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PRIMARY RESEARCH PAPER

Impacts of UV radiation on respiration, ammonia excretion, and survival of copepods with different feeding habits

Zengling Ma · Wei Li · Kunshan Gao

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Abstract Solar ultraviolet radiation (UVR) is known to harm aquatic organisms by damaging key molecules. Here, we showed that UV-A as well as UV-B affected differentially the respiration, ammonia excretion, and mortality of the copepods *Pseudodiaptomus marinus* (herbivorous) and *Labidocera bipinnata* (omnivorous). Adding UV-A (320–400 nm, 62.4 W m^{-2}) to PAR (400–700 nm, 278 W m^{-2}) decreased respiration by 10.2% in *P. marinus* and 46.1% in *L. bipinnata*, and additionally, the presence of UV-B (280–320 nm, 2.63 W m^{-2}) further decreased it by 8.1 and 18.8%, respectively. The ammonia excretion of *P. marinus* was suppressed by 13.9% in 30 min exposures to PAR + UV-A compared with those receiving PAR only; however, in the presence of UV-B, it decreased by 13.8% compared to the control. In *L. bipinnata*, exposure to PAR decreased the ammonia excretion by 33.4%, while the presence of UV-B caused additional suppression by 15.8%. The mortalities of both copepod species increased with prolonged duration under all radiation treatments. More carotenoids and UV-absorbing compounds were found in *P. marinus* than in *L. bipinnata*, which could have been responsible for the higher resistance of the former to solar UVR.

Keywords Ammonia excretion · Copepod · *Labidocera bipinnata* · *Pseudodiaptomus marinus* · Mortality · Respiration · UV

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Z. Ma
College of Life and Environmental Science, Wenzhou University, Wenzhou 325035, China

Z. Ma · W. Li · K. Gao (✉)
State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361005, China
e-mail: ksgao@xmu.edu.cn

Introduction

Solar ultraviolet radiation (UVR, 280–400 nm) is known to harm both primary producers and their consumers in aquatic ecosystems, decreasing productivity and disturbing reproduction and development (Häder et al., 2011). Although enforcement of the Montreal Protocol has slowed down ozone depletion, recent studies still indicate increased UV-B irradiance reaching the earth surface due to cloud cover change interacted with climate change and depleted ozone (Josefsson, 2006; Mackenzie et al., 2011; Manney et al., 2011). More and more attention is being paid to the effects of solar UVR on the metabolic activities of zooplankton (Hansson & Hylander, 2009; Häder et al., 2011).

Solar UVR not only harms secondary producers (zooplankton) directly (Aarseth & Schram, 2002; Tartarotti & Torres, 2009; Ma et al., 2012) but also affects them indirectly (Scott et al., 1999;

De Lange & Van Reeuwijk, 2003) by changing the biochemical composition of the phytoplankton (Nahon et al., 2010). UVR is notorious for decreasing zooplankton reproduction, deforming nauplii, and increasing mortality (Kouwenberg et al., 1999; Dattilo et al., 2005). Most of the negative impacts are attributed to UV-B, which is known to damage biologically important molecules, such as proteins and nucleic acids (Malloy et al., 1997; Browman et al., 2003), due to the very high-energy content in each photon compared with irradiance in longer wavelength (Johnsen, 2012). Although high levels of UV-A are harmful, moderate or low levels of UV-A are necessary for the expression of some genes (encoding metabolism related enzymes or proteins) and repair of UV-B induced DNA damage (Britt, 1996; Casati & Walbot, 2003).

Copepods are primary consumers and one of the most important zooplankton groups in the oceans (Verity and Smetacek, 1996; Ohman & Hirche, 2001; Bradford-Grieve, 2002; Beaugrand et al., 2002). In addition, they play important roles in influencing both coastal and pelagic food web structures (Kiørboe, 1997; Katechakis et al., 2002; Schnetzer & Caron, 2005; Schultes et al., 2006). Previously, it has been shown that copepods can sense and avoid UVR both vertically (Rocco et al., 2001; Wold & Norrbin, 2004; Hansson et al., 2007) and horizontally (Ma et al., 2010). It is also known that the UV-related resistance of copepods is associated with photo-protective compounds, such as mycosporine-like amino acids (MAAs) and carotenoids, accumulated in their bodies (Hansson et al., 2007; Hansson & Hylander, 2009). No biosynthetic pathways for photo-protective compounds are found in copepods (Karentz, 2001 and references therein). They acquire these substances from their diets (Hylander & Jephson, 2010) and MAAs-rich diets contribute to the accumulation of these compounds (Pérez et al., 2012). Consequently, different feeding habits may lead to different accumulation levels of the photo-protective compounds, since MAAs and carotenoids are richer in phytoplankton (Laurion et al., 2002) than in zooplankton (Persaud et al., 2007) based on dry weight.

We hypothesized that copepods, with different feeding habits such as herbivorous and omnivorous, might exhibit differential responses to UV-exposures. We tested this hypothesis using the calanoid copepods *Pseudodiaptomus marinus* and *Labidocera bipinnata*. The former grazes on phytoplankton alone while the latter feeds on both phytoplankton and small zooplankton. These two species are distributed along the coastal waters of the Pacific Ocean (Zheng et al., 1965; Uye et al., 1983). In Xiamen Bay (24°26′N, 118°02′E), the abundance of both species increased from spring to be dominant in early summer. Since respiration and the ammonia excretion rates of zooplankton are used as indicators of physiological stresses (Kiørboe et al., 1985; Danford & Uglow, 2001; Li & Gao, 2012), we investigated the impacts of simulated solar radiation on the respiration, ammonia excretion, and mortality of *P. marinus* and *L. bipinnata*. Excretion of ammonia by zooplankton is known to contribute to the nitrogen requirements for primary production in natural waters (Kiørboe et al., 1985; Alcaraz et al., 1994), and respiratory carbon loss by migrant copepods influences the efficiency of the marine CO_2 pump (Longhurst et al., 1990; Zhang & Dam, 1997). The results in this study built up the knowledge on the effects of diet on regulating the tolerance of copepods to solar UVR.

Materials and methods

Sampling of zooplankton

Zooplankton individuals were collected with a plankton net (mesh diameter 112 μm) using vertical hauls in the waters (with depth of 3–4 m) of Xiamen Bay in June 2009, when *P. marinus* and *L. bipinnata* were still the dominant species. The depth of 1% penetration of PAR, UV-A, and UV-B were 4.42–5.01, 2.70–2.84, and 1.50–1.66 m, respectively, in the sampling waters during the experimental period (Li et al., 2011). The samples were immediately transported to the laboratory and were temporarily reared in an aquarium (5 l) at 20°C and 40 μmol m^{-2} s^{-1} of fluorescent light (12 L:12 D) with seawater (filtered, 0.22 μm) collected from the sampling site. A mixture (about 4.0×10^4 cells mL^{-1}) of the chlorophyte *Chlorella vulgaris* and the diatom *Phaeodactylum tricornutum* with equal cell density was used to feed them. Both *C. vulgaris* and *P. tricornutum* contain MAAs and carotenoids (Cerón García et al., 2006; Sonntag et al., 2007; Liewellyn & Airs, 2010). In addition, *Chlorella* spp. are used as carotenoid sources for rainbow trout in aquaculture (Gouveia et al., 1996, 1998) and diatoms are the dominant primary producers in Xiamen Bay waters

(Li et al., 2011). Healthy (actively moving) individuals were selected and used for the following experiments within 3 days after sampling.

Illumination source and measurement

A solar simulator (Sol 1200W, Dr. Hönle, Martinsried, Germany) was used to transmit irradiances similar to those of solar radiation, and the transmission spectrum is available elsewhere (Gao et al., 2008). The intensities of PAR, UV-A, and UV-B used in the experiments were 278 (1,278 μmol m^{-2} s^{-1}), 62.4, and 2.63 W m^{-2}, respectively. It should be noted though that the solar simulator spectrum output had slightly higher intensities for UV-A and UV-B as compared to that of solar radiation in tropical China (Villafañe et al., 2007). The natural UV-A and UV-B intensities measured with the same photometer under the same PAR level were 43.9 and 1.33 W m^{-2}, respectively. The PAR level was close to 60%, but UV-A and UV-B levels were approximately 85 and 118% of local noontime solar irradiance on sunny days during the harvesting period. The irradiance was measured using a broadband ELDONET filter radiometer (Real Time Computer, Möhrendorf, Germany) that has three channels for PAR (400–700 nm), UV-A (315–400 nm), and UV-B (280–315 nm) (Häder et al., 1999).

Radiation treatments for tested copepods

To investigate the effects of UVR on the respiration, ammonia excretion, and mortality of the copepods *P. marinus* and *L. bipinnata*, different radiation treatments were carried out using cut-off filters. These were PAR (P) treatment: the beakers were covered with a GG395 filter (Schott, Mainz, Germany), allowing the individuals to receive irradiance above 395 nm; PAR + UV-A (PA) treatment: beakers were covered with a WG320 Schott filter, the copepods receiving irradiance above 320 nm; and PAR + UV-A + UV-B (PAB) treatment: the beakers were covered with a Schott WG280 Schott filter, the copepods receiving irradiance above 280 nm [refer to Ma et al. (2010) for transmittance spectrum of above filters]. The beakers were not UV-transparent, and so exposure was directed from above, such that the organisms were exposed to the radiation treatments without any sheltering from the glass beaker wall.

Determination of respiration rate

To investigate the effects of PAR, UV-A, and UV-B on the respiration of both species, each group including 15 individuals of *P. marinus* or *L. bipinnata* was transferred to a beaker (diameter 55 mm, height 70 mm) containing 200 ml filtered seawater and placed under the solar simulator so as to receive the above-mentioned P, PA or PAB treatments for 30 min. Triplicates were done for each treatment and each species. The beakers were water bathed for temperature control at 20°C with a circulating cooler (Eyela, CAP-3000, Tokyorikakikai Co. Ltd., Tokyo, Japan). Ten individuals were picked out from each beaker and transferred to a 100 ml electrode chamber with sterile seawater (algae free). Oxygen consumption was measured with a Clark-type oxygen electrode (YSI Model 5300, Ohio, USA) in air-equilibrated seawater with the copepods from different treatments. An extra five individuals were put in one beaker receiving the same irradiance treatment to void effects on oxygen measurement in case any individuals died during the exposure period. Three electrode chambers were used to measure the respiration of the pre-exposed individuals at the same time. The oxygen concentrations at the beginning and end of the incubation (6 h, during which a linear decrease was confirmed) were used to calculate the respiration rate per individual. No dead (non-moving) individuals were observed at the end of the incubation.

Determination of ammonia excretion

To determine the effects of different irradiance on the ammonia excretion of both species, the individuals were pre-exposed to P, PA, and PAB treatments for 30 min in the beakers as mentioned above. Then the copepods were transferred to flasks with 10 individuals per 100 ml sterile seawater. The ammonia content of the seawater after 6 h incubation was determined spectrophotometrically using Koroleff's indophenol method according to Slawyk & MacIsaac (1972). A linear relationship between the absorbencies and ammonia concentration were confirmed within 0–3 μg NH_4^+-N. The absorbance was measured at 630 nm using a Beckman DU spectrophotometer with a 5 cm path-length cuvette. Accumulation of ammonia was determined according to the changes in concentration of ammonia in the bottles.

Determination of mortality

To investigate the relationship between UV-exposure and mortality, *P. marinus* and *L. bipinnata* individuals in 1,000 ml beakers (diameter 90 mm, height 150 mm) with 800 ml seawater, and about one individual per 10 ml water, were exposed to P, PA, and PAB treatments. This may have been more crowded than in nature, but it was acceptable for indoor cultures due to the fact that a density of the harpacticoid copepod *Nitokra lacustris* of 100,000 individuals l^{-1} in small culture containers was possible (Rhodes, 2003). Triplicates were carried out for each treatment and each species. The intensities of PAR, UV-A, and UV-B were the same as above. No food (microalgae) was supplied during exposure. The mortality was expressed as ratio of dead (immovable when disturbed) individuals to the total at the beginning. The median lethal time ($T_{1/2}$) was derived from the curve-fitted equation (logistic equation).

Determination of photo-protective compounds

To determine the relationship between the concentrations of the photo-protective compounds and the UV-tolerance of copepods, equal wet mass (hundreds of individuals) of both species were harvested by filtering on GF/F filters, sonicated with ultrasonic homogenizer (CPX600, Cole-Parmer, USA) in icy water and then extracted at 4°C for 12 h in the dark in 100% methanol (Hansson et al., 2007). The absorption spectra of the supernatant after centrifugation (5 min at 5,000×*g*) were measured from 300 to 700 nm using a Beckman DU 800 spectrophotometer. Quantification of the MAAs with absorption peaks between 310 and 360 nm (Sinha & Häder, 2008) and carotenoids was estimated using the peak heights for equal wet masses of the individuals (Dunlap et al., 1995).

Statistical analysis

A one-way ANOVA using the *F* test was applied to analyze the differences among treatments. When significant ANOVA differences occurred, Tukey's HSD test was used to identify these differences. A confidence level of 95% was used in all analyses.

To estimate the inhibitory effect of UV-A and UV-B on respiration and ammonia excretion of the two copepod species (relative to that in the P control) over the exposure period, the inhibition was calculated as:

$$\text{UV-A inhibition } (\%) = [(Y_P - Y_{PA})/Y_P] \times 100,$$

$$\text{UV-B inhibition } (\%) = \{[(Y_P - Y_{PAB}) - (Y_P - Y_{PA})/Y_P] \times 100,$$

where Y_P, Y_{PA}, and Y_{PAB} are the respiration or ammonia excretion rates under the P, PA, and PAB treatments.

Results

Effects on respiration

The ANOVA analysis results for the effects of UV-A and UV-B on respiration were $F = 255.88$ ($F > F_{0.01,2,6} = 10.92$, $P < 0.001$) for *P. marinus*; and $F = 26.38$, ($F > F_{0.01,2,6} = 10.92$, $P = 0.001$) for *L. bipinnata* (Table 1). The results indicated that both UV-A and UV-B significantly suppressed the respiration of *P. marinus* and *L. bipinnata*. In the presence of UV-A (62.4 W m^{-2}) and PAR, the respiration rates of *P. marinus* and *L. bipinnata* were suppressed by 10.2 and 46.1% compared with those receiving PAR alone (1,278 μmol m^{-2} s^{-1}) for the 30 min exposure. Addition of UV-B (2.63 W m^{-2}) brought about further ($P < 0.05$) reductions, by 8.1% in *P. marinus* and 17.8% in *L. bipinnata* (Figs. 1A, B). The UV-induced inhibition of respiration of *L. bipinnata* was greater, although it had a higher value (0.69 ± 0.02 mg O_2 ind.$^{-1}$ h^{-1}) compared with that of *P. marinus* (0.61 ± 0.03 mg O_2 ind.$^{-1}$ h^{-1}) under PAR.

Effects on ammonia excretion

The ANOVA analysis results for the effect of UV-A and UV-B on ammonia excretion were $F = 5.30$, ($F > F_{0.05,2,6} = 5.143$, $P = 0.047$) for *P. marinus* and $F = 29.47$ ($F > F_{0.01,2,6} = 10.92$, $P < 0.001$) for *L. bipinnata* (Table 1). Ammonia excretion in both *P. marinus* and *L. bipinnata* was significantly depressed by UV-A and UV-A + UV-B compared with those receiving PAR alone. The inhibition induced by UV-A or UV-A + UV-B was about 13.9 and 27.4% (Fig. 2A) in *P. marinus* and 33.4 and 49.2% in *L. bipinnata* (Fig. 2B).

Table 1 One-way ANOVA statistical results for respiration, ammonia excretion, and mortality of the herbivorous copepod *Pseudodiaptomus marinus* (A) and the omnivorous copepod *Labidocera bipinnata* exposed to P, PA, and PAB treatments

Parameters	*Pseudodiaptomus marinus*				*Labidocera bipinnata*			
	N	df	*F*	*P*	*N*	df	*F*	*P*
Respiration	3	2	255.88	<0.001	3	2	26.38	0.001
Ammonia excretion	3	2	5.30	0.047	3	2	29.47	<0.001
Mortality	3	2	17.17	<0.001	3	2	16.96	<0.001

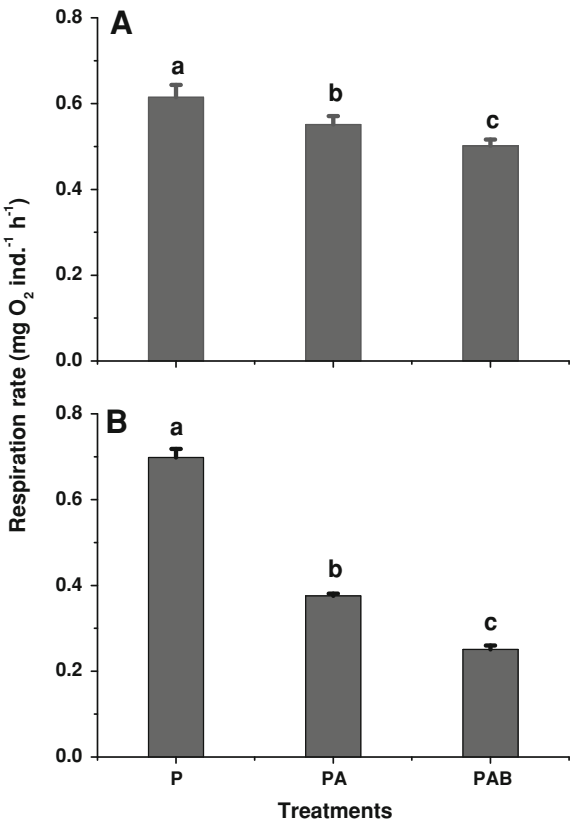

Fig. 1 Respiration rates of herbivorous copepod *Pseudodiaptomus marinus* (**A**) and omnivorous copepod *Labidocera bipinnata* (**B**) adults pre-exposed to PAR (*P* treatment), PAR + UV-A (*PA* treatment), and PAR + UV-A + UV-B (*PAB* treatment) for 30 min. Triplicate incubations for each radiation treatment were carried out. *Different letters* on the *bars* indicate significant ($P < 0.05$) difference between the treatments

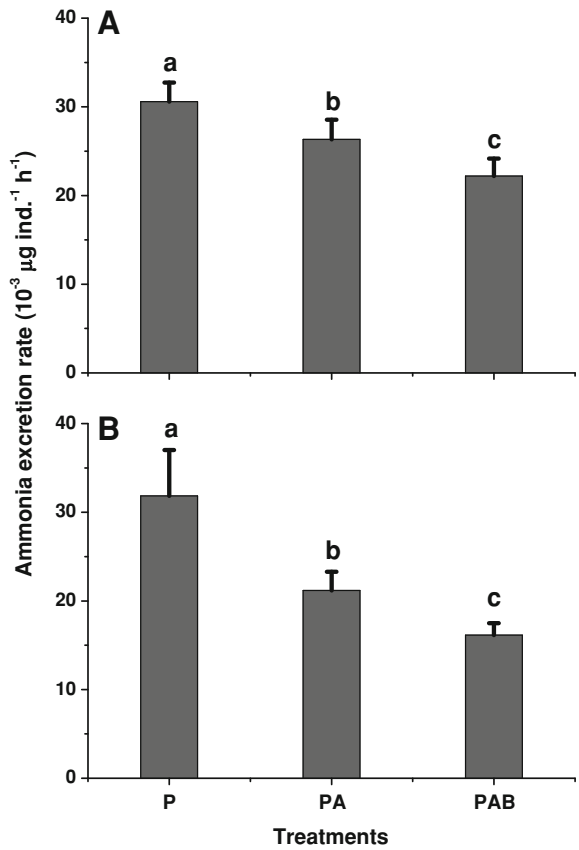

Fig. 2 Ammonia excretion rate of herbivorous copepod *Pseudodiaptomus marinus* (**A**) and omnivorous copepod *Labidocera bipinnata* (**B**) pre-adults exposed to PAR (*P* treatment), PAR + UV-A (*PA* treatment), and PAR + UV-A + UV-B (*PAB* treatment) for 30 min. Triplicate incubations for each radiation treatment were carried out. *Different letters* on the *bars* indicate significant ($P < 0.05$) difference between the treatments

Effects on mortality of the copepods

When exposed to the simulated solar radiation, an increased number of dead individuals were observed with prolonged duration in both *P. marinus* and *L. bipinnata* (Figs. 3A, B). A PAR level of about 60% local noontime irradiance in June led to lower mortality; however, addition of UV-A increased the mortality, and adding both UV-A and UV-B induced the highest mortality. The ANOVA analysis results for the effects of UV-A and UV-B on mortality were

$F = 17.17$ ($F > F_{0.01,2,60} = 4.98$, $P < 0.001$) for *P. marinus* and $F = 16.96$ ($F > F_{0.01,2,60} = 4.98$, $P < 0.001$) for *L. bipinnata* (Table 1). Mortality of *P. marinus* and *L. bipinnata* was significantly enhanced by UV-A + UV-B. When comparing the two species, the mortality was generally lower in *P. marinus* than in *L. bipinnata.* In the presence of UV-B, maximal mortality of *P. marinus* was observed in about 4 h (Fig. 3A), while that of *L. bipinnata* appeared in about 2 h (Fig. 3B); UV-B led to mortality in 1.5 h exposure of 13.7% in *P. marinus* and of 68.6% in *L. bipinnata*. The median lethal time ($T_{1/2}$) of *P. marinus* receiving P, PA, and PAB treatments was 6.7, 4.4, and 1.7 h, and that of *L. bipinnata* was 3.6, 2.3, and 0.8 h, respectively.

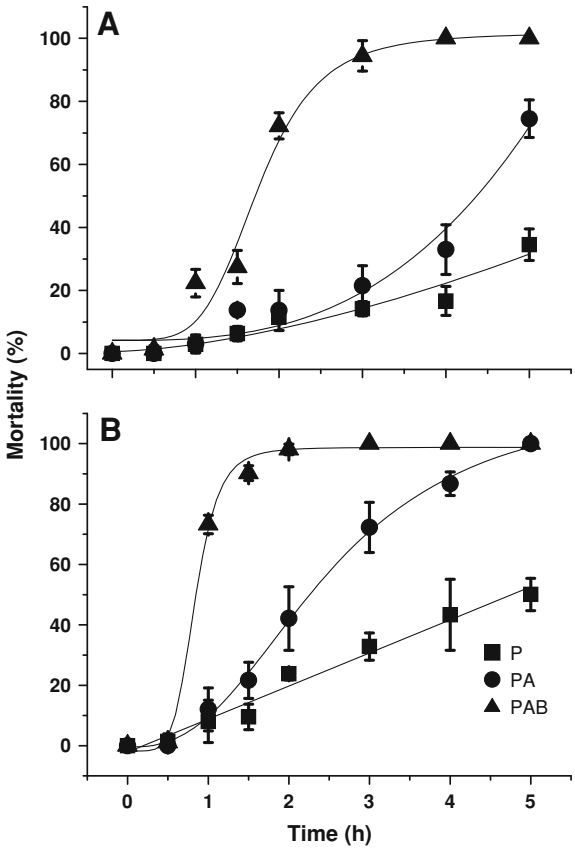

Fig. 3 Mortality of herbivorous copepod *Pseudodiaptomus marinus* (**A**) and omnivorous copepod *Labidocera bipinnata* (**B**) pre-adults exposed to PAR (*P*), PAR + UV-A (*PA*), and PAR + UV-A + UV-B (*PAB*). The intensities of PAR, UV-A, and UV-B being 278 (1,278 μmol m^{-2} s^{-1}), 62.4, and 2.63 W m^{-2}, respectively. Triplicate incubations for each radiation treatment were carried out

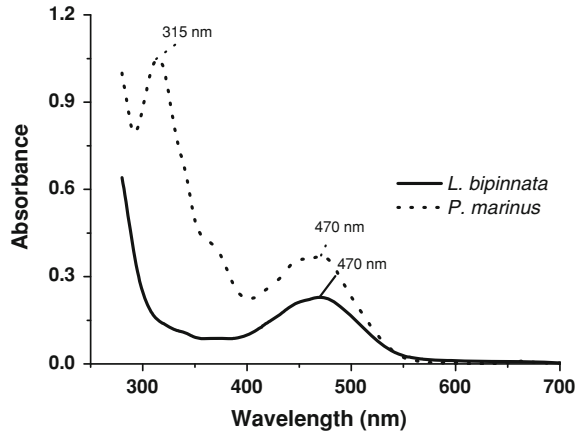

Fig. 4 Absorption spectra of the methanol extract of the copepods *Pseudodiaptomus marinus* and *Labidocera bipinnata*. The absorbance compounds were extracted immediately after the copepods were collected from Xiamen Bay

UV-absorbing compounds in the copepods

The methanol extraction of *P. marinus* individuals showed absorbance peaks at 315 and 477 nm (Fig. 4), which should be caused by MAAs with absorbance peaks between 310 and 360 nm, and carotenoids, respectively. For *L. bipinnata*, only one (and smaller) absorbance peak at 477 nm was found, reflecting undetectable MAAs and less carotenoids. The ANOVA analysis result of carotenoids content between the two copepods species concluded from the highest of the absorption peaks was $F = 2009.82$ ($F > F_{0.01,1,4} = 21.20, P < 0.001$). When normalized to fresh body weight, the contents of carotenoids were about 30% higher in *P. marinus* than in *L. bipinnata*.

Discussion

The respiration and ammonia excretion of both copepods were significantly suppressed by UV-A and UV-B radiation during a 30 min exposure, and the presence of both UV-A and UV-B led to higher mortality. In comparison, *P. marinus* was more resistant to UV than *L. bipinnata*, and the higher contents of MAAs and carotenoids in the former might have been responsible for the differential responses.

In addition to the decreased egg production and increased proportion of naupliar deformities (Kouwenberg & Lantoine, 2007), exposure to UVR can kill marine copepods directly (Lacuna & Uye, 2000;

Ban et al., 2007; Ma et al., 2012). Strategies which the zooplankton uses to alleviate UVR induced damage include photoprotection, photorepair, and behavioral response (Hansson & Hylander, 2009; Ma et al., 2010; Häder et al., 2011). Zooplankton species with smaller size or at younger developmental stages are more sensitive to UV-B (Damkaer et al., 1980; Lacuna & Uye, 2000).

Labidocera spp. mainly inhabit the surface waters of tropical to warm temperate regions (Fleminger, 1967; Hassett & Boehlert, 1999; Jeong et al., 2009), and the *Pseudodiaptomus* group distributes to deeper waters than the *Labidocera* species (Walter, 1986, Fleminger & Kramer, 1988; Liang & Uye, 1997). In our study, however, the respiration, ammonia excretion, and survival of smaller sized *P. marinus* were less affected by UV compared to the larger sized *L. bipinnata* (Figs. 1, 2, 3). *P. marinus* is herbivorous (Uye & Kasahara, 1983), feeding only on phytoplankton, while *L. bipinnata* is herbivorous at the nauplius and copepodite stages but omnivorous as adults. Marine copepods are unable to synthesize UV-protective compounds (Karentz, 2001 and references therein), but they can acquire these substances when there is sufficient phytoplankton as a food source (Hylander & Jephson, 2010). Therefore, different feeding habits can lead to different accumulation levels of photo-protective compounds, such as MAAs and carotenoids, which usually are much higher in phytoplankton (Laurion et al., 2002) than in zooplankton (Persaud et al., 2007) on a dry weight basis. In addition, there is evidence that MAAs-rich diets lead to the accumulation of these compounds in copepods (Pérez et al., 2012). The higher levels of photo-protective compounds in *P. marinus* could be related to the abundant phytoplankton cells in Xiamen Bay (Yang, 2007). *L. bipinnata* mainly feeds on zooplankton (such as *Paracalanus parvus*) which has a smaller body size than itself (Yang, 2001) and, therefore, accumulated less photo-protective compounds (Fig. 4). The MAAs and other UV-absorbing compounds can be accumulated to a higher extent in the herbivorous copepod than the omnivorous one (Fig. 4), since most of the phytoplankton species studied so far accumulate these compounds to screen off UV irradiance (Hannach & Sigleo, 1998; Sinha et al., 2007).

The respiration rates of *P. marinus* were suppressed by both UV-A (62.4 W m^{-2}) and UV-B (2.63 W m^{-2}) in the presence of PAR (1,278 μmol m^{-2} s^{-1}) (Fig. 1A); furthermore, the existence of UV-A and UV-B stress decreased the respiration of *L. bipinnata* to a further extent (Fig. 1B). It is reported that the respiration of *Daphinia catawba* is improved by 31.8% at low levels of UV-B (2.08 kJ m^{-2} over a 12 h period) compared to the dark control, whereas it is inhibited by 70.3% when the UV-B level is doubled (Fischer et al., 2006). Different physiological responses among zooplankton species when exposed to similar radiation treatments indicate the existence of species-specific metabolic activities and defense strategies. Both stimulation and inhibition of copepod metabolism were adverse for them: increases in metabolism could significantly reduce the energetic reserves available for growth and reproduction; however, inhibition in the metabolic activities would threaten survival (Ylönen et al., 2004). The effects of UVR on the ammonia excretion of marine zooplankton were first reported in our study (Figs. 2A, B). Metabolic responses of copepods to UVR can be a combined result of UVR-induced tissue damage, the cell repair system and induction of a cellular antioxidant (Fischer et al., 2006; Alton et al., 2012). UVR can cause damage through absorption of high-energy photons by proteins and DNA (Malloy et al., 1997), and indirectly through the creation of reactive oxygen species that can cause widespread damage to proteins, nucleic acids, and lipids (Charron et al., 2000; Borgeraas & Hessen, 2002; Ma & Gao, 2010). Prolonged UV-exposure decreased the survival of *P. marinus* and *L. bipinnata* (Fig. 3A, B), and may be a cumulative result of inhibition in metabolic activity and damage to cellular components (Ma et al. 2012). The local noontime solar UVR radiation levels are comparable with that employed in the present study, although noontime PAR levels would be higher than that during exposure. Therefore, the observed suppression of metabolic activities of both copepods could reflect somehow natural UV impacts on them, although the exposures only lasted for 30 min, considering that copepods are known to escape from UV by either vertical or horizontal migrations (Hansson et al., 2007; Ma et al., 2010). The mortality of both species under the PAR alone treatment might have been due to the individuals' health being weakened during preculture when they were fed with low quality food (*Phaeodactylum*). However, these results would not influence the significance of this study because we aimed to investigate the different physiological responses when copepods with different feeding habits were exposed to harmful irradiance simultaneously. This study indicated

that solar radiation induced photodamage would last for some time even when the stressful irradiance was removed.

In conclusion, the resistance of copepods to PAR, UV-A, and UV-B seemed to be feeding habit-dependent: the omnivorous species was more sensitive to solar spectra compared with the herbivorous one (Figs. 1, 2, 3). The *Pseudodiaptomus* group is distributed in deeper waters and the *Labidocera* species mainly inhabit surface waters in coastal seawater (Fleminger, 1967; Walter, 1986, Fleminger & Kramer, 1988; Liang & Uye, 1997; Hassett & Boehlert, 1999; Jeong et al., 2009). Thus, the possibility of *P. marinus* having higher adaptability to UV-exposure than *L. bipinnata* can be excluded. In fact, the resistance of copepods to solar irradiance depended on the photoprotective compounds they contained (Fig. 4): those which contained more MAAs and carotenoids are less sensitive to high solar radiation (Moeller et al., 2005; Hansson et al., 2007). The different resistance of herbivorous *P. marinus* and omnivorous *L. bipinnata* adults to simulated solar radiation may alter community and ecosystem structure and function during anticipated changes in underwater UVR environments.

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