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Research Article

Short-term effect of UVR on vertical distribution of *Cyrtograpsus altimanus* and *Alexandrium tamarense* from Atlantic Patagonia

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ABSTRACT. Many marine species spend part of their development in upper layers of the water column, where they may be exposed to solar ultraviolet radiation (UVR). For many of these species, light is one of the key environmental clues which triggers behaviorally-mediated adjustments in vertical distribution. We incubated planktonic larvae of the crab *Cyrtograpsus altimanus* in column-like aquaria to study their responses with/without UVR (under a solar simulator) and with/without a potential prey (the dinoflagellate *Alexandrium tamarense*). Their vertical distribution was recorded and used to evaluate the combined effects of UVR and the presence of the dinoflagellate on larval behavior. When UVR was absent, most larvae showed a tendency to swim upwards and to aggregate near the surface, regardless of the dinoflagellate presence. However, UVR inhibited this tendency and induced a repellent effect, which resulted in a more homogeneous vertical distribution of larvae. *A. tamarense* did not affect the vertical distribution of larvae. These results suggest that UVR-triggered, quick adjustments in vertical distribution might be an important strategy for *C. altimanus* larvae to cope with high solar radiation, which typically occur during the hatching season.

Keywords: *Cyrtograpsus altimanus*, Decapoda, crab larvae, ultraviolet radiation (UVR), vertical distribution, Atlantic Patagonia.

Efectos a corto plazo de la RUV en la distribución vertical de *Cyrtograpsus altimanus* y *Alexandrium tamarense* de la Patagonia Atlántica

RESUMEN. Muchas especies marinas pasan parte de su ciclo vital en las capas superficiales de la columna de agua, donde pueden estar expuestas a radiación ultravioleta (RUV). En muchos casos la luz constituye el factor ambiental que provoca ajustes del comportamiento en la distribución vertical. Se incubaron larvas planctónicas del cangrejo *Cyrtograpsus altimanus* en acuarios verticales para estudiar sus respuestas con/sin RUV y con/sin una potencial presa (el dinoflagelado *Alexandrium tamarense*). La distribución vertical de los plancteres fue registrada y se usó para evaluar el efecto combinado de la RUV y la presencia del dinoflagelado en el comportamiento larval. Cuando la RUV estaba ausente, las larvas de *C. altimanus* tendieron a nadar hacia arriba y agregarse cerca de la superficie, independientemente de la presencia del dinoflagelado. Sin embargo, la RUV inhibió esta tendencia e indujo un efecto repelente que llevó a una distribución vertical de larvas mucho más homogénea. Las larvas no parecieron ser afectadas en ningún caso por la presencia de *A. tamarense*. Los resultados sugieren que *C. altimanus* podría ajustar rápidamente su distribución vertical en respuesta a RUV, lo cual sería una estrategia importante para hacer frente a los altos niveles de radiación solar que típicamente ocurren durante sus primeros estadios de desarrollo.

Palabras clave: *Cyrtograpsus altimanus*, Decapoda, larvas de cangrejo, radiación ultravioleta (RUV), distribución vertical, Patagonia Atlántica.

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INTRODUCTION

Zooplankton vertical distribution has profound ecological consequences for the whole pelagic realm, both in oceans and lakes. Many planktonic organisms may adjust their vertical distribution (hereafter referred to as VD) in response to different environmental cues. Usually vertical distribution of zooplankton is the result

of conflicting factors such as solar radiation, food and predators (Speekmann *et al.*, 2000; Boeing *et al.*, 2004; Fischer *et al.*, 2006; Cooke *et al.*, 2008; Hylander & Hansson, 2010). Larvae of virtually all decapods control to some extent their VD (Queiroga & Blanton, 2005) and the same happens with several phytoplankton species (*e.g.*, Richter *et al.*, 2007a). In planktonic larvae of meroplanktonic organisms, this behavioral trait maximizes dispersion/retention of individuals into favorable areas/layers to enhance recruitment. A number of species-specific patterns of VD have been observed, related to different, sometimes interactive, factors such as tide phase, temperature, food conditions, predation pressure, etc. (Sulkin, 1984; Cohen & Forward Jr., 2009). Many crab larvae remain near the surface during certain periods, sometimes including daytime when they may be exposed to sunlight (Morgan & Christy, 1996). Solar radiation reaching the surface of the water column includes visible light (PAR, wavelengths between 400 and 700 nm) and ultraviolet radiation (UVR, 280-400 nm) which in turn comprises ultraviolet A (UVA, 315-400 nm) and ultraviolet B (UVB, 280-315 nm) radiation. In general, UVR has detrimental effects on plankton (Gonçalves *et al.*, 2010; Llabrés *et al.*, 2013) and several species are able to detect and avoid high-UVR surface waters (Speekmann *et al.*, 2000; Richter *et al.*, 2007a; Cohen & Forward Jr., 2009). An exposure of a few hours under UV radiation may produce negative effects on crab larvae (Morgan & Christy, 1996; Hovel & Morgan, 1999; Hernández-Moresino & Helbling, 2010; Hernández-Moresino *et al.*, 2011). Therefore, a quick downward migration response in the presence of UVR would be a selective advantage for crab larvae, especially in mid-latitude areas with high solar UVR like Atlantic coast of Patagonia (which may be exposed to low-ozone events, *e.g.*, Orce & Helbling, 1997). Regardless of the ultimate causes of crab larvae vertical distribution, light and tidal factors act as major proximal cues (Cohen & Forward Jr., 2009), which makes larval photobehavior an important trait among meroplanktonic species. However, very little is known about the short-term effects of UVR on VD of crab larvae.

Another important factor which may affect VD of zooplankters is food availability (Lindley *et al.*, 1994), as they are able to remain within patches of phytoplankton (Leising & Franks, 2002). In the case of potentially toxic species such as *Prorocentrum* sp. or *Alexandrium* sp., crab larvae may instead show avoidance by means of downward migration (Sulkin *et al.*, 2003). Therefore, a trade-off between UVR and the potentially toxic prey in the larval VD could be expected.

Given the myriad of potentially confounding factors affecting VD in the field (Queiroga & Blanton, 2005), laboratory experiments improve our mechanistic understanding of larval behavior. Thus, the aim of this study was to experimentally evaluate the short-term (*i.e.*, h) responses of larvae of the common shore crab *Cyrtograpsus altimanus* when exposed to a combination of UVR and a potentially toxic prey (the dinoflagellate *Alexandrium tamarense*).

C. altimanus (Rathbun, 1914) is a common species along the South Atlantic Ocean (Spivak, 1997); its hatching season coincides with high UVR levels, when daily doses of UVB at the sea surface often exceed 30 kJ m^{-2} (Villafañe *et al.*, 2004). During this period, blooms of potentially toxic dinoflagellates such as *A. tamarense* (Lebour) are common (Gayoso & Fulco, 2006).

Our working hypothesis is that VD of larvae will be affected by both UVR and the presence of *A. tamarense*. The dinoflagellate will act either as repellent (toxic cells) or attraction (palatable cells) factor in the water column.

MATERIALS AND METHODS

Ovigerous females of *C. altimanus* were collected in intertidal rocky pools at Puerto Madryn, Argentina (Atlantic Patagonian coast, 42°47'S, 65°00'W) and kept in aquaria (19-20°C; 12:12 h photoperiod) until their embryos hatched. Newly-hatched larvae (<24 h) from one female at the time were used in each experiment. *A. tamarense* was obtained from own cultures at EFPU. Three independent experiments were done with different females and in different dates to cover the extension of the hatching season for this species. In each experiment we used six glass aquaria (8x15x61 cm; length x width x depth) containing ~6100 mL of sterilized seawater. The contents of the six aquaria were: two with crab larvae only, two with dinoflagellates only, and two with crab larvae together with dinoflagellates. Each pair of aquaria represented the two radiation levels (with-without UVR). Crab larvae (400 individuals) were added to four aquaria. Dinoflagellates (final concentration 2500 cel mL^{-1}) were added also to four aquaria to have two levels (with-without *A. tamarense*). The water column was gently homogenized before starting the exposure to ensure a uniform vertical distribution as the initial state.

All aquaria were simultaneously exposed under a solar simulator (Hönle, Sol 1200). The irradiances at the water surface (70 cm from the lamp) were 166.3, 64.4, and 1.58 W m^{-2} for PAR, UVA radiation (315-400 nm) and UVB (280-315 nm), respectively. The

exposure time of 240 min under these conditions resulted in a sublethal UVB dose of 22.8 kJ m^{-2}. Thermocline formation (*i.e.*, due to heat from the UV lamp) was prevented using air refrigeration, keeping the temperature stable at 18°C in the whole water column. Aquaria were exposed in a homogeneous horizontal radiation field using a rotating platform (Fig. 1). Differences in vertical attenuation of UVR and PAR in aquaria from all treatments (*i.e.*, including aquaria with phytoplankton) were negligible, as measured with a high-resolution spectrometer (optic fiber, HR2000 CG-IV-NIR, Ocean Optics, USA). Larvae were inspected 24 h after the end of the exposure to record mortality.

The two levels of the radiation factor were a) PAR+UVR: aquaria covered with Ultraphan 290 filter -Opak Digefra-, so samples received PAR, UVA and UVB, and b) PAR: aquaria covered with Ultraphan UV filter, organisms received only PAR. This statistical factor applies to both dinoflagellates and crab larvae. The other factor was the presence of predators or prey (when VD of dinoflagellate or crab larvae, respectively, was considered). The levels of this factor are simply "with" and "without" the presence of the corresponding organism. Therefore, each of the six aquaria represented a combination of radiation and presence/ absence of the dinoflagellate and crab larvae. Due to the lack of space under the solar simulator, and in order to keep a homogeneous radiation field, only six aquaria were fit under the solar simulator in each experiment. This precluded the use of replicates (*i.e.*, more aquaria at the same time); however, exactly the same experiment was independently conducted three times under the same conditions, and each aquarium from each experiment was considered a replicate.

Using marks on the outer walls, aquaria were divided into four equal depth intervals. Vertical distribution of plankters was recorded every 1 h during 240 min. High-resolution, digital images were taken at each depth interval, from where crab larvae were counted using the software ImageJ (Abràmoff *et al.*, 2004). Dinoflagellate cells were counted under a microscope from samples collected using a device with four syringes and four silicon tubes -one for each depth level- operated from above the aquaria. Samples were *ca*. 5 mL in order to prevent changes in the total volume of aquaria. The syringes were operated very gently to avoid generating mixing/turbulence in the water column.

Average and standard error of plankters concentrations are reported using experiments as replicates. Data is expressed as percentage of individuals or cells (for larvae or dinoflagellate, respectively) at each interval (100% being the whole aquarium). Based on preliminary trials, the concentration (stable after 180 min of exposure) of individuals or cells was used as the dependent variable, while radiation and presence of *A. tamarense* (or *C. altimanus*) were the factors when evaluating vertical distribution of crab larvae (or the dinoflagellate). Since the total concentration of larvae and dinoflagellate cells was limited by the initial number of organisms at the beginning of the exposure, their concentration at a given depth level is not independent from the other depths. Therefore a two-way, repeated measures ANOVA test was used to determine interactions between depth, radiation and presence of larvae/ dinoflagellate for both organisms. Concentrations at each level were the "repeated measures" of the dependent variable. Data were arcsine-transformed to meet ANOVA assumptions of homoscedasticity (Zar, 1999). When significant differences were found, *post-hoc* (Tukey HSD) pairwise comparisons were calculated. Significance level was $P < 0.05$.

RESULTS

After starting with an initially homogeneous vertical distribution (VD), larvae started moving randomly at the beginning of the exposure under PAR + UVR. This was translated into initial fluctuations during the first 120 min (data not shown), while from 180 to 240 min, larvae showed a stable distribution. Therefore we used data from 180 min of exposure as it was the minimum time required to reach a stable VD under experimental conditions. Mortality 24 h after the end of each exposure was in all cases less than 6%.

There were differences in VD of larvae between PAR+UVR and PAR treatments ($P = 0.037$, Table 1). When UVR was absent, larvae showed a clear tendency to swim upwards and stay near the surface (under PAR treatment, an average of *ca*. 60% of individuals remained in the upper depth interval, Figs. 2a-2c). However, under PAR + UVR this tendency was inhibited and larvae were distributed more homogeneously (Fig. 2a). When the dinoflagellate was present (Fig. 2c), there was not a clear tendency to stay in or avoid the upper layers ($P = 0.564$, Table 1). Overall (with and without dinoflagellates), the tendency of crab larvae to swim upward and stay near the surface was inhibited when UVR was present, when the average presence of larvae in the upper level was almost half (34%) compared to PAR treatment. Therefore the presence of dinoflagellates cells had no significant effect on VD of crab larvae. As revealed by visual inspection, the downward response of larvae was either by active swimming or longer periods of sinking in the typical 'hop-and-sink' locomotion pattern. Conversely,

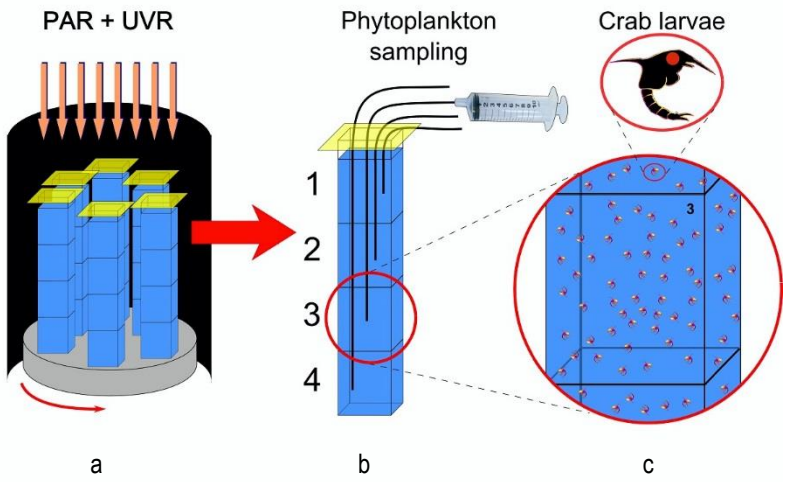

Figure 1. Schematic drawing of the experimental setup. a) Exposure setup, with glass columns on a rotating platform, b) detail of each column with the radiation filter (yellow), tubes and syringe for phytoplankton sampling, c) detail of one depth level used to quantify concentration of free-swimming crab larvae.

Table 1. Two-way repeated measures ANOVA for vertical distribution of larvae of the crab *C. altimanus* a) and the dinoflagellate *A. tamarense*, b) after 180 min of exposure to UVR. The experiment was replicated three times. Significant differences ($P < 0.05$) indicated in bold.

a) *C. altimanus* (crab larvae)	SS	d.f.	MS	F	*P*
Intercept	38984.3	1	38984.3	4760.55	**<0.001**
Radiation	7.85	1	7.85	0.96	0.356
Dinoflagellate	0.75	1	0.75	0.09	0.770
Radiation x Dinoflagellate	1.16	1	1.16	0.14	0.716
Error	65.51	8	8.19		
Depth	3171.12	3	1057.04	7.12	**0.001**
Depth x Radiation	1476.59	3	492.2	3.31	**0.037**
Depth x Dinoflagellate	309.46	3	103.15	0.69	0.564
Depth x Radiation x Dinoflagellate	116.04	3	38.68	0.26	0.853
Error	3565.28	24	148.55		

b) *A. tamarense* (dinoflagellate)	SS	d.f.	MS	F	*P*
Intercept	40905.42	1	40905.42	11965.92	**<0.001**
Radiation	1.21	1	1.21	0.36	0.568
Larvae	0.07	1	0.07	0.02	0.886
Radiation x Larvae	0.91	1	0.91	0.27	0.619
Error	27.35	8	3.42		
Depth	1226.94	3	408.98	5.50	**0.005**
Depth x Radiation	37.22	3	12.41	0.17	0.918
Depth x Larvae	185.52	3	61.84	0.83	0.489
Depth x Radiation x Larvae	349.20	3	116.40	1.57	0.223
Error	1783.36	24	74.31		

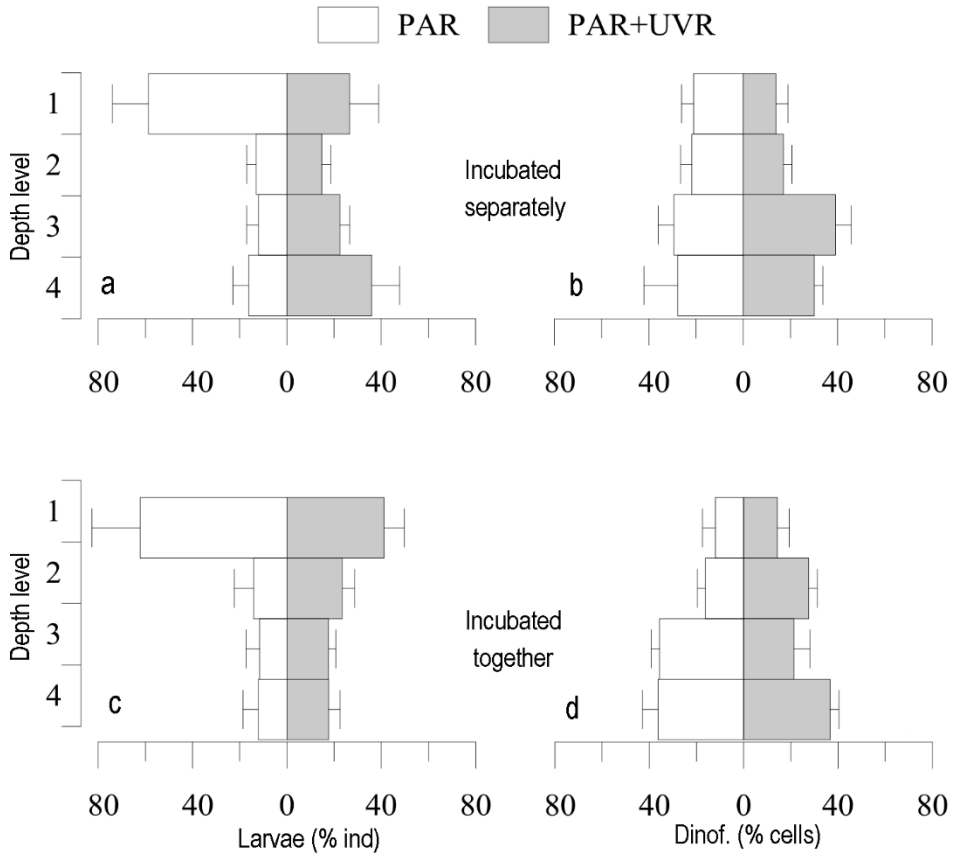

Figure 2. Vertical distribution (VD) of larvae of the crab *C. altimanus* (% of individuals) and the dinoflagellate *A. tamarense* (% cells) after 180 min of exposure under PAR (white bars) or PAR+UVR (grey bars). a) VD of larvae when incubated without dinoflagellates, b) VD of dinoflagellates when incubated without crab larvae, c) VD of larvae when incubated together with dinoflagellates, d) VD of dinoflagellates when incubated with larvae. Error bars denote one standard error.

the VD of the dinoflagellate *A. tamarense* was not significantly affected by the presence of larvae or UVR (Figs. 2b-2d, Table 1).

As mentioned, VD of crab larvae was not significantly affected by the presence of *A. tamarense*. This allowed us to pool these data (*i.e.*, concentration of larvae with and without *A. tamarense*) together for each depth interval, so only radiation treatments were compared (Fig. 3a). Similarly, the dinoflagellate *A. tamarense* was not affected by radiation or larval presence, so these data (*i.e.*, concentration of cells of *A. tamarense* with and without UVR, with and without crab larvae) were also pooled for each depth interval (Fig. 3b). HSD tests confirmed the overall pattern that a most larvae receiving only PAR remained near the surface, while larvae receiving PAR+UVR were more homogeneously distributed (Fig. 3a). Differences in VD of *A. tamarense* were only related to depth, as the general tendency of the dinoflagellate was to migrate downwards in all cases (Fig. 3b) irrespective of larvae or radiation ($P = 0.489$ and $P = 0.918$, respectively; see Table 1).

DISCUSSION

Ontogenetic vertical migration is common in decapods, where the planktonic larvae hatch from bottom-dwelling females, feed at surface and subsequently return to the bottom at settlement. At population level, changes in vertical distribution are considered to affect larval dispersion/retention to enhance recruitment. However, in order to better understand the processes involved, one must consider how physical environment affects biological variables such as behavior (Queiroga & Blanton, 2005). Most decapod larvae can exert some degree of behavioral control on their vertical distribution in response to a number of factors. Light is a proximal cue in marine environments and can trigger vertical movements in planktonic larvae. In laboratory conditions, many decapod larvae display positive

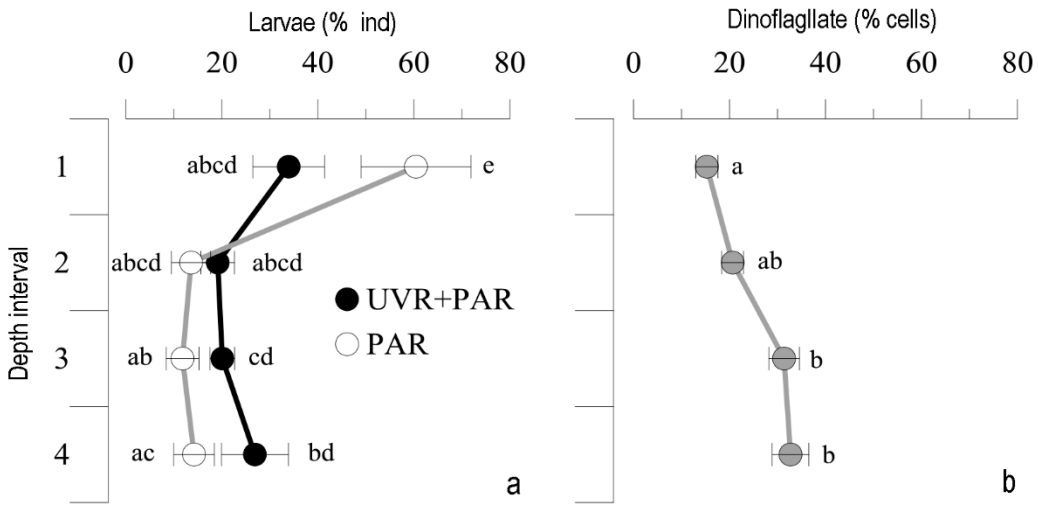

Figure 3. Pooled data showing only factors with statistically significant effects. a) Concentration of larvae of the crab *C. altimanus* (% of individuals) combining data of aquaria with and without dinoflagellates (*i.e.*, only the significant factor; radiation is shown), b) *A. tamarense* (% cells) at each depth interval, combining all radiation and larvae presence treatments (both factors were statistically non-significant; hence one line groups all the data). Lowercase letters next to symbols indicate Tukey HSD similarities ($P < 0.05$ in all cases) between the concentration individuals at different depth intervals and radiation levels a) or depth intervals, b) error bars denote one standard error.

phototaxis (Forward Jr., 1989; Queiroga & Blanton. 2005; Cohen & Forward Jr., 2009), which means that larvae would aggregate near the surface. However, this is rarely observed in nature. This may be due to the spectral composition of light sources: when illuminated only with visible light (PAR) *C. altimanus* did aggregate at the surface, but when spectral composition of light was closer to sunlight (*i.e.*, it included UVR) then this positive phototaxis was much weaker (Fig. 2a). Our results suggest that all other factors remaining equal, UVR may have its own short-term effect on VD of larvae of *C. altimanus*. To our best knowledge, there are no previous studies specifically evaluating the short-term effects of UVR on vertical distribution of marine zooplankton species in Patagonia or in Argentina.

The more homogeneous distribution of crab larvae after a period of UVR exposure in principle agrees with the light-dependent negative feedback model of depth regulation formulated by Sulkin (1984) and modified by Forward Jr. (1989). However, if UVR is absent (PAR treatment), the model does not apply, and distribution is more concentrated near surface as it has been observed for crab larvae of several species (Morgan & Christy, 1996). Our results suggest that larvae are able to detect UVR, although it is not clear how UVR inhibits the upward-swimming tendency observed in the PAR treatment. Crayfishes (presumably adults) (Cummins & Goldsmith, 1981), and megalopae of at least two species of crabs (Cronin & Forward, 1986; Miner *et al.*, 2000) have chromatophores which absorb in the UVR range. If this is the case of *C. altimanus*, then UVR may be part of the proximal cues for its short-term regulation of VD.

The general pattern of downward migration of *A. tamarense* may indicate a reaction to high PAR intensities. Although the reaction seems to be stronger in presence of a potential predator (compare Figs. 2b, 2d), the statistic support is too weak (maybe due to low sample size) so we refrain from further speculation on this. Regarding their response to light conditions, it has been shown that some species of phytoplankton change their gravitaxis from negative to positive when exposed to high irradiances (Richter *et al.*, 2007a, 2007b). Contrary to our expectations, the presence of *A. tamarense* did not show any effect on the VD of larvae. Brachyuran zoeae may ingest several species of *Alexandrium* sp., even toxic ones (García *et al.*, 2011) but *A. tamarense* is not the preferred (Perez & Sulkin, 2005). Therefore, our results may simply reflect the poor palatability of this dinoflagellate, and at the same time an apparent non-toxicity given the lack of avoidance reaction. Another alternative could be that *C. altimanus* needs a higher concentration of *A. tamarense* to show significant avoidance. However, higher cell numbers of the dinoflagellate are not common in nature, and in our experiments it would have affected the attenuation coefficient in the experimental columns, somewhat confounding the observed behavior.

As with any laboratory results, caution is needed to extrapolate these findings to the field, as behavior of crab larvae in laboratory is often simpler (Cronin & Forward, 1986). However, precisely due to the very complex nature of these responses, our experimental approach is useful to pursue a mechanistic underpinning of the photo behavior of *C. altimanus*, whose hatching season coincides with high daily doses of solar radiation (Villafañe *et al.*, 2004), with UVB levels similar to the one used in our study.

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