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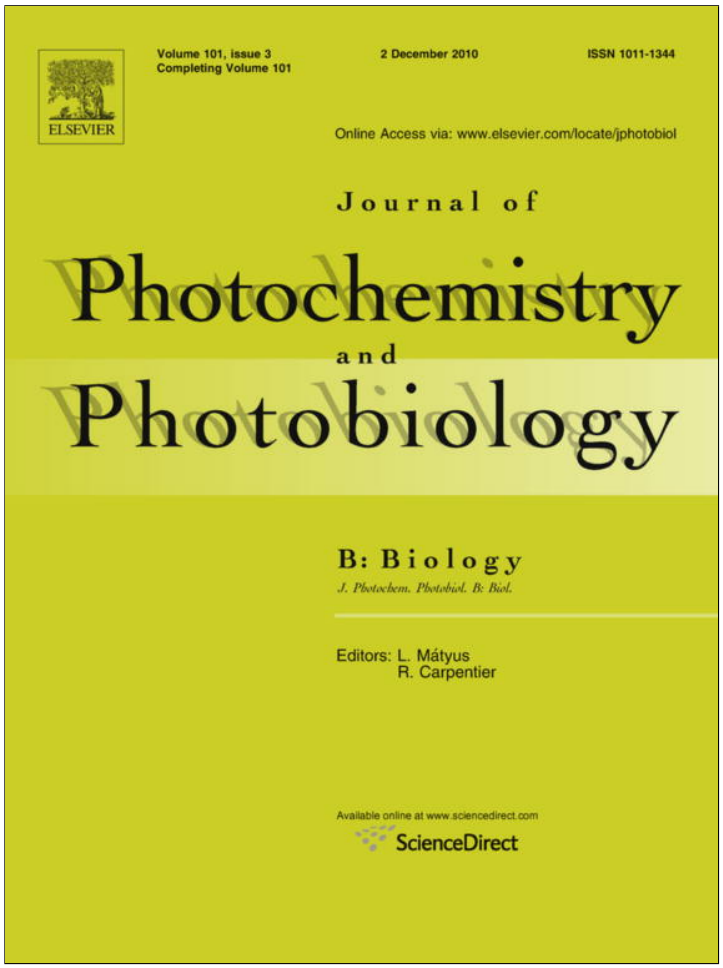

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Horizontal migration of *Acartia pacifica* Steuer (copepoda) in response to UV-radiation

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ABSTRACT

It is known that zooplankton migrate vertically to avoid UV-radiation (UVR, 280–400 nm), but little is known if such avoidance happens horizontally. Here, we showed that the copepod *Acartia pacifica* avoided UV irradiated fields horizontally. Exposure of *A. pacifica* to PAR or PAR + UV-A for 30 min did not make any difference in the horizontal distribution of the individuals. However, addition of UV-B radiation, that is PAR + UV-A + B, resulted in uneven distributions among the treatments, with significant less individuals compared to the PAR or PAR + UV-A treatments. More carotenoids and UV-absorbing compounds were found in the *A. pacifica* individuals that chose to stay under the radiation treatments with UV. It is concluded that *A. pacifica* can migrate horizontally to avoid UV-related harms and those contains more protective compounds were less sensitive to UVR.

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1. Introduction

Increased solar UV-B radiation (280–320 nm) due to stratospheric ozone reduction caused by industrial activities is threatening the aquatic ecosystems because of its harms on biological activities [1]. In addition, recent studies indicate a 10% increase in UVR (280–400 nm) reaching north temperate regions due to alteration in cloudiness from 1983 to 2003 [2]. The physiological and ecological impacts of enhanced UVR on marine organisms have extensively been studied in the past decades (see review by Beardall et al. [3] and literatures therein). UVR cannot only influence primary producers [4–6] but also harms secondary producers (herbivorous zooplankton) both directly [7,8] and indirectly by reducing the food quality [9,10]. The negative effects of UVR on zooplankton include increased mortality, lowered reproductive capability and increased malformation of nauplii [7,11,12]. The negative effects have been attributed to UV-B in most of the studies that damages biologically important molecules, such as proteins and nucleic acids [13]. UV photons absorbed by the nitrogen base of DNA molecules result in formation of photoproducts such as pyrimidine dimmers or 6–4 photoproducts [14].

To defend against UVR, zooplankton can migrate vertically to deeper depths to avoid its harms [15–18]. They can also synthesize or accumulate photo-protective compounds (such as melanin, carotenoids and mycosporine-like amino acids (MAAs)) that function either as sunscreens or as scavengers of photo-produced radicals [19,20]. In small crustaceans commonly found in freshwaters, melanin is the most important photo-protective compound [15,21]. Among copepods, the photo-protective compounds are carotenoids and MAAs [18,21], which were mainly gained from the grazed phytoplankton [23].

Herbivorous individuals are commonly faced with a trade-off situation: algal food is close to the surface where UV levels are high during daytime. Accordingly, behavioral responses to UVR have been widely studied in zooplankton [15,24]. The diel vertical migration (DVM) had been explained by the avoidance of predators [25–28] or grazing of phytoplankton [29,30]. In recent years, such DVM has been related to avoidance of UVR [15,16,18,30] or a compromise between threats from both predators and UV-radiation [31]. Vertical migration of copepods to avoid UVR has been widely confirmed [16–18]. However, to the best of our knowledge, it is unknown whether copepods can perform horizontal migration in response to UV.

In the South China Sea (SCS), effects of UVR on phytoplankton have been carried out in recent years [4,5]. However, little is known on the impacts of UV on zooplankton in this area. Shadings provided by seaweeds or reefs in coastal waters may provide some shelters for zooplankton to avoid harmful UVR. Consequently, we hypothesized that the copepod *Acartia pacifica* could use horizontal phototaxic sensing to avoid UVR.

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2. Materials and methods

2.1. Sampling of zooplankton and preculture in the lab

The calanoid copepod, *A. pacifica*, is widely distributed along the coastal waters of China. In Xiamen Bay (24°26′N, 118°02′E) of the South China Sea (SCS), a semi-enclosed bay with a dike connecting Xiamen Island and the mainland, this species appears in winter and reaches an annual maximum density in spring, then declines and completely disappears in summer. Its resting eggs represent a potential source for the recruitment of nauplii into the water column [32]. The copepods were collected with a plankton net (mesh diameter 0.112 mm) by horizontal hauling in surface seawater in the central area of Xiamen Bay. The collection was carried out at night in April 2009, when *A. pacifica* was abundant as a dominant species. The samples were transported to laboratory within 1 h and then the individuals were separated into two groups using meshes of 0.25 and 0.50 mm pore sizes. The individuals sized 0.25–0.50 mm, with *A. pacifica* accounted for more than 90% of the total, were temporarily reared in an aquarium (5 L) at 20 °C and 40 μmol m^{-2} s^{-1} of cool-white light (12 L: 12 D) with the seawater (filtered through 0.22 μm pore size filters) collected from the sampling site. A mixture (about 4.0×10^4 cells mL^{-1}) of *Chlorella vulgaris* and *Prymnesium parvum* with equivalent proportion were used to feed them. Healthy (actively moving around) individuals were used for the following experiments within 2 days.

2.2. Experiments to test horizontal behavior under different PAR levels

To test the phototaxis under different PAR levels, a rectangular container (length × width × depth = 50 × 6 × 10 cm) made of opaque plastic was used. It was equally divided into six chambers by symmetrical grooves on the sides and bottom, into which plastic plates could be slid in perpendicularly. The length of each chamber was 8 cm and the depth of water column in the chambers was about 8 cm also. The PAR levels of 0, 45, 90, 135, 180 and 225 W m^{-2} (1035 μmol m^{-2} s^{-1}) were got by placing black plastic or neutral filters on each chamber. About 600 *A. pacifica* individuals were transferred to the container that were not yet separated with the sliding plates. *A. pacifica* in the container were shaken to allow the individuals homogeneously distributed in the container before the exposures. Upon the exposures, they were allowed to freely move about to the irradiated areas. The exposures lasted for 30 min before the plates were perpendicularly inserted to separate the areas receiving the different radiation treatments. The individuals and the seawater in each compartment were transferred to a beaker and then counted immediately. The containers were maintained in a big water tank and the temperature was controlled at 20 °C with a circulating cooler (Eyela, CAP-3000, Tokyorikakikai Co. Ltd., Tokyo, Japan). The individuals with no mobility were regarded as dead ones. The experiment was repeated three times with the same container that had six chambers.

2.3. Experiments to test horizontal behavior of A. pacifica under different radiation treatments

To investigate if *A. pacifica* avoids UVR, about 380 individuals with similar body size were put into the container (only three adjacent chambers were used in this experiment, the other three chambers were separated with the plates). Different radiation treatments were performed with different cut-off filters placed on the top of the chambers: (1) PAR treatment (P), covered with a GG395 filter (Schott, Mainz, Germany) with 50% transmittance at 395 nm; (2) PAR + UV-A treatment (PA), covered with a Schott WG320 filter with 50% cutoff at 320 nm and (3) PAR + UV-A + UV-B treatment (PAB), covered with a Schott WG280 filter with 50% cutoff at 280 nm, allowing the individuals exposed to the irradiances above 280 (Fig. 1A). A solar simulator (Sol 1200 W, Dr. Hönle, Martinsried, Germany) was employed to provide the irradiation (Fig. 1B), with the intensities of PAR, UV-A and UV-B being 225 (1035 μmol m^{-2} s^{-1}), 50.5 and 2.18 W m^{-2}, respectively, which was equivalent to half local noontime solar radiation. The individuals were counted as mentioned above after the exposures and the dead individuals (less than five) were ignored.

The illuminations were measured using a broadband ELDONET filter radiometer (Real Time Computer, Möhrendorf, Germany) that has three channels for photosynthetically active radiation (PAR, 400–700 nm), ultraviolet-A radiation (UV-A, 315–400 nm) and ultraviolet-B radiation (UV-B, 280–315 nm), respectively [33]. This instrument has been calibrated regularly with the help of the maker.

2.4. Determination of photo-protective compounds

To determine the relationship between photo-protective compounds and the UV-tolerance of *A. pacifica*, the individuals were harvested by filtering to GF/F filters and were extracted at 4 °C for 12 h in the dark in 100% methanol after sonicated with ultrasonic homogenizer (CPX600, Cole-Parmer, USA) in icy water [18]. The absorption spectra of the supernatant after centrifugation (5 min at 5000*g*) were measured from 300 to 700 nm using a Beckman DU 800 spectrophotometer. Quantification of the carotenoids was performed according to Parsons and Strickland [34]. The absorptivity of MAAs, with typical absorption peaks between 310 and 360 nm [35], was estimated using the ratios of peak height (at 317 nm) to the dry mass of the individuals used [36].

The ratio of dry to wet weight was established in order to estimate dry mass changes in later experiments to determine the dry weight (DW) and photo-protective compounds contents. About

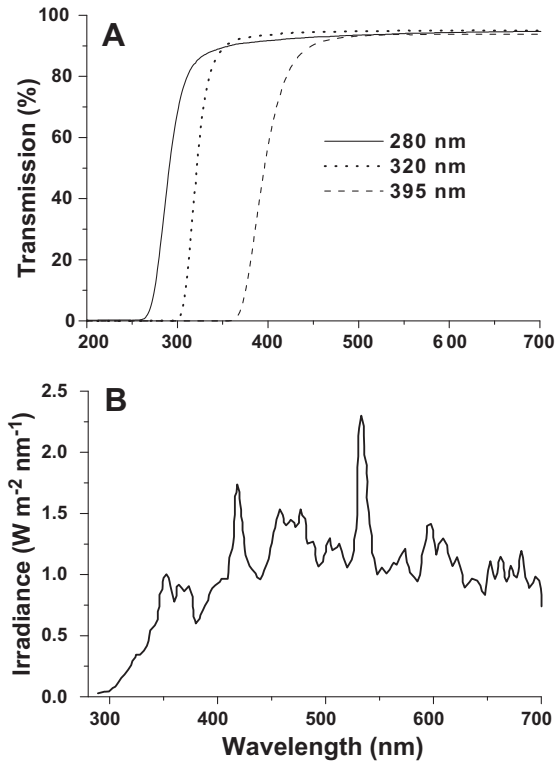

Fig. 1. Transmission of cut-off filters (A) and spectrum of the simulator solar radiation (B).

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4000 individuals were used to determine the ratio. The dry weight was determined with an electronic balance after drying in an oven at 80 °C for 24 h and cooling off in a desiccators.

2.5. Statistical analysis

Data were analyzed by One-Way ANOVA followed by a multiple comparison using Tukey-test. A confidence level of 95% was used in all analyses.

3. Results

3.1. Effects of radiation levels on horizontal migration of A. pacifica

A. pacifica showed differential horizontal migrations under different PAR levels. The number of individuals increased with increased PAR intensity and reached a maximum at level of 173.4 W m^{-2} (800 μmol m^{-2} s^{-1}) (Fig. 2), at which nearly 50% of the individuals were found. Further increase of PAR resulted in a sharp decrease of the individuals (Fig. 2). Significant ($p < 0.05$) difference in the individual abundance was found among the radiation levels except those under the darkness and 45 W m^{-2} (207 μmol m^{-2} s^{-1}) PAR level.

3.2. Effects of different radiation treatments on horizontal migration of A. pacifica

A. pacifica showed significant avoidance of UV-B, however, it was insensitive to UV-A (Fig. 3). The individuals under PAR + UV-A + B (PAB) treatment were much less ($p < 0.01$) than those under PAR (P) and PAR + UV-A (PA) treatments; however, there were no significant ($p > 0.05$) difference between P and PA treatments. The individuals under PAR, PAR + UV-A and PAR + UV-A + B proportioned as 39.2%, 39.7% and 21.1%, respectively.

3.3. The photo-protective compounds contents in A. pacifica distributed to different radiation treatments

The methanol extraction of *A. pacifica* showed four absorbance peaks at 317, 451, 477 and 665 nm (Fig. 4A). The peaks of 451 and 665 nm relate to chlorophyll *a* and those peaked at 317 nm and 477 nm ought to be caused by MAAs and carotenoids, respectively. The individuals that were found under PA treatment

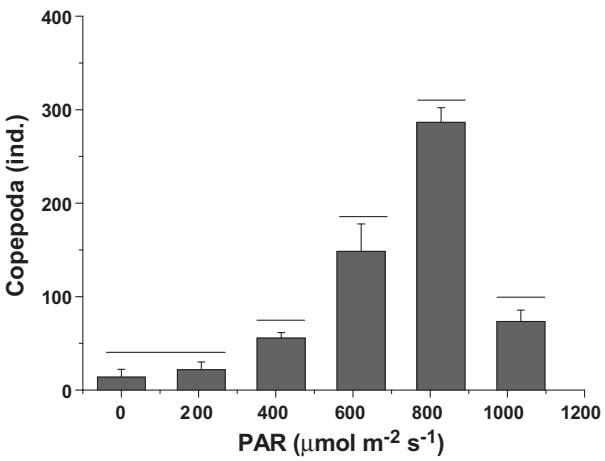

Fig. 2. Number of *A. pacifica* individuals distributed to the different PAR levels after 30 min exposure. The means and standard errors were based on triplicate incubations. Horizontal bars at different levels above the columns indicate significant ($p < 0.05$) differences among the treatments.

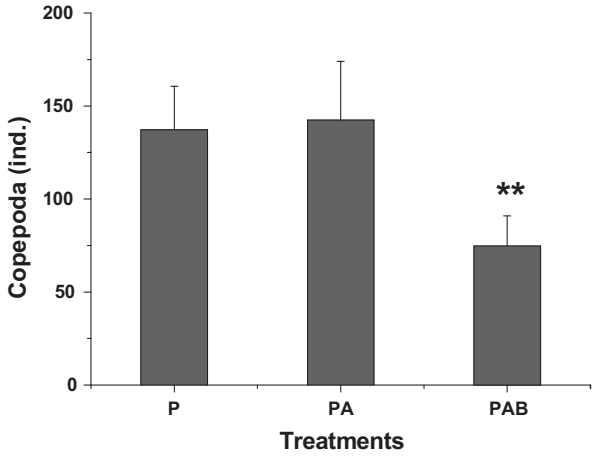

Fig. 3. Number of *A. pacifica* individuals distributed to the different radiation treatments (PAR alone (P), PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB) after 30 min exposure. The irradiance levels were 225 (1035 μmol m^{-2} s^{-1}) for PAR, 50.5 for UV-A and 2.18 W m^{-2} for UV-B, respectively. The means and standard errors were based on three times repeated incubations. The symbol "**" above the columns indicate significant ($p < 0.01$) differences between P and other treatments .

contained more ($p < 0.05$) carotenoids compared with those distributed to pure PAR, and those that sustained under PAB treatment contained the highest level of carotenoids ($p < 0.01$) (Fig. 4B). On the other hand, the individuals found under PAR or PAR + UV-A treatments had similar levels of MAAs, but those resistant to UV-B (stayed under PAB treatment) possessed the highest contents of MAAs ($p < 0.01$) (Fig. 4C).

4. Discussion

The copepod *A. pacifica* responded to changes in the PAR intensity as well as quality of simulated solar radiation. Addition of UV-A to PAR had insignificant impact on its horizontal distribution; however, supplement of UV-B forced most of the individuals leaving off.

The protective compounds in copepods have been identified using HPLC as carotenoids and MAAs [18,22]. The absorption peak at 317 nm in the *A. pacifica* extract was representative of MAAs [36]. The higher contents of carotenoids can play a sheltering role to reduce damages caused by UV-radiation, though increasing susceptibility to visual predators [18,37]. Although the individuals stayed under P and PA treatments were almost equal, the content of carotenoids of the individuals under PA treatment was higher, reflecting a photoprotective role of carotenoids. The individuals tolerant to UV-B contained more carotenoids and the UV-screening MAAs. Field survey and mechanistic examinations showed that pigmentation of copepods was an inducible defense against prevailing threats from predators or UV-radiation [19,23,37,38]. The MAAs in copepods have been considered as UV photoprotectants in zooplankton [39,40]. These colorless compounds could protect the individuals from UV without causing the susceptibility to visual predation. The UV-protective compounds can be induced in days to weeks [41]. However, the short exposures of 30 min in the present study were less likely to induce these compounds in *A. pacifica*. Nevertheless, the individuals with higher levels of MAAs and carotenoids prior to the exposures were more tolerant to high PAR or/and UVR (Fig. 4C). These individuals can therefore benefit in grazing under high levels of solar radiation. The UV-protective compounds in *A. pacifica* could be obtained from the grazed phytoplankton [42].

The present study demonstrated that the copepod was able to sense both PAR (Fig. 2) and UVR (Fig. 3). Furthermore, they could

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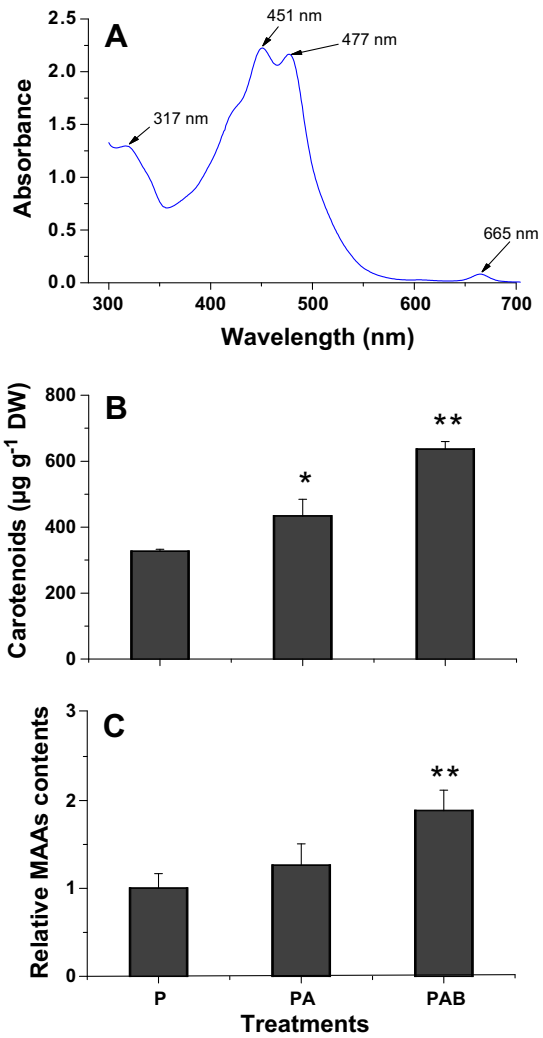

Fig. 4. Absorption spectrum of the methanol extract of *A. pacifica* (A), the contents ($\mu g\ g^{-1}$ DW) of carotenoids (B) and relative contents of MAAs (C) extracted from those copepods distributed to different treatments after 30 min exposure. The means and standard errors were based on triplicate incubations. The symbols "$*$" and "$**$" indicate significant differences between P and other treatments at $p < 0.05$ and $p < 0.01$, respectively. The MAAs content of *A. pacifica* under P treatment was set as 1 and those under other treatments were normalized to it.

horizontally escape from the harmful UV irradiance or migrate to the preferred PAR levels, reflecting its positive phototaxis and protective capability. Photoenzymatic repair of damaged DNA and antioxidants may also function as protective strategies [16,43]. The depth of water column in the chambers was 8 cm only, it was impossible for the individuals to escaping from the harmful radiation by vertical migration in this depth limited device. The individuals may get enough protection by downward migration in the water column in Xiamen bay. However, the individuals can easily move to the nearest shadings for possible protection by horizontal migration because vertical migrating zooplanktons have to cross pressure and temperature gradients in the water column that cost additional energy for them to move down [44,45]. Moreover, the depth necessary for them to avoid visually orienting predators generally exceeds that harmful UVR penetrates [46,47]. The ecological implication of horizontal migration by zooplankton lies in that the individuals can benefit in saving energy to avoid harmful UV and predators. The shadings provided by marine macrophytes or reefs would facilitate zooplankton's horizontal migration.

Behavioral adaptation by a species to avoid a particular environmental stress has been related to the capacity physiologically to withstand it, and the behavioral responses to natural environmental stressors could reduce selection pressure of physiological adaptation [48,49]. The diurnal horizontal migration from and to macrophyte had been proved and the macrophyte bed was regarded as an important refuge for potentially migrating pelagic cladocerans against fish predation [50,51]. Such a diurnal movement might also be related to avoidance of UV. We showed here that *A. pacific* can horizontally migrate to the areas with less harmful UVR or to their preferred radiation PAR levels without predation pressure (Figs. 2 and 3). The illumination received by zooplankton eyespots results in spiral swimming towards the light by changing the beating rate of adjacent cilia [52]. The harmful UV-B radiation could be sensed by their UV receptors [53] and caused the escaping responses. UV-protective compounds (i.e. carotenoids and MAAs) made the individuals of *A. pacifica* less sensitive to UV, indicating their sheltering effects.

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