

Impacts of solar UV radiation on grazing, lipids oxidation and survival of *Acartia pacifica* Steuer (Copepod)

MA Zengling^{1,3}, LI Wei², GAO Kunshan^{2*}

¹ College of Life and Environmental Science, Wenzhou University, Wenzhou 325035, China

² State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361005, China

³ Key and Open Laboratory of Marine and Estuary Fisheries (Ministry of Agriculture), East China Sea Fisheries Research Institute, Chinese Academy of Fisheries Science, Shanghai 200090, China

Received 11 March 2011; accepted 25 July 2011

©The Chinese Society of Oceanography and Springer-Verlag Berlin Heidelberg 2012

Abstract

UV radiation is known to affect aquatic primary producers and their grazers. However, little has been documented on its effects on zooplankton grazing. In this study, the authors investigated the effects of photosynthetically active radiation (PAR, 400–700 nm), ultraviolet-A (UV-A, 320–400 nm) and ultraviolet-B (UV-B, 280–320 nm) radiation on grazing, mortality and lipids oxidation of the copepod *Acartia pacifica* collected from the Xiamen Bay. After 30 min of the exposures, the copepod was fed in darkness with the diatom *Phaeodactylum tricornutum* at two cell concentrations (2.5×10^4 and 2.5×10^5 cells/ml). At the low cell concentration, the individuals pre-exposed to PAR (218.0 W/m^2)+UV-A (48.2 W/m^2) or PAR+UV-A+UV-B (2.1 W/m^2) showed suppressed clearance and grazing activities compared with those receiving PAR alone, by 22.7% and 17.1% for clearance and by 22.6% and 5.5% for grazing rates, respectively. However, the suppression on clearance and grazing became indistinctive at the high food concentration. Exposures to UV-A and UV-B led to increased lipid oxidation and higher mortality, furthermore, the mortality linearly increased with enhanced oxidation of lipid.

Key words: *Acartia pacifica*, copepod, grazing, malonaldehyde (MDA), mortality, UVR

1 Introduction

Solar UV radiation (280–400 nm) is known to impair both primary producers and their consumers in aquatic ecosystems, decrease productivity and disturb reproduction and development, which then may result in a reduced sink capacity for atmospheric carbon dioxide, affect species diversity, ecosystem stability, and trophic interactions and ultimately global biogeochemical cycles (Häder et al., 2011). Although enforcement of the Montreal Protocol has slowed down the ozone depletion, recent studies indicate a 10% increase in UV radiation (UVR, 280–400 nm) reaching north temperate regions from 1983 to 2003 (Josefsson, 2006). The physiological and ecological impacts of enhanced UVR on marine organisms have been extensively examined in the past decades (Williamson and Rose, 2009; Häder et al., 2007).

UVR reduces photosynthesis of phytoplankton (Beardall et al., 2009; Gao et al., 2007; Helbling et al., 2003), has direct adverse impacts on secondary producers (herbivorous zooplankton) (Tartarotti and Torres, 2009; Aarseth and Schram, 2002) and indirect ones through the food web (De Lange and Van Reeuwijk, 2003; Scott et al., 1999), since UVR can alter the nutritious composition of phytoplankton (Finkel, 2010; Guihéneuf et al., 2010; Nahon et al., 2010). The presence of UVR is notorious for decreasing zooplankton's reproduction, deformed nauplii and mortality (Dattilo et al., 2005; Lacuna and Uye, 2001; Kouwenberg et al., 1999). Most of the negative impacts were attributed to UV-B, while effects of UV-A are often ambiguous. UV-B is known to damage biologically important molecules, such as proteins and nucleic acids (Häder et al., 2011; Browman et al., 2003; Sinha and Häder, 2002; Mitchell, 1996).

Foundation item: The Changjiang Scholars and Innovative Research Team Program under contract No. IRT0941; Shanghai Municipal Natural Science Foundation under contract No. 11ZR1449900; Visiting Scholarship of State Key Laboratory of Marine Environmental Science, Xiamen University under contract No. MELRS0919.

*Corresponding author, E-mail: ksgao@xmu.edu.cn

Copepods are primary consumers and one of the most dominant zooplankton species in ocean (Camus and Zeng, 2009; Feinberg and Dam, 1998). They and their nauplii are natural preys of many juvenile fish and crustaceans (Pinto et al., 2001), typically accounting for more than 50% of their stomach contents (Støttrup, 2000). Copepods play an important role in regulating phytoplankton population dynamics (Schultes et al., 2006; Schnetzer and Caron, 2005) in addition to their basic roles in the food chain. The food quality, especially, the content of fatty acids, forms the bases of energy transport. Most species use lipids as a primary energy storage for survival before and after the short productive season (Falk-Petersen et al., 1999). The transfer of lipids from diatoms to herbivorous zooplankton is of particular importance in aquatic ecosystems (Falk-Petersen et al., 2007). Zooplankton grazing on phytoplankton can transfer more than 50% of carbon fixed by primary production to higher trophic levels (Laws et al., 1988; Scavia, 1980). However, to the best of our knowledge, the effects of UVR on the grazing activity and lipid oxidation of copepod have rarely documented.

The calanoid copepod, *Acartia pacifica*, which shows higher feeding intensity in the evening, is widely distributed in the coastal waters of China. In the Xiamen Bay (24°26'N, 118°02'E), 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 (Wang et al., 2005; Jiang et al., 2004). The changes in their grazing and population density may have an impact on the local ecosystem. UVR and water temperature show the highest levels in summer in the Xiamen Bay, which might be responsible for the disappearance. However, zooplankton's photobiological response to UV in this area has only been carried out recently (Ma et al., 2010).

The aim of this study is to investigate the effects of UV radiation on grazing activity, lipid oxidation and mortality of *A. pacifica*, and distinguish the effects of UV-A and UV-B on this important species, which may aid in understanding the ecological behavior of zooplanktons in the Xiamen Bay.

2 Materials and methods

2.1 Sampling of zooplankton and preculture in the laboratory

Zooplankton was collected with a plankton net

(mesh diameter 0.112 mm) by horizontal hauling at surface water in the central area of the Xiamen Bay, at night during April 2009, when *A. pacifica* was abundant as a dominant species (Wang et al., 2005; Jiang et al., 2004). The samples were immediately transported to the laboratory and then were separated into two groups using meshes of 0.25 and 0.50 mm pore sizes. The individuals sized 0.25 to 0.5 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 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ 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) of *Chlorella vulgaris* and *Phaeodactylum tricornerutum* with equal density was used to feed them. Healthy (actively moving) individuals were picked out and used for the following experiments within 2 d after each sampling.

2.2 Radiation treatments, illumination source and measurement

To investigate the effects of different radiation treatments on grazing activity, lipids oxidation and mortality of the copepod *A. pacifica*, different radiation treatments were carried out using cut-off filters: (1) PAR (P treatment), covered with a GG395 filter (Schott, Mainz, Germany), allowing the copepod to receive the irradiances above 395 nm; (2) PAR+UV-A (PA treatment), covered with a Schott WG320 filter, exposed to the irradiances above 320 nm; (3) PAR+UV-A+UV-B (PAB treatment), covered with a Schott WG280 filter, allowing the individuals exposed to the irradiances above 280 nm.

A solar simulator (Sol 1200W, Dr. Hönle, Martinsried, Germany) was used to perform the radiation exposures and the artificial solar radiation showed similar output spectrum with the solar radiation (Gao et al., 2008). The irradiances were 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), respectively (Häder et al., 1999).

2.3 Determination of grazing and filtering rate

To eliminate the disturbance of the zooplankton's excrement on the measurement of phytoplankton cell density, the copepods were pre-starved for 24 h to clean up alimentary canal (Icely and Nott, 1985). Nine groups of *A. pacifica*, 25 individuals each, were

transferred to nine beakers (diameter 55 mm, height 70 mm) containing 100 ml filtered seawater. Then, the beakers were exposed to different radiation treatments with or without UVR using the cutoff filters as mentioned above for 30 min. Triplicate beakers were placed under each radiation treatment and in a water bath for the temperature control at 20°C with a circulating cooler (Eyela, CAP-3000, Tokyorikakikai Co. Ltd., Tokyo, Japan). The irradiance levels for PAR, UV-A and UV-B were 218 [1 000 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$], 48.2 and 2.1 W/m^2 , respectively, which approximated 60% of the local solar PAR in April. The UV-A and UV-B were 54.7% and 128.9% higher than the natural radiations at the same PAR intensity. Ten individuals under each treatment were randomly sampled from each beaker using a pipette in 10 min and transferred to a 50 ml bottle full of the filtered seawater containing the diatom *P. tricornutum* as food at a concentration of 2.5×10^4 or 2.5×10^5 cells/ml. Changes in the diatom cell concentration over time were determined using a Z2™ Coulter Counter (Beckman Coulter, Buckinghamshire, UK), while the bottles were maintained in darkness at 20°C. In addition, three bottles without the copepod but the diatom of the same concentration were incubated under the same condition for evaluation of the grazing. The clearance rate (CR) and grazing rate (GR) were determined according to the formula of Frost (1972).

2.4 Determination of mortality

To test how UVR would harm *A. pacifica*, the individuals were transferred to 800 ml seawater in a 1 000 ml beaker (diameter 90 mm, height 150 mm) and were exposed to two levels of solar radiation, with PAR of 218 or 362 W/m^2 [1 000 or 1 667 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$], accounting for 60% and 100% of the local noontime solar radiation in April, and with UV-A of 48 or 79 W/m^2 and UV-B of 2.1 and 3.4 W/m^2 , respectively. The exposures lasted for 4 h and no food was supplied. The mortality of *A. pacifica* was expressed as ratio of dead (immovable when disturbed) individuals to the total. Triplicate incubations were done under each treatment.

2.5 Determination of malondialdehyde (MDA)

To test oxidation of lipids by reactive oxygen species (ROS) during the exposures, the contents of malondialdehyde (MDA, the final production of lipid oxidation) in the zooplankton after the exposures to the different radiation treatments (as mentioned

above, approximating 100% local noontime level in April) were measured according to Heath and Packer (1968). Briefly, the individuals were collected and homogenized in 10% trichloroacetic acid (TCA) and then centrifuged at 5 000 g for 10 min. Two milliliters supernatant was taken and mixed with 2 ml 0.6% thiobarbituric acid (TBA), heated in boiling water for 15 min, and then re-centrifuged after cooling. The absorbance of the supernatant was measured using a Beckman DU 800 spectrophotometer, then the concentration (c , $\mu\text{mol}/\text{L}$) of MDA was determined as follows: $c = 6.54 \times A_1 - 0.56 \times A_2$, where A_1 and A_2 denotes the absorbance at 532 and 450 nm, respectively.

2.6 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 solar radiation on grazing of *A. pacifica*

During the incubations at a low *P. tricornutum* cell density of about 2.5×10^4 cells/ml, the cell concentration decreased with prolonged culture time due to the grazing of *A. pacifica*. However, the descent rate decelerated with prolonged cultures, with higher rates ($p < 0.05$) in the first 4 h under all the treatments. The cell concentration in cultures with PAR-irradiated *A. pacifica* individuals (control group) decreased faster ($p < 0.05$) than those received PA treatment in 4 h, and those with the individuals exposed to PAR+UV-A+UV-B declined by the least extent (Fig. 1a), reflecting the inhibitory effects of UVR on grazing. The cell concentration cultured with *A. pacifica* pre-exposed to PAR, PAR+UV-A and PAR+UV-A+UV-B decreased to 0.86, 0.98 and 1.20 ($\times 10^4$ cells/ml) in 4 h from 2.5×10^4 cells/ml, addition of UV-A and UV-B to *A. pacifica* slowed down the decrease rate of cell density by 14% and 39% compared with those cultured with the individuals pre-exposed to PAR only. During the incubations at a high cell (*P. tricornutum*) density of 2.5×10^5 cells/ml, no significant ($p > 0.05$) difference in cell concentration could be detected among the treatments throughout though they all decreased with prolonged duration (Fig. 1b).

To evaluate the effects UV-A and UV-B on grazing of *A. pacifica*, the average rates of clearance and grazing in the initial 4 h period when the cell concen-

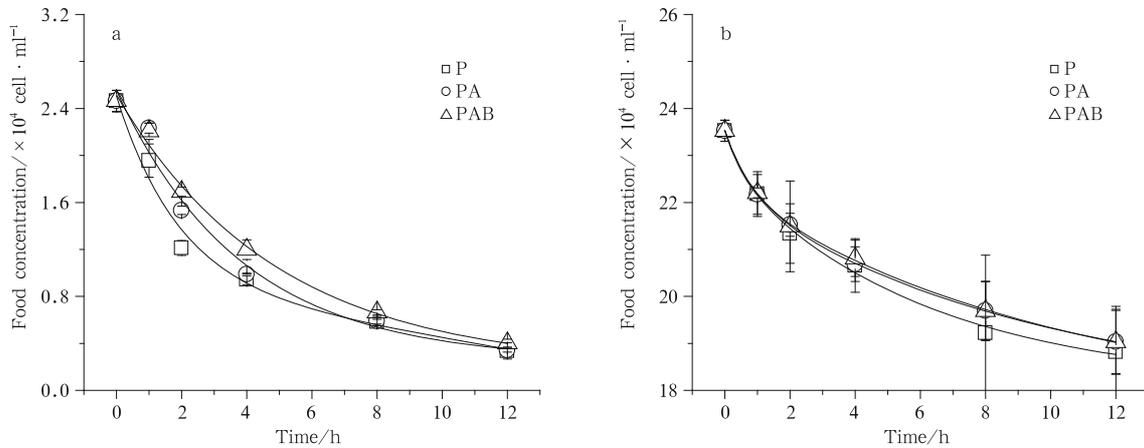


Fig.1. Changes in cell concentration of *P. tricornutum* with initial densities of $\sim 2.5 \times 10^4$ cells/ml (a) $\sim 2.5 \times 10^5$ cells/ml (b) in presence of *A. pacifica* individuals which were pre-exposed to P (PAR), PA (PAR+UV-A) and PAB (PAR+UV-A+UV-B) treatments for 30 min. The means and standard errors were based on triplicate incubations. The irradiance levels for PAR, UV-A and UV-B were 218 [1 000 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$], 48.2 and 2.1 W/m^2 , respectively, which approximated 60% of the local solar PAR in South China Sea during mid spring.

tration dropped off linearly almost were analyzed. Addition of UV-A ($48.2 \text{ W}/\text{m}^2$) led to a decrease ($p < 0.05$) in the clearance compared with those receiving PAR only, and presence of UV-A and UV-B ($2.1 \text{ W}/\text{m}^2$) led to the lowest ($p < 0.01$) clearance rate (Fig. 2a). On the other hand, at the high algal cell concentration, pre-exposures to PAR+UV-A and PAR+UV-A+UV-B showed insignificant ($p > 0.05$) influence on the clearance rate (Fig. 2b). In view of the grazing rate, similarly both UV-A and UV-B resulted in a significant ($p < 0.05$) decrease at low food density (Fig. 3a). Furthermore, the clearance rate was much higher ($p < 0.05$) at low food concentration (Figs 2a and b), while, the grazing rate was much higher ($p < 0.05$) at

high food concentration (Figs 3a and b).

3.2 Effects of solar radiation on mortality of *A. pacifica*

When exposed to the solar radiation with UVR, some of *A. pacifica* individuals were killed. Exposures to PAR alone of 60% and 100% of local noontime level led to little mortality, addition of UV-A increased the mortality, and adding both UV-A and UV-B gave rise to the highest mortality (Figs 4a and b). When compared between the two levels of solar radiation (60% and 100% of the local noontime level), higher mortality of *A. pacifica* was found under the higher radiation level. The mortalities in 4 h after the exposures to P,

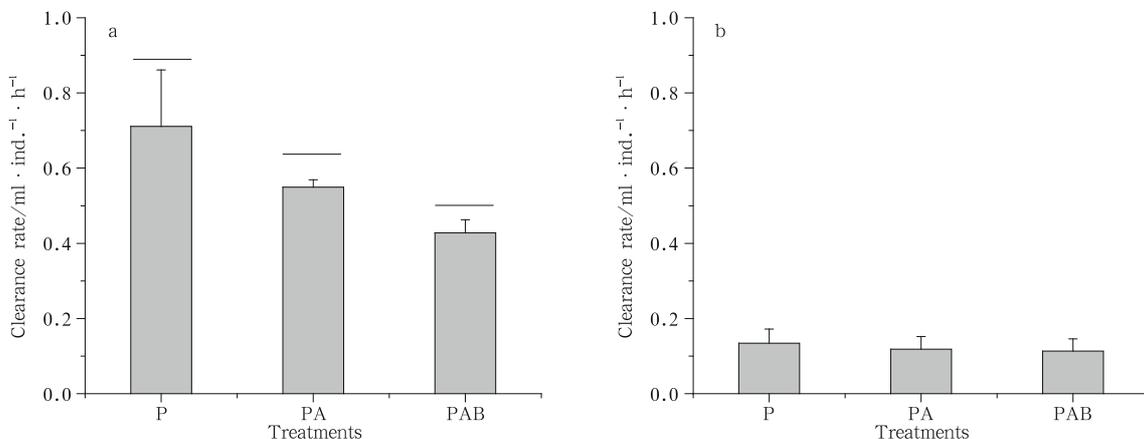


Fig.2. Effects of different irradiation treatments on clearance rates of *A. pacifica* on *P. tricornutum* with initial concentration of $\sim 2.5 \times 10^4$ cells/ml (a) and $\sim 2.5 \times 10^5$ cells/ml (b). The means and standard errors were based on triplicate incubations and the horizontal bars at different levels above the columns indicate significant ($p < 0.05$) differences among the treatments.

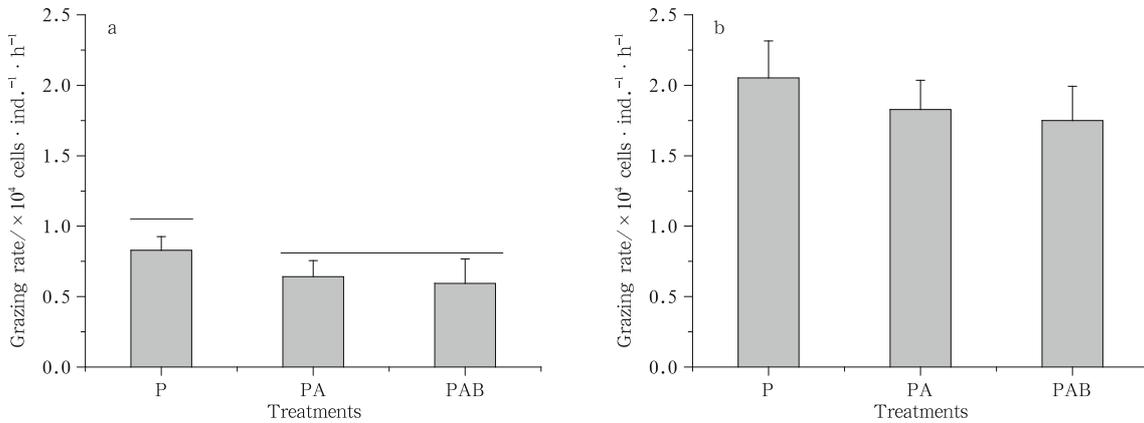


Fig.3. Effects of different irradiation treatments on grazing rates of *A. pacifica* on *P. tricornutum* with initial concentration of 2.5×10^4 cells/ml (a) and 2.5×10^5 cells/ml (b). The means and standard errors were based on triplicate incubations and the horizontal bars at different levels above the columns indicate significant ($p < 0.05$) differences among the treatments.

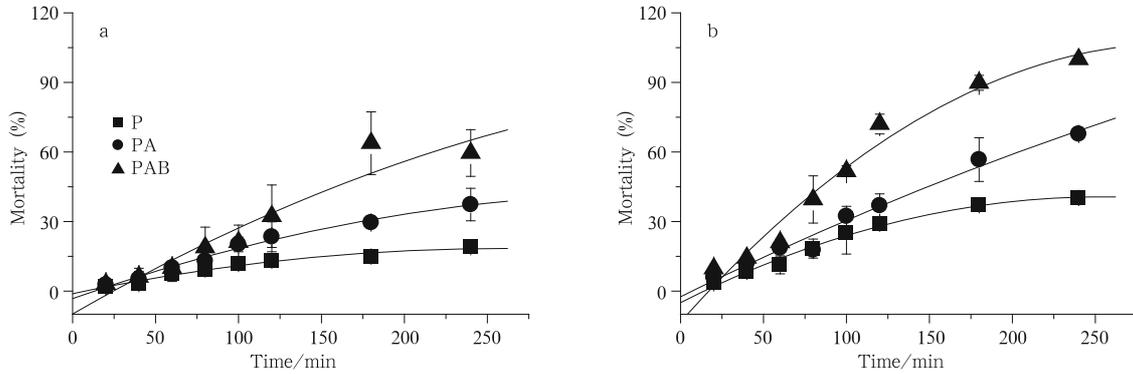


Fig.4. Effects of different irradiation treatments, which accounting for 60% (a) and 100% (b) of noontime solar radiation in the South China Sea during mid spring, on mortality of *A. pacifica*. The means and standard errors were based on triplicate incubations. The PAR levels were 218 or 362 W/m^2 [1 000 or 1 667 $\mu mol/(m^2 \cdot s)$], and with corresponding UV-A of 48 or 79 W/m^2 and UV-B of 2.1 and 3.4 W/m^2 , respectively.

PA and PAB treatments were, 18.89% ($\pm 2.63\%$), 37.33% ($\pm 7.04\%$) and 59.56% ($\pm 10.05\%$) at the 60% local noon solar radiation (Fig. 4a); 40.20% ($\pm 2.46\%$), 67.71% ($\pm 1.47\%$) and 100% ($\pm 0.00\%$) at the 100% local noon solar radiation (Fig. 4b), respectively.

3.3 Effects of solar radiation on lipid oxidation of *A. pacifica*

When *A. pacifica* individuals were exposed to 100% local noontime solar radiation in the presence of UV-A or UV-A+UV-B, the oxidation of lipids increased with prolonged time (Fig. 5). Addition of UV-A or UV-A+UV-B to PAR led to higher ($p < 0.01$) lipids oxidation (Fig. 5). The contents of malondialdehyde (MDA, the final product of lipids oxidation) were 11.33 (± 2.06), 31.71 (± 2.01) and 46.32 (± 2.26) $\mu g/g$ dry mass after 4 h exposures to P, PA and PAB treatments, respectively (Fig. 5). UV-A and UV-B respectively led to 179.8% and 128.9% stimulation of

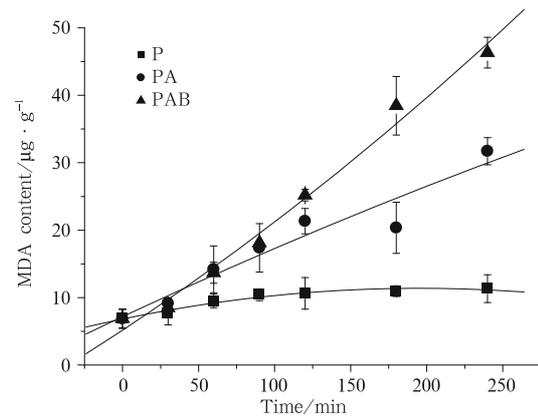


Fig.5. Effects of different irradiation treatments, which accounting for 100% of noontime solar radiation in South China Sea during mid spring, on MDA production in *A. pacifica*. The means and standard errors were based on triplicate incubations. The irradiance levels for PAR, UV-A and UV-B were 362 [1 667 $\mu mol/(m^2 \cdot s)$] 79 and 3.4 W/m^2 , respectively.

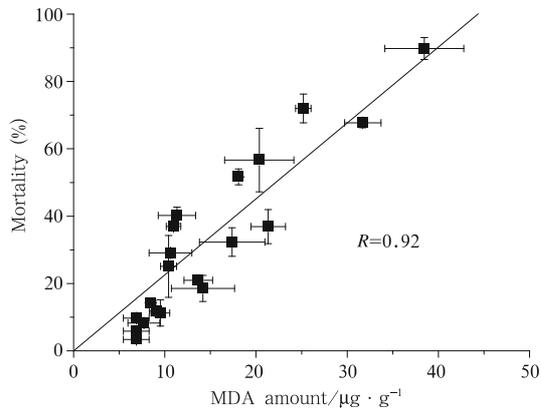


Fig. 6. The relationship between mortality of *A. pacifica* and MDA production. The means and standard errors were based on triplicate incubations.

MDA production. When the mortality of *A. pacifica* was plotted against the formation of MDA, a linear ($R^2=0.85$, $p < 0.01$) relationship was established (Fig. 6).

4 Discussion

The grazing activity of *A. pacifica* was inhibited in the presence of UV-A and UV-B at a PAR level corresponding to 60% noontime solar radiation of sunny days in the South China Sea during mid-spring. The mortality and lipids peroxidation increased with prolonged exposures, with higher pace in the presence of UV-A and/or UV-B.

The grazing and ingestion of copepods commonly increased with increased food availability (Setälä et al., 2009; Kozłowski-Suzuki et al., 2006). In this study, the impact of UV radiation on grazing of *A. pacifica* was affected by food concentration. The phytoplankton cell densities ($\sim 2.5 \times 10^4$ cells/ml, $\sim 2.5 \times 10^5$ cells/ml) used in the present study was much higher than natural cells density than one to three orders, which enhanced the encounter rates of food. Pre-exposures to UVR significantly inhibited the grazing at lower food density (2.5×10^4 cells/ml), but the effects became negligible when the cells' concentration ten times increased (Figs 3a and b). High clearance rate is not a representative of high grazing when taking into consideration the encounter rates (Rothschild and Osborn, 1988). At the lower food density, the individuals must have filtered more water to get the food they needed, and their clearance capability was impaired by UV-A and UV-B (Fig. 2a). The individuals might have not received enough food when their

clearance capability was inhibited by UV-A and UV-B, thus their grazing became impaired by UV (Fig. 3a).

Zooplankton's grazing affects the structure of the lower levels via trophic cascades (Schnetzer and Caron, 2005; Gliwicz, 2002; Carpenter and Kitchell, 1988) and usually causes a decrease in phytoplankton biomass (Mayzaud et al., 2002). It has been reported that biologically effective levels of solar ultraviolet radiation could penetrate into at least 20 m even in highly productive coastal waters (Whitehead et al., 2000). The average depth of sea water in the Xiamen Bay was 14 m (Zhang et al., 2007), much lower than solar UV penetrated. Therefore, the zooplankton living in the waters must face the stressful radiation on sunny day, especially at noontime though they may move to bottom by vertical migration. As shown in the present study, both UV-A and UV-B harm the grazing capability of *A. pacifica*, phytoplankton abundance and/or community structure may change in response to changes in zooplankters' grazing performance.

For *Artemia franciscana*, exposure to UVR led to high mortality (Dattilo et al., 2005). In this study, a PAR level of about 60% noontime solar radiation of sunny days during local mid-spring led to death of *A. pacifica*, and addition of UV-A and UVB increased the mortality (Fig. 4), showing a linear relationship with production of MDA (Fig. 5). The antioxidant enzyme activities of glutathione peroxidase (GPx) and glutathione disulfide reductase (GR) in the copepod *Schmacheria inopinus* increased first but then declined with prolonged exposure to UV radiation (Yu et al., 2009), reflecting non-sufficient protection by the enzymes. Oxidative stress resulting from the formation of reactive oxygen species (ROS) may be responsible for the damaging effects of UV on aquatic organisms (Ma and Gao, 2010; Charron, 2000). The deleterious effects of ROS on aquatic organisms include lipid peroxidation, DNA strand breaks, cyclobutane pyrimidine dimers (CPD's) and enzyme inactivation (Karantz et al., 2004; Livingstone, 2001; Di Giulio et al., 1989). Lipid peroxidation is a well-known mechanism of cellular injury induced by oxidative stress in cells and tissues (Charron et al., 2000). MDA is a decomposition product of lipid peroxides derived from polyunsaturated fatty acids and therefore widely used as an indicator of lipid peroxidation. In this study, the mortality of *A. pacifica* increased linearly with increased MDA contents (Fig. 6). It reflects damages caused by UVR that induces formation of ROS in *A. pacifica*.

5 Conclusions

The clearance and grazing activities of *A. pacifica* were impaired by solar UVR, however, the negative effects could be alleviated by increased food encounter rates. Adding UV-A and UV-A+UV-B to PAR led to increased mortality and lipid oxidation of *A. pacifica*, thus, the mortality caused by UVR may be compounded results of PAR, UV-A and UV-B exposures. In view of the elevated ratio of UV-B to PAR in the present work and the effects observed, enhanced solar UV radiation can be expected to deteriorate the zooplankton ecological behavior in the Xiamen Bay and its ecosystem by decreasing the survival rate of dominant zooplankton species or by affecting the energy flow between trophic levels.

Acknowledgements

The authors are grateful to Liu Yuting, Yang Guiyuan and Liu Shouhai for their assistance during the experiments.

References

- Aarseth K A, Schram T A. 2002. Susceptibility to ultraviolet radiation in *Calanus finmarchicus* and *Lepeophtheirus salmonis* and the adaptive value of external filtering (Crustacea: Copepoda). *Journal of Plankton Research*, 24: 661–679
- Beardall J, Sobrino C, Stojkovic S. 2009. Interactions between the impacts of ultraviolet radiation, elevated CO₂, and nutrient limitation on marine primary producers. *Photochemical and Photobiological Science*, 8: 1257–1265
- Browman H I, Vetter R D, Rodriguez C A, et al. 2003. Ultraviolet (280–400 nm)-induced DNA damage in the eggs and larvae of *Calanus finmarchicus* G. (Copepoda) and Atlantic Cod (*Gadus morhua*). *Photochemistry and Photobiology*, 77: 397–404
- Camus T, Zeng C. 2009. The effects of stocking density on egg production and hatching success, cannibalism rate, sex ratio and population growth of the tropical calanoid copepod *Acartia sinjiensis*. *Aquaculture*, 287: 145–151
- Carpenter S R, Kitchell J F. 1988. Consumer control of lake productivity. Large-scale experimental manipulations reveal complex interactions among lake organisms. *BioScience*, 38: 764–769
- Charron R A, Fenwick J C, Lean D R S, et al. 2000. Ultraviolet-B radiation effects on antioxidant status and survival in the zebrafish, *Brachydanio rerio*. *Photochemistry and Photobiology*, 72: 327–333
- Dattilo A M, Bracchini L, Carlini L, et al. 2005. Estimate of the effects of ultraviolet radiation on the mortality of *Artemia franciscana* in naupliar and adult stages. *International Journal of Biometeorology*, 49: 388–395
- De Lange H J, Van Reeuwijk P L. 2003. Negative effects of UVB-irradiated phytoplankton on life history traits and fitness of *Daphnia magna*. *Freshwater Biology*, 48: 678–686
- Di Giulio R T, Washburn P C, Wenning R J, et al. 1989. Biochemical responses in aquatic animals: A review of determinants of oxidative stress. *Environmental Toxicology and Chemistry*, 8: 1103–1123
- Falk-Petersen S, Pedersen G, Kwasniewski S, et al. 1999. Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. *Journal of Plankton Research*, 21: 1249–1264
- Falk-Petersen S, Timofeev S, Pavlov V, et al. 2007. Climate variability and possible effects on arctic food chains. The role of *Calanus*. In: Ørbæk J B, Kallenborn R, Tombre I, et al., eds. *Arctic-Alpine Ecosystems and People in a Changing Environment*. Berlin: Springer Verlag, 250
- Feinberg L R, Dam H G. 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Marine Ecology Progress Series*, 175: 87–96
- Finkel Z V. 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry. *Journal of Plankton Research*, 32: 119–137
- Frost B W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, 17: 805–815
- Gao Kunshan, Li Ping, Watanabe T, et al. 2008. Combined effects of ultraviolet radiation and temperature on morphology, photosynthesis and DNA of *Arthrospira (Spirulina) platensis*. *Journal of Phycology*, 44: 777–786
- Gao Kunshan, Wu Yaping, Li Gang, et al. 2007. Solar UV radiation drives CO₂ fixation in marine phytoplankton: A double-edged sword. *Plant Physiology*, 144: 54–59
- Gliwicz Z M. 2002. On the different nature of top-down and bottom-up effects in pelagic food webs. *Freshwater Biology*, 47: 2296–2312
- Guihéneuf F, Fouqueray M, Mimouni V, et al. 2010. Effect of UV stress on the fatty acid and lipid class composition in two marine microalgae *Pavlova lutheri* (Pavlovophyceae) and *Odontella aurita* (Bacillariophyceae). *Journal of Applied Phycology*, 22: 629–638
- Häder D-P, Helbling E W, Williamson C E, et al. 2011. Effects on aquatic ecosystems and interaction with climate change. *Photochemical and Photobiological Science*, 10: 242–260

- Häder D-P, Kumar H D, Smith R C, et al. 2007. Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. *Photochemical and Photobiological Science*, 6: 267–285
- Häder D-P, Lebert M, Marangoni R, et al. 1999. ELDONET-European light dosimeter network hardware and software. *Journal of Photochemistry and Photobiology B: Biology*, 52: 51–58
- Heath R L, Packer L. 1968. Photoperoxidation in isolated Chloroplasts: I. Stoichiometry of fatty acid peroxidation. *Archives of Biochemistry and Biophysics*, 125: 189–198
- Helbling E W, Gao K, Gonçalves R, et al. 2003. Utilization of solar UV radiation by coastal phytoplankton assemblages off SE China when exposed to fast mixing. *Marine Ecology Progress Series*, 259: 59–66
- Icely J D, Nott J A. 1985. Feeding and digestion in *Corophium volutator* (Crustacea: Amphipoda). *Marine Biology*, 89: 183–195
- Jiang Xiaodong, Wang Guizhong, Li Shaojing. 2004. Age, distribution and abundance of viable resting eggs of *Acartia pacifica* (Copepoda: Calanoida) in Xiamen Bay, China. *Journal of Experimental Marine Biology and Ecology*, 312: 89–100
- Josefsson W. 2006. UV-radiation 1983–2003 measured at Norrköping, Sweden. *Theoretical and Applied Climatology*, 83: 59–76
- Karentz D, Bosch I, Mitchell D. 2004. Limited effects of Antarctic ozone depletion on sea urchin development. *Marine Biology*, 145: 277–292
- Kouwenberg J H M, Browman H, Cullen J J, et al. 1999. Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I Atlantic cod (*Gadhus morhua*) eggs. *Marine Biology*, 134: 269–284
- Kozlowsky-Suzuki B, Carlsson P, Ruhl A, et al. 2006. Food selectivity and grazing impact on toxic *Dinophysis* spp. by copepods feeding on natural plankton assemblages. *Harmful algae*, 5: 57–68
- Lacuna D G, Uye S. 2001. Influence of mid-ultraviolet (UVB) radiation on the physiology of the marine planktonic copepod *Acartia omorii* and the potential role of photoreactivation. *Journal of Plankton Research*, 23: 143–156
- Laws E A, Bienfang P K, Ziemann D A, et al. 1988. Phytoplankton population dynamics and the fate of production during the spring bloom in Auke Bay, Alaska. *Limnology and Oceanography*, 33: 57–65
- Livingstone D R. 2001. Contaminant-stimulated reactive oxygen species production and oxidative damage in aquatic organisms. *Marine Pollution Bulletin*, 42: 656–666
- Ma Zengling, Li Wei, Gao Kunshan. 2010. Horizontal migration of *Acartia pacifica* Steuer (copepoda) in response to UV-radiation. *Journal of Photochemistry and Photobiology B: Biology*, 101: 233–237
- Ma Zengling, Gao Kunshan. 2010. Photosynthetically active and UV radiation act in an antagonistic way in regulating buoyancy of *Arthrospira (Spirulina) platensis* (cyanobacterium). *Environmental and Experimental Botany*, 66: 265–269
- Mayzaud P, Tirelli V, Errhif A, et al. 2002. Carbon intake by zooplankton. Importance and role of zooplankton grazing in the Indian sector of the Southern Ocean. *Deep-Sea Res II*, 49: 3169–3187
- Mitchell D L. 1996. Radioimmunoassay of DNA damaged by ultraviolet light. In: Pfeifer G, ed. *Technologies for Detection of DNA Damage and Mutation*. New York: Plenum, 73–85
- Nahon S, Charles F, Lantoine F, et al. 2010. Ultraviolet radiation negatively affects growth and food quality of the pelagic diatom *Skeletonema costatum*. *Journal of Experimental Marine Biology and Ecology*, 383: 164–170
- Pinto C S C, Souza-Santos L P, Santos P J P. 2001. Development and population dynamics of *Tisbe biminiensis* (Copepoda: Harpacticoida) reared on different diets. *Aquaculture*, 198: 253–267
- Rothschild B J, Osborn T R. 1988. Small-scale turbulence and plankton contact rates. *Journal of Plankton Research*, 10: 465–474
- Scavia D. 1980. An ecological model of Lake Ontario. *Ecological Modelling*, 8: 49–78
- Schnetzer A, Caron D A. 2005. Copepod grazing impact on the trophic structure of the microbial assemblage of the San Pedro Channel, California. *Journal of Plankton Research*, 27: 959–971
- Schultes S, Verity P G, Bathmann U. 2006. Copepod grazing during an iron-induced diatom bloom in the Antarctic Circumpolar Current (EisenEx): I. Feeding patterns and grazing impact on prey populations. *Journal of Experimental Marine Biology and Ecology*, 338: 16–34
- Scott J D, Chalker-Scott L, Foreman A E, et al. 1999. *Daphnia pulex* fed UVB-irradiated *Chlamydomonas reinhardtii* show decreased survival and fecundity. *Photochemistry and Photobiology*, 70: 308–313
- Setälä O, Sopanen S, Autio R, et al. 2009. Grazing and food selection of the calanoid copepods *Eurytemora affinis* and *Acartia biflosa* feeding on plankton assemblages containing *Dinophysis* spp. *Boreal Environment Research*, 14: 837–849
- Sinha R P, Häder D-P. 2002. UV-induced DNA damage and repair: A review. *Photochemical and Photobiological Science*, 1: 225–236
- Støttrup J G. 2000. The elusive copepods: their production and suitability in marine aquaculture. *Aquaculture Research*, 3: 702–711

- Tartarotti B, Torres J J. 2009. Sublethal stress: Impact of solar UV radiation on protein synthesis in the copepod *Acartia tonsa*. *Journal of Experimental Marine Biology and Ecology*, 375: 106–113
- Wang Guizhong, Jiang Xiaodong, Li Shaojing, et al. 2005. A potential source of recruitment of *Acartia pacifica* nauplii: viable benthic resting eggs. *Acta Oceanologica Sinica*, 24: 151–158
- Whitehead R F, De Mora S J, Demers S. 2000. Enhanced UV radiation—a new problem for the marine environment. In: De Mora S J, Demers S, Vernet M, eds. *The Effect of UV Radiation in the Marine Environment*. Cambridge: Cambridge University Press, 1–34
- Williamson C E, Rose K C. 2009. Ultraviolet insights: attempting to resolve enigmatic patterns in pelagic freshwaters—the historical context and a view to the future. *International Review of Hydrobiology*, 94: 129–142
- Yu Juan, Yang Guipeng, Tian Jiyuan. 2009. Effects of UV-B radiation on ingestion, fecundity, population dynamics and antioxidant enzyme activities of *Schmackeria inopinus* (Copepoda Calanoida). *Journal of Experimental Marine Biology and Ecology*, 381: 74–81
- Zhang Luoping, Ye Xin, Feng Huan, et al. 2007. Heavy metal contamination in western Xiamen Bay sediments and its vicinity, China. *Marine Pollution Bulletin*, 54: 974–982