology of Puerto Rican anoline lizards: habitat light and spectral sensitivity. *J Comp Physiol A* 181:446-460.
- Forward RB, Cronin TW, Douglass JK, 1988. The visual pigments of crabs II. Environmental adaptations. *J Comp Physiol A* 162:479-490.
- Fuller RC, 2002. Lighting environment predicts the relative abundance of male colour morphs in bluefin killifish (*Lucania goodei*) populations. *Proc Royal Soc of Lond B* 269:1457-1465.
- Gamble S, Lindholm AK, Endler JA, Brooks R, 2003. Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behavior and sexual selection in guppies. *Ecology Letters* 6:463-472.
- Guevara-Fiore P, Skinner A, Watt PJ, 2009. Do male guppies distinguish virgin females from recently mated ones? *Animal Behaviour* 77:425-431.
- Hailman JP, 1977. Chapter 7: Noise. In: *Optical Signals - Animal communication and light*. Bloomington, IL: Indiana University Press; 191-248.
- Hailman JP, 1979. Environmental light and conspicuous colors. In: *The behavioral significance of color* (Burt EH, ed). New York: Garland STPM Press; 456.
- Hailman JP, Dzelzkalns JJI, 1974. Mallard tail-wagging: Punctuation for animal communication? *Am Nat* 108:236-238.
- Hazlett BA, Lawler S, Edney G, 2007. Agonistic behavior of the crayfish *Euastacus armatus* and *Cherax destructor*. *Mar Fresh Behav Physiol* 40:257-266.
- Hebets EA, 2005. Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology* 16:75-82.
- Hebets EA, 2008. Seismic signal dominance in the multimodal courtship display of the wolf spider *Schizocosa stridulans* Stratton 1991. *Behavioral Ecology* 19:1250-1257.
- Hebets EA, Papaj DR, 2005. Complex signal function: developing a framework of testable hypothesis. *Behav Ecol Sociobiol* 57:197-214.
- Heindl M, Winkler H, 2003. Interacting effects of ambient light and plumage color patterns in displaying Wire-tailed Manakins (Aves, Pipridae). *Behav Ecol Sociobiol* 53:153-162.
- Jackson RR, 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Anim Behav* 25:953-957.
- Loew ER, McFarland WN, 1990. The underwater visual environment. In: *The visual system of fish*, 1st ed (Djamgoz M, ed). London: Chapman and Hall; 1-43.
- Long KD, Rosenqvist G, 1998. Changes in male guppy courting distance in response to a fluctuating light environment. *Behav Ecol Sociobiol* 44:77-83.
- Lythgoe JN, 1990. *The ecology of vision*. Oxford: Clarendon Press.
- McFarland WN, Loew ER, 1983. Wave produced changes in underwater light and their relations to vision. *Env. Bio. Fish.* 8:173-184.
- McFarland WN, Munz FW, 1975. Part II: The photic environment of clear tropical seas during the day. *Vision Res* 15:1063-1070.

- McLennan DA, 1994. Changes in female colour across the ovulatory cycle in the brook stickleback, *Culaea inconstans* (Kirtland). *Can J Zool* 72:144-153.
- McNaught MK, Owens IPF, 2002. Interspecific variation in plumage color among birds: species recognition or light environment? *J Evol Biol* 15:505-514.
- Mead KS, Koehl MAR, O'Donnell MJ, 1999. Stomatopod sniffing: the scaling of chemosensory sensillae and flicking behavior with body size. *JEMBE* 241:235-261.
- Morin JG, Cohen AC, 1991. Bioluminescent displays, courtship and reproduction in ostracodes. In: *Crustacean Sexual Biology* (Martin J, ed). New York: Columbia University Press; 1-16.
- Ord TJ, Stamps JA, 2008. Alert signals enhance animal communication in "noisy" environments. *PNAS* 105:18830-18835.
- Peters RA, Evans CS, 2003. Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends on duration. *J Exp Biol* 206:4293-4307.
- Reynolds JD, Gross MR, Coombs MJ, 1993. Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. *Anim Behav* 46:145-152.
- Rodd FH, Hughes KA, Grether GF, Baril CT, 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc Royal Soc of Lond B* 269:475-481.
- Rowe MP, Baube CL, Loew ER, Phillips JC, 2004. Optimal mechanisms for finding and selecting mates: how threespine stickleback (*Gasterosteus aculeatus*) should encode male throat colors. *J Comp Physiol A* 190:241-256.
- Rypstra AL, Schlosser AM, Sutton PL, Persons MH, 2009. Multimodal signalling: the relative importance of chemical and visual cues from females to the behaviour of male wolf spiders (Lycosidae). *Animal Behaviour* 77:937-947.
- Salmon M, 1967. Coastal distribution, display and sound production by Florida fiddler crabs (genus *Uca*). *Anim Behav* 15:449-459.
- Salmon M, Astsaides SP, 1968. Visual and acoustical signalling during courtship by fiddler crabs (Genus *Uca*). *Am Zool* 8:623-639.
- Taylor PW, Hasson O, Clark DL, 2000. Body postures and patterns as amplifiers of physical condition. *Proc Royal Soc of Lond B* 267:917-922.
- Thèry M, 2001. Forest light and its influence on habitat selection. *Plant Ecology* 153:251-261.
- VanderSal ND, Hebets EA, 2007. Cross-modal effects on learning: a seismic stimulus improves color discrimination learning in a jumping spider. *J Exp Biol* 210:3689-3695.
- Zeil J, Hofmann M, 2001. Signals from 'crabworld': cuticular reflections in a fiddler crab colony. *J Exp Biol* 204:2561-2569.

## Figure legends

Figure 1. Behaviours of *Gonodactylus smithii*. Upper left panel: *G. smithii* exhibiting the “meral spread” and antennule (black arrows) spread, and telson curl behaviours. Lower left panel: *G. smithii* performing a meral and antennule spread from within its domicile in coral head. Upper right panel: Resident *G. smithii* (right) displaying antennules to an intruder (left). Bottom right panel: Mating of male (lower) and female grasping eggs within maxillipeds (upper).

Figure 2.A. Irradiance spectra of fluorescent lighting used in behavioral assays with *Gonodactylus smithii*. The thick line represents the reduced spectrum “blue” light and the thin line represents the full-spectrum light treatment. The reduced intensity light was approximately 20% the irradiance of the full-spectrum light treatment. Irradiance was measured with an Ocean Optics USB2000 spectrometer, using a 50 $\mu$ m fiber optic fitted with a cosine correcting head.

B. Downwelling irradiance measured at Cobia Hole near Lizard Island on a clear, sunny day at approximately noon in July 2002. Each trace represents 1 meter depth starting at the water surface (top trace) down to 18 meters. Reproduced from Cheroske and Cronin 2005.

Figure 3. Categorized reactions from intrasexual (A) and intersexual (B) *G. smithii* behavioral assays conducted in blue (gray bars) or white light (white bars). See text for definitions of “aggressive contacts.” Data are mean percent of total responses + 1 SD. Sample sizes are five animals for blue light and six animals for white light treatments. Significant differences at  $p < 0.05$  are designated with an asterisk.

Figure 4. Mean performance distances of antennular flicking and meral spreads under blue (gray bars) and white light (white bars) conditions in both intrasexual and intersexual behavioral trials. Error bars represent + 1 standard deviation. Numbers in parentheses are sample sizes. Differences in performance distance were analyzed using a t-test for unequal sample sizes. Significant differences at  $p < 0.05$  are designated with an asterisk.

Figure 5. Mean number of responses (+ 1 SD) to the viewing of a conspecific under low (grey bars) or high intensity (white bars) light during 2006 intersexual behavioral trials. Significant differences at  $p < 0.05$  are designated with an asterisk (Aggressive acts: Wilcoxon test:  $W = 18$ ,  $z_{15} = -2.521$ ; Antennular flicking: Wilcoxon test:  $W = 60$ ,  $z_{15} = -2.215$ ).

Figure 6. Mean number of antennular flicks (+1 SD) performed by *G. smithii* in response to introduced seawater, seawater from a container with a conspecific, and seawater from a container with 1 cm<sup>3</sup> of macerated fish. Significant differences at  $p < 0.05$  are designated with an asterisk (Friedman’s test:  $X^2 = 11.63$ ,  $df = 2$ ,  $n = 15$ ).

Figure 7. Mean number of antennular flicks (+1 SD) performed by *G. smithii* in response to introduced seawater, seawater from a container with a conspecific, and seawater from a container with 1 cm<sup>3</sup> of macerated fish. Data were recorded prior to, 1 day after and 5 days after freshwater treatment of antennules. Significant differences at  $p < 0.05$  are designated with an asterisk (Pre-ablation vs. post-ablation: Wilcoxon tests. conspecific:  $W = 60$ ,  $z_{15} = -2.045$ ; food:  $W = 115.5$ ,  $z_{21} = -3.007$ ; Post-ablation vs. recovered: Wilcoxon tests. conspecific:  $W = 14$ ,  $z_7 = -2.366$ ; food:  $W = 10.5$ ,  $z_6 = -1.992$ ).



Figure 1.

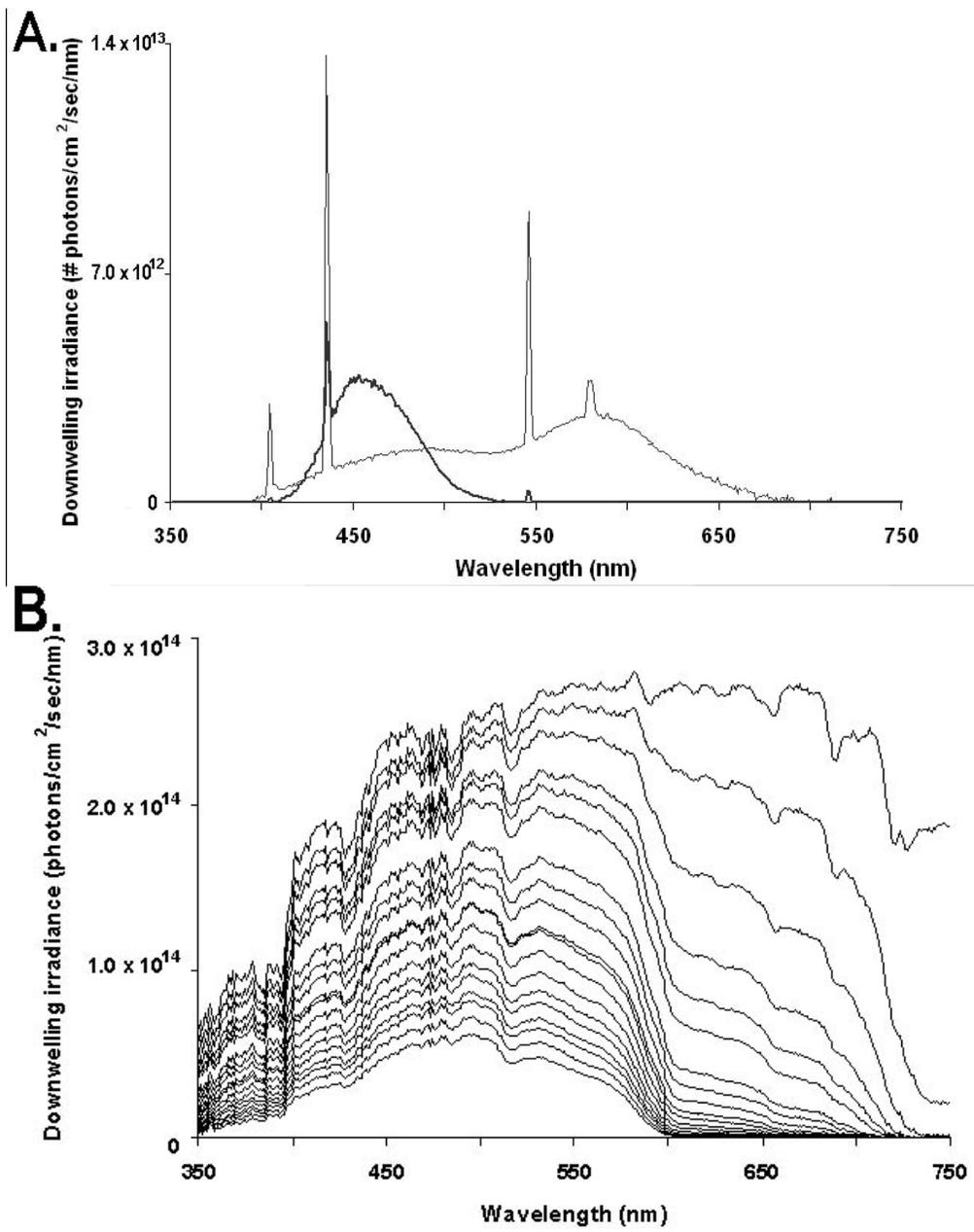


Figure 2.

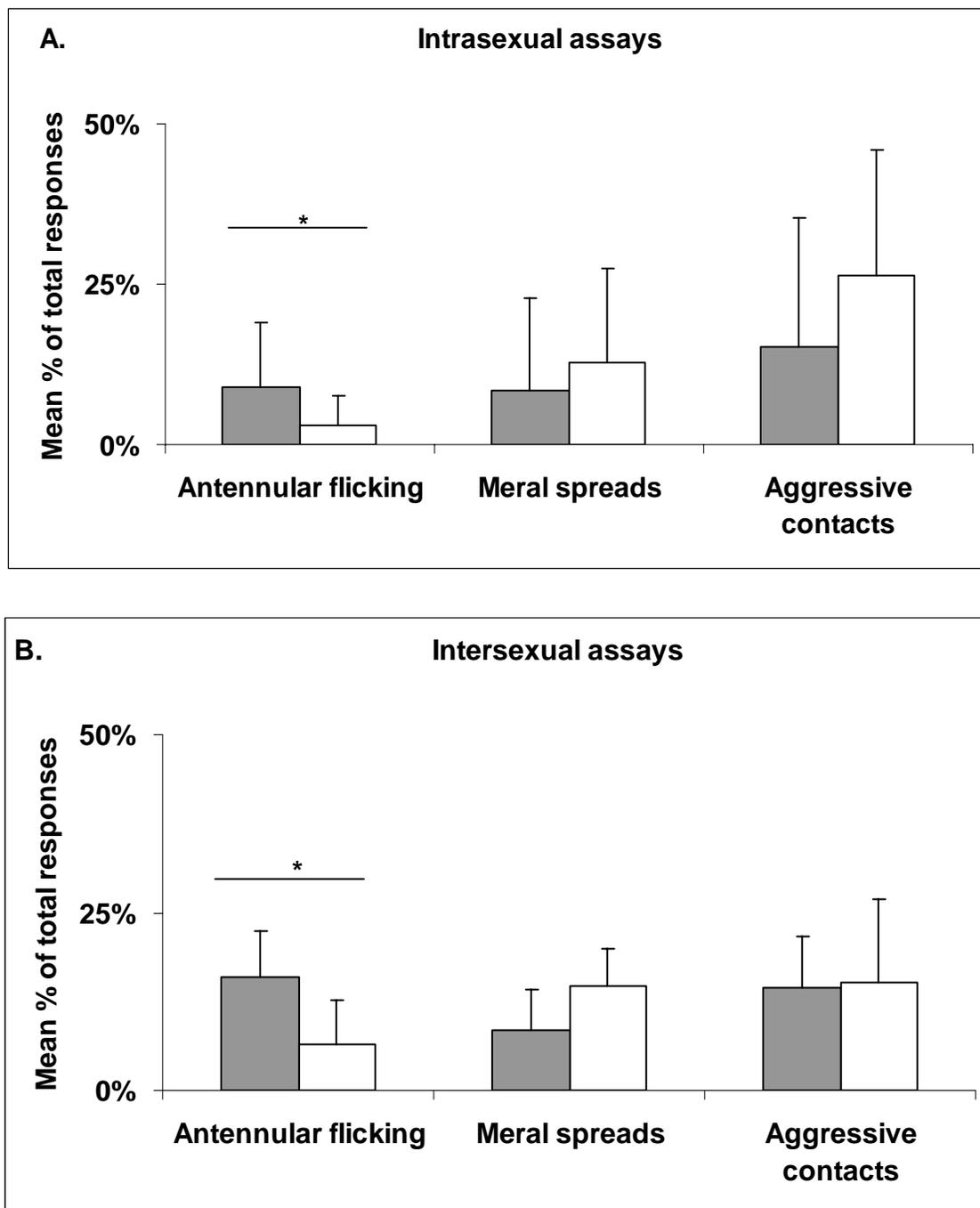


Figure 3.

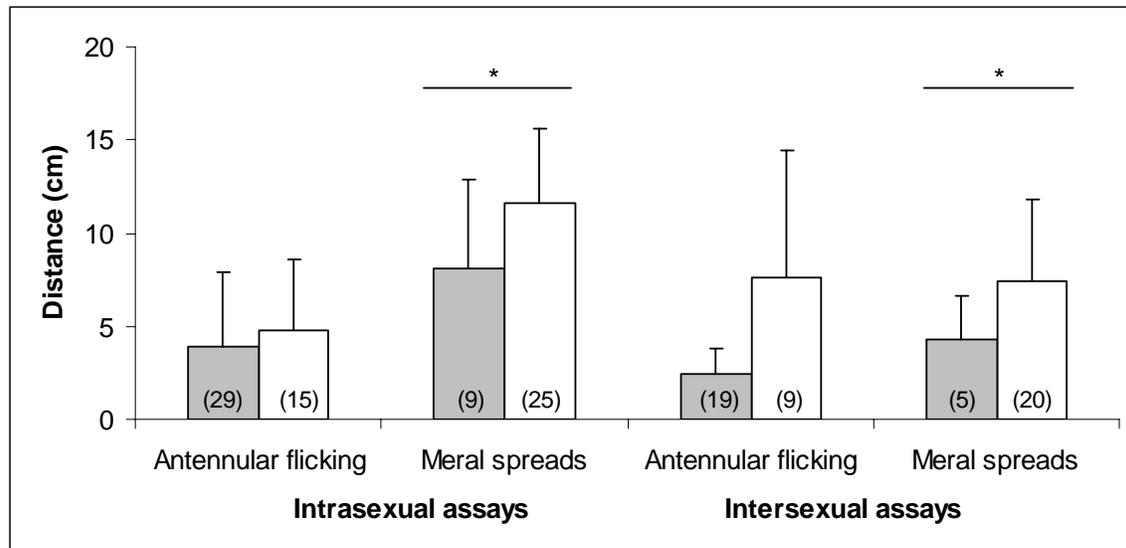


Figure 4.

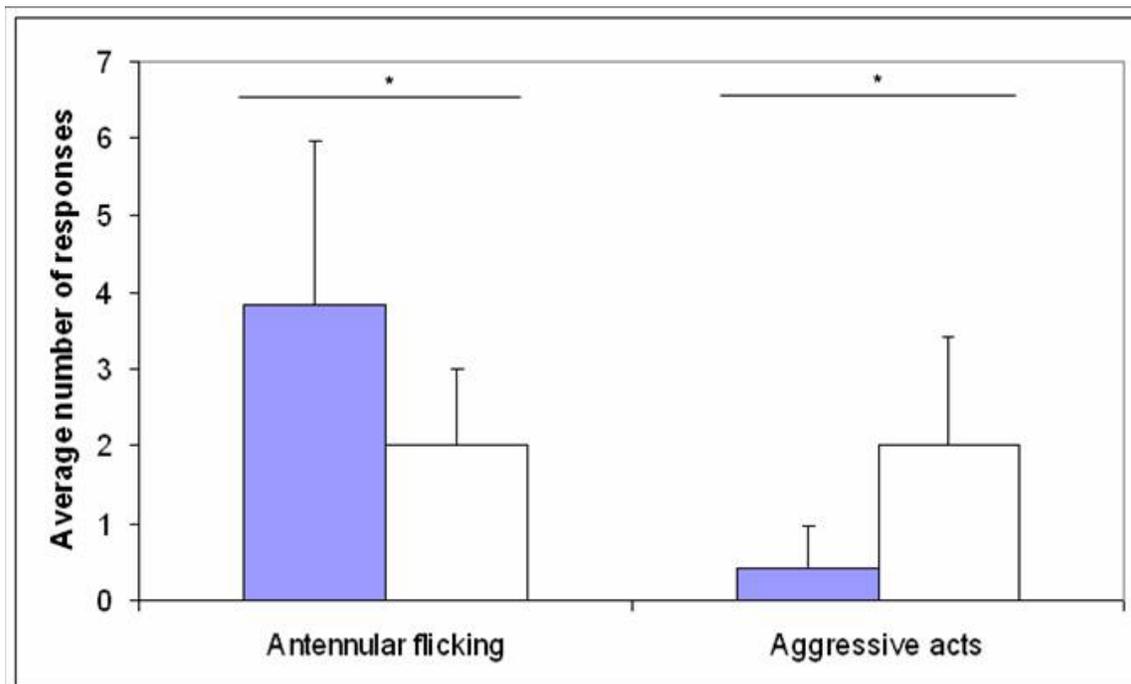


Figure 5.

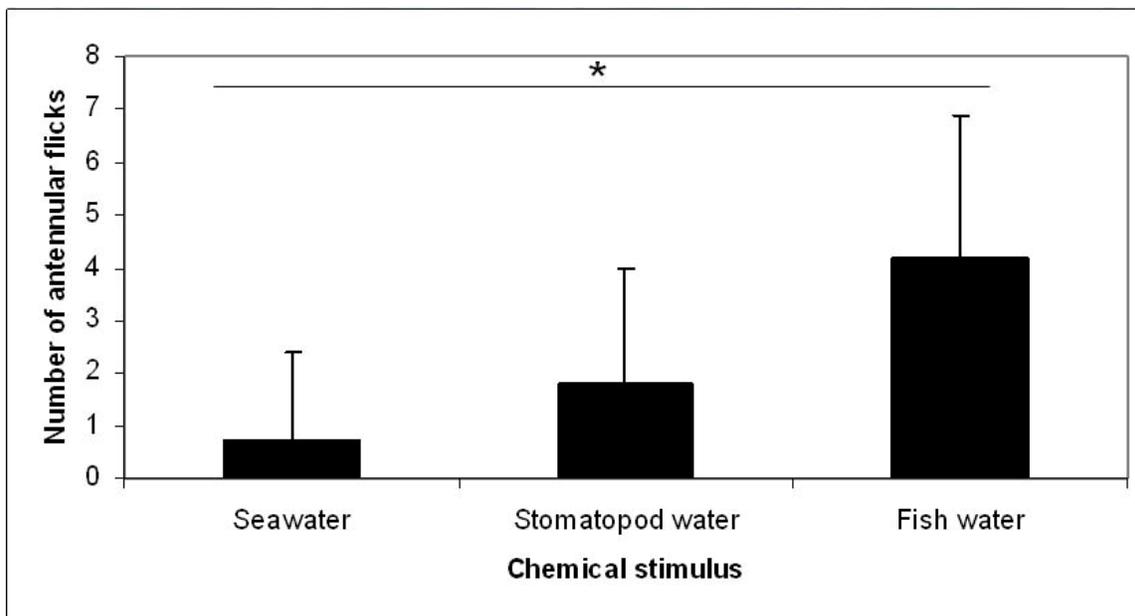


Figure 6.

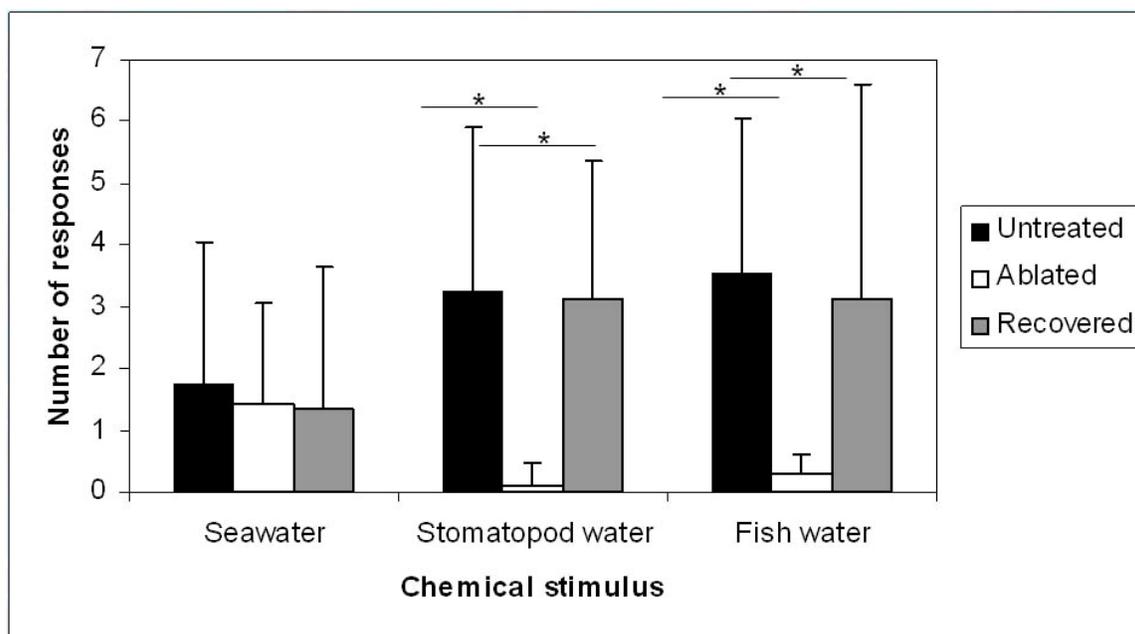


Figure 7.