

Behavioral Response to Light in Hydromedusae: Effects of Photoreceptor Complexity Across Three Hydrozoan Species

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ABSTRACT

Cnidarians possess a simple and diffuse nervous system, yet they are capable of exhibiting behavioral responses to light stimuli. Examining the relationship between photoreceptor complexity and the extent to which hydromedusae translate light cues into behavioral responses can provide critical insights into the evolutionary development of nervous systems. We tested the behavioral responses of three marine hydrozoan species in their hydromedusa stage: *Sarsia tubulosa*, *Clytia gregaria*, and *Mitrocoma cellularia*. We exposed ten individuals from each species first to different constant light intensities to observe behavioral differences, then to a half-illuminated environment to assess phototactic preferences. Consistent with previous studies, none of the three species exhibited significant differences in swimming behavior across light intensities. Under the half-illuminated condition, only *S. tubulosa* displayed positive phototaxis, whereas *C. gregaria* and *M. cellularia* showed no significant preference for either illuminated or dark regions. These findings suggest that greater photoreceptor complexity does not necessarily correspond to different behavioral responses, despite enabling the detection of additional visual cues, including the presence of a shadow in a light environment.

INTRODUCTION

Light is an important environmental cue that coordinates many processes in the aquatic invertebrate world, including life stages such as reproduction (Roosen-Runge 1962) and settlement (Rodriguez et al. 1993), biological interactions such as predation (Pangle & Peacor 2009) and symbiosis (Ayalon et al. 2021), and behaviors such as vertical migration and navigation (Navarro-Barranco & Hughes 2015). Light availability in marine environments varies substantially with depth (Lythgoe 1988), turbidity (Stern 1978), season (Martí et al. 2005), and latitude (Sakshaug & Slagstad 1991). As a result, marine organisms are often required to behaviorally manage these changing light conditions in ways that enhance survival and reproductive success.

Cnidaria was one of the first phylums to evolve a simple and diffuse nervous system in animal evolutionary history, capable of detecting light and responding to these stimuli through active behaviors (Kelava 2015; Watanabe et al. 2009). Light is used in Cnidaria as a reproductive cue, for circadian rhythm regulation, larval settlement, tentacle contraction and expansion, and cnidocyte discharge (Kitsui et al. 2026; Leach and Reitzel 2020; Levy et al. 2003; Roosen-Runge 1962). Light in Cnidaria is detected via both ocular and extraocular reception, depending on the species. Photosensitive cells that are either scattered or localized and form light-sensitive structures can mediate extraocular photoreception (EOP), which is a form of photoreception widely distributed throughout the phylum Cnidaria. Some species possess photoreceptive organs called ocelli (eyes), which are composed of photoreceptive cells responsible for ocular reception (Martin 2002; Taddei-Ferretti & Musio 2000). Ocelli usually appear as red, brown, or black spots at each tentacular bulb or as up to hundreds of ocelli around the bell margin (Martin 2002).

There are four classes under the phylum Cnidaria: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa (Grimmelikhuijzen & Westfall 1995). Within the class Hydrozoa, the life cycle is complex and typically includes both a colonial polyp stage, which reproduces asexually by budding, and a hydromedusa stage, which reproduces sexually (Kitsui et al. 2026). The behavior of hydromedusae is generally categorized as swimming, feeding, and defensive behavior (“crumpling”)

(Anderson & Schwab 1982; Anderson & Spencer 1989). These behaviors can vary widely across species and can change with light intensity (Arkett 1989; Colin & Costello 2002).

In addition to categorical behavioral responses, positive phototactic behavior in hydromedusae has also been examined in several studies (Kim et al. 2024; Lüsckow et al. 2026; Martin 2002; Plickert & Schneider 2004). It is crucial to examine light responses across hydromedusae species because this may provide important insights into the evolutionary development of neural systems controlling active behaviors, as Cnidaria is among the earliest animal phyla to evolve an organized but decentralized nervous system that coordinates behavior (Cunningham et al. 2024; Miljkovic-Licina et al. 2004). Because many hydromedusae behaviors are influenced by light, these organisms may also play an important role in carbon transport within coastal ecosystems. As carnivorous predators, many hydromedusae undergo diel vertical migration, ascending to surface waters at night to feed on zooplankton such as copepods and the larvae of other marine species (D'Ambra et al. 2013; Mills 1983).

While swimming and feeding behaviors have been compared across species, responses to light have been less frequently studied in a comparative context. In particular, phototactic behavior in hydromedusae remains understudied across species. It is still unclear whether these responses are conserved or species-specific, and knowledge gaps exist regarding whether the presence or absence of ocelli and EOP contributes to differences in behavioral responses to light. Studies have implied that the structural complexity of photoreceptors is positively correlated with their functions (Arkett 1989; Colin et al. 2003; Colin & Costello 2002). The photic responses in *Hydra* species of the class Hydrozoa have been well documented, including contraction pulses and behavioral changes that vary with the wavelength and intensity of illumination, while few studies using the same approaches have been conducted on species with a hydromedusa life stage (Passano & McCullough 1964; Rushforth 1971; Singer et al. 1963). Furthermore, while *Hydra* provides evidence that extraocular photoreception can mediate photobehavior, relatively few studies have compared the behavioral responses of species possessing centralized photoreceptive structures such as ocelli with those relying solely on dispersed photoreceptive cells (Taddei-Ferretti & Musio 2000).

In this study, we compared behavioral responses such as swimming activity and bell pulsation rate of three hydrozoan species under varying light intensities and spatially mixed illumination to assess whether they exhibit phototactic behavior (Fig. 1). We hypothesized that species with different photoreceptive structures would both exhibit differences in preference and respond differently to light stimuli.

MATERIALS & METHODS

Animal Collection & Care

We tested three hydrozoan species in their hydromedusa life stage: *Clytia gregaria*, *Mitrocoma cellularia*, and *Sarsia tubulosa* (Fig. 1). All hydromedusae, with bell diameters ranging from half a centimeter to four centimeters, were captured when tides were changing rapidly at various times of the day within the top meter of the water column off the Friday Harbor Laboratories floating dock, San Juan County, WA. We used plastic cups to retrieve the species from the water, and they were kept in a glass jar in a sea table with constantly flowing Natural Sea Water (NSW) at 13 °C until the start of the experimental trials. Species were identified using the key in The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon, Fourth Edition (J.T. Carlton, editor). University of California Press, Berkeley. The entire process of collecting, transferring, keeping, and experimenting involved no hand contact to minimize artificial disturbances. All containers used to hold the hydromedusae were pre-rinsed with seawater.

Experimental Procedure

All trials were conducted in a dark room in one laboratory of the Friday Harbor Laboratories with minimal light intensity. Trials were conducted in a corner-rounded, half-translucent 23.6 cm × 10.8 cm × 13.8 cm rectangular Tupperware containing 1700 mL of NSW so the hydromedusa could move freely without becoming trapped. The Tupperware was placed in another glass tray containing ice water to maintain the water temperature in the Tupperware at a constant 13 °C throughout the experiment. Before the start of each trial, we transferred one individual hydromedusa to the Tupperware containing still water and allowed it to acclimatize in the dark for fifteen minutes to avoid recording the physiological response of the hydromedusa to the handling stress associated with transfer.

Reaction to Varying Light Intensity

Hydromedusae were acclimated in darkness for fifteen minutes, after which the number of bell contractions in response to three varying light intensities: dark (control, $0 \mu\text{mol m}^{-2} \text{s}^{-1}$), medium ($13 \mu\text{mol m}^{-2} \text{s}^{-1}$), and high ($65 \mu\text{mol m}^{-2} \text{s}^{-1}$), was recorded with a four-digit tally counter. Light intensity was measured with an MQ-510 Full-Spectrum Quantum Meter with Underwater Sensor. The dark environment was monitored under the illumination of a red LED light, while the medium and high light intensities were controlled using a $3\text{W} \times 2$ white-light LED Dual Gooseneck Illuminator with Dual Controls. LED bulbs were used instead of regular bulbs to prevent heat from radiating from the light source.

Each trial started with 300 seconds of recording bell contractions in a dark environment, followed by sequential exposure to varying light intensities in a bracketed order (medium–dark–medium–high–medium). The order was designed such that the same light condition could be tested multiple times as a control. The number of bell contractions was recorded for 300 seconds under each light intensity. Each individual from the three species was tested independently ($n = 10$ individuals per species; $n = 30$ individuals in total).

Phototaxis

A randomized side of the Tupperware container was wrapped in black felt to create a half-dark, half-light environment while minimizing light reflection from the container walls. Hydromedusae were acclimated in complete darkness for fifteen minutes prior to testing. An adjustable white LED light was then positioned directly above the container, illuminating exactly half of the container at an intensity of $60 \mu\text{mol m}^{-2} \text{s}^{-1}$. The amount of time each individual spent in the illuminated half of the container was recorded with a stopwatch over a 600-second observation period. Each individual from the three species was tested independently ($n = 10$ individuals per species; $n = 30$ individuals in total). The same individuals were first used in the light-intensity experiment and were then allowed to recover in the sea table for 24 hours before being tested in the phototaxis experiment.

Statistical Analysis

We used RStudio version 2025.05.1+513 to perform statistical analyses and generate figures. A Linear Mixed Model (LMM) was fitted using the lme4 package to determine whether the number of bell contractions varied linearly with light intensity and the order of light exposure. The model included light intensity and exposure order as fixed effects on the number of bell contractions. A paired Wilcoxon signed-rank test was conducted using the MASS package to analyze the phototaxis experiment. The test was used to determine whether the paired differences between time spent in the light and dark were significantly different from zero for each individual tested. Both tests were performed separately for the three hydromedusa species.

RESULTS

Reaction to Varying Light Intensity

A linear mixed model was used with the number of bell contractions as the response variable and light intensity and trial order as fixed effects. The number of bell contractions was included as the dependent variable, with light intensity and trial order as fixed effects. Each individual hydromedusa was added as a random effect, since one individual was used throughout multiple trials. The model specification was as follows: Bell_Contractions ~ Light_intensity + Order + (1 | Subject).

A threshold of $|t\text{-value}| \geq 2$ was used to determine the significance of the results. There were no significant effects of light intensity on the number of bell contractions for *C. gregaria* ($\beta = -0.098$, SE = 0.37, $t = -0.26$), *M. cellularia* ($\beta = -0.40$, SE = 0.48, $t = -0.83$), or *S. tubulosa* ($\beta = 0.03715$, SE = 0.40203, $t = 0.092$). A negative t -value coefficient indicated that contractions decreased as light intensity increased, while a positive t -value coefficient indicated that contractions increased as light intensity increased.

Similarly, trial order also did not have any significant effects on the number of bell contractions for either *M. cellularia* ($\beta = -10.94$, SE = 6.23, $t = -1.755$) or *S. tubulosa* ($\beta = -3.42$, SE = 5.20, $t = -0.66$). However, there was a significant effect of trial order on the number of bell contractions for *C. gregaria* ($\beta = -17.85$, SE = 4.83704, $t = -3.69$). A negative t -value coefficient indicated that contractions decreased over successive trials (Fig. 4).

Phototaxis

A paired Wilcoxon signed-rank test showed that *S. tubulosa* spent significantly more time in the light (529.4 ± 180.1 s) than in the dark (70.6 ± 180.1 s, $\alpha = 0.05$, $p = 0.018$). In contrast, neither *C. gregaria* nor *M. cellularia* showed a significant difference in time spent under light or dark conditions. *C. gregaria* spent 275.8 ± 46.8 s in the light and 324.2 ± 46.8 s in the dark ($p =$

0.236), whereas *M. cellularia* spent 172.1 ± 207.1 s in the light and 427.9 ± 207.1 s in the dark ($p = 0.153$) (Fig. 5).

DISCUSSION

Primary Findings

This study investigated the effects of light on the swimming and phototactic behavior of three hydrozoan species in their hydromedusa stage. We hypothesized that different complexities of photoreceptive structures would cause hydromedusae to respond differently in their swimming behaviors and exhibit different preferences when presented with light stimuli. The main findings contrasted with our hypothesis, as light intensity did not have a significant effect on hydromedusae's rhythmic swimming contraction behavior. Instead, the order in which individuals were exposed to the light intensities had a stronger effect than the varying light intensities themselves. Consistent with our hypothesis, one species did exhibit a preference for the lit side of the container over the dark side, with *S. tubulosa* being positively phototactic by spending significantly more time on the illuminated half of the container. In contrast, *C. gregaria* and *M. cellularia* showed neither positive nor negative phototaxis, as they did not show a significant preference for either side of the container.

Implications

The absence of significant effects of varying constant light intensity on hydromedusae swimming behavior was consistent with previous literature showing that most hydromedusae do not exhibit behavioral differences across varying light intensities, with the current known exception of *Polyorchis penicillatus* (Arkett 1985). The results of the present study are therefore consistent with previous research and suggest that the three species examined similarly do not alter their swimming behavior across the tested light intensity levels. We expected the treatment to matter for the number of bell contractions, but we found that order had a greater effect than light intensity. This finding suggests that behavioral changes in the hydromedusae were driven more strongly by repeated exposure to experimental conditions than solely by light intensity. Physiological responses associated with acclimation or prolonged confinement in the container may have affected bell

contraction frequency, potentially masking any direct effects of light intensity on swimming behavior.

The lack of significant behavioral responses under different constant light intensities across all three species suggests that the presence of ocelli alone, or the degree of complexity of hydromedusae's photoreceptive structures, may not be the determining factor for such behavioral responses. Although *S. tubulosa* possesses ocelli, while *C. gregaria* and *M. cellularia* do not, all three species exhibited similar behavioral patterns under the experimental conditions. In contrast, other hydrozoans, such as *Hydra*, have been reported to alter their behavior in response to changes in light intensity and wavelength despite only having opsins in sensory neurons and lacking specialized visual organs (Hanson 2023). These observations imply that behavioral responses to light may be less dependent on the complexity of photoreceptive structures and more dependent on how photoreceptive information is processed by the nervous system. The presence of photoreceptors may allow organisms to detect light, but whether this information produces observable behavioral changes may depend on neural organization, sensory integration, and the ecological relevance of the light stimulus to specific species in the class Hydrozoa.

It can be implied that the reason *S. tubulosa* had a preference for actively staying on the illuminated side of the container was due to its possession of four ocelli, a more complex and localized photoreceptive structure than delocalized photoreceptive cells, at the base of each tentacle (Fig. 1, B1). The presence of ocelli in hydromedusae was necessary for detecting shadows, and *S. tubulosa* did exhibit the ability to swim away from the shadow, which experienced a drastic change in light intensity when the light–dark boundary was crossed from $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Arkett 1985). *C. gregaria* and *M. cellularia* lack ocelli at the base of their marginal bells (Artigas 2017; Mills 1983). Since they do not have ocelli for detecting shadows, we could hypothesize that this is the reason neither species exhibited significant phototactic behavior or a consistent swimming direction toward the illuminated side. The observed preference of *M. cellularia* for the dark side was likely influenced by physiological stress during prolonged experimental trials, resulting in individuals being less active in performing swimming behaviors in

general. Each individual was frequently observed remaining near the boundary between light and dark conditions and drifting passively between the two regions without visible contractions to swim toward a particular region (Fig. 5).

Limitations and Future Directions

Further investigation using more rigorous experimental designs, such as increasing the order of magnitude to tenfold differences between the high-light and dark treatments, is needed to determine whether the lack of behavioral responsiveness to changing light intensities is a reproducible characteristic of these species. According to the Weber–Fechner law, visual systems often respond to changes in light intensity logarithmically rather than linearly (Longcore 2023; Rider et al. 2019). Mitigation of the potential acclimation effects can be achieved by reducing trial duration, increasing recovery periods between treatments, or using different individuals for each treatment. These modifications would help distinguish behavioral responses to light intensity from physiological responses associated with repeated experimental exposure.

The reason for the light preference of *S. tubulosa* remained unclear. Some hydromedusae have been shown to exhibit a “shadow response” when experiencing a sudden decrease in light intensity levels, reacting with sudden, rapid bell contractions (Tamasige & Yamaguchi 1967). However, *S. tubulosa*’s response to swim away from the shadow exhibited more directionality than contraction-related behavioral changes. Future studies could further examine the reason for this directional response, rather than the conventional “shadow response,” which has been observed primarily in relation to diel vertical migration in hydromedusae (Arkett 1985; Mills 1983).

More research is needed on both *C. gregaria* and *M. cellularia*, or their closely related species, which are known to use light cues for various purposes without exhibiting phototactic behaviors. Members of the genus *Clytia* and the species *M. cellularia* have been reported to undergo diel vertical migration (Artigas 2017; Mills 1983). Diel vertical migration is the daily migration of zooplankton, including some hydromedusae, involving ascent to surface waters at dusk to feed and descent to deeper waters at dawn, with migration likely being cued by changes in

light intensity (Brierley 2014; Hays 2003; Mills 1983). Furthermore, reproduction in the species *Clytia hemisphaerica* is strongly regulated by light cues, with synchronized gamete release stimulated by light–dark transitions despite the absence of ocelli (Kitsui et al. 2026). The reason why *Clytia* do not exhibit strong phototactic responses under constant light conditions, while still being capable of perceiving and responding to light for biological processes, remains unclear. One possible explanation is that both species possess EOP cells that allow detection of changes in environmental light without the need for specialized visual organs. Such photoreceptive structures could facilitate behaviors such as vertical migration and light-cued spawning while producing little or no directional swimming response under the experimental conditions used in this study. Future research should focus on identifying specific photoreceptive structures and their functions in *C. gregaria* and *M. cellularia*. Determining how these species detect light in the absence of ocelli would help explain how they synchronize reproductive events and perform vertical migration despite showing no significant phototactic behavior in the present study.

Conclusion

Collectively, our results suggest that the presence of ocelli and the complexity of photoreceptive structures may be associated with directionality in phototactic behavior, but do not necessarily predict behavioral responses to different constant light intensities. Behaviors cued by light stimuli in hydrozoans were likely dependent on both photoreceptive structures and the neural mechanisms that process the information collected by these structures. Future studies identifying photoreceptor types in specific species and the neural pathways used to process this information may help explain how different hydrozoan species utilize light cues for ecological functions such as diel vertical migration and reproduction.

FIGURES

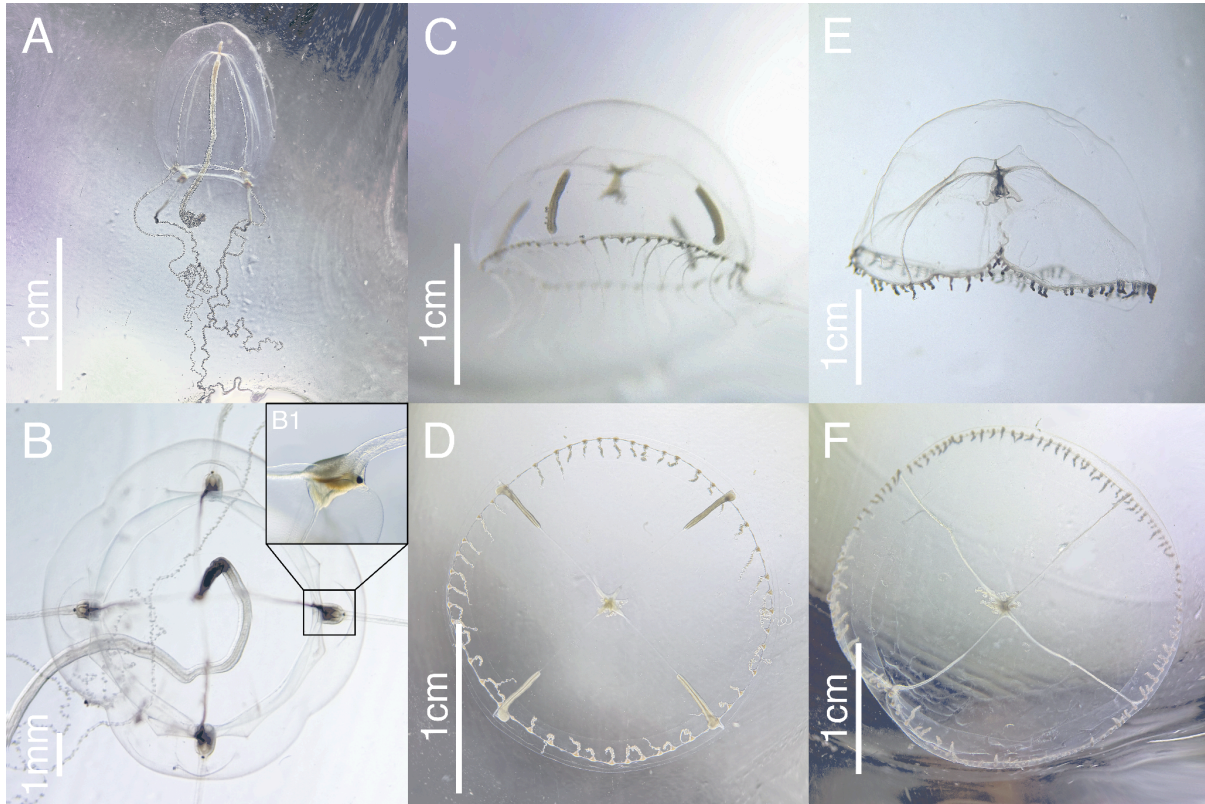


Fig. 1. Photographs of three hydrozoan species in their hydromedusa stage viewed under a dissection microscope. Side view (A) and top view (B) of adult *S. tubulosa*, with a total of four ocelli present, one at each tentacular bulb (B1). Side view (C) and top view (D) of adult *C. gregaria*. Side view (E) and top view (F) of adult *M. cellularia*.

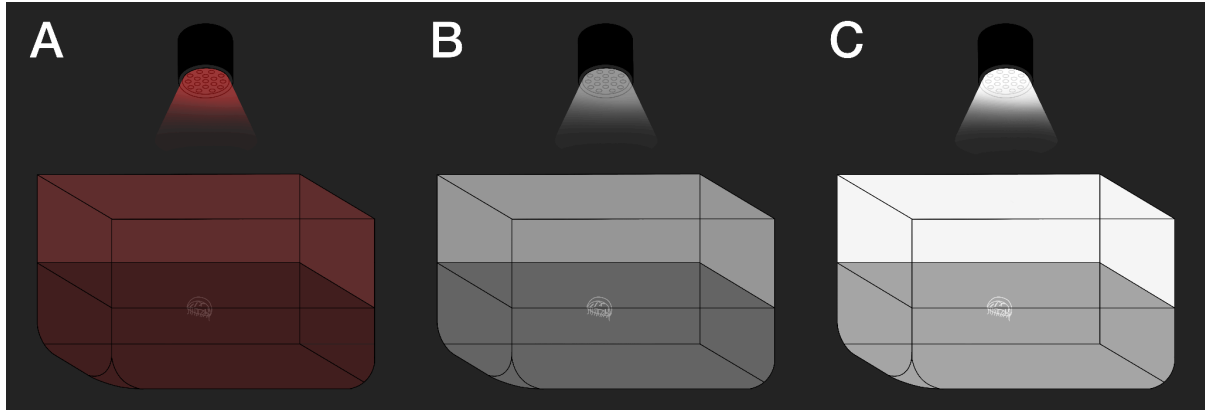


Fig. 2. Experimental setup used for testing behavioral reactions to different light intensities. Each individual hydromedusa was placed in a half-transparent container, then acclimated in the dark for fifteen minutes. The entire container was then sequentially exposed to three light intensity treatments: (A) dark (control, $0 \mu\text{mol m}^{-2} \text{s}^{-1}$), (B) medium ($13 \mu\text{mol m}^{-2} \text{s}^{-1}$), and (C) high ($65 \mu\text{mol m}^{-2} \text{s}^{-1}$). Bell contractions were recorded during each five-minute trial.

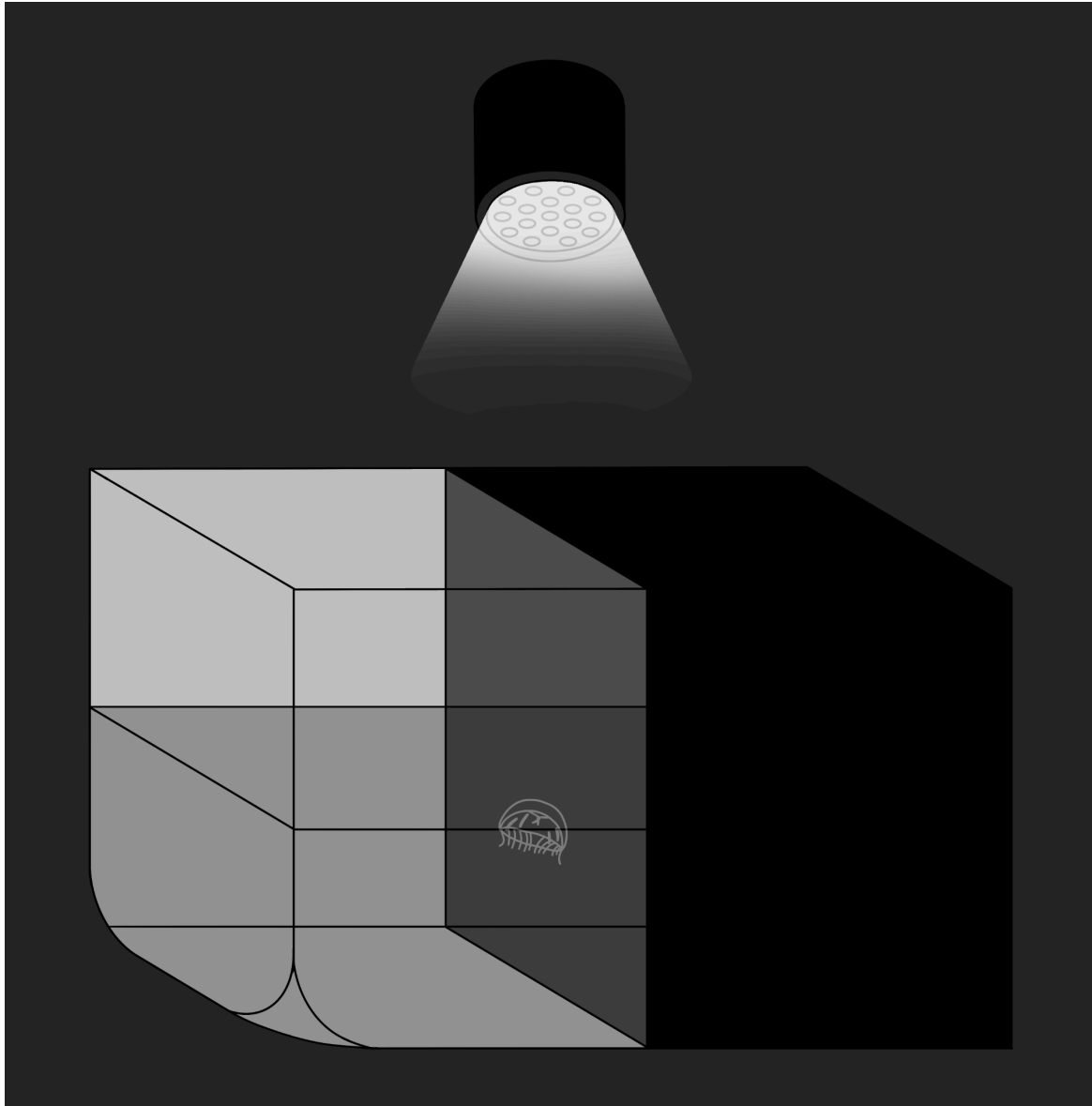


Fig. 3. Experimental setup used for testing the phototaxis of hydromedusae. Each individual hydromedusa was placed in a half-transparent container and then acclimated in darkness for fifteen minutes. A light ($60 \mu\text{mol m}^{-2} \text{s}^{-1}$) was shone directly above the container, with half of the container wrapped in black felt to create a half-dark, half-light environment. The time each hydromedusa spent in the illuminated side was measured throughout the total ten-minute trial.

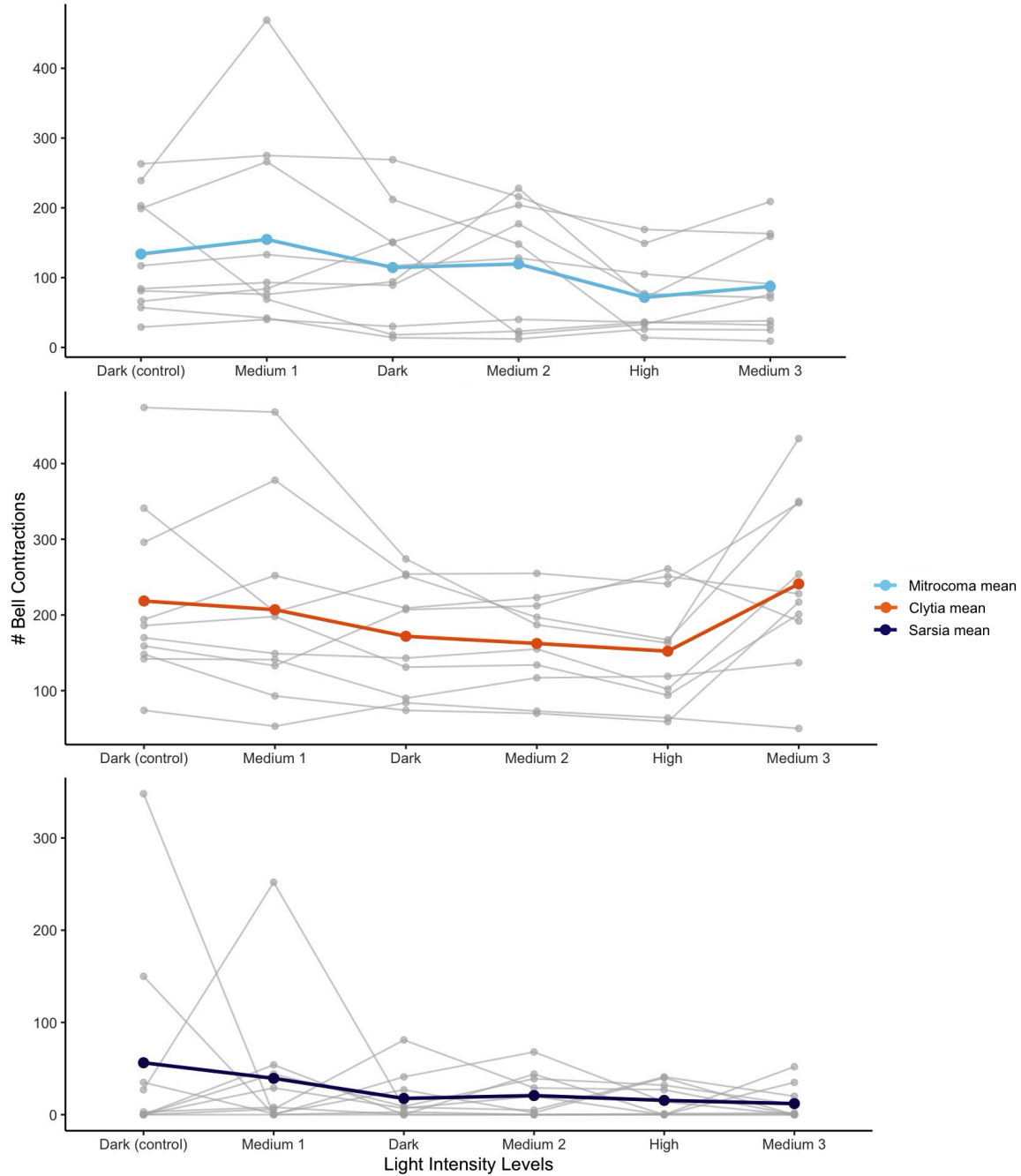


Fig. 4. Average number of bell contractions of hydromedusae exposed to different light intensities. Grey lines represent each individual hydromedusa ($n = 10$), and colored lines represent species means. Individuals were exposed sequentially in the order dark–medium–dark–medium–high–medium (dark: control, $0 \mu\text{mol m}^{-2} \text{s}^{-1}$; medium: $13 \mu\text{mol m}^{-2} \text{s}^{-1}$; high: $65 \mu\text{mol m}^{-2} \text{s}^{-1}$). Statistical analysis was performed using a linear mixed model with a significance threshold of $|t\text{-value}| \geq 2$ (*S. tubulosa*: $t = -0.66$; *M. cellularia*: $t = -1.755$; *C. gregaria*: $t = -3.69$).

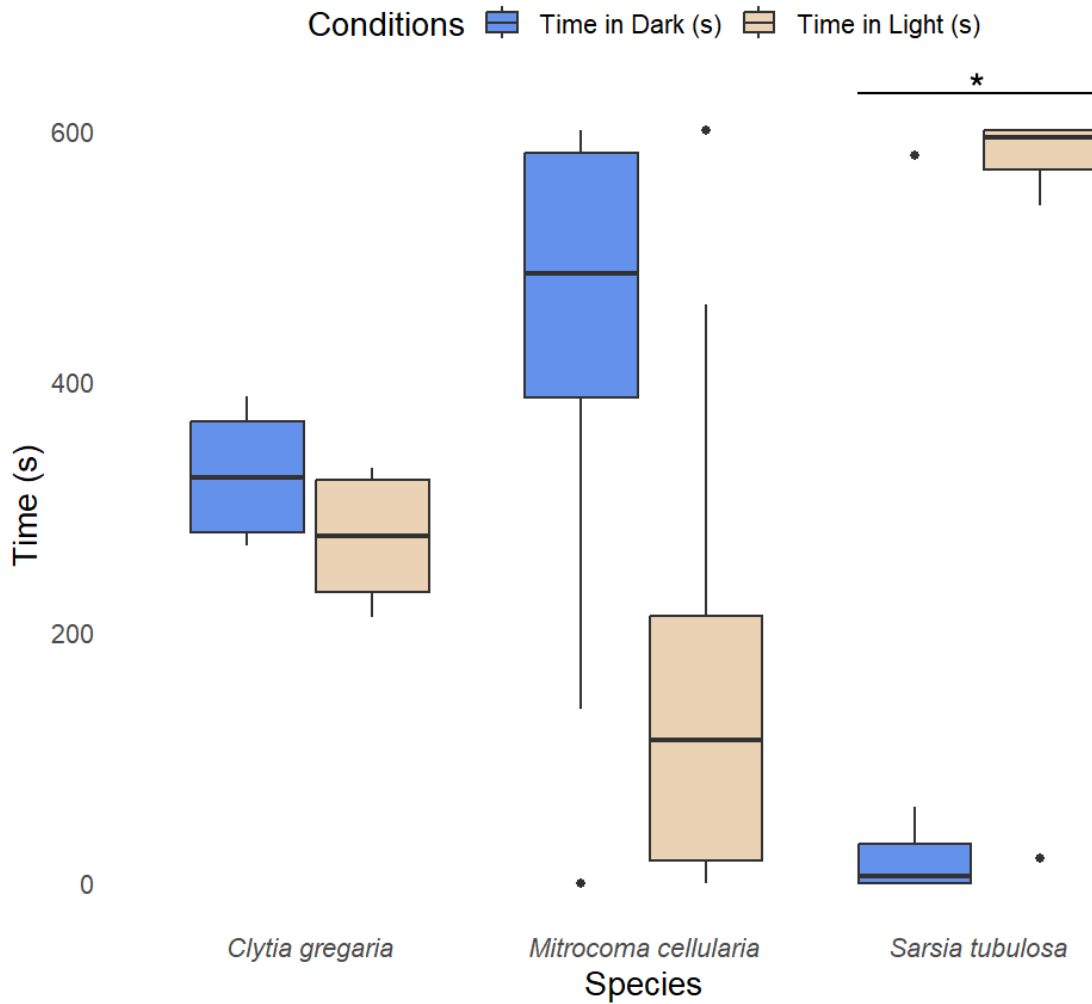


Fig. 5. Box-and-whisker plots of the time spent on the dark or illuminated side of the container by *C. gregaria* (n = 10), *M. cellularia* (n = 10), and *S. tubulosa* (n = 10) during the phototaxis experiment. Boxes represent the interquartile range (IQR) from the 25th to 75th percentile, with thick lines indicating the median, whiskers extending to values within $1.5 \times \text{IQR}$, and data points beyond the whiskers representing outliers. A paired Wilcoxon signed-rank test was conducted using a significance threshold of $\alpha = 0.05$. Only *S. tubulosa* exhibited a significant preference for the illuminated region ($p = 0.018$).

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