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Effect of light environment on prey consumption in two species of larval stomatopods, *Gonodactylaceus falcatus* (Forskål, 1775) and *Gonodactylellus* sp. (Stomatopoda: Gonodactylidae)

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ABSTRACT

While adult stomatopod crustaceans are relatively well studied, understanding of larval stomatopod ecology is lacking, largely due to difficulties studying larvae in their natural habitat. This study investigated how light environment (i.e., spectral composition) and time of day affected prey consumption in two species of larval stomatopod, *Gonodactylaceus falcatus* (Forskål, 1775) and *Gonodactylellus* sp. Individual larvae were placed with 20 *Artemia* nauplii prey in feeding chambers treated to produce different light environments with respect to ultraviolet (UV) light: full spectrum light UV+, full spectrum UV–, and a dark control. Chambers were lowered to a depth of 3 m for 2 hours at three times of day (noon, twilight, and night) to test 1) if larval feeding rates changed at different times of day and 2) if UV vision was involved in prey capture. We found that light was important for successful feeding, with both species eating significantly more in lighted treatments than the dark controls during daytime experiments. *Gonodactylellus* sp. also had a significantly higher feeding rate at twilight in the UV+ treatment than in the dark control. Both species showed decreased consumption at night compared to daytime rates, and decreased consumption in all dark controls. This study is one of the first to examine how ecological conditions affect feeding behavior in larval stomatopods. Our results suggest that light is important for larval stomatopod feeding, with differences between species in daily feeding activity periods. There was also a difference in total consumption between the two species, with the slightly larger *Gonodactylaceus falcatus* consuming nearly double the prey items as *Gonodactylellus* sp. at peak feeding times. Follow up studies should incorporate a variety of prey types to test how feeding changes based on food source and density.

KEY WORDS: Crustacea, feeding, plankton, visual ecology, ultraviolet light

INTRODUCTION

One of the primary tasks for many larval crustaceans is finding food, which is required to successfully molt between larval stages, and ultimately undergo metamorphosis (Cronin & Forward, 1980; Anger & Dawirs, 1981; Anger 1987). Starvation is one of the main causes of larval mortality in the ocean, which can be exacerbated by the patchy distribution of prey items in pelagic habitats (Omori & Hamner, 1982; Cianelli *et al.*, 2009; Messié & Chavez, 2017;). Early-stage pro-pelagic larval stomatopods have yolk sacs and do not require feeding, but laboratory trials have shown that they require food to successfully molt into the next stage once larvae reach the first pelagic stage (Manning & Provenzano, 1963; Provenzano & Manning, 1978; Williams *et al.*, 1985; Morgan & Goy, 1987). While laboratory trials show that stomatopod larvae need to feed, very little is currently known about feeding behaviors in the wild. There is a large body of literature on the ecology of adult stomatopods (e.g., Marshall *et al.*, 2007; Franklin *et al.*, 2016, 2019; Patel & Cronin, 2020) but information on the ecology of larval stomatopods, including feeding behaviors, is lacking.

Previous studies have suggested that larval stomatopods undergo diel vertical migrations, remaining in deep, dark waters to avoid visual predators during the day and rising to the surface at sunset and through the night to feed (Reaka & Manning, 1987). If larval stomatopods are undergoing a strong diel vertical migration, peak feeding would be expected to occur either at twilight or at night when they are rising to the surface. Little to no research, however, has measured vertical migration in

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larval stomatopods directly (Feller, 2013). In fact, there is some evidence that early-stage larval stomatopods remain in shallow water, only moving to deeper waters as late-stage larvae, and the benthos, when they molt (Kodama *et al.*, 2006; Ohtomi *et al.*, 2006). For some shrimp larvae, particularly in the early stages, light at night is not sufficient to drive feeding and they will instead feed primarily during the day (Gomes *et al.*, 2014).

Recent work has found that larval stomatopods are likely efficient hunters, with a fast strike similar to the adult counterparts (Harrison *et al.*, 2021). It is likely that, similar to the adults, a sophisticated visual system is used to direct this rapid strike. Based on this, we hypothesized that one of the main sensory modes of prey detection in larval stomatopods is visual cues, and effective prey capture is likely to be affected by light environment. Therefore, we tested how light environment affected prey consumption in larval stomatopods. We did this in two ways. First, we tested if the rate of feeding was affected by times of day in order to identify optimal feeding times for early-stage larval stomatopods. We also tested how the spectral composition of light, particularly the presence or absence of UV light, affected larval stomatopod feeding rates. Larval stomatopods were recently found to have UV vision (McDonald *et al.*, 2022), and one of the leading hypotheses for the presence of UV vision in planktonic marine animals is its use in hunting and prey capture. Even though many plankton are transparent, many planktonic animals have UV photoprotective pigments which decrease their transparency in these wavelengths (Morgan & Christy, 1996; Johnsen & Widder, 2001). Because UV light is scattered in marine waters, animals with UV vision have increased detection of nearby UV-absorbing objects as silhouettes against the bright UV background (Browman *et al.*, 1994; Siebeck & Marshall, 2007; Cronin & Bok, 2016). The hypothesis that UV vision assists pelagic planktivores in feeding has so far been mainly studied in larval reef and adult planktivorous fishes (Browman *et al.*, 1994; Siebeck & Marshall, 2007). With the recent evidence that larval stomatopod shrimps have UV vision (McDonald 2022; McDonald *et al.*, 2022) and as likely visual predators (Harrison *et al.*, 2021), it is possible that stomatopod larvae are similarly utilizing UV light to aid in the detection and capture of smaller transparent prey.

We investigated prey consumption in the larvae of two stomatopod species commonly found in the Hawaiian Islands, *Gonodactylaceus falcatus* (Forskål, 1775) (Fig. 1A) and *Gonodactylellus* sp. (as "*Gonodactylellus* n. sp." in Steck, 2022, but yet undescribed) (Fig. 1B). Prey consumption experiments were completed in the field under three different light treatments to determine the impact of the spectral composition and intensity of light: full spectrum + UV light (300–700 nm), full spectrum – UV light (400–700 nm), and full dark (i.e., no light), at each of three time periods (day, twilight, and night). By measuring prey consumption under different light conditions, we provide the first insights into the feeding ecology of larvae of this important, yet enigmatic, group of crustaceans.

MATERIALS AND METHODS

Collection and identification

We collected two species of stomatopod larvae from nearshore habitats on O'ahu, Hawai'i: *Gonodactylaceus falcatus* and *Gonodactylellus* sp. (Fig. 1). All *Gonodactylellus* sp. larvae were collected as egg clutches from Wailupe Beach park. All *Gonodactylaceus falcatus* larvae were collected at night using underwater flashlights and dipnets from the Makai Research Pier taking advantage of their inherent positive phototactic behavior (Barber & Boyce, 2006). We used a subset of individuals to confirm the identity of *Gonodactylaceus falcatus* using DNA barcoding (see below).

All larvae of both species, upon hatching or collection, were placed in 1 l containers of filtered seawater (salinity of ~30 ppt) under a full spectrum aquarium light (Willis 165 W aquarium light; Willis Electric, DongGuang City, China) on a 12 h light/dark cycle until experimentation. Collected egg masses were placed on a table rocker (Benchmark Scientific BR1000, Sayreville, NJ, USA) until hatching. All hatched larvae were supplied with a diet of 1–2 day old *Artemia* nauplii (San Francisco Bay Brand, San Francisco, CA, USA); seawater was changed daily. Larvae were only used in trials once it was established they were in the early pelagic larval stages. When freshly hatched and in the propelagic stages, larvae were observed to be clustered in a tight ball with yolk sacs at the bottom of the container, until around day 8–9, which is consistent with previous observations of gonodactyloid larval development (Morgan & Goy, 1987; Harrison *et al.*, 2021). Prior to experimentation, we determined that larvae were in the pelagic stage by: 1) establishing that there

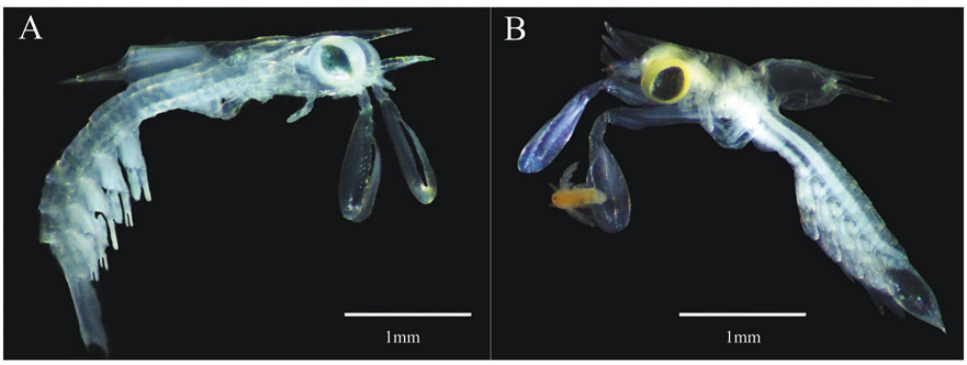

Figure 1. Representative images of early pelagic stages of the two focal species, *Gonodactylaceus falcatus* (**A**) and *Gonodactylellus* sp. (**B**), with approximate scale bars. *Gonodactylellus* sp. is seen with an *Artemia* nauplius, which was observed speared on the raptorial appendage at the time of death. Images taken by MM and MP, respectively.

was no evidence of a yolk sac; 2) observing that the larvae were free swimming in the water column, rather than showing the positive thigmotaxis characteristic of the propelagic stage (Morgan & Goy, 1987); and 3) observing that larvae demonstrated positive phototaxis to a point light source. We also ensured that all individuals were observed actively feeding in the laboratory, through examination of visible orange prey in the stomach. When trials were completed, laboratory grown *Gonodactylellus* sp. were aged between 10–18 d after hatching. The wild-caught *Gonodactylaceus falcatus* larvae were captured using their inherent positive phototaxis to lights at night, and all larvae were used within 12 d of capture. Wild-caught larvae were not used until feeding was actively observed in the laboratory. Full descriptions of larval stages have not been published for either species. Based on behavior, length of time maintained in the laboratory, and size ranges (3.5–4.2 mm for *Gonodactylellus* sp., 3.7–4.3 mm for *Gonodactylaceus falcatus*), we estimated that all larvae used were in the early pelagic stages (fourth and fifth larval stages) at the time of trials (Morgan & Goy 1987; Harrison *et al.*, 2021).

DNA barcoding

For wild-caught larvae, larval stomatopods were sorted from other plankton upon collection. Larvae were further sorted into morphological groups, and individuals that were thought to be *Gonodactylaceus falcatus* based on size and morphology were removed to separate containers. To verify that these samples belong to this species, a subset of 25 individuals were randomly pulled from four different collection periods for COI barcode confirmation. COI barcoding is a standard method of identifying larval stomatopod crustaceans (Palecanda *et al.*, 2020). To complete barcoding, the DNA of each individual larva was extracted using a DNeasy Kit (Qiagen, Hilden, Germany), following manufacturer protocols. The cytochrome oxidase I (COI) mitochondrial gene was then amplified through polymerase chain reaction (PCR). We used 5–10 ng of DNA for each reaction, Phire Hot Start Taq mix (ThermoFisher Scientific, Waltham, MA, USA) following manufacturer protocols in 20 µl reactions with 0.5 µl of 1× forward and reverse primers. The cycling parameters used consisted of a single 2 min incubation at 94 °C, 40 cycles of 20 s 94 °C denaturing, 10 s 46 °C annealing, and 1 min 65 °C elongation, and a final elongation at 65 °C for 7 min. The success of each PCR was verified using gel electrophoresis. For successful PCRs, amplicons were cleaned with EXO-SAP-IT (ThermoFisher Scientific) and sent to the Advance Studies in Genomics, Proteomics, and Bioinformatics facility at the University of Hawai'i at Mānoa (Honolulu, HI, USA) for sequencing. Sequences were assembled in Geneious (Kearse *et al.*, 2012) and run through NCBI's Basic Local Alignment Tool (BLAST) (Altschul *et al.*, 1990) to verify species identity. All samples returned a hit with *Gonodactylaceus falcatus* with less than 3% divergence. To further verify species identity, samples were aligned with a curated list of stomatopod reference sequences from MLP's laboratory and placed in a Neighbor Joining Tree with a Tamura-Nei distance model, which was resampled using Bootstrapping with 100 replicates. All samples were identified to be *Gonodactylaceus falcatus* with a bootstrap value of 96%.

Trial set-up

Feeding trials were conducted during October-November 2021 at the Makai Research Pier, Waimanalo, HI. We tested how prey consumption was affected by two factors: 1) time of day, and 2) presence or absence of UV light. We used 2-hr feeding trials, as in initial laboratory trials this was the time required to induce a measurable feeding response in the two larval stomatopod species used. To measure feeding differences related to time of day, trials were completed at three time points: day (~12:00–14:00), twilight (~17:00–19:00), and night (~20:00–22:00). All twilight trials started 1 h prior to sunset and ran until 1 h after sunset to evenly assess this time frame in the given feeding window. To test the impact of UV light on total prey consumption, we used three light treatments at each time of day: full spectrum light (UV+), full spectrum – UV light (UV–) and a dark control (dark) (Fig. 2). We had a minimum sample size of 20 individual larvae for each combination of light treatment and time of day. Twilight trials for *Gonodactylaceus falcatus* had a sample size of 25 individuals, and day and night sample sizes of 20. Day trials for *Gonodactylellus* sp. had a sample size of 27 individuals, and twilight and night samples of 25.

To establish UV+ and UV– light treatments, cylindrical 20 ml borosilicate liquid scintillation vials, which have high transmission across the UV-visible spectrum (28 mm diameter by 61 mm height; Wheaton #986561, NJ, USA) were used. No changes were made to the vials for UV+, as the material was chosen because it had high UV transmission (Fig. 2). For UV– treatments, each vial was treated to block UV light while keeping approximately the same visible spectrum luminance as untreated vials. Following the methods of Franklin *et al.* (2016), UV– vials were lightly sprayed with sunscreen (Banana Boat Ultra Sport SPF 50+, Clearwater, FL, USA), allowed to dry for 45 seconds, then coated with a layer of superglue (Krazy Glue Elmer Products, Columbus, OH, USA), and finally covered with a layer of clear nail varnish (Orly, Los Angeles, CA, USA) to seal in the sunscreen and increase luminance in the visible spectrum. The transmission of the vials was measured with a handheld radiometer (StellarRad_UVN, StellarNet Inc, Keystone, FL, USA) to confirm that the treated vials were blocking UV light, whereas the UV+ vials were allowing full UV transmission (Fig. 2). A dark control was created by coating vials with black spray paint (Krylon Fusion All-in-One Matte Black, Krylon, Philadelphia, PA, USA), which obstructed any light from reaching the interior of the vials.

In situ field trials

Prior to trials, larval stomatopods were starved for 24 h to induce a measurable feeding response (Yen, 1983). *Artemia* nauplii were used as prey item in all trials, as this is the food source that has been most successful in raising stomatopod larvae in past studies (Dingle, 1969; Morgan & Goy, 1987; Harrison *et al.*, 2021). Prior to the field trials, 20 *Artemia* nauplii (1–2 days old, ~0.5 mm) were counted into individual vials in the laboratory, for a prey density of 1 nauplii ml^{-1}. These vials were then stored in a cooler at ambient temperature for transportation to the Makai Research Pier. A single larval stomatopod was added to each vial at the field site, and the vials were then tied to a weighted line and submerged to an experimental depth of 3 m.

At the end of each trial, vials were recovered, and feeding was immediately arrested with ~1 ml of formalin. Vials were transported back to the laboratory, where the remaining prey items were counted under a light microscope. Trials were conducted during October-November 2021, and only completed on days when weather was sunny or partially cloudy, as we did not want high cloud cover or storms to affect behavior. Data from time points run on different days were pooled for statistical analysis.

Statistical analysis

Total consumption was determined as the difference between the beginning prey total and ending prey total. Consumption was compared for factor 1, time of day (noon, twilight, night) and factor 2, light treatment (UV+, UV–, dark). As this was count data and does not fit the assumptions of normality, the data were modeled with a count data regression model. The model was tested for zero inflation, and it was identified to be underfitting zeros in the data (Lüdecke *et al.*, 2021). Because of this, a zero-inflated count data regression model with a Poisson distribution was used to model the data in R (Tables 1, 2) (Zeileis *et al.*, 2008). Relationships between groups were then established with a Tukey post hoc correction on the model (Lenth, 2016). The results were plotted as the average consumption per trial ±standard error of the mean (s.e.m) with letters to denote significant differences between light treatments and time of day ($a = 0.05$) (Fig. 3).

RESULTS

Our results show that light availability is important for feeding in both species of larval stomatopods. *Gonodactylaceus falcatus* displayed significantly higher ($P < 0.05$) total consumption during day trials under both UV+ and UV– light treatments compared to the dark control (Fig. 3A). All other light treatments at night and twilight displayed significantly lower consumption than the two lighted day treatments (Fig. 3A).

We saw different results in *Gonodactylellus* sp. This species had the highest total consumption during two time periods, day and twilight, under the UV+ and UV– light treatments. Total consumption in the UV+ treatment was significantly higher ($P < 0.05$) than the dark control during these time periods, but the UV– treatment was not significantly different from the dark control (Fig. 3B). *Gonodactylellus* sp. larvae were seen to have decreased consumption, at all other time points measured, including all night trials, although the night trials were not significantly lower than the dark controls at other time points (Fig. 3B).

DISCUSSION

We found that time of day and light availability both had a significant effect on total prey consumption (*Artemia* larvae) in both species, but the observed results were not the same between species. We observed the highest total consumption during the daytime trials in both the UV+ and UV– treatments for the wild caught *Gonodactylaceus falcatus* larvae. These two treatments displayed significantly higher consumption than any other time point, or light treatment measured (Fig. 3A). It appears that the presence or absence of UV light does not affect prey

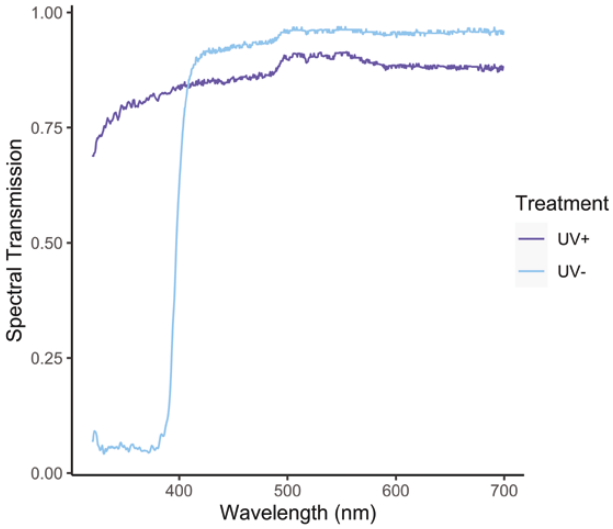

Figure 2. Spectral irradiance measurements of each of the vials used in the UV+ and UV– light treatments were measured with a handheld radiometer of sunlight, and the irradiance through each of the vials. Transmission was calculated by dividing the irradiance of each of the vials by sunlight for both the UV+ and UV– vials.

Table 1. Model results and sample sizes shown for *Gonodactylaceus falcatus* trials when run through the Poisson zero-inflated regression count model. The results of the model were then run through a Tukey comparison to establish relationships between groups (*< 0.05, **< 0.01, ***< 0.001).

Treatment	*N*	Estimate	Standard error	Z value	*P* value
Daytime UV+	27	1.8137	0.263	6.896	> 0.001***
Daytime UV–	27	2.0361	0.2655	7.67	> 0.001***
Daytime dark	27	–0.2113	0.2425	–0.871	0.383628
Twilight UV+	25	0.5908	0.2918	2.025	0.042891*
Twilight UV–	25	0.974	0.3161	3.081	0.002064**
Twilight dark	25	–0.1335	0.343	–0.389	0.697033
Night UV+	25	1.0885	0.3071	3.544	> 0.001***
Night UV–	25	0.2985	0.3947	0.756	0.449486
Night dark	25	0.3302	0.4515	0.731	0.464591

Table 2. Model results and sample sizes shown for *Gonodactylellus* sp. trials when run through the Poisson zero inflated regression count model. The results of the model were then run through a Tukey comparison to establish relationships between groups (*< 0.05, **< 0.01, ***< 0.001).

Treatment	*N*	Estimate	Standard Error	z value	*P* value
Daytime UV+	20	0.86207	0.34765	2.48	0.01315*
Daytime UV–	20	0.88504	0.36264	2.441	0.01467*
Daytime dark	20	0.02684	0.31232	0.086	0.93151
Twilight UV+	25	1.08307	0.34742	3.117	0.00182**
Twilight UV–	25	0.37861	0.35401	1.07	0.28484
Twilight dark	25	0.13442	0.47051	0.286	0.77511
Night UV+	20	0.51221	0.40899	1.252	0.21043
Night UV–	20	0.1519	0.42905	0.354	0.72331
Night dark	20	0.21588	0.42844	0.504	0.61436

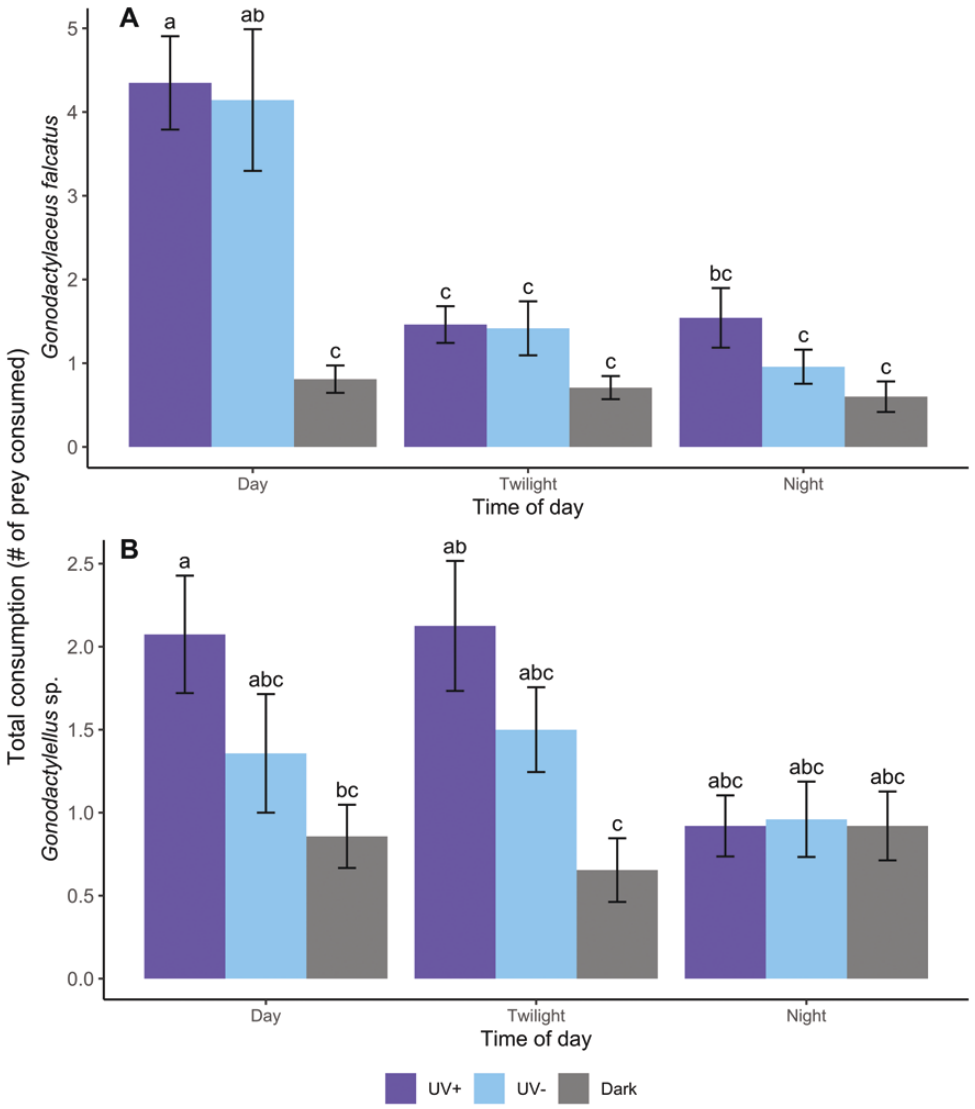

Figure 3. Total consumption of prey items displayed by time of day and light treatment for both species of stomatopods. Consumption of *Gonodactylaceus falcatus* is shown for day trials ($N = 20$ per treatment), twilight trials ($N = 25$ per treatment), and night trials ($N = 20$ per treatment) (**A**). Consumption for *Gonodactylellus* sp. is also displayed for daytime trials ($N = 27$ per treatment), twilight trials ($N = 25$ per treatment), and night trials ($N = 25$ per treatment) (**B**). Results are plotted as the mean consumption per trial ± standard error of the mean. Results were run through zero-inflated count data regression model with a Poisson distribution, followed by a Tukey comparison between groups. Letters indicate significant differences between light treatments and time of day ($\alpha = 0.05$).

consumption in *Gonodactylaceus falcatus*, and instead the larvae were observed to be mainly feeding during daytime, which may indicate they need high levels of irradiance to drive efficient prey capture.

The highest total consumption in *Gonodactylellus* sp. was seen at both day and twilight in both lighted conditions (UV+ and UV–) (Fig. 3B). The dark controls during the day had significantly lower consumption than the UV+ treateatments. These larvae appeared to consume fewer *Artemia* larvae at night, although these results were not significant. Based on these results, feeding by *Gonodactylellus* sp. was driven by light availability, and there was sufficient light at twilight times to drive feeding in both the UV+ and UV– vials. While the highest total consumption was seen in UV+ treatment, the total consumption was not significantly higher than in the UV– vial. Like *Gonodactylaceus falcatus*, the larvae of *Gonodactylellus* sp. did not appear to be actively feeding at night.

These results suggested that larvae of *Gonodactylellus* sp. ate more prey when UV light was present during both day and twilight, although this possibility requires further study (Fig. 3B). Increased consumption under UV light may be even more pronounced with transparent food sources found in the wild, which are otherwise difficult to see without the aid of UV vision (Browman *et al.*, 1994; Siebeck & Marshall, 2007; Yoshimatsu *et al.*, 2020). The *Artemia* nauplii we used were orange (Fig. 1B). While we have observed wild-caught stomatopods with bright orange prey items in their stomach at the time of capture, it is likely that transparent zooplankton are also a component of the larval diet. To better understand how prey type affects feeding, it would be beneficial for future studies to investigate larval stomatopod feeding rates on a variety of prey types that vary in body color and transparency, which may be more similar to the prey diversity that the larvae would naturally encounter in the wild. We used only one prey density and variations in prey density could also be examined in future studies, to determine if encounter rate of prey also affected the observed predation.

The highest prey consumption was seen in daylight trials for *Gonodactylaceus falcatus*, and day and twilight in *Gonodactylellus* sp., indicating that larval stomatopods are likely using visual predation and require a certain level of light to feed effectively. This was somewhat surprising, as we expected the highest feeding rates at twilight when it is hypothesized the larvae would be vertically migrating to the surface to feed (see Reaka & Manning, 1987). It is nevertheless possible that early-stage pelagic larvae, such as the ones tested, are remaining in relatively shallow water with sufficient light to drive feeding during the day. This would also align with observations seen in other zooplankton. Small, transparent zooplankton have been found to remain shallower and have less vertical migratory movement than pigmented zooplankton, instead relying on transparency to reduce visual predation in the upper waters (Johnsen, 2001; Hylander & Hansson, 2013). Some early-stage decapod larvae appear to perform a reverse diel vertical migration (DVM) behavior, remaining at the surface in the day and moving to depth at night, before reverting back to a normal diel vertical migration at later stages (Barth *et al.*, 2014). It is possible that early-stage pelagic stomatopod larvae will also exhibit different DVM behaviors across ontogeny, but follow-up studies would be needed to test this hypothesis.

Our results do show that there is still some degree of feeding taking place in the dark controls and at night (Fig. 3), so it is possible that the larval stomatopods are switching to an alternate type of prey detection other than vision at night, such as olfactory or mechanosensory, in the absence of light. Based on our results, however, feeding appears to be less efficient in the absence of environmental light. There is also a chance that either prey or predator behavior was altered by complete darkness in our control vials. We were unable to track the prey dynamics in the field to determine if the *Artemia* nauplii were evenly distributed in the vials, or if there were any clustering behaviors taking place in any of the vials. *Artemia* nauplii are known to be positively phototactic (Bradley & Forward, 1984; Dojmi Di Delupis & Rotondo, 1988) and may be more likely to remain towards the bottom of the chamber in complete darkness (Villamizar *et al.*, 2011), which could result in decreased predator-prey interactions. As larval stomatopods are also positively phototactic, we are unsure how full darkness may affect their behaviors.

We also recorded one instance of a *Gonodactylellus* sp. larva seemingly feeding with raptorial appendages. We found a larva with an *Artemia* nauplii impaled on the raptorial appendages after feeding was arrested (Fig. 1B), indicating it may have been in the middle of a feeding event when the trial was ended. The biomechanics of the larval raptorial appendage strike has been characterized with strike speeds sufficient for prey capture, but actual prey capture was not observed (Harrison *et al.*, 2021). Recent high-speed video recordings show that larvae of *Gonodactylaceus falcatus* impale prey using their raptorial appendages. Surprisingly, instead of a rapid strike, they appear to capture nearby larvae simply by grabbing at them (Suzzanne Cox, personal communication).

Both species studied in this project are included in the superfamily Gonodactyloidea and are similar in size, morphology, and larval stages (Fig 1). Further testing of larvae from species in different stomatopod superfamilies would be needed to learn whether or not the patterns of feeding we observed here occur only in gonodactyloid species or are common to larval stomatopods in general. It would also be of interest to test larvae across ontogeny, particularly in later and larger larval stages, as all larvae used in this study were in the early pelagic larval stages. In theory, larval stomatopods all inhabit similar environments and may therefore have similar ecological needs. There is nevertheless a wide range of morphological types (Ahyong *et al.*, 2014; Haug *et al.*, 2016) in larval stomatopods, which can range in size from a few millimeters to several centimeters long (Townsley, 1953; Feller, 2013; Haug *et al.*, 2016). The larvae we used were small for stomatopod larvae, measuring ~4 mm long (Fig 1). There may be further differences in feeding behaviors that were not observed here in larvae of different sizes and morphologies. For example, some species have large shields that nearly enclose the body, making them very round, which may affect mobility (Haug *et al.*, 2016). There are also differences in the size and shape of the larval raptorial appendage that is used for feeding that may affect feeding efficiencies and behavior (Haug *et al.*, 2016). Larvae of species in the family Nannosquillidae have visual specializations that are hypothesized to be associated with prey capture, potentially at night, which may also lead to differences in feeding ecologies (Feller *et al.*, 2019). With these

differences in mind, future studies should investigate feeding behaviors in different species, particularly with different morphologies and visual specializations.

Larval stomatopods are difficult to study in their natural environment, largely due to their small size and transparency. This work provides one of the first studies of stomatopods utilizing *in-situ* experiments to understand larval feeding ecology and to document how light environment affects larval stomatopod prey capture. The highest prey consumption was observed during the daytime in both species, in contrast to expectations based on the current understanding of larval stomatopods as vertical migrators that should have peak feeding times at twilight and nighttime periods. Based on the times of day that consumption was highest, and the lack of consumption in the dark controls at those times, our results strongly suggest that successful feeding in these two species of stomatopods requires light. The significantly lower total consumption observed in the dark controls suggests that if larvae were switching to other senses, such as olfactory or chemical, for feeding in the absence of light, they may be less efficient than visual cues. It is possible, however, that multiple senses, such as vision and mechanoreceptors, are being used simultaneously in lighted environments to sense prey movement (Doall *et al.*, 2002). Both time of day and light availability are important for larval stomatopod prey capture and feeding, but peak consumption periods and preferred light environments may vary between species. Follow up-studies should be completed to investigate how these factors are affected by other environmental conditions, such as depth or prey item.

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