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# Costs and compensation in zooplankton pigmentation under countervailing threats of ultraviolet radiation and predation

Samuel M. Bashevkin<sup>1,3</sup> · John H. Christy<sup>2</sup> · Steven G. Morgan<sup>1</sup>Received: 18 March 2019 / Accepted: 8 April 2020 / Published online: 21 April 2020  
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## Abstract

Evolutionary responses to opposing directions of natural selection include trade-offs, where the phenotype balances selective forces, and compensation, where other traits reduce the impact of one selective force. Zooplankton pigmentation protects from ultraviolet radiation (UVR) but attracts visual predators. This trade-off is understudied in the ocean where planktonic larvae in surface waters face ubiquitous UVR and visual predation threats. We tested whether crab larvae can behaviorally reduce UVR risk through downward swimming or expansion of photoprotective chromatophores. Then we examined whether more pigmented larvae are more heavily predated by silverside fish under natural sunlight in the tropics in three UVR treatments (visible light, visible + UVA, visible + UVA + UVB). Lastly, we tested the behavioral chromatophore response of larvae to predation threats in two light treatments. *Armases ricordi* avoided surface waters after exposure to sunlight with UVR. *Armases ricordi*, *Armases americanum*, and *Eurypanopeus* sp. consistently expanded chromatophores in UVR or visible light, while *Mithraculus sculptus* and *Mithraculus coryphe* showed no response. Fish preferred pigmented larvae on sunnier days in visible light lacking UVR. Lastly, both *M. coryphe* and *M. sculptus* unexpectedly expanded chromatophores in fish cues, but responses were inconsistent over trials and across light treatments. The more consistent larval responses to UVR than to predator cues and the lack of predator preferences in natural light conditions suggest that UVR may have a stronger influence on pigmentation than predation. This study improves our understanding of planktonic adaptation to countervailing selection caused by visual predation and exposure to UVR.

**Keywords** Trade-off · Brachyura · Larva · Behavior · Color change

Communicated by Pablo Munguia.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00442-020-04648-2>) contains supplementary material, which is available to authorized users.✉ Samuel M. Bashevkin  
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## Introduction

Different modes of selection on a given trait can favor different phenotypes (Arnold 1992; Zera and Harshman 2001). One common evolutionary response is a trade-off in which an intermediate phenotype maximizes net fitness within the genetic capability of the species. For example, sexual selection favors brighter lizard coloration whereas survival selection favors duller, camouflaged coloration, resulting in a coloration that balances the two selective forces (Husak et al. 2006). Compensation is another evolutionary response in which an additional trait reduces the strength of a selective force on the original trait. For example, freshwater snails with cheaper, thinner shells were more vulnerable to predation but compensated with greater behavioral avoidance of predators (Rundle and Brönmark 2001).

Both types of evolutionary responses are evident in the coloration of zooplankton in response to countervailing selection from exposure to ultraviolet radiation (UVR) and

visual predators. Zooplankters are largely transparent except for pigmented chromatophores. More transparent zooplankton with smaller or fewer chromatophores are less often consumed by visual predators but die much more quickly in UVR (Hairston 1976; Luecke and O'Brien 1983; Herbert and Emery 1990; Utne-Palm 1999; Hessen et al. 1999; Bashevkin et al. 2019a). Thus, predation selects for smaller chromatophores while UVR selects for larger chromatophores. The ultimate evolutionary response would be limited by energetic and phylogenetic constraints. A number of studies have documented a trade-off in freshwater cladocerans and copepods that have reduced pigmentation but increased susceptibility to UVR damage in lakes with visual predators compared to those without predators (Hairston 1976; Luecke and O'Brien 1983).

Zooplankton can compensate in several ways for selection on chromatophore size. They can remain below brightly lit surface waters during the daytime when susceptibility to UVR and visibility to fishes is greatest (Hairston 1980; Hansson et al. 2007; Hylander et al. 2009). They can change pigmentation in response to fish or UVR cues (Pautsch 1951; Hunter et al. 1979; Miner et al. 2000; Hansson et al. 2007; Hylander et al. 2009, 2012; Brüslein et al. 2016). They can increase photoprotective antioxidants in the presence of fish cues (Hylander et al. 2012). Lastly, they can deter predators with Batesian mimicry of unpalatable species (Greer et al. 2016). Thus, compensation circumvents the “tug-of-war” in the phenotype between the countervailing selection by exposure to UVR and predators that hunt visually.

However, no studies have yet investigated the effects of UVR on the selectivity of planktivorous fish for pigmented prey and most studies of changes in pigmentation by plankters have focused on relatively slow changes on the scale of days to months rather than rapid changes in color over minutes in response to shifting threats. Furthermore, few studies have investigated this potential trade-off in the ocean, and fewer still in the planktonic larval stages of benthic adults. Selection on coloration is complex for planktonic larvae that cannot swim against currents. Stratified currents flowing in opposing directions, in both estuaries and coastal environments, serve as a “conveyor belt” transporting larvae from adult to larval habitats in surface currents and returning them to adult habitats in bottom currents (Queiroga and Blanton 2005; Pineda et al. 2007; Morgan et al. 2014). Because successful recruitment depends on occupying surface currents during early larval life, larvae of many species cannot minimize exposure to UVR and visibility to fishes by descending into deeper waters throughout their entire planktonic phase (Morgan and Christy 1996; Morgan and Anastasia 2008).

In a companion study (Bashevkin et al. 2019a), we found that pigmentation was advantageous in protecting crab larvae from UVR (UVR protection hypothesis; Fig. 1a, H1). In the present study, we examined the potential disadvantages of

pigmentation in attracting predators and possible compensatory mechanisms these larvae may use to escape the trade-off (Fig. 1a, H2-5). Pigmented larvae may compensate for increased predator exposure by expanding chromatophores in UVR and contracting them in the presence of predators or swimming to darker waters in the daytime when their visibility and exposure to UVR is highest (Fig. 1, H2,3,5). Predation is thought to be a significant source of mortality for marine larvae and crab larvae are subject to heavy visual predation from planktivorous fishes (Bashevkin and Morgan 2020; Morgan 1990). This study stands to increase our understanding of how selection from exposure to UVR and visual predators affects the pigmentation and behavior of planktonic larvae. More generally, we hope to advance understanding of the links between morphological and behavioral evolution by investigating behavioral compensation for morphological traits.

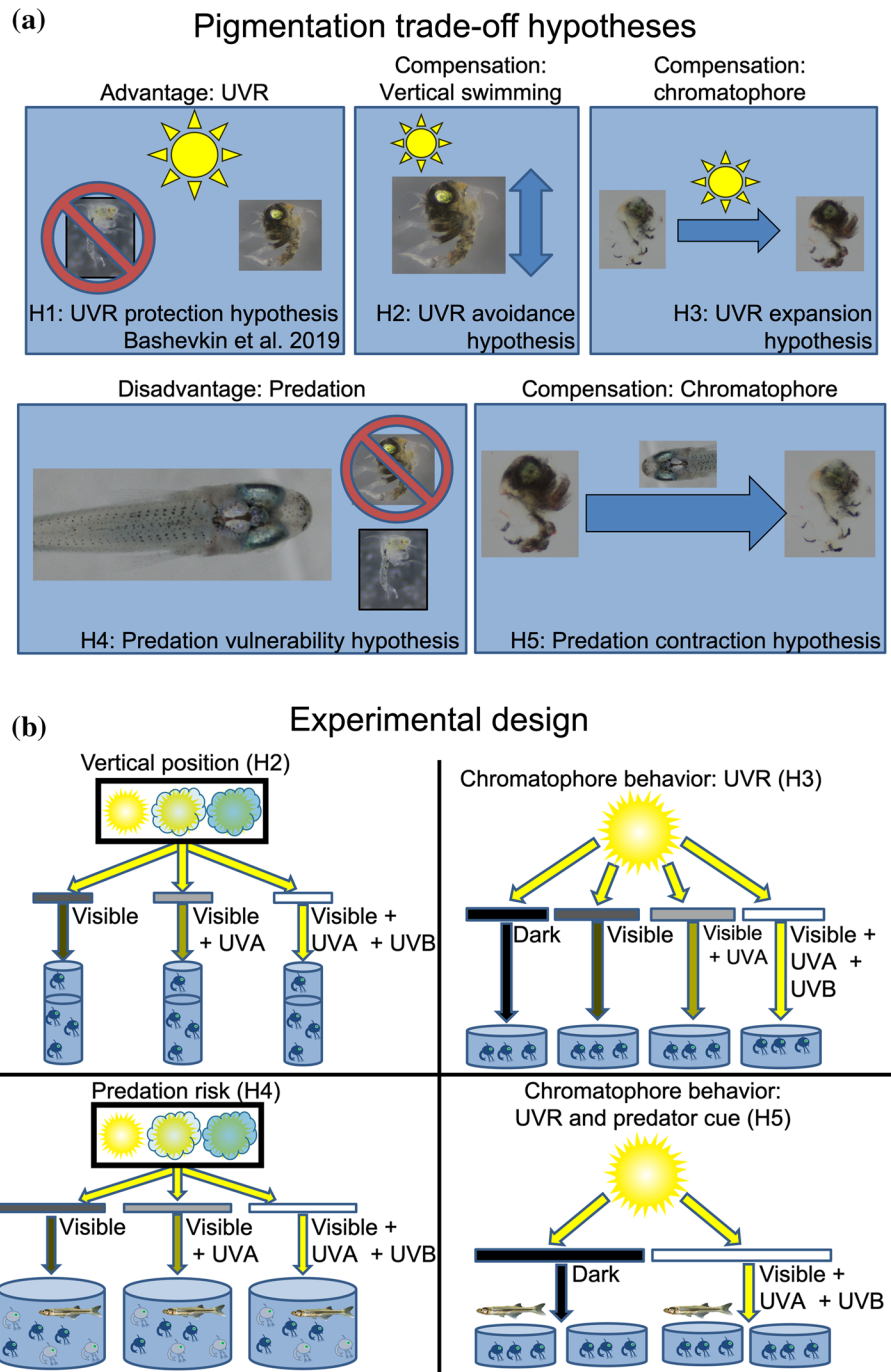
We tested each of our hypotheses (Fig. 1a) in separate experiments. To test the ability of crab larvae to avoid UVR through behavioral compensation, we measured the vertical distributions of larvae exposed to different UVR conditions and sunlight intensities and the expansion or contraction of their chromatophores in response to UVR. To examine the predatory costs of pigmentation, we conducted predation trials with reef silversides that were offered a choice of different species of crab larvae with dissimilar pigmentation in different UVR treatments. This allowed us to parse the effects of the wavelength and intensity of light on the selectivity of fish. We quantified pigmentation as total percent cover by visible pigments regardless of color because lack of pigmentation is the cheapest camouflage. This also enables a direct comparison of these results with our previous study (Bashevkin et al. 2019a) where we found a strong relationship between total pigmentation and UVR protection. This direct comparison is important to determine if a true trade-off is operating. Lastly, we tested the behavioral chromatophore response of crab larvae to predator cues and whether that response would be influenced by light treatment in a 2 × 2 factorial experiment (Fig. 1b). We expected that (1) larvae will descend to deeper water in the presence of UVR (UVR avoidance hypothesis; Fig. 1a, H2), (2) larvae will expand chromatophores in UVR (UVR expansion hypothesis; Fig. 1a, H3), (3) more pigmented larvae will be subject to higher visual predation (predation vulnerability hypothesis; Fig. 1a, H4), and (4) larvae in the presence of predator cues will contract chromatophores (predation contraction hypothesis; Fig. 1a, H5).

## Materials and methods

### Study site and species

We conducted our study at the Smithsonian Tropical Research Institute (STRI) Galeta Marine Laboratory

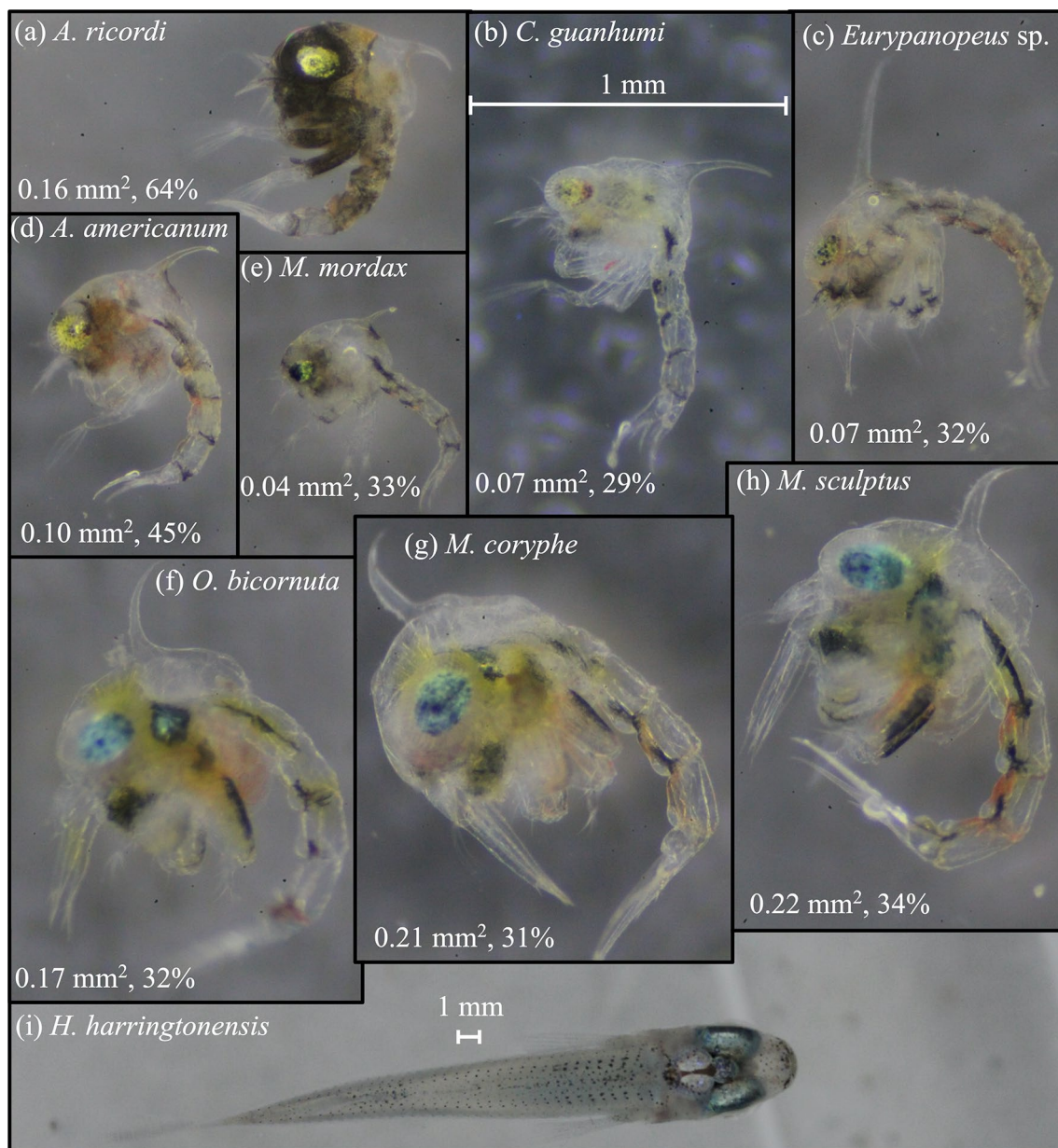
**Fig. 1** Conceptual framework and experimental designs. **a** Conceptual diagram illustrating the theoretical background for this study. The UVR protection hypothesis (H1: pigmentation protects from UVR) was tested by Bashevkin et al. (2019a). The UVR avoidance hypothesis (H2: larvae avoid intense UVR by descending to deeper waters), UVR expansion hypothesis (H3: larvae expand chromatophores in UVR to reduce photodamage), predation vulnerability hypothesis (H4: pigmentation increases visual predation risk), and predation contraction hypothesis (H5: larvae contract chromatophores when visual fish predators are present to reduce visibility) are all tested in this study. **b** The experimental designs for the four experiments in this study, along with the hypotheses they address. Sample sizes are for illustrative purposes only and diagrams are not to scale. The varying cloud covers in the vertical position and predation risk experimental designs represent that these experiments were conducted on multiple days with different levels of sun intensity so we were able to incorporate sun intensity as a covariate in our models. A color version of this figure is available online



on the Caribbean coast of Panama (9°24'10.35"N, 79°51'39.26"W) in July–October 2015 and June–July 2016. Gravid females of eight species of crabs (*Armases ricordi*, *Armases americanum*, *Cardisoma guanhumii*, *Mithraculus sculptus*, *Mithraculus coryphe*, *Omhalacantha bicornuta*, *Eurypanopeus* sp., and *Minuca mordax*) were collected by hand on Galeta Island (Fig. 2). Crabs were identified to species with Rathbun (1918, 1925, 1930), Klompmaker et al. (2015), Abele (1976, 1992), and Crane (1975). One species, *Eurypanopeus* sp., could not

be identified to species. *M. sculptus*, *M. coryphe*, *O. bicornuta*, and *Eurypanopeus* sp. were collected during the day. The other species were primarily collected at night using a flashlight. Gravid females were held individually in 1-L plastic containers partially submerged in a table with flowing seawater at ambient temperatures until they released larvae. Each container was checked every morning for newly hatched larvae and the water was changed. The abundant, planktivorous reef silverside *Hypoatherina harringtonensis* was collected with a hand net and flashlight





**Fig. 2** Photographs of the eight study species of crab larvae are at the same scale (a–h) and the fish predator is at a smaller scale (i). Numbers on larval photos represent the average pigmentation area and percent cover for each species. A color version of this figure is available online

from the dock at night, the day before each experiment. Fish collection, handling, and care conformed with the STRI IACUC protocols. Concurrent with our experiments, light intensity was recorded 100 m away from the experiments at a monitoring station maintained by the Physical Monitoring Program at STRI (Steven Paton, STRI, unpublished data). Solar radiation (400–1100 nm) was measured with two LiCor Model Li200x pyranometers every minute, and the data were averaged every 15 min. Experiments were conducted with newly hatched larvae of species available on the day of each experiment.

### Vertical position experiments

In 2016, we determined whether *A. ricordi* larvae compensate for UVR exposure by descending into deeper waters (UVR avoidance hypothesis; Fig. 1a, H2, b). We observed the vertical position of larvae in three UVR treatments: visible light only, visible + UVA (VUVA), or visible + UVA + UVB (VUVAB). A visible + UVB treatment was not included because it does not naturally occur in the environment, given that UVB attenuates much more rapidly than UVA. Larvae were observed in tall glass jars

(18 cm tall × 6 cm diameter) filled with 500 ml of seawater. The glass jars were then placed in Styrofoam coolers filled with newly collected seawater to maintain natural temperatures. The UVR treatments were created using square plastic filters (38 × 38 cm) composed of polycarbonate (transmits > 400 nm), Mylar (transmits > 320 nm) and UVR transparent plexiglass (transmits > 270 nm) for visible, VUVA and VUVAB treatments, respectively (Bashevkin et al. 2019a). Plastic filters were partially open at the sides to permit air circulation and avoid warming by the greenhouse effect. One hundred larvae were introduced into each of three or four replicate jars per treatment and larvae swimming in the top third of each container were photographed from the side every 30 min for 2 h. The number of larvae in photographs was counted. We conducted a total of 5 experiments (48 unique replicates in total and 4800 larvae tested) on different days between 11 AM and 2 PM.

### Chromatophore behavior in response to UVR

Experiments were conducted in 2015 to determine whether light or UVR would induce crab larvae to expand or contract their chromatophores (UVR expansion hypothesis; Fig. 1a, H3, b). Larvae were placed individually into compartments of opaque blue plastic ice cube trays (20-ml compartments) with seawater. Blue ice cube trays were used to mimic planktonic background colors. The trays were then floated in Styrofoam coolers (26 × 32 × 19 cm) filled with newly collected seawater to maintain ambient temperature under intense sunlight.

Larvae were exposed to one of the four light treatments: darkness, visible light, VUVA, or VUVAB. The four light treatments were then randomly assigned to different coolers (one cooler per treatment) and the treatments were applied by covering the coolers with the plastic filters described above. Darkness was achieved by floating the trays in a cooler made of rigid opaque plastic that was closed for the duration of each experiment. Between 12 and 16 larvae in each treatment were exposed for 0.5–2 h. We conducted experiments with *A. ricordi*, *Eurypanopeus* sp., and *M. sculptus* for 1 h, and one experiment with *A. ricordi* for 0.5 h to determine if larvae could respond to UVR cues within 0.5 h.

At the end of each experiment, larvae were quickly removed from the trays and photographed through a dissecting microscope at 45X with a Canon EOS Rebel T3 Digital SLR Camera fitted with a microscope adapter. A live larva was pipetted onto a depression slide, isolated in a few drops of seawater, and photographed against a white background while illuminated from above with natural sunlight. Larvae were photographed alive and from the lateral view while still. Crab larvae need around 30 min to adjust their chromatophores (Pautsch 1961; Lawinski and Pautsch

1965) so larvae could not have expanded or contracted them in the few minutes it took to take photographs, and no such changes were observed.

The total area of pigmentation was quantified from the photographs of the larvae using the image analysis program ImageJ through the Fiji platform (Schindelin et al. 2015). Images were first converted to binary format, which transformed all pigmentation to black and all transparent segments to white. The black (pigment) surface area was then measured in this binary image. A pilot experiment demonstrated no effect of different overhead lighting conditions on the pigment measurement by this method nor did natural lighting change perceptibly while larvae were photographed during each experiment. This approach to quantifying pigmentation is identical to that used by Bashevkin et al. (2019a, 2020a) and very similar to the approach described by Siegenthaler et al. (2017) that was used to study background matching in shrimp (Siegenthaler et al. 2018). This approach was found superior in speed, accuracy, and precision to traditional methods that rank chromatophore size with an index from 1 to 5 (Siegenthaler et al. 2017).

### Predation experiments

Predation experiments (testing the predation vulnerability hypothesis; Fig. 1a, H4, b) were conducted in 2016 using 19-L light blue-tinted plastic carboys (31 cm height × 25 cm diameter) with the top removed to allow UVR to enter. These open-topped carboys were exposed to 3 UVR treatments during predation experiments: visible light, VUVA, or VUVAB. The UVR treatments were applied by covering the carboys with the same plastic filters as above. The plastic covers were secured over the carboys with Velcro, leaving a 5-cm gap between the plastic cover and carboy opening that was large enough to allow air exchange but small enough to prevent sunlight from entering directly without first passing through a plastic filter during the hours these experiments were conducted (when the sun was close to directly overhead). Fish predators were collected and placed singly in carboys that were partially filled (10 cm) with seawater the evening before experiments were conducted allowing them to acclimate. Individual fish were used in only one experimental trial. On the morning of an experiment, 12 L of newly collected unfiltered seawater and 200 crab larvae with equal numbers of each species (Table 1) were added to each carboy. There were 4 replicate experimental carboys and 1 control carboy (without a fish) per light treatment, for a total of 15 carboys. Sometimes there were not enough larvae of a species to conduct 15 predation trials in a day, so all carboys were not used, but we always evenly divided fish predators among the light treatments. Carboys were partially submerged in shallow subtidal seagrass and coral rubble habitat, where the fish predators and many of the adult crabs



**Table 1** Experimental design for predation experiments indicating how many experiments were conducted with larvae from four species of crabs and how many total reef silversides *Hypoatherina harringtonensis* were offered each of 4 combinations of larvae

Prey choices	Number of experiments	Total fish
100 AR 100 OB	9	100
100 AR 100 CG	3	41
100 AR 100 MM	4	56
67 AR 67 OB 67 MM	2	28

AR *Armases ricordi*, OB *Omalacantha bicornuta*, CG *Cardisoma guanhumi*, MM *Minuca mordax*. Each experiment was conducted on a different day and each fish was only used once so the total number of fish is equivalent to the number of predator trials. In some cases, there were not enough larvae of a species to conduct 15 predation trials in a day so some experiments consisted of fewer than 15 trials

were collected, providing natural temperatures and lighting conditions. Predation trials were conducted in sunlight for 2–3 h starting around 11 AM. Predator preferences were calculated relative to the total number of larvae consumed in each trial to account for differences in trial duration and fish hunger. At the end of the experiment, fish were removed with a hand net and their total lengths were measured. The contents of each carboy were then poured through a sieve (100  $\mu\text{m}$ ) to concentrate the surviving larvae, which were counted and identified in the laboratory.

We conducted 16 experiments (197 trials) on 16 different days in which fish were offered a choice between 2 species. In each of these experiments, fish were offered the abundant and darkly pigmented *Armases ricordi* and one of three species (*Minuca mordax*, *Omalacantha bicornuta*, or *Cardisoma guanhumi*). We also conducted two experiments (hereafter referred to as Experiment 1 and 2; 28 trials) in which fish were offered three species: *A. ricordi*, *O. bicornuta*, and *M. mordax* (Table 1). On average, 98% of larvae were recovered from carboys without fish and no fewer than 92% were recovered. The number of missing larvae was unrelated to larval species or UVR treatment, indicating that we were recovering unbiased larval samples at the end of experiments, so these controls were not included in analyses. Trials were excluded when fish consumed fewer than 10% (selectivity would be based on too few predation events) or greater than 90% (selectivity may be artificially biased as preferred prey is depleted) of prey.

Fish used in these experiments ranged from 20 to 36 mm long (standard length) with mouth gapes of 1.9 to 4.0 mm. The average spine-to-spine lengths (distance from the tip of the antennal or rostral spine to the tip of the dorsal spine, corresponding to the minimum mouth gape required to consume them) of these crab larvae were 0.5, 0.7, 0.9, and 1.2 mm for *M. mordax*, *C. guanhumi*, *A. ricordi*, and *O. bicornuta* respectively. Thus, all larvae were small enough

to be consumed by fish and fish readily ate all species (SMB, pers. obs.).

### Chromatophore behavior in response to predator cue and UVR

To determine whether larvae would contract chromatophores in fish cues (predation contraction hypothesis; Fig. 1a, H5, b), we conducted experiments with the same methods as described above (Chromatophore behavior in response to UVR) except with the treatments described here. In these experiments, larvae were exposed to two fish treatments (presence or absence of cue) and two light treatments (VUVAB or darkness) in a factorial design. We included two UVR treatments to determine whether any larval response to predator cues would be affected by light cues. We filled two containers (1 L) with seawater and placed a fish into one of the containers for 2 h to allow the dissolution of mucus-born cues known to stimulate larval crabs (Rasch and O'Connor 2012; Charpentier and Cohen 2014) before pouring the water into the ice cube trays. We conducted two 1-h experiments on *A. ricordi* and one each on *M. coryphe* and *M. sculptus*, as well as longer 2-h experiments on *A. ricordi*, *A. americanum*, and *M. sculptus* to determine if longer exposures would induce a stronger response.

### Statistical analyses

Statistical models were fit in a Bayesian framework with Stan (Stan Development Team 2016) run through the *R* package brms (Bürkner 2017) to best account for the unbalanced nature of these opportunistic experiments (Gelman et al. 2013; McElreath 2015). Our priors were weakly informative as recommended by the package authors, using the Stan language manual (Stan Development Team 2016), Gelman and Hill (2006) and McElreath (2015) as references. All models were run on three chains for 10,000 iterations each, including 2500 warmup iterations that were discarded. In all analyses, we started with models including all interactions up to three ways, then paired down the nonsignificant interactions until we found the best model fit by WAIC, or parsimony when WAIC differences were equivocal (i.e., overlapping standard errors). For each model, the diagnostics and posterior predictive checks were thoroughly inspected before proceeding. All models were used to produce fitted values with 95% confidence intervals for hypothesis tests. To assess and visualize the interactive effects of continuous covariates, discrete categories were chosen representing the range of values from the experiments. Model predictions were then plotted for visual representation of our statistical results. Analogous frequentist models produced equivalent results (Online Resource: Figs. S1–S3).

To test the UVR avoidance hypothesis (Fig. 1a, H2), vertical position data were analyzed with a binomial generalized linear mixed model (GLMM) fit to the proportion of larvae swimming in the top 1/3 of each jar. We included main effects for hours since the start of the experiment, average brightness at each sampling time (calculated as above), and light treatment, along with all two-way interactions. We also included a random intercept for each unique replicate jar to account for repeated measures.

The data from each chromatophore expansion experiment were analyzed with separate Gaussian linear models for each species and hypothesis. To test the UVR expansion hypothesis (Fig. 1a, H3), the light cue experiments were each analyzed with a fixed effect for light treatment. To test the predation contraction hypothesis (Fig. 1a, H5), the fish cue experiments were each analyzed with fixed effects for light treatment, fish treatment, and their interaction. An additional fixed effect for experiment and all resulting interactions were added in cases where more than one experiment was conducted on a species.

To test the predation vulnerability hypothesis (Fig. 1a, H4), we fit separate GLMMs for the two-choice and three-choice predation experiments. For the two-choice predation experiments, we fitted a binomial GLMM to the number of *A. ricordi* consumed out of the total number of larvae consumed in that trial. We included fixed effects predictors for the light treatment coded as an ordinal variable (0 for visible light, 1 for VUVA, 2 for VUVAB), difference in pigmentation (see below) between *A. ricordi* and the other species, brightness, and fish length, as well as two-way interactions between light treatment and pigment difference, pigment difference and brightness, and brightness and fish length. We also included a random intercept for each unique fish predator (= unique experimental unit with 200 larvae + 1 fish) to account for random differences in fish preference or larval prey quality. Brightness was calculated as the average solar radiation intensity over the duration of the experiment. Pigment difference was the difference in average pigmented area of the two species offered to fish predators in each experiment, from data previously collected on these species (Bashevkin et al. 2019a, b, 2020a) with the method described above for the chromatophore expansion experiments.

For the predation experiments in which fish were offered a choice between three larval prey species, we fit a multinomial GLMM to the number of each species consumed. We included fixed effects for experiment, fish length, light treatment coded as an ordinal variable, and the interaction between fish length and light treatment. Since only two experiments were performed, we were unable to include brightness as a predictor, so we included the fixed effect for experiment instead. We also included a random intercept for

each unique fish predator to account for random differences in fish preference or larval prey quality.

## Results

### Behavioral compensation: UVR avoidance hypothesis

*A. ricordi* larvae generally avoided the surface as sunniness and exposure time increased (Fig. 3). Larvae exposed to VUVA or VUVAB behaved similarly and avoided the surface most, while larvae exposed to visible light spent significantly more time at the surface on cloudier days for shorter exposures (Fig. 3b, Online Resource: Table S1).

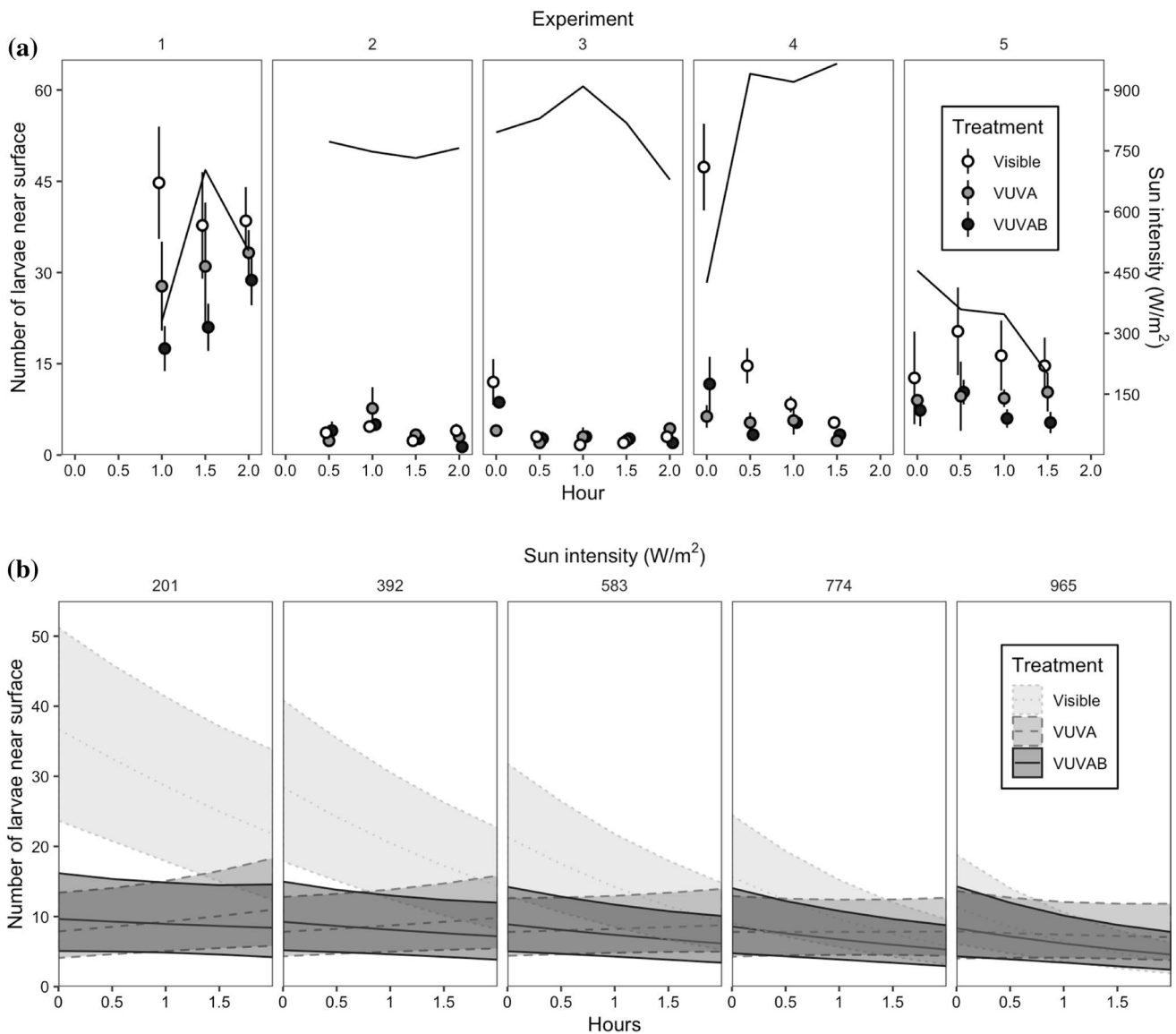
### Behavioral compensation: UVR expansion hypothesis

In response to different light cues, *A. ricordi*, *A. americanum*, and *Eurypanopeus* sp. expanded chromatophores, but *M. sculptus* and *M. coryphe* did not. *A. ricordi* significantly expanded chromatophores in response to visible light, VUVA, and VUVAB, and *A. americanum* similarly expanded chromatophores in VUVAB (visible light and VUVA treatments were not tested for this species), while *Eurypanopeus* expanded chromatophores only in response to VUVA or VUVAB (Fig. 4, Online Resource: Table S1).

### Predation vulnerability hypothesis

In the two-species choice experiments, fish predators significantly preferred the more pigmented *A. ricordi* on sunnier days, when the contrast in pigmentation between species of larval prey was greatest, when less UVR was present, and when fish were larger (Fig. 5a,b, Online Resource: Table S1). However, while small and medium fish preferred more pigmented prey on sunnier days, they significantly preferred the more transparent species on cloudy days. Sunniness did not affect the preference of large fish.

The more pigmented *A. ricordi* and *O. bicornuta* were also significantly preferred over the lightly pigmented *M. mordax* in the three-species choice experiments (Fig. 5a, c). This preference was again highest when less UVR was present. Significant preferences for *A. ricordi* or *O. bicornuta* over *M. mordax* were observed for small and medium fish from Experiment 2 in the visible and VUVA treatments (Fig. 5c). Similar non-significant trends were evident in Experiment 1 (Fig. 5c). *A. ricordi* and *O. bicornuta* were generally consumed with equal preference but there was a slight trend toward a preference for *O. bicornuta* (Fig. 5c, Online Resource 1: Table S1).



**Fig. 3** Vertical position of *Amases ricordi* larvae in response to UVR cues and light intensity. **a** Number of larvae near the surface is represented by points (mean  $\pm$  SE) in five replicate experiments performed on separate days. The line represents sun intensity over the duration

of the experiment. **b** Predicted number of larvae near the surface over a range of sun intensities with 95% confidence intervals from a Bayesian binomial GLMM

### Behavioral compensation: predation contraction hypothesis

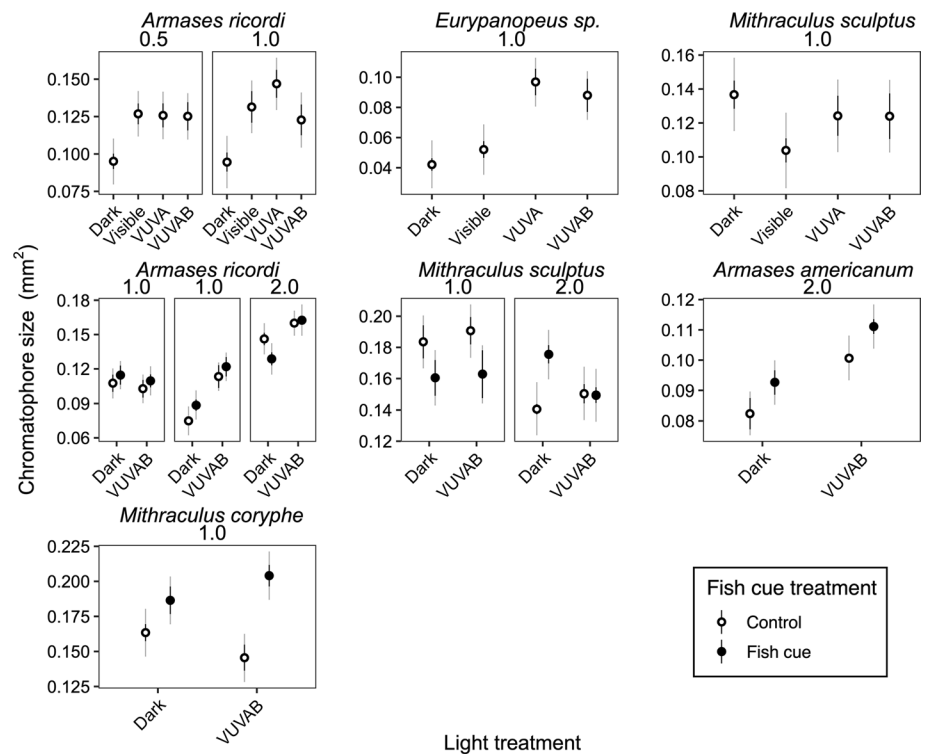
In experiments manipulating fish cues, *M. coryphe* expanded chromatophores in response to fish cues in VUVAB but not darkness in one experiment but tended to contract chromatophores in response to fish cues in the other experiment. *M. sculptus* significantly expanded chromatophores in response to fish cues in darkness, with the same trend in VUVAB. *A. americanum* and *A. ricordi* showed no significant reaction to fish cues but tended nonsignificantly to expand chromatophores when fish

cues were present in 3 of 4 experiments (Fig. 4, Online Resource: Table S1).

### Discussion

Larvae exhibited consistent behavioral avoidance of UVR through vertical swimming and chromatophore expansion. The one species we tested avoided UVR by descending to deeper waters and three of four species tested expanded chromatophores in response to sunlight. Pigmented larvae were subjected to higher predation risk in some circumstances

**Fig. 4** Chromatophore response to light and predatory fish cues. Points represent the mean for each treatment, black error bars are the SE, and gray error bars are the 95% confidence interval predicted from a Bayesian regression. Multi-paneled subplots represent repeated replicate experiments performed on the same species and numbers above each plot indicate experimental duration in hours



(sunnier days, less UVR, and larger fish) but larval chromatophore responses to predator cues were inconsistent. Fish cues had no consistent effect on larval chromatophores, and, surprisingly, induced larvae to expand their chromatophores in two cases.

*Armases ricordi* larvae avoided surface water more when sun intensity was high, exposure was long, or UVR was present, supporting our UVR avoidance hypothesis (Fig. 1a, H2). This behavior could minimize exposure to the most intense UVR present in surface waters. Furthermore, descending to subsurface waters under intense sunlight could also help shield pigmented larvae from visual predation since we found fish preferred more pigmented *A. ricordi* prey under more intense sunlight. Diving in response to UVR has been previously observed in sea urchin, barnacle, and herring larvae (Pennington and Emler 1986; Speckmann et al. 2000; Chiang et al. 2007) as well as numerous holoplankton (Hairston 1980; Hansson et al. 2007; Hylander et al. 2009). *A. ricordi* seems well adapted to UVR exposure, exhibiting two behavioral responses to minimize UVR damage as well as surviving better than most species after prolonged UVR exposure (Bashevkin et al. 2019a).

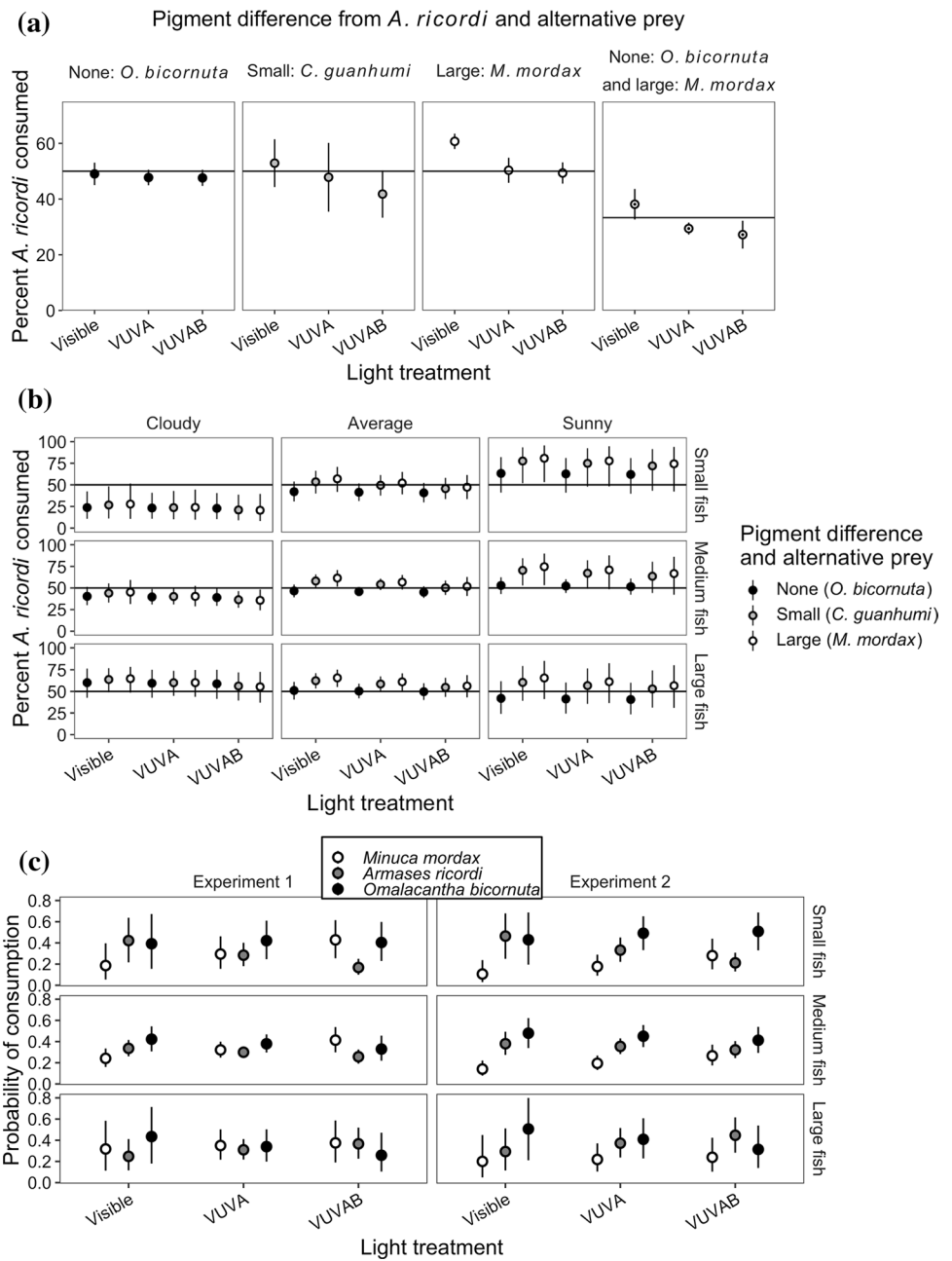
Larvae of three of five species (*A. ricordi*, *A. americanum*, and *Eurypanopeus sp.*) consistently responded to light and UVR cues by expanding their chromatophores, supporting our UVR expansion hypothesis (Fig. 1a, H3). While predation is thought to be an important source of mortality for larval crabs (Bashevkin and Morgan 2020; Morgan 1990), intense tropical UVR may be more important where

the present study was conducted. Pigmentation plasticity in response to UVR has been observed before in crab postlarvae (Miner et al. 2000), crab adults (Coohill et al. 1970), shrimp larvae (Pautsch 1951), fish larvae (Hunter et al. 1979), *Daphnia* (Hansson et al. 2007), and copepods (Brüsin et al. 2016), likely because it increases protection from damaging UVR (Hairston 1976; Luecke and O'Brien 1983; Bashevkin et al. 2019a). Notably, only the studies on decapods found UVR-induced pigment changes within the same timescale we observed (minutes to hours). These rapid, reversible chromatophore responses enable animals to respond to small-scale variation in the environment due to changes in time of day, turbidity, and weather. Long-term pigmentation plasticity (over days to weeks) such as that observed in copepods is an appropriate response to seasonal changes or consistent spatial differences in UVR.

Larvae with more pigmentation were more preferred as prey by silversides, supporting our predation vulnerability hypothesis (Fig. 1a, H4). Predators increasingly preferred *A. ricordi* as its pigmentation difference with the alternative prey increased. *A. ricordi* larvae are dark brown to black with 0.164 mm<sup>2</sup> pigmentation; *O. bicornuta* larvae have green, blue, black, and red pigmentation covering 0.168 mm<sup>2</sup>; *C. guanhumii* larvae are gray with 0.067 mm<sup>2</sup> pigmentation; and *M. mordax* larvae have scattered black-grey pigmentation covering 0.036 mm<sup>2</sup> (Bashevkin et al. 2019b, 2020a). Thus, it is not surprising that we observed the strongest preference for *A. ricordi* over *M. mordax*, no preference between *A. ricordi* and *O. bicornuta* in two-choice experiments, and



**Fig. 5** Reef silverside *Hypoatherina harringtonensis* preference for larvae of crab species with different pigmentations. In **(a)** and **(b)** Y-axes represent the proportion of the darkly pigmented *Armases ricordi* consumed of all larvae consumed. Points above the black line represent disproportionate consumption of (i.e., preference for) *A. ricordi*. **a** Mean ( $\pm$ SE) fish preference for *A. ricordi* from four types of prey choice trials, ordered by increasing pigmentation difference with alternative prey choice (noted above plots). Fish were offered 200 prey, split evenly among prey species. **b** Predicted values with 95% confidence intervals from a Bayesian binomial GLMM. Fish sizes correspond to 2, 2.8, and 3.6 cm. **c** Predicted values with 95% confidence intervals from Bayesian multinomial GLMM fit to the number of each species consumed in the three-way choice experiments. Fish sizes correspond to 2.3, 3, and 3.7 cm long



a slight preference for *O. bicornuta* in three-choice experiments (Fig. 5).

Fish preference for pigmented larvae was not as strong as expected and depended on a number of covariates. Small fish ate more pigmented larvae on sunnier than cloudier days, while feeding preferences of large fish were mostly unaffected by ambient light conditions. This could reflect changes in feeding ability and visual acuity as fish grow. Both the visual acuity of fish and the distance at which they react to zooplankton prey tend to increase as fish grow and in brighter light (Breck and Gitter 1983; Aksnes and Giske 1993). However, in our experiments, small fish increasingly

preferred more transparent and presumably less visible prey as sun intensity decreased. This change in feeding preference with sun intensity could be due to (1) pigmented *A. ricordi* contracting chromatophores on cloudy days eliminating or reversing the difference in pigmentation between prey, or (2) different optical environments on cloudy days increasing the visibility of transparent prey. This raises the possibility that selective predation varies with cloud cover, e.g., predation risk for pigmented prey increases with sunlight intensity.

The preference of fish predators for pigmented larvae tended to increase with decreasing UVR. The reduced predator preference for pigmented larvae in the presence of UVR

could be due to differences in the visibility of larvae. Many planktivorous fishes can see in the UV range, including other species of silversides (Loew et al. 1996; Losey et al. 1999; Siebeck and Marshall 2007). If larvae appearing transparent under visible light absorb or scatter UVR, they may be more visible in UVR to predators that can see UVR. Invisible photoprotective compounds such as mycosporine-like amino acids (MAAs) are accumulated by some crab larvae (Moresino et al. 2014). MAAs only absorb in UVR, thus protecting larvae from UVR while maintaining transparency in the visible spectrum despite reducing transparency to UVR. Thus, prey that are transparent in UVR as well as visible light may best avoid these predators, although susceptibility to UVR damage would increase (Johnsen and Widder 2001). Furthermore, if larvae produce or consume compounds that fluoresce in UVR, their conspicuousness in the visible range could increase in the presence of UVR as well.

Predator preferences may also be related to interspecific prey differences in behavioral, morphological, or chemical defenses. All species of larval prey were quickly and easily consumed by our fish predators (SMB, pers. obs.), so differences in behavioral defenses are unlikely. Prey species differed in size and the minimum gape width needed to consume them ranged from 0.5 mm (*M. mordax*) to 1.2 mm (*O. bicornuta*; Bashevkin et al. 2019b, 2020a). However, fish used in this study had gape widths of 1.9 mm or larger and the best defended prey with the longest spine–spine length (*O. bicornuta*) was also the most preferred. Chemical defenses are rare in crustaceans and have never been discovered in crustacean larvae (Bashevkin and Morgan 2020).

Copepods contract chromatophores in response to fish cues (Hylander et al. 2009, 2012; Brüsin et al. 2016) and we expected crab larvae to do so too. However, larvae did not consistently contract chromatophores in responses to fish cues, in contrast to the much clearer responses we observed to light and UVR. In two cases, larvae even expanded their chromatophores when fish cues were present. Thus, our predation contraction hypothesis was not supported (Fig. 1a, H5). The chromatophore expansion we observed in response to fish cues could be due to background matching. Crab larvae are known to match backgrounds (Pautsch 1967), and they might have expanded chromatophores to blend in against the dark background of the ice cube trays used in our experiments. However, experiments with related temperate species on light and dark backgrounds found similarly inconsistent reactions to predator cues regardless of background color (Bashevkin 2019). These inconsistencies may be related to the early age of larvae used in these experiments. We used all first-stage larvae, and Pautsch (1967) found that late-stage but not first-stage larvae of *Rithropanopeus harrisi* respond to backgrounds or chromatophore-dispersing hormones. Why first-stage larvae would show inconsistent responses to background and predation but

consistent responses to light cues is unclear. One possibility is that visual predation is a more variable threat than UVR due to interspecific and ontogenetic differences in the visual systems of predator fishes (Levine and MacNichol 1979; Pankhurst 1987) and spatial and temporal variability in optical properties of seawater (Johnsen 2014). However, if so, we would expect larval behavioral responses to predator cues to be even stronger and more consistent due to this variability, which should favor behavioral flexibility over fixed morphology. Another possibility is that *H. harringtonensis* is not an important predator of crab larvae, although it readily consumed crab larvae in our experiments and related species prey heavily on crab larvae (Bashevkin and Morgan 2020). Alternatively, the lack of a consistent response to predator cues may indicate that mortality caused by exposure to UVR is a more pervasive threat than predation, at least for first-stage larvae.

Our results indicated that UVR may be a stronger selective pressure than predation on pigmentation of tropical crab larvae. Larvae adjusted their pigmentation in response to UVR but not predators. Transparent larvae only had slightly higher survival from visual predators in the absence of UVR, while in a related study (Bashevkin et al. 2019a), pigmented larvae had much higher survival from UVR damage. To tease apart these selective pressures, future studies could survey the vertical distributions of crab larvae in the field to determine how larvae of different pigmentations respond to vertical gradients in fish predation and UVR.

These results have implications for our understanding of the factors determining the survival and vertical distribution of marine larvae and other members of the plankton community. We provide evidence for the impacts of weather (sunniness) and UVR on selective planktivory, vertical position, and behavioral color change in crab larvae. A better understanding of the factors determining the survival and vertical migrations of larvae will be key to constructing better mechanistic models of larval survival and dispersal under current conditions and future climate change scenarios (Bashevkin et al. 2020b). More broadly, these results improve our understanding of the selective pressures acting on pigmentation and vertical distribution of holoplankters as well as meroplankters in both freshwater and marine systems. Our results also enhance our understanding of the environmental drivers of prey selection in planktivorous fishes and potential species interactions in plankton communities. Furthermore, by documenting a trade-off between UVR and predation in which UVR seems to be a stronger selective force, we suggest the potential for using studies of trade-offs and compensation to evaluate the relative influences of threats in systems like plankton that are difficult to study in situ. Lastly, improved understanding of the behavioral mechanisms through which animals can circumvent countervailing selective forces on their morphology can help

us understand broader patterns of morphological evolution in relation to behavior and environment.

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**Author contribution statement** SMB, JHC, and SGM conceived and designed the experiments. SMB performed the experiments, analyzed the data, and wrote the manuscript. JHC and SGM provided editorial advice.

### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

### References

- Abele LG (1976) Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panamá. *Mar Biol* 38:263–278
- Abele LG (1992) A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. *Smithson Contrib Zool* 527:1–60
- Aksnes DL, Giske J (1993) A theoretical model of aquatic visual feeding. *Ecol Model* 67:233–250. [https://doi.org/10.1016/0304-3800\(93\)90007-F](https://doi.org/10.1016/0304-3800(93)90007-F)
- Arnold SJ (1992) Constraints on phenotypic evolution. *Am Nat* 140:S85–S107
- Bashevkin SM (2019) The Adaptive Arsenal of Crustacean Larvae Against Predatory and Environmental Stresses of the Plankton. Ph.D., University of California, Davis
- Bashevkin SM, Christy JH, Morgan SG (2019a) Photoprotective benefits of pigmentation in the transparent plankton community: a comparative species experimental test. *Ecology* 100:e02680. <https://doi.org/10.1002/ecy.2680>
- Bashevkin SM, Christy JH, Morgan SG (2019b) Data from: adaptive specialization and constraint in morphological defenses of planktonic larvae. Dryad Digit Repos. <https://doi.org/10.5061/dryad.sxksn02z8>
- Bashevkin SM, Christy JH, Morgan SG (2020a) Adaptive specialization and constraint in morphological defenses of planktonic larvae. *Funct Ecol* 34:217–228. <https://doi.org/10.1111/1365-2435.13464>
- Bashevkin SM, Dibble CD, Dunn RP et al (2020b) Larval dispersal in a changing ocean with an emphasis on upwelling regions. *Ecosphere* 11:e03015. <https://doi.org/10.1002/ecs2.3015>
- Bashevkin SM, Morgan SG (2020) Predation and competition. In: Anger K, Harzsch S, Thiel M (eds) *The natural history of the crustacea*, Vol 7, Developmental biology and larval ecology. Oxford University Press, New York (in press)
- Breck JE, Gitter MJ (1983) Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. *Can J Fish Aquat Sci* 40:162–167. <https://doi.org/10.1139/f83-026>
- Brüsin M, Svensson PA, Hylander S (2016) Individual changes in zooplankton pigmentation in relation to ultraviolet radiation and predator cues. *Limnol Oceanogr* 61:1337–1344. <https://doi.org/10.1002/lno.10303>
- Bürkner P-C (2017) brms: an R package for Bayesian multilevel models using Stan. *J Stat Softw* 80:1–28. <https://doi.org/10.18637/jss.v080.i01>
- Charpentier CL, Cohen JH (2014) Effects of predator odor on photo-behavior, visual sensitivity, and morphology of crab larvae. *Integr Comp Biol* 54:E35–E35
- Chiang W-L, Wu RS-S, Yu PK-N, Au DW-T (2007) Are barnacle larvae able to escape from the threat of UV? *Mar Biol* 151:703–711. <https://doi.org/10.1007/s00227-006-0508-9>
- Cohill TP, Bartell CK, Fingerman M (1970) Relative effectiveness of ultraviolet and visible light in eliciting pigment dispersion directly in melanophores of the fiddler crab, *Uca pugilator*. *Physiol Zool* 43:232–239
- Crane J (1975) Fiddler crabs of the world: Ocypodidae: genus *Uca*. Princeton University Press, Princeton, New Jersey
- Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge
- Gelman A, Stern HS, Carlin JB et al (2013) Bayesian data analysis. Chapman and Hall/CRC, Boca Raton
- Greer AT, Woodson CB, Guigand CM, Cowen RK (2016) Larval fishes utilize Batesian mimicry as a survival strategy in the plankton. *Mar Ecol Prog Ser* 551:1–12. <https://doi.org/10.3354/meps11751>
- Hairston NG Jr (1976) Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. *Proc Natl Acad Sci* 73:971–974
- Hairston NG Jr (1980) The vertical distribution of diaptomid copepods in relation to body pigmentation. Evolution and ecology of zooplankton communities. Univ Press of New England, Lebanon, pp 98–110
- Hansson L-A, Hylander S, Sommaruga R (2007) Escape from UV threats in zooplankton: a cocktail of behavior and protective pigmentation. *Ecology* 88:1932–1939. <https://doi.org/10.1890/06-2038.1>
- Herbert PDN, Emery CJ (1990) The adaptive significance of cuticular pigmentation in *Daphnia*. *Funct Ecol* 4:703–710
- Hessen DO, Borgeraas J, Kessler K, Refseth UH (1999) UV-B susceptibility and photoprotection of Arctic *Daphnia* morphotypes. *Polar Res* 18:345–352. <https://doi.org/10.1111/j.1751-8369.1999.tb00313.x>
- Hunter JR, Taylor JH, Moser HG (1979) Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the pacific mackerel, *Scomber japonicus*, during the embryonic stage. *Photochem Photobiol* 29:325–338. <https://doi.org/10.1111/j.1751-1097.1979.tb07055.x>
- Husak JF, Macedonia JM, Fox SF, Saucedo RC (2006) Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology* 112:572–580. <https://doi.org/10.1111/j.1439-0310.2005.01189.x>
- Hylander S, Larsson N, Hansson L-A (2009) Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnol Oceanogr* 54:483–491. <https://doi.org/10.4319/lo.2009.54.2.0483>
- Hylander S, Souza MS, Balseiro E et al (2012) Fish-mediated trait compensation in zooplankton. *Funct Ecol* 26:608–615. <https://doi.org/10.1111/j.1365-2435.2012.01976.x>

- Johnsen S (2014) Hide and seek in the open sea: pelagic camouflage and visual countermeasures. *Annu Rev Mar Sci* 6:369–392. <https://doi.org/10.1146/annurev-marine-010213-135018>
- Johnsen S, Widder EA (2001) Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. *Mar Biol* 138:717–730. <https://doi.org/10.1007/s002270000499>
- Klompaker AA, Portell RW, Klier AT et al (2015) Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracidae. *PeerJ* 3:e1301. <https://doi.org/10.7717/peerj.1301>
- Lawinski L, Pautsch F (1965) System of the chromatophores and their behaviour in the larva of the crab, *Rhithropanopeus harrisi* (Gould) subsp. *tridentatus* (Maitland). *Acta Biol Med Gdansk* 9:5–14
- Levine JS, MacNichol EF (1979) Visual pigments in teleost fishes: Effects of habitat, microhabitat, and behavior on visual system evolution. *Sens Processes* 3:95–131
- Loew ER, McAlary FA, McFarland WN (1996) Ultraviolet visual sensitivity in the larvae of two species of marine atherinid fishes. In: Lens P, Hartline D, Purcell J, Macmillan D (eds) *Zooplankton sensory ecology and physiology*. Gordon and Breach, Sydney, pp 195–209
- Losey GS, Cronin TW, Goldsmith TH et al (1999) The UV visual world of fishes: a review. *J Fish Biol* 54:921–943. <https://doi.org/10.1111/j.1095-8649.1999.tb00848.x>
- Luecke C, O'Brien WJ (1983) Photoprotective pigments in a pond morph of *Daphnia middendorffiana*. *Arctic* 36:365–368
- McElreath R (2015) *Statistical rethinking: A Bayesian course with examples in R and Stan*. CRC Press, Boca Raton
- Miner BG, Morgan SG, Hoffman JR (2000) Postlarval chromatophores as an adaptation to ultraviolet radiation. *J Exp Mar Biol Ecol* 249:235–248
- Moresino RDH, Gonçalves RJ, Helbling EW (2014) Direct and indirect acquisition of photoprotective compounds in crab larvae of coastal Patagonia (Argentina). *J Plankton Res* 36:877–882
- Morgan SG (1990) Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology* 71:1640–1652
- Morgan SG, Anastasia JR (2008) Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proc Natl Acad Sci* 105:222–227
- Morgan SG, Christy JH (1996) Survival of marine larvae under the countervailing selective pressures of photodamage and predation. *Limnol Oceanogr* 41:498–504
- Morgan SG, Fisher JL, McAfee ST et al (2014) Transport of crustacean larvae between a low-inflow estuary and coastal waters. *Estuaries Coasts* 37:1269–1283
- Pankhurst NW (1987) Intra- and interspecific changes in retinal morphology among mesopelagic and demersal teleosts from the slope waters of New Zealand. *Environ Biol Fishes* 19:269–280. <https://doi.org/10.1007/BF00003228>
- Pautsch F (1951) Colour adaptation of the zoea of the shrimp *Crangon crangon* L. *Bull Acad Sci B II Cracoe* 7–10:511–523
- Pautsch F (1961) The larval chromatophoral system of the crab, *Carcinus maenas* (L). *Acta Biol Med (Gdansk)* 5:105–119
- Pautsch F (1967) On some responses of chromatophores in larvae and megalopa of crab *Rhithropanopeus harrisi* (Gould) Subsp *tridentatus* (Maitland). *Gen Comp Endocrinol* 9:480–481
- Pennington JT, Emlet RB (1986) Ontogenetic and diel vertical migration of a planktonic echinoid larva, *Dendraster excentricus* (Eschscholtz): occurrence, causes, and probable consequences. *J Exp Mar Biol Ecol* 104:69–95
- Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:22–39
- Queiroga H, Blanton J (2005) Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv Mar Biol* 47:107–214
- Rasch JA, O'Connor NJ (2012) Development and behavior of megalopae of the non-native crab *Hemigrapsus sanguineus* in response to chemical cues from coastal fishes. *J Exp Mar Biol Ecol* 416–417:196–201. <https://doi.org/10.1016/j.jembe.2011.12.012>
- Rathbun MJ (1925) The spider crabs of America. *U S Natl Mus Bull* 129:1–613
- Rathbun MJ (1930) The cancrroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. *U S Natl Mus Bull* 152:1–609
- Rathbun MJ (1918) The grapsoid crabs of America. *US Natl Mus Bull* 97:1–461
- Rundle SD, Brönmark C (2001) Inter- and intraspecific trait compensation of defense mechanisms in freshwater snails. *Proc R Soc Lond B Biol Sci* 268:1463–1468
- Schindelin J, Rueden CT, Hiner MC, Eliceiri KW (2015) The ImageJ ecosystem: An open platform for biomedical image analysis. *Mol Reprod Dev* 82:518–529. <https://doi.org/10.1002/mrd.22489>
- Siebeck UE, Marshall NJ (2007) Potential ultraviolet vision in pre-settlement larvae and settled reef fish—a comparison across 23 families. *Vision Res* 47:2337–2352. <https://doi.org/10.1016/j.visres.2007.05.014>
- Siegenthaler A, Mastin A, Dufaut C et al (2018) Background matching in the brown shrimp *Crangon crangon*: adaptive camouflage and behavioural-plasticity. *Sci Rep* 8:3292. <https://doi.org/10.1038/s41598-018-21412-y>
- Siegenthaler A, Mondal D, Benvenuto C (2017) Quantifying pigment cover to assess variation in animal colouration. *Biol Methods Protoc* 2:1–8. <https://doi.org/10.1093/biomethods/bpx003>
- Speckmann CL, Bollens SM, Avent SR (2000) The effect of ultraviolet radiation on the vertical distribution and mortality of estuarine zooplankton. *J Plankton Res* 22:2325–2350. <https://doi.org/10.1093/plankt/22.12.2325>
- Stan Development Team (2016) *Stan modeling language users guide and reference manual*, Version 2.14.0
- Utne-Palm AC (1999) The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *J Fish Biol* 54:1244–1258. <https://doi.org/10.1111/j.1095-8649.1999.tb02052.x>
- Zera AJ, Harshman LG (2001) The physiology of life history trade-offs in animals. *Annu Rev Ecol Syst* 32:95–126