Journal of Plankton Research Vol.22 no.12 pp.2325–2350, 2000

The effect of ultraviolet radiation on the vertical distribution and mortality of estuarine zooplankton

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Abstract. The effect of UV-B radiation on the vertical distribution of three calanoid copepod species (*Tortanus dextrilobatus*, *Acartiura* spp. and *Acanthacartia* spp.) and three larval stages of Pacific herring, *Clupea pallasi* (1-, 7-, and 14-day-old larvae) was investigated. A series of 2 m high columnar tanks equipped with infra-red light and video-microscopy was used to investigate the vertical distribution of zooplankton in the presence and absence of UV-B radiation. In the presence of UV-B radiation, *T.dextrilobatus* and 1-day-old *C.pallasi* resided about 50 cm deeper than in the absence of UV-B, while *Acartiura* spp. and *Acanthacartia* spp. showed no (or only minimal) change in vertical distribution. Mortality experiments were also conducted outdoors in which each copepod species was exposed to full or reduced natural radiation levels. Only *T.dextrilobatus* showed an increase in mortality when exposed to full radiation. Our results showed that *T.dextrilobatus* and 1-day-old *C.pallasi* larvae were sensitive to UV radiation (UVR), and to reduce or eliminate UV-induced stress, they avoided the surface of the water column when UV-B radiation was present. Copepod species were chosen to span a range of pigmentation: *T.dextrilobatus* (heavily pigmented), *Acartiura* spp. (moderately pigmented) and *Acanthacartia* spp. (not pigmented). The pigmentation did not appear to play a role in UVR tolerance of the copepods, but may be a factor determining UV tolerance of *C.pallasi*.

Introduction

Ultraviolet radiation (UVR) is divided into three categories: UV-A (320–400 nm), UV-B (280–320 nm) and UV-C (<280 nm). UV-A radiation is considered to be relatively biologically harmless, but UV-B radiation is biologically damaging (Karentz and Lutze, 1990). UV-B radiation is usually absorbed by the ozone layer, but as the ozone layer is thinning, higher levels of radiation are reaching the earth's surface (Madronich *et al.*, 1995). UV-C radiation is also biologically damaging, but because these wavelengths are so short, the ozone layer, even in its reduced state, is 100% efficient in absorbing all the radiation (Madronich *et al.*, 1995). Thus, much of the recent biological research on UVR has focused on the effect UV-B radiation has on behavior and physiology of terrestrial and aquatic plants and animals.

The downwelling irradiation depth in the ocean is a function of the attenuation coefficient of light, which, in turn, is dependent on the absorption and scattering of radiation due to particle type and concentration (Kirk, 1994). Eutrophic waters, similar to those of San Francisco Bay which are high in chlorophyll (Chl *a*) and dissolved organic matter (DOM), usually have the highest attenuation coefficient and shallowest downwelling irradiance depth (Häder, 1997a). For instance, in open ocean oligotrophic waters 10% of surface UV-B can penetrate up to 30 m, while in coastal eutrophic waters 10% of UV-B may penetrate only 3 m (Kirk, 1994). However, there have been no studies on UVR penetration in San Francisco Bay. There have been very few studies on UVR within estuarine waters throughout the world. In the estuarine waters of the Gulf of St Lawrence,

the attenuation coefficient for UV-B ranged between 0.7 and 4.5 m^{-1} with a 10% penetration depth between 0.5 and 4 m; this is enough radiation to be potentially biologically damaging (Kuhn *et al.*, 1999). Chlorophyll *a* and DOM levels during late summer and early fall in the Gulf of St Lawrence are comparable to those in San Francisco Bay (Cole and Cloern, 1984; Baylosis *et al.*, 1997; Kuhn *et al.*, 1999) and thus, UV penetration depths are also likely to be comparable.

There have been conflicting reports of the effect of UV-B radiation on the mortality, behavior, growth rate and fecundity of zooplankton. Karanas *et al.* determined that enhanced levels of artificial UV-B radiation increased mortality and lowered the reproductive capability of the calanoid copepod *Acartia clausii* (Karanas *et al.*, 1979). In the freshwater cladoceran *Daphnia*, mortality increased significantly when *Daphnia* were exposed to increased levels of artificial and natural UVR (Zagarese *et al.*, 1994). The calanoid copepod *Calanus sinicus* showed a reduction in hatching rate and an increase in the number of deformed nauplii when exposed to an increase in artificial UV-B radiation (Naganuma *et al.*, 1997). Although the calanoid copepod *Boeckella gracilipes* showed increased mortality with enhanced artificial and natural UV-B exposure over a 3-day period, *B.gribbosa* and *B.brevicaudata* did not (Zagarese *et al.*, 1997a; Zagarese *et al.*, 1998). A longer-term study over 48 days by Cabrera *et al.* (Cabrera *et al.*, 1997) concluded that *B.gracilipes* was tolerant to natural UV-B exposure, but that the cladoceran *Chydorus sphaericus* was not. The harpacticoid copepod *Tigriopus californicus* was found to tolerate a significant increase in artificial UV-B radiation (Chalker-Scott, 1995).

There have also been a few studies on the effect of increased UVR on ichthyoplankton. Increased levels of UV-B radiation have been found to reduce the successful hatching and development of eggs and larvae of plaice (*Pleuronectes platessa*), Pacific mackerel (*Scomber japonicus*), northern anchovy (*Engraulis mordax*) and sunfish (*Lepomis*) (Siebeck *et al.*, 1994; Williamson *et al.*, 1999). The sunfish, *Lepomis*, was also shown to be susceptible to natural UVR levels of 1.01 kJ m^{-2} nm^{-1} in surface waters (Williamson *et al.*, 1999). UV-B radiation has been shown to increase egg mortality of Atlantic cod (*Gadus morhua*) in estuarine waters of the Gulf of St Lawrence (Kuhn *et al.*, 1999). The UV-B dosage which a given species can tolerate is often dependent on the amount of protective pigments, such as cuticular melanin, in the epidermis. The epidermis in larval fish is very thin and lacks numerous scales, pigments and mucous cells; this morphology allows UVR to penetrate into the body and cause lesions in tissues (Hunter *et al.*, 1982), which leads to a breakdown in the immune system and an increase in fungal infections (Siebeck *et al.*, 1994).

Zooplankton have adapted three mechanisms to cope with UV-B exposure: (i) possession of protective UV-absorbing compounds such as mycosporine-like amine acids, cuticular melanin and carotenoid pigments; (ii) repair of DNA damage; and (iii) avoidance via vertical migration (Karentz, 1994; Siebeck *et al.*, 1994). Similar to phytoplankton, the degree of pigmentation zooplankton have seems to be related to their tolerance of UVR (Karentz *et al.*, 1991; Zagarese *et al.* 1997a). Zagarese *et al.* have provided evidence that the calanoid copepods *B.brevicaudata* and *B.gibbosa*, which have carotenoid pigments, can tolerate

UVR better than *B.gracilipes*, which lacks such pigments (Zagarese *et al.*, 1997a). In addition, tolerance of *B.brevicaudata* and *B.gibbosa* to UV-B radiation was dependent on the presence of photosynthetically-active radiation (PAR), which appears to stimulate photoreactivation (Zagarese *et al.*, 1997a). Similarly, UV-B induced damage to *C.sinicus* was reduced when they were exposed to UV-B radiation in combination with PAR (Naganuma *et al.*, 1997).

It has been suggested that some zooplankton, especially those without protective pigments, may migrate deeper in the water column to avoid UV-B radiation (Barcelo and Calkins, 1979). For instance, UV-B radiation stimulated changes in vertical distribution of the echinoid larvae *Dendraster excentrics*, i.e. larvae resided at the bottom of 4 cm deep vials in the presence of natural and artificial UVR (Pennington and Emlet, 1986). Two small crustaceans, *Cyclops* and *Cyprus*, were also tested for their tolerance and avoidance of 'simulated solar UV-B' by Barcelo and Calkins (Barcelo and Calkins, 1979). Only *Cyclops* was affected by UV-B radiation and was shown to migrate deeper to avoid the radiation. A combination of natural and artificial UV-B radiation has been shown to stimulate changes in the vertical distribution of the marine copepod *Acartia hudsonica*, resulting in a 0.5 m deeper distribution in summer, but no change in the winter (Jeon, 1995). Zaragese *et al.* determined that *B.gracilipes*, which lacks pigmentation, avoided the top 9 m of the water column, while the pigmented *B.gibbosa* avoided only the top 3 m (Zaragese *et al.*, 1997a, b).

However, there have also been studies on marine zooplankton which have shown that increased levels of UV-B radiation do not effect vertical distribution. For instance, the vertical distribution of *A.hudsonica* was shown by Bollens and Frost (Bollens and Frost, 1990) to be unaffected by reduced natural UV-B radiation levels, in contrast to findings by Jeon (Jeon, 1995). The discrepancy in the two studies may be a result of a difference in sampling resolution. Bollens and Frost (Bollens and Frost, 1990) used a sampling resolution of 1 m, while Jeon (Jeon, 1995) used a sampling resolution of 0.63 m. Similarly, Damkaer and Dey (Damkaer and Dey, 1982) concluded that the vertical migrations of two species of meroplankton, *Pandalus danae* and *P.hypsinotus*, were not affected by UV-B radiation. Unfortunately, no data are available on icthyoplankton avoidance of UV-B radiation, which we hypothesize may be an important UVR protection mechanism, especially because of their small size and lack of protective pigments.

Very few studies have been undertaken on the ecology of zooplankton in San Francisco Bay (Ambler *et al.*, 1985; Kimmerer *et al.*, 1994; Bollens *et al.*, 1999), and none on the effects of UVR. We have chosen to look at several of the dominant taxa in San Francisco Bay, which are *Tortanus dextrilobatus*, *Acartiura* spp., *Acanthacartia* spp. and Pacific herring, *Clupea pallasi*. *Tortanus dextrilobatus* is an obligate carnivore about 2 mm in length, which was introduced into San Francisco Bay in 1992, possibly from Asia (Orsi, 1995), and is now broadly distributed and abundant in the Bay (Bollens *et al.*, 1999; Bollens *et al.*, unpublished data). *Acartiura* spp. and *Acanthacartia* spp. are native, herbivorous species, about 1 mm in length, which are abundant in the Bay year-round (Ambler *et al.*, 1985; Bollens *et al.*, 1999; Bollens *et al.*, unpublished data). *Clupea pallasi* larvae were examined

because herring is both economically important and abundant in the Bay during the late fall, winter and early spring (Griffin *et al.*, 1998).

The purpose of this study was to determine whether vertical distribution and mortality of several zooplankton species common to temperate estuaries were affected by increased exposure to UVR. The four specific goals of this study were to determine: (i) if increased levels of UV-B radiation affect the vertical distribution of copepods and herring larvae; (ii) if changes in distribution differ between species with different degrees of pigmentation; (iii) if enhanced UVR increases mortality of calanoid copepods; (iv) if mortality rates differ between copepod species with different pigmentation.

Method

Irradiance measurements

PAR radiation was taken with a radiometer (Biospherical Instruments Inc., model QRS-250) and UV readings were taken with a UVX radiometer and sensor (UVP Inc.). Two UV sensors were used: UVX-31 with peak sensitivity at 300 nm and UVX-36 with peak sensitivity at 365 nm. All measurements were taken at the Romberg Tiburon Center for Environmental Studies in Tiburon, CA, USA (122º35.30′W; 37º55.65′N). Surface UVR readings were taken hourly throughout one summer day under clear skies and several times throughout the day during each outdoor experiment.

Specimen collection

The selection of calanoid copepod species (*T.dextrilobatus*, *Acartiura* spp. and *Acanthacartia* spp.) for this study was based on pigmentation, ecological importance and local access. In the latter two taxa, individuals were identified only to sub-genera because the species composition of *Acartia* (*Acartiura*) spp. in San Francisco Bay is not known (although we suspect at least two species), and for *Acanthacartia* spp. it was not possible for us to differentiate between live *A.californiensis* and *A.tonsa*. For the remainder of the paper these copepods will be referred to only by their sub-genera. *Tortanus dextrilobatus* was classified as heavily pigmented, *Acartiura* spp. as moderately pigmented and *Acanthacartia* spp. as not pigmented, using ordinal rankings based on visual observations with a microscope. Chemical analyses of pigments in these species were not performed in this study nor, to our knowledge, in any previous studies.

All copepods were collected from the North (122º22.4′W; 33º1.7′N) or Central (122º52.8′W; 37º52.8′N) San Francisco Bay, the day of the experiment, using nets with either a 153 µm mesh and 0.5 m diameter or a 253 µm mesh and 0.25 m diameter. Collections were made during late morning or early afternoon on the following dates: July 18, 1998, July 23, 1998, August 13, 1998, August 27, 1998, September 3, 1998, September 11, 1998, October 8, 1998, October 19, 1998, October 29, 1998, August 5, 1999, and August 23, 1999. The net was towed obliquely for 5–15 min at a boat speed of about 0.5 m s^{-1}. The temperature (ºC) and salinity (ppt) at the collecting site were measured at the time of the tow using

a hand held oxygen, conductivity, salinity and temperature system (YSI Inc., model 85). Zooplankton samples were taken to the laboratory within 1 h of collection and kept in a temperature-controlled room under ambient (collection site) temperature and salinity conditions. Within 2–3 h of collection, individual copepods were sorted from the sample using a dissecting microscope and glass pipette. Only sexually mature females were used in the study.

The three stages examined were 1-day-old (7 mm), 7-day-old (8 mm) and 14-day-old (9 mm) larvae. Fertilized *C.pallasi* eggs were obtained from Bodega Marine Laboratory (Bodega Bay, CA) from January to March of 1999. Upward of several thousand eggs from each female were kept in separate tanks in 1 μm filtered San Francisco Bay water of 15 ppt and allowed to hatch in a temperature-controlled cold room (11–13ºC). A diel 12 h light/12 h dark cycle was created by illuminating the 7 liter holding tanks with a 65 W GE Grow Bulb. The 7-day-old larvae were fed rotifers at a concentration of about 20 ml^{-1}. The 14-day-old larvae were fed rotifers (20 ml^{-1}) and *Artemia* nauplii at a concentration of about 10 ml^{-1}. Just prior to any given experiment, larvae of the appropriate age class were carefully removed from the hatching tank with a plastic spoon and placed into a 200 ml beaker of filtered bay water.

Vertical distribution experiments

Ten vertical distribution experiments were carried out during the course of this study. Two experiments were conducted with each of the following species: *T.dextrilobatus, Acartiura* spp., *Acanthacartia* spp. and 7-day-old *C.pallasi* larvae. One experiment each was conducted on 1-day-old and 14-day-old *C.pallasi* larvae.

At the beginning of each experiment, 20–30 sexually mature female copepods or 10 herring larvae of the appropriate stage were placed into each of two columnar tanks (described below) containing 1 μm filtered San Francisco Bay water. The temperature and salinity in the tanks were measured using a hand held oxygen, conductivity, salinity and temperature system (YSI Inc., model 85) and any adjustments to salinity were made by adding artificial sea salts (Instant Ocean) or de-ionized water. Temperature and salinity measurements were taken every 20 cm in each tank on the initial and final day of each experiment. Surface UV-A and UV-B radiation readings were taken on the first and last days of the experiment using a UVX radiometer and sensor (UVP Inc.). Eight pairs of valves, placed at 25 cm intervals down the length of the tank, were used to introduce algae (i.e. food) and take water samples for fluorometric analysis of Chl *a*. The initial food concentration for the *Acartiura* spp. and *Acanthacartia* spp. experiments was 15 μg ml^{-1} Chl *a* of *Thalassiosira weisflogii*. Four, 10 ml water samples were taken from the tank at 30, 85, 115 and 195 cm depths to measure chlorophyll density (Smith *et al.*, 1981; Parsons *et al.*, 1984) and to insure that food levels in each tank were similar. No attempt was made to maintain constant Chl *a* levels for the duration of any of the experiments. Water collected from each valve was replaced with filtered bay water in order to keep the water level in the tank, and thus the distance between the water surface and UV source (14 cm), constant. The 7-day-old *C.pallasi* larvae were fed rotifers at an initial concentration of 20

rotifers ml^{-1}. Fourteen-day-old *C.pallasi* larvae were fed a mixture of 15 rotifers ml^{-1} and 10 *Artemia* nauplii ml^{-1}. Food was not added to the experiments on *T.dextrilobatus* nor 1-day-old (yolk sac) *C.pallasi* larvae.

Details of the experimental vertical migration apparatus are given in Bollens *et al.* (Bollens *et al.*, in preparation). Briefly, custom designed Plexiglas tanks (200 $\times$ 7.6 $\times$ 5.1 cm) were used, which allowed the copepods sufficient room to migrate vertically. An infra-red light-emitting diode (LED) was used so that video could be recorded both during the day and at night without altering the organisms' normal behavior. A plano-convex lens was placed in front of the light and behind the tank. The lens was used to convert the point light source of the infra-red light into a columnated light source. A monochrome video camera (Cohu) with a macro/zoom lens ran up or down the length of the tank. The video was recorded on video cassette time lapse recorders (Panasonic, model AG-6124) with a date/time recorder. The whole system, which included the camera, lens and LED light, was mounted on a motorized linear bearing/rail system. The motor, camera, lights and VCR were all programmed and controlled by the X-10 Home Control System version 2.4.1 for Apple Macintosh. The system was programmed to turn on once an hour and took 6 min for the camera to traverse and record the entire length of the tank.

The experiments were performed in a temperature-controlled room maintained at the ambient temperature at which each species was collected (copepods) or reared (herring larvae). A diel light cycle was created by illuminating the chambers with two 65 W GE Grow Bulbs. A daylight and dark cycle was generated that was comparable with those experienced in nature. The lights were turned on between 06:45 and 07:15 h and turned off between 18:00 and 19:30 h. Visible light intensity at the surface of the water was 0.3×10^{15} Quanta s^{-1} cm^{-2} measured using a radiometer (Biospherical Instruments Inc., QSL-100 BOX). This value is about 1% of natural visible radiation at noon during summer and 6% of natural visible radiation at noon during winter at the Romberg Tiburon Center (122º35.30′W; 37º55.65′N). UV-B radiation was produced by a 15 W UV-B lamp with peak emission at 302 nm (VWR, UVM-57). The UV-B lamp was placed above the tank and water surface and between the two Grow Bulbs. A piece of frosted plastic was placed below the Grow Bulb and above the UV-B lamp to diffuse the visible light. Two treatment tanks 'UV-B present' and 'UV-B absent', were used in each experiment. Mylar (three sheets, each 0.13 mm thick) was placed under the UV-B lamp in the UV-B absent treatment to nearly eliminate UV-B irradiance. Surface UV-B irradiance averaged 650 µW cm^{-2} in the UV present tank and 10 µW cm^{-2} over the UV-B absent tank. The UV-B irradiance intensity in the UV-B present treatment was half of the maximum natural UV-B intensity measured outdoors on August 13, 1998 in Tiburon, CA. The UV-B lamps were turned on from 10:00–15:00 h during each day of each experiment. The UV-B intensity and exposure time were chosen in order to provide sufficient UV radiation for the organisms to detect and possibly respond to the radiation, although not enough to be lethal.

Video recordings of vertical distribution of organisms were analyzed visually by noting the date, time and depth of each animal.

Mortality experiments

Mortality experiments were conducted in an outdoor sea water table with constantly running bay water at the Romberg Tiburon Center in Tiburon, CA. Six separate experiments were conducted: two with *T.dextrilobatus* (August 13–17 and August 27–29, 1998); three with *Acanthacartia* spp. (September 11–20, October 8–11 and October 19–22, 1998); and one with *Acartiura* spp. (October 29–November 4, 1998).

Eight to ten sexually mature females were placed into each 1 l plastic jar containing 900 ml of filtered San Francisco Bay water. The initial salinity and temperature of the water were the same as that of the ambient water from which subjects were collected earlier that day. There were two treatments: (i) full radiation, in which organisms were exposed to full visible and UV radiation, and (ii) reduced radiation. As in the vertical distribution experiments, Mylar sheets (three sheets, each 0.13 mm thick) were used, which reduced PAR by 20%, UV-A by 50% and UV-B by 90%. Because UV is absorbed by the plastic jars, UV radiation was only able to penetrate the water from above (i.e. through the very top of the open jars). There were either four or five replicates of each treatment for each experiment. Jars with subjects were placed in the sea water table at dusk in order to avoid shocking the copepods with full daylight radiation. Two to four times per day for the duration of each experiment (3–10 days), we measured the temperature, salinity and radiation in each jar, and also made visual inspections of the number of copepods dead and alive. Temperature readings were taken using a thermometer (±0.5ºC), and salinity readings were taken by a hand held refractometer (±0.5 ppt) (Reichert-Jung). The water temperature in all jars increased slightly, but never by more than 4ºC above ambient sea surface temperature. The experiments were terminated when fewer than two living individuals were seen in the majority of jars. In all but one experiment with *Acanthacartia* spp., the copepods were not fed. In this one experiment, 15 µg l^{-1} of *T.weisflogii* were added initially to all jars and 10 ml water samples were taken every other day for the duration of the experiment to monitor food levels. However, algal growth in the jars during this experiment made accurate visual assessment of the copepods difficult, so food additions were discontinued in subsequent experiments.

Statistical analysis

The statistical program Statistical Package for the Social Sciences (SPSS) version 7.5 was used to perform the general linear model test of repeated measures using Type III sum of squares with an experiment-wide alpha level of 0.05. The repeated measure used was the mean depth of the copepods on each hourly scan in each treatment tank (UV-B present and absent). The repeated measures test of the mean depths was performed in order to determine if there was a difference in vertical distribution (i.e. depth) in the presence/absence of UV-B radiation and over time. Statistical analysis was performed for each day of UV exposure by analyzing three time intervals separately: before the UV light was on (07:00–09:00 h), while the UV light was on (11:00–15:00 h) and after the UV light was turned

off (17:00–19:00 h). When only one observation (vertical scan) was available due to natural changes in the diel light cycle or system errors, SPSS Student's independent *t*-test was used to test for a difference in mean depth between the two tanks. Time intervals during which either the UV or grow light were turned on or off were excluded from the statistical analysis. The data from the mortality experiments were analyzed with SPSS Student's independent *t*-tests to test for a difference in the number of individuals seen alive for each day of each experiment ($\alpha = 0.05$).

Results

Irradiance

On one typical summer day, August 13, 1998, surface UV-B irradiance in San Francisco Bay increased throughout the day from 500 μW cm^{-2} at 09:00 h to a maximum of 1500 μW cm^{-2} between 13:00–14:00 h, and then declined to 100 μW cm^{-2} at 19:00 h.

In order to determine the depth to which visible light penetrates the water column, the extinction coefficient for visible radiation (k) was calculated from Secchi disk depth measurements using (Idso and Gilbert, 1974):

$$k = 1.7\ (Z_{SD})^{-1}$$

The average Secchi depth (z_{SD}) was taken off the sea wall at the Romberg Tiburon Center on October 23, 1998. The depth of the euphotic zone, or the depth to which 1% of surface irradiance penetrates, was determined from the following equation (Idso and Gilbert, 1974):

$$I_z = I_o\ e^{-kz}$$

where I_z is irradiance at depth z, I_o is surface irradiance, k is the extinction coefficient, and z is the depth to which 1% of surface irradiance penetrates. I_o was assumed to be 100%, I_z to be 1%, k was determined as described above, and then the above equation was solved for z. The average Secchi depth reading in early fall for San Francisco Bay was 1.9 m, from which we calculated an extinction coefficient of visible radiation of 0.89 m^{-1}, and a euphotic zone depth (1% of surface visible radiation) of 5.2 m. This Secchi depth and 1% light level are consistent with long-term datasets collected in Central San Francisco Bay (Baylosis *et al.*, 1997; Wilkerson *et al.*, 1999).

We assume UV-B penetration is about 10% of visible light penetration in San Francisco Bay, as it was off the coast of Tampa, FL (Smith and Baker, 1979) and in the Baltic Sea (Häder, 1997b). Using our estimate of 5.2 m for the depth of penetration of 1% of surface visible light, we estimate the depth of 1% of surface UV-B to be 0.52 m in San Francisco Bay. This estimate of UV-B penetration in San Francisco Bay is slightly less than that in other estuarine and coastal water bodies. For instance, 10% UV-B was found to penetrate between 0.5 and 4.0 m in the Gulf of St Lawrence (Kuhn *et al.*, 1999), to 2.7 m off the coast of Tampa,

FL (Smith and Baker, 1979), and to 4.1 m and 3.2 m in Batemans and Jervis Bays, New South Wales (Kirk, 1994).

Vertical distribution experiments

Tortanus dextrilobatus appeared to be able to detect and avoid UV-B radiation, residing about 50 cm deeper in the presence of UV-B compared with the absence of UV-B (Figure 1). The treatment (UV-B) effect, which tested for a difference in vertical distribution between the UV-B present and the UV-B absent tank averaged across time, was significant during UV-B exposure in the first experiment (Figure 1; Table I) on days 1 ($P < 0.001$), 2 ($P < 0.001$) and 3 ($P < 0.01$). There was also a significant difference between treatments during daylight hours prior to UV-B exposure on days 1 ($P < 0.05$) and 3 ($P < 0.05$) and after UV-B exposure on day 2 ($P < 0.01$) of the first experiment. The within subject time effect tested for a difference in vertical distribution over time averaged between the UV-B present and UV-B absent tank. The within subject interaction effect (UV-B * time) tested for a change in vertical distribution as a result of the treatment and time effects. There were time effects and interaction effects for several time periods throughout both experiments (Table I). In the second *T.dextrilobatus* experiment (data not shown), the treatment effect during UV-B exposure was significant on days 1 ($P < 0.01$), 2 ($P < 0.05$) and 3 ($P < 0.05$), and after UV-B exposure on day 1 ($P < 0.01$).

Acartiura spp. showed a mixed response to UV-B radiation. In the first experiment the mean depth of the copepods appeared to be about 50 cm deeper when UV radiation was present (Figure 2), with significant effects on days 1 ($P < 0.001$), 2 ($P < 0.01$) and 3 ($P < 0.01$) (Table II). There were significant differences between treatments prior to UV-B exposure on day 2 ($P < 0.01$) and after UV-B exposure on days 1 ($P < 0.001$), 2 ($P < 0.01$) and 3 ($P < 0.05$). Due to equipment failure, no data were available for the time prior to UV-B on day 3 of the first experiment. There were several significant within subject time effects and interaction effects throughout both experiments (Table II). However, unlike the first experiment, in the second experiment (data not shown) there was no significant effect of UV-B; mean depths of the copepods were similar between treatments.

Acanthacartia spp. did not respond to UV-B exposure (Figure 3, Table III). Neither the first (Figure 3) nor second (data not shown) experiments had an apparent change in copepod distribution in the presence of UV-B radiation. The time effect was significant during and after UV-B exposure for several days for each experiment. There were also several significant interaction effects in both sets of experiments.

The most dramatic effect of UV-B radiation was seen with 1-day-old *C.pallasi* yolk sac larvae, which resided substantially deeper (i.e. 60 cm or more) in the UV-B tank when UV-B radiation was present (Figure 4, Table IV). The effect of UV-B radiation was significant for all 3 days of UV-B exposure: day 1 ($P < 0.05$), day 2 ($P < 0.01$) and day 3 ($P < 0.01$). There was also a significant difference prior to UV-B exposure on day 1 ($P < 0.001$) and after UV-B exposure on days 1 ($P < 0.01$) and 2 ($P < 0.01$). The effect of time was only significant on day

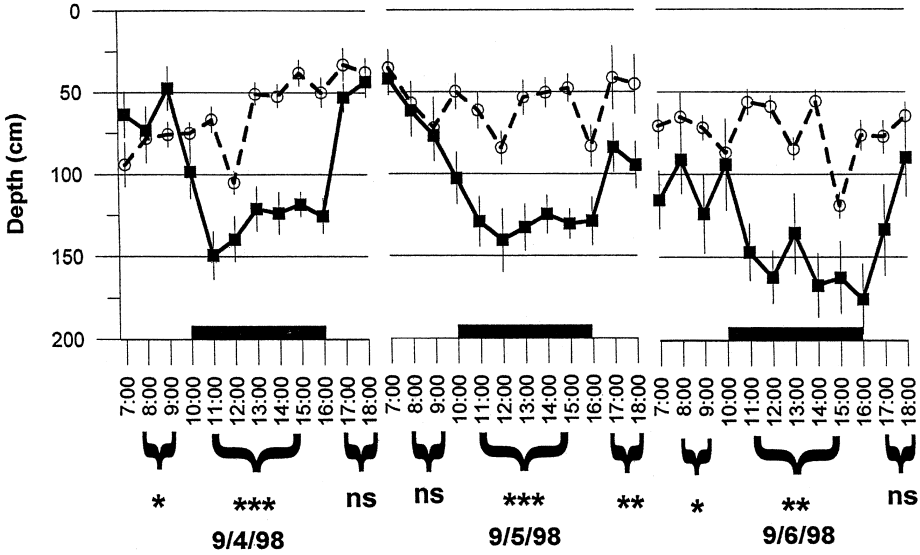

Fig. 1. The daytime vertical distribution of *Tortanus dextrilobatus* over 3 days of UV-B exposure (September 4–6, 1998). Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. . (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

3 after UV exposure. There were no significant interaction effects during UV exposure (Table IV).

Seven-day-old *C.pallasi* larvae appeared to be less affected by UV-B radiation than the younger larvae (Figure 5). The only significant effects of UV-B on these larvae were found in the first experiment on the last two days during UV-B exposure: day 2 ($P < 0.05$) and day 3 ($P < 0.01$) (Table V). There were no significant treatment effects prior to UV-B exposure in either experiment, but there was a significant treatment effect after exposure on day 3 ($P < 0.05$) of the first experiment. There were several significant time effects and interaction effects throughout the duration of both experiments (Table V). Data from the second experiment are not shown.

Clupea pallasi larvae older than 14 days also did not show a response to UV-B radiation (Figure 6). The only significant treatment effect on this larval stage was during UV exposure on day 1 ($P < 0.05$) and day 3 prior to UV-B exposure ($P < 0.01$). There were several significant time effects and interaction effects throughout the experiment (Table VI).

Mortality experiments

The mortality of *T.dextrilobatus* was significantly higher when exposed to full radiation than when exposed to reduced radiation filtered by Mylar (Table VII).

Table I. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for *Tortanus dextrilobatus*; September 4–6, 1998; AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, *F* = *F*-value, *P* = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
AM (pre-UV exposure)									
treatment (UV)	1,4	8.73	0.05*	1,4	5.20	ns	1,4	15.35	0.05*
time	1,4	4.65	ns	1,4	10.14	0.01**	1,4	29.25	0.001***
treatment*time	1,4	8.65	0.05*	1,4	5.21	ns	1,4	4.86	ns
UV exposure									
treatment (UV)	1,31	26.90	0.001***	1,21	22.62	0.001***	1,13	13.77	0.01**
time	3,90	58.08	0.01**	3,82	7.45	0.01**	3,32	6.76	0.01**
treatment*time	3,90	18.36	0.01**	3,82	2.98	0.001***	3,32	1.67	ns
PM (post-UV exposure)									
treatment (UV)	1,32	1.57	ns	1,24	5.20	0.01**	1,10	2.19	ns
time	1,32	0.03	ns	1,24	1.03	ns	1,10	1.25	ns
treatment*time	1,32	15.00	0.001***	1,24	0.40	ns	1,10	1.34	0.001***

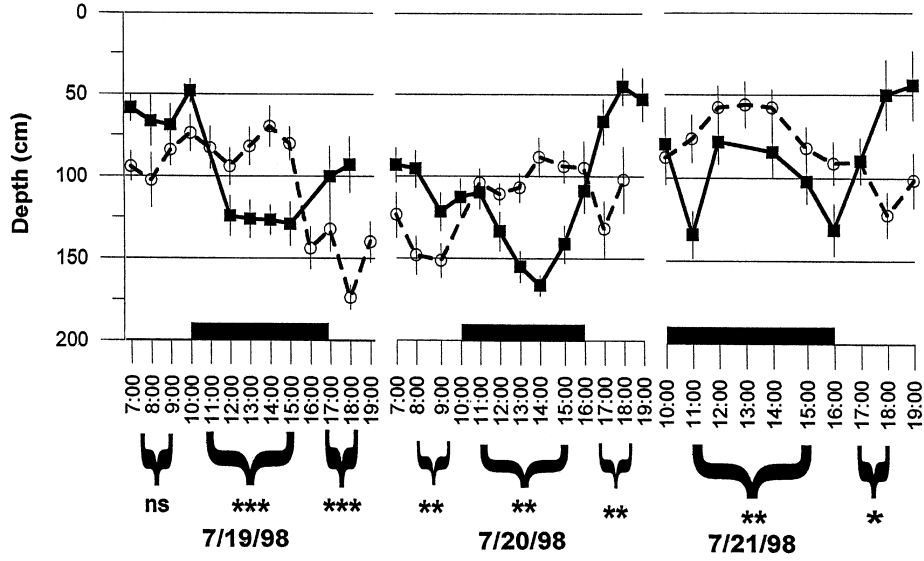

Fig. 2. The daytime vertical distribution of *Acartiura* spp. over 3 days of UV-B exposure (July 19–21, 1998). Time period prior to UV on day 3 was not recorded due to system failure. Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

Average noontime surface UV-B irradiance was 1027 μW cm^{-2} during the 3 days that *T.dextrilobatus* experiments were conducted. The mortality for *Acartiura* spp., exposed for 7 days, with noontime surface UV-B exposure averaging 810 μW cm^{-2}, was not statistically different between those copepods exposed to reduced and full radiation (Table VII). For *Acanthacartia* spp. exposed to radiation from 1 to 10 days, with an average mid-day UV-B level of 1002 μW cm^{-2}, the mortality for those organisms exposed to full radiation was significantly higher ($P < 0.05$) in only one of the three experiments.

Discussion

Tortanus dextrilobatus was sensitive to both artificial and natural UVR. Its vertical distribution was significantly affected by UV-B radiation in both vertical distribution experiments, in which it avoided the top 50 cm of the tank in the presence of UV-B radiation. By residing well below 50 cm, and usually below 100 cm in the presence of UV-B radiation, *T.dextrilobatus* appeared to be able to avoid the harmful radiation. UV-B radiation has been shown to be harmful to several zooplankton species [e.g. (Karanas *et al.*, 1979; Damkaer *et al.*, 1980; Damkaer and Dey, 1982; Zagarese *et al.*, 1994, 1997a; Naganuma *et al.*, 1997; Stutzman, 1999)], and changing their vertical distribution is one possible way to avoid the radiation. There were two instances in our experiments when organisms that had

Table II. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for *Acartiura* spp., July 19–21, 1998. Time period prior to UV on day 3 was not recorded due to system failure. AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, *F* = *F*-value, *P* = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
AM (pre-UV exposure)									
treatment (UV)	1,37	1.74	ns	1,43	6.75	0.01**			
time	1,37	27.35	0.001***	1,43	5.35	0.01**			
treatment*time	1,37	4.82	0.05 *	1,43	5.19	0.01**			
UV exposure									
treatment (UV)	1,38	9.37	0.001***	1,17	13.9	0.01**	1,24	5.55	0.01**
time	2,72	35.88	0.01**	2,69	16.97	0.01**	3,72	8.09	0.001***
treatment*time	2,72	4.78	0.05 *	2,69	43.36	0.01**	3,72	3.65	0.01*
PM (post-UV exposure)									
treatment (UV)	1,36	9.52	0.001***	1,34	6.88	0.01**	1,22	4.73	0.05 *
time	1,36	4.18	0.05*	1,34	40.98	0.001***	2,44	1.18	ns
treatment*time	1,36	36.17	0.001***	1,34	2.87	ns	2,44	22.46	0.001***

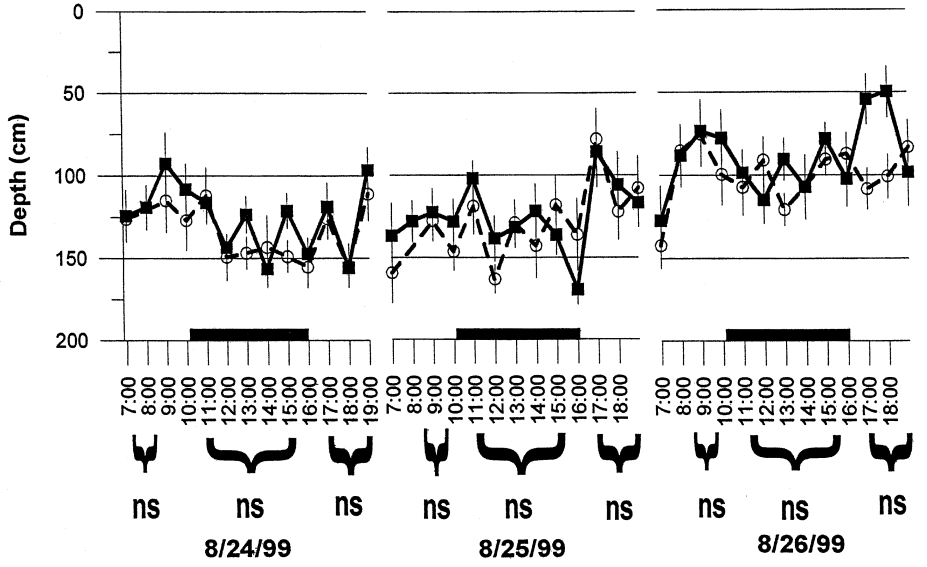

Fig. 3. The daytime vertical distribution of *Acanthacartia* spp. over 3 day UV-B exposure (August 24–26, 1999). Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

been previously exposed to UV-B resided deeper in the tank even though the UV-B lamp was not on. The displacement of the copepods deeper in the tank during UV-B exposure may have been so great that it took longer for them to rise to their 'normal' shallow depth, or perhaps after a prolonged UV-B exposure of more than a day, they simply remain deeper in the tank throughout the day. In any event, *T.dextrilobatus* appeared to be sensitive to artificial UVR exposure, and migrated deeper in the tank to avoid the damaging radiation.

The change in the vertical distribution of *T.dextrilobatus* and the increase in mortality when exposed to UVR suggest that its pigmentation does not aid in UVR absorption, which is contrary to previous work on other species. For instance, migrating cladocerans (*Daphnia galeata*) usually had low pigment levels and showed an immediate downward response in the presence of artificial UV-B (Hessen, 1994; Siebeck and Bohm, 1994). Although the pigment composition of *T.dextrilobatus* is not known, we hypothesize that its pigmentation does not absorb radiation in the ultraviolet range.

In several experiments on *T.dextrilobatus,* as well as with other organisms, there were time and interaction (treatment*time) effects. The time effect occurred as the result of a slight downward trend in the morning and the upward trend in the evening. *Tortanus discaudatus* (Bohrer, 1983) and *A.tonsa,* which is in the sub-genus *Acanthacartia* (Stearns and Forward, 1984), have been shown to display strong normal vertical migration, in which organisms are at depth during

Table III. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for *Acanthacartia* spp., September 24–26, 1998. On days 1 and 2 a *t*-test was used to determine if there was a significant difference in mean depth in the AM. AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, F = F-value, t = t-value, P = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	F (t)	P	d.f.	F (t)	P	d.f.	F	P
AM (pre-UV exposure)									
treatment (UV)	1,16	0.30	ns						
time	1,16	0.87	ns						
treatment*time	1,16	18.57	0.001***						
t-test	26	0.82	ns	25	0.34	ns			
UV exposure									
treatment (UV)	1,15	0.09	ns	1,17	0.60	ns	1,12	0.03	ns
time	2,59	18.39	0.01**	3,69	23.44	0.01**	3,50	17.83	0.01**
treatment*time	2,59	5.29	0.01**	3,69	11.98	0.01**	3,50	4.84	0.01**
PM (post-UV exposure)									
treatment (UV)	1,24	0.06	ns	1,19	0.12	ns	1,9	1.62	ns
time	2,48	80.74	0.001***	2,38	25.76	0.001**	2,18	4.86	0.05*
treatment*time	2,48	7.43	0.001**	2,38	8.62	0.001**	2,18	38.21	0.01**

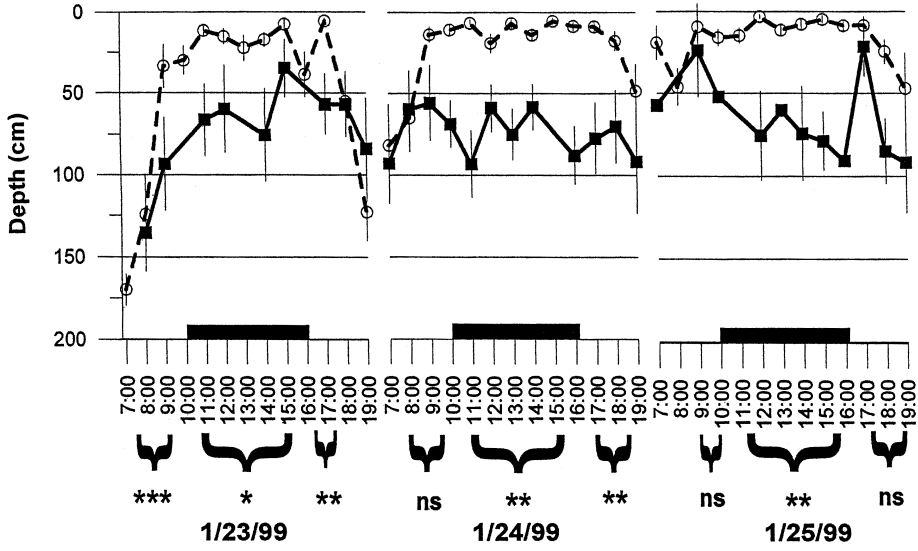

Fig. 4. The daytime vertical distribution of 1-day-old *Clupea pallasi* larvae over 3 days of UV-B exposure (January 23–25, 1999). Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

the day and nearer the surface during the night. The significant time effects may be the result of these diel vertical distribution patterns associated with endogenous rhythms that triggered the organisms to start to migrate (Enright and Hamner, 1967; Hough and Naylor, 1992). The interaction (treatment*time) effect is interpreted to be due to the downward trend in the morning and the upward trend in the evening (i.e. time effect) in combination with the downward trend of organisms exposed to UV-B radiation, compared with the upward trend or constant depth held by organisms in the tank without UV-B (i.e. treatment effect).

Acartiura spp. responses to UV-B radiation varied between experiments. In the first experiment, *Acartiura* spp. avoided the top 50 cm of the tank in the presence of UV-B, residing deeper during all 3 days of UV-B exposure. Because *Acartiura* spp. is moderately pigmented, a change in vertical distribution in order to avoid the radiation was not expected by us. However, as we hypothesize for *T.dextrilobatus*, pigmentation may not absorb in the UV range or may be a secondary defence against UV radiation, with avoidance being the primary defense.

Interestingly, in the first experiment, there seemed to be a counter effect of UV-B radiation after the UV-B light had gone off, i.e. the organisms in the UV-B tank resided significantly shallower than those in the tank without UV-B. One possible explanation is that after the UV-B light went off, the copepods overcompensated by moving higher in the UV-B present tank.

Table IV. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for 1-day-old *Clupea pallasi* larvae, January 23–25, 1999. A *t*-test was used to determine if there was a significant difference in mean depth on day 3 AM, and day 1, 2, and 3 PM. AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, *F* = *F*-value, *t* = *t*-value, *P* = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	*F* (*t*)	*P*	d.f.	*F* (*t*)	*P*	d.f.	*F* (*t*)	*P*
AM (pre-UV exposure)									
treatment (UV)	1,15	13.56	0.001***	1,16	3.72	ns			
time	1,15	2.92	ns	1,16	1.79	ns			
treatment*time	1,15	0.61	ns	1,16	0.39	ns			
t-test							15	0.31	ns
UV exposure									
treatment (UV)	1,6	8.02	0.05*	1,5	85.94	0.01**	1,7	102.02	0.01**
time	1,19	0.52	ns	2,19	1.45	ns	1,20	0.34	ns
treatment*time	1,19	0.30	ns	2,19	1.02	ns	1,20	0.47	ns
PM (post-UV exposure)									
t-test	8	2.63	0.01**	9	2.95	0.01**	12	1.84	ns

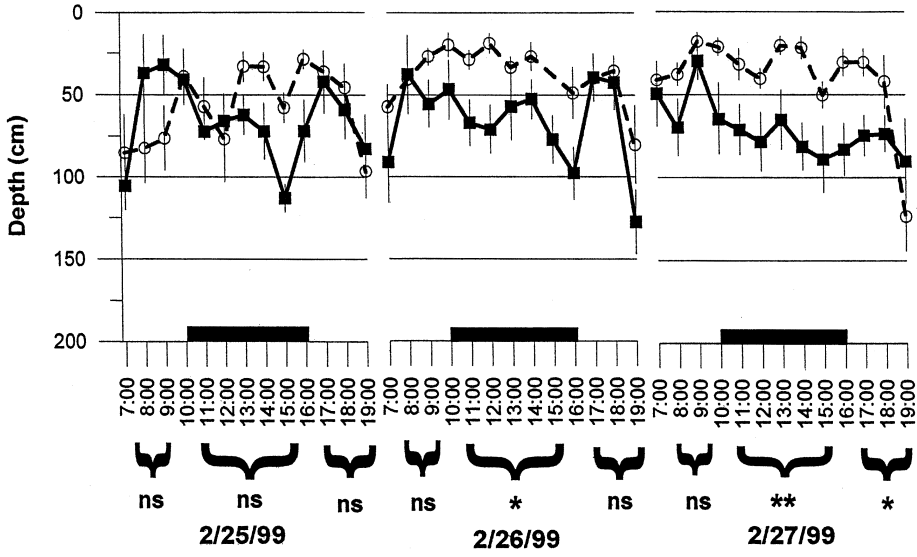

Fig. 5. The daytime vertical distribution of 7-day-old *Clupea pallasi* larvae over 3 days of UV-B exposure (February 25–27, 1999). Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

However, there was no difference in vertical distribution of *Acartiura* spp. during the second vertical distribution experiment, i.e. copepods in both tanks resided at about 150 cm during UV-B exposure, compared with the first experiment when copepods resided at about 100 cm. Because UV-B penetration greatly decreases with depth, it is possible that the copepods in experiment 2 were already so deep (presumably due to some other, unmeasured factor) that they were not able to detect sufficient radiation to cause them to change their vertical distribution. The mortality experiments showed that *Acartiura* spp. were not sensitive to a natural increase in UVR. The mortality results support those of the second vertical distribution experiment, which showed there was no effect of UV-B on mean depth, but are at odds with the first vertical distribution experiment showing an effect of UV-B. The conflicting results of the two vertical distribution experiments are hard to reconcile. The *Acartiura* spp. responses to UV-B radiation appeared to be variable.

Acanthacartia spp. did not change their vertical distribution in response to UV-B radiation in either experiment. *Acartiura* spp. and *Acanthacartia* spp. are about the same size, but *Acartiura* spp. has more pigmentation. Thus, a greater response to UV-B radiation in the form of avoidance of UV-B radiation in the surface layers by *Acanthacartia* spp. was expected, as was found for *B.gracilipes* by Zagarese *et al.* (Zagarese *et al.*, 1997a). Throughout the experiments, *Acanthacartia* spp. resided primarily between 75 and 150 cm in the absence of UV-B. In

Table V. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for 7-day-old *Clupea pallasi* larvae, February 25–27, 1999. AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, *F* = *F*-value, *P* = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
AM (pre-UV exposure)									
treatment (UV)	1,13	0.05	ns	1,12	1.69	ns	1,14	1.25	ns
time	2,26	19.51	0.001***	1,15	14.25	0.01**	2,28	15.867	0.001***
treatment*time	2,26	1.55	ns	1,15	0.90	ns	2,28	0.89	ns
UV exposure									
treatment (UV)	1,13	4.04	ns	1,12	4.60	0.05*	1,14	5.48	0.01**
time	2,28	6.99	0.01**	2,17	6.86	0.01**	4,56	22.193	0.001***
treatment*time	2,28	7.29	0.01**	2,17	5.27	0.05*	4,56	4.99	0.001***
PM (post-UV exposure)									
treatment (UV)	1,15	0.44	ns	1,15	0.11	ns	1,15	4.51	0.05*
time	1,15	14.38	0.001***	1,15	40.02	ns	1,15	1.09	ns
treatment*time	1,15	3.00	ns	1,15	9.31	ns	1,15	1.61	ns

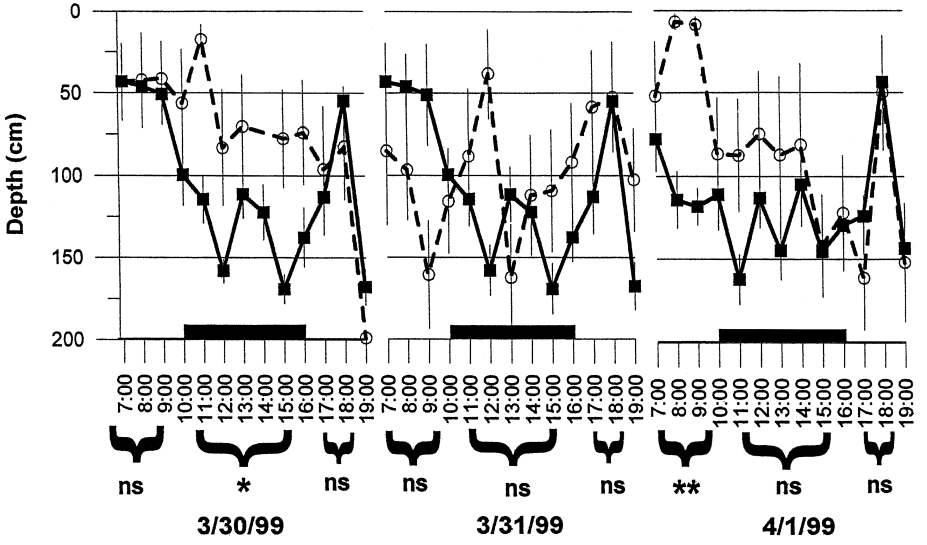

Fig. 6. The daytime vertical distribution of 14-day-old *Clupea pallasi* larvae over 3 days of UV-B exposure (March 30- April 1, 1999). Dark bars are times in which UV-B lamps were on (10:00–15:00 h). The dashed line represents organisms in the tank without UV-B and the solid line represents organisms in the tank with UV-B. Vertical bars are ± S.D. (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$, ns = not significant for repeated measure ANOVA treatment effect of UV-B).

contrast, *Acartiura* spp. resided somewhat shallower, between 40 and 150 cm, in the absence of UV-B. Because *Acanthacartia* spp. resided deeper in the tanks than *Acartiura* spp., the effect of UV-B radiation may have been sufficiently reduced as a result of attenuation to the extent that the organisms did not respond with significant changes in vertical distribution. Perhaps *Acanthacartia* spp. resided deeper in the tank due to its lack of pigmentation. These results are consistent with other findings on *A.hudsonica*, which did not appear to change their migration pattern over 3 m in the presence of natural summer UVR (Bollens and Frost, 1990). *Acartia hudsonica* is similar in size and pigmentation to *Acanthacartia* spp., suggesting that their behavior might be expected to be similar as well. However, our results, and those of Bollens and Frost (Bollens and Frost, 1990), are not consistent with findings by Jeon (Jeon, 1995) who concluded that *A.hudsonica* did reside about 0.5 m deeper in the water column during summer UVR exposures. In this study *Acanthacartia* spp. does not appear to be effected by an increase in artificial UV-B radiation.

One-day-old *C.pallasi* yolk sac larvae appeared to be the most sensitive to UVR of all the species and stages we studied. In the absence of UV-B radiation, yolk sac larvae resided in the upper 25 cm, but in the presence of UV-B radiation, resided at about 75 cm. Herring larvae have a similar body plan to northern anchovy and rainbow smelt larvae, i.e. they have translucent bodies with a thin epidermis, no protective pigmentation or scales and few mucous secreting cells (Hunter *et al.*, 1982). In addition, younger *C.pallasi* larvae appeared to display a

Table VI. Summary of repeated measures ANOVA for mean depth with time as the repeated measure factor for 14-day-old *Clupea pallasi* larvae, March 30–April 1, 1999. AM = daylight period prior to UV exposure, UV = time period during UV exposure, PM = daylight period after UV exposure, treatment = between subject effect of UV, time = within subject effect of time, treatment*time = within subject effect of UV and time; d.f. = degrees of freedom, *F* = *F*-value, *P* = significance (* = significant at $\alpha \leq 0.05$; ** = significant at $\alpha \leq 0.01$; *** = significant at $\alpha \leq 0.001$; ns = not significant at $\alpha \leq 0.05$)

	Day 1			Day 2			Day 3		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
AM (pre-UV exposure)									
treatment (UV)	1,18	0.67	ns	1,7	0.25	ns	1,6	11.122	0.01**
time	2,18	3.63	0.05*	2,14	9.04	0.001***	2,12	2.49	ns
treatment*time	2,18	1.73	ns	2,14	1.38	ns	2,12	1.48	ns
UV exposure									
treatment (UV)	1,9	9.28	0.05*	1,7	4.95	ns	1,5	1.94	ns
time	3,24	12.25	0.01**	3,22	9.95	0.01**	4,20	3.03	0.01**
treatment*time	3,24	1.27	ns	3,22	5.22	0.01**	4,20	2.79	0.05*
PM (post-UV exposure)									
treatment (UV)	1,8	0.04	ns	1,8	2.33	ns	1,3	0.32	ns
time	1,8	6.58	0.01**	1,8	14.68	0.05*	1,3	7.50	ns
treatment*time	1,8	3.72	ns	1,8	10.81	0.01**	1,3	0.11	ns

Table VII. Independent *t*-test of number of dead individuals after exposure of reduced or full natural radiation for three copepod species; *Tortanus dextrilobatus*, *Acartiura* spp. and *Acanthacartia* spp. (** = significant at $\alpha \leq 0.01$, ns = not significant at $\alpha \leq 0.01$)

Species	df	*t*	*P*
Tortanus dextrilobatus	10	2.50	0.01**
	8	2.56	0.01**
Acartiura spp.	8	3.14	ns
Acanthacartia spp.	8	2.13	ns
	6	2.83	0.01**
	8	1.62	ns

positive phototactic behavior, in which they were attracted to the visible light. Heath *et al.* found that medium sized (10.0–13.9 mm) *C.harengus* larvae were photo-positive and small larvae (6.0–9.9 mm) were 'photo-aggressive' under natural light conditions, meaning they would group together near the light (Heath *et al.*, 1988). It is likely that the lack of protective skin characteristics and the positive phototactic behavior increased the larvae's susceptibility to UV-B damage, especially to the eyes and brain (Hunter *et al.*, 1982; Siebeck *et al.*, 1994). Hunter *et al.* showed that 4-day-old northern anchovy and mackerel larvae had a greater number of eye and brain lesions after exposure to natural UV-B radiation than older larvae (Hunter *et al.*, 1982). In our study, *C.pallasi* larvae as old as 7 days already displayed less phototactic behavior and in the absence of UV-B, resided at about 75 cm, while 14-day-old larvae resided even deeper, usually below 100 cm. Since older *C.pallasi* larvae resided deeper, it was possible that the UV-B radiation at this depth was insufficient to be detected or was less harmful to the larvae. These data clearly show that larvae less than a week old were the most sensitive to UV-B radiation and changed their position in the water column in order to reduce their exposure to UVR.

The outdoor mortality experiments showed that summer and early fall UVR levels reaching the surface at San Francisco Bay were lethal to *T.dextrilobatus* but not *Acartiura* spp. and *Acanthacartia* spp. These results are somewhat surprising because *T.dextrilobatus* is larger and more pigmented than either *Acartiura* spp. or *Acanthacartia* spp. Previous work has concluded that pigmented species are more tolerant of UVR, e.g. *Diaptomus* (Hariston, 1979; Byron, 1982), *B.brevicaudata* and *B.gibbosa* (Zagarese *et al.*, 1997a,b), *Acanthodiaptomus denticornis* (Ringelberg *et al.*, 1984) and *Tigriopus californicus* (Chalker-Scott, 1995). However, these previous studies have been on species that have a red–orange appearance due in part to the presence of carotenoids, which absorb in the UV range and contribute to their increased tolerance of UVR. In contrast, *T.dextrilobatus* has brown rather than red–orange coloration, suggesting that its pigmentation is not composed largely of carotenoids. These findings suggest that the pigmentation of *T.dextrilobatus* may not contribute to UVR tolerance, although the composition of these pigments and their absorption properties are not currently known.

Of all the species and age classes studied, *T.dextrilobatus* and 1-day-old *C.pallasi* larvae responded the most dramatically to UVR. *Tortanus dextrilobatus* was sensitive to both natural and artificial UVR. Because *T.dextrilobatus* migrated deeper in the tanks in the presence of UV-B radiation and had a higher mortality when exposed to full radiation, we conclude that they respond to the harmful effects of UVR by avoiding it rather than absorbing radiation with pigments. One-day-old *C.pallasi* yolk sac larvae were the most sensitive to artificial UV-B of all the organisms studied, most likely due to their transparent body which lacked protective scales and mucus. In addition, in the absence of UVR the youngest larvae were attracted to the light and resided in the upper portion of the water column where UVR levels would be the highest in nature. Our results suggest that the youngest stages of *C.pallasi* avoided the damaging effects of UV-B in our tanks by migrating deeper in the water column, a behavior that was necessitated by their lack of natural protective characteristics and their otherwise photo-positive behavior to visible light.

There are several explanations for the lack of response to UV-B radiation by *Acanthacartia* spp. and the mixed response by *Acartiura* spp. One explanation is that the addition of 15 µg of Chl *a* in the *Acartiura* spp. and *Acanthacartia* spp. experiments might lower the UV-B radiation to non-lethal levels. The depth to which UV-B radiation can penetrate is highly dependent on water clarity (Smith and Baker, 1979). Another possibility is that the UV-B lamps produced radiation at a different spectrum and quality from that of the sun, resulting in less harmful UVR in our tanks than in nature. However, both species appeared to be relatively unaffected by the natural UVR in our mortality experiments, which implies these species are indeed more tolerant of UVR. In addition, some of the other copepods (e.g. *T.dextrilobatus*) were responsive, suggesting our experimental system did an adequate job of simulating quasi-natural conditions. Photoreactivation is another possible mechanism to explain why *Acartiura* spp. or *Acanthacartia* spp. have a higher tolerance to natural and artificial UVR. Photoreactivation is a repair mechanism in which a single enzyme recognizes and repairs UV-B induced cis-syn cyclobutane dimers only in the presence of UV-A (320–400 nm) (Karentz, 1994). UV-B induced damage to *C.sinicus* was reduced when they were exposed to UV-B radiation in combination with PAR (Naganuma *et al.*, 1997). Zagarese *et al.* studied *Boeckella* and suggested that an organism's photoreactivation ability was not only a function of exposure to PAR, but also the organism's pigment composition, and that in the absence of protective pigments and photoreactivation, zooplankton may attempt to avoid UVR (Zagarese *et al.*, 1997a). Our mortality experiments showed that *Acartiura* spp. and *Acanthacartia* spp. were generally not sensitive to a natural increase in UVR, which supports our vertical distribution results showing that these species exhibited little or no response to UV-B radiation. *Acartiura* spp. tolerance to UVR was somewhat expected because of their moderate amount of pigmentation, but the tolerance of *Acanthacartia* spp. was not expected due to their lack of pigmentation. Knowledge of the actual pigment composition in these three species may help further explain their response to UVR.

For *C.pallasi*, natural morphological defences, such as pigmentation, scales and

mucous cells, may explain why older (7- and 14-day-old) larvae appeared less sensitive to UV-B. In addition, the older larvae resided deeper in the tank, in much the same way *Acartiura* spp. and *Acanthacartia* spp. did. Thus, the radiation at this depth may not be as damaging to *C.pallasi* and/or the older larvae are better able to tolerate the increase in radiation.

In summary, this study shows that one copepod species (*T.dextrilobatus*) and the earliest larval stage of *C.pallasi* avoided the surface layer of water when exposed to UVR, possibly to avoid UVR damage. The copepods' tolerance of UVR did not appear to be a function of pigmentation, in that the less heavily pigmented species (*Acanthacartia* spp. and *Acartiura* spp.) did not show a response to UVR. Our findings are contrary to the literature in that the largest, most heavily pigmented species (*T.dextrilobatus*) was the most affected by UVR. However, natural defences such as pigmentation and scales may play a role in UVR tolerance of *C.pallasi* larvae. If changing vertical distribution proves to be an effective way of reducing the damaging effect of UVR, organisms that would otherwise reside close to the surface may be forced to reside deeper. This could cause changes in spatial overlap between predators and prey, and thus food web dynamics. For instance, a shift in zooplankton depth of 0.5 m (or less) due to UVR may have significant effects within shallow ecosystems such as San Francisco Bay, where the vast majority of the Bay is less than 3 m deep. In order to more fully understand the effects of UVR on zooplankton in San Francisco Bay, we need a better understanding of the temporal and spatial distribution of the natural zooplankton assemblage. In addition, more well controlled laboratory experiments, as well as field experiments using mescosms similar to those of Bollens and Frost (Bollens and Frost, 1990), will add to our understanding of the effects of UVR on zooplankton.

Acknowledgements

We thank L.Lougee for assisting with experimental set up and data collection. We greatly appreciate the help of C.Vines at Bodega Marine Laboratory for providing us with fertilized herring eggs. We also thank R.Dugdale, F.Wilkerson, A.Markie and V.Hogue for the use of the fluorometer and assistance with fluorometry procedures, and use of the outdoor Biospherical Instruments PAR sensor. We appreciate the use of the Biospherical Instruments hand held PAR meter from W.Cochlan and R.Kudela and the UVP Inc. radiometer and UV-B sensor from G.Martin of Occidental College. The authors would also like to thank A.Arp and T.Niesen for their comments and suggestions while serving as thesis committee members for C.L.S. Funding for this project was provided by the Office of Naval Research Young Investigator Award (grant N00014–94–1–0495) to S.M.B. and a Department of Education fellowship, the Graduate Assistance in Areas of National Need awarded to C.L.S. This work was completed in partial fulfilment of the requirement of a Masters Degree in Marine Biology, Department of Biology, San Francisco State University.

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Received on April 19, 2000; accepted on August 14, 2000