ABSTRACT

Title of Document: THE EFFECTS OF ULTRAVIOLET RADIATION ON THE GROWTH, REPRODUCTION AND SURVIVAL OF THE LOBATE CTENOPHORE *MNEMIOPSIS LEIDYI* IN CHESAPEAKE BAY

Kristen Alyssa Rathjen, Master of Science, 2010

Directed By: Dr. Denise Breitburg
Smithsonian Environmental Research Center
Professor Michael Roman
Marine, Estuarine and Environmental Sciences

Solar ultraviolet radiation (UVR) is an environmental stressor that can have a variety of negative effects on aquatic organisms. The ctenophore *Mnemiopsis leidyi* is a highly transparent organism that has not been shown to actively avoid UVR or possess photoprotective compounds and may therefore be vulnerable to deleterious effects of UVR. Results of this study indicate that summertime UVR exposure equivalent to average UVR conditions within the top 0.5 m of the water column of the Rhode River, Maryland, USA, can cause mortality and reduced size of *M. leidyi*. Exposures tested did not, however, affect egg production. Experiments indicated a sharp threshold for the tolerance of *M. leidyi* to biologically effective UVR exposure. *Mnemiopsis leidyi* is an important component in many ecosystems; thus, changes in its abundance have the potential to significantly affect coastal and estuarine food webs and oyster, fish and sea nettle populations in systems like Chesapeake Bay.

THE EFFECTS OF ULTRAVIOLET RADIATION ON THE GROWTH, REPRODUCTION AND SURVIVAL OF THE LOBATE CTENOPHORE *MNEMIOPSIS LEIDYI*

By

Kristen Alyssa Rathjen

Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2010

Advisory Committee:
Dr. Denise Breitburg, Co-Advisor
Professor Michael Roman, Co-Advisor
Dr. Patrick Neale
Professor Christopher Rowe

Dedication

To my husband, Bill, without whose never-ending patience and support, this goal would never have been achieved.

Acknowledgements

First and foremost, I would like to thank my advisor Dr. Denise Breitburg for her guidance, insight and for always having her door open to me over the last several years. I owe a debt of gratitude to Pat Neale for his endless patience in answering my many questions, and also his logistical and analytical support. I would also like to thank my co-advisor, Mike Roman and also Chris Rowe for serving on my committee and for providing their support and advice.

I wish to thank Rebecca Burrell for imparting her knowledge of all things gelatinous on me; for traipsing to sites with me with tons of luggage; for her sincere willingness to assist wherever needed; and for her friendship throughout this experience. I also want to thank the Smithsonian Environmental Research Center's Marine Ecology Lab and Photobiology Lab for their friendship, assistance and support over the last three years. I would also like to thank Courtney Richmond for diversions into the philosophical complexities of science and her continued willingness to comment on various drafts and revisions. I also want to thank Darryl Hondorp for allowing me to distract him with statistical dilemmas. And finally I am grateful to Debbie Morrin-Nordlund for always having the answers to the sea of administrative uncertainties.

This research was funded in part by Maryland Sea Grant, and the Smithsonian Marine Science Network; funds to present my work at the Coastal and Estuarine Research Federation conference came from the Jacob K Goldhaber travel award and the Atlantic Estuarine Research Society.

Table of Contents

List of Tables

List of Figures

Introduction

Solar ultraviolet radiation (UVR) is an important and dynamic feature in aquatic ecosystems. Incident UVR is affected by factors such as sea surface state, solar zenith angle, altitude, cloud cover and stratospheric ozone concentration. Attenuation of UVR within the water column of aquatic ecosystems is mainly influenced by absorption and scattering, which depend on the optical properties of the water. Attenuation of UVR in marine ecosystems varies with trophic state (Tedetti and Sempéré 2006); in oligotrophic open oceanic waters, UVR penetration is high, while in eutrophic coastal ecosystems UVR is rapidly attenuated, mainly due to absorption by the chromophoric component of dissolved organic matter (CDOM). Consequently, seasonal fluctuations in CDOM and particulates alter the amount and depth of UVR penetration in coastal ecosystems.

Solar UVR is an environmental stressor that can affect individual organisms and community structure in aquatic ecosystems. The mechanisms of UVR stress vary among species and life stages (Vincent and Neale 2000). Exposure to UVR can have a variety of direct effects on aquatic organisms including DNA damage, slowed growth, and changes in reproduction and development, as well as indirect effects such as disruption of primary production and food web dynamics (Mostajir et al. 1999, Zagarese and Williamson 2001, Palen et al. 2005, Häder et al. 2007). Blaustein et *al.* (1994) suggested that ultraviolet radiation can be a contributing factor in geographic distribution and population declines for amphibian species that are sensitive to UVR,

although it has been shown that many sensitive species alter their breeding behavior to reduce embryonic UVR exposure (Palen et al. 2005). For zooplankton, UVR has been shown to induce vertical migration, damage DNA, reduce fecundity and increase mortality (Karanas et al. 1981, Grad et al. 2001, Williamson et al. 2001, Leech et al. 2005, Häder et al. 2007).

Ultraviolet radiation is classified into three components based on wavelengths; UV-A (320-400 nm), UV-B (280-320 nm), and UV-C (< 280 nm). The energy per photon of UVR increases with decreasing wavelength; highly energetic shorter wavelengths are more damaging than longer wavelengths. For this reason it is often suggested that UV-B is more biologically damaging to organisms than UV-A.

Each component of UVR has characteristic effects. The effects of UV-A can be both detrimental and beneficial. UV-A is capable of indirectly damaging DNA, inhibiting growth and survival of zooplankton (Williamson et *al.* 1994) and fish (Williamson et *al.* 1997) and reducing primary production, but is also necessary for initiating photorepair mechanisms and for vision in some organisms. In *Daphnia pulicaria*, for example, UV-A was found to be a key factor in initiating photoenzymatic repair systems at low irradiance levels but at higher irradiance levels UV-A was suggested to have a net negative effect (Williamson et *al*. 2001). UV-B exposure is detrimental to all organisms because strong absorption of the high-energy, shorter UV-B wavelengths by DNA and RNA can damage and structurally change these molecules, cause toxic photoproducts and disrupt many cellular processes (Vincent and Neale 2000, Buma et *al.* 2003). Methods to investigate the response of organisms to specific wavelengths have demonstrated that biological damage

increases with decreasing wavelength in the UVR spectrum (Williamson et *al*. 2001). These reasons again lead to suggestions that UV-B is more biologically damaging to organisms than UV-A. Presently, there is no risk of damage from UV-C as no wavelengths shorter than 290 nm reach the surface of the Earth due to absorption by atmospheric gases, mainly ozone, in the stratosphere.

Negative effects of UVR can be manifested in many ways. On an individual level, growth and reproduction can be negatively affected by UVR due to both direct damage and an allocation of energy to repair UVR damage to DNA and tissues (Speakman 1997, Fischer et. al. 2006). Elevated investment in repair and resulting lower investment in growth and reproduction may decrease individual fitness of organisms exposed to high levels of UVR, which could in turn decrease population size. Subtle genetic changes due to UVR may accumulate through several generations damaging biological functioning and potential fitness of later generations (Vincent and Neale 2000).

Tolerances and responses of organisms to UVR vary depending on intensity, duration and spectral composition of the exposure, the efficiency of protection and repair strategies, and interactions with other variables (Vincent and Neale 2000). Detrimental effects from UVR occur once the amount of absorbed UVR either no longer provides a benefit or if repair mechanisms are unable to keep pace with the damage; at this threshold, effects of UVR rapidly increase, often from negligible to severe. The threshold for irradiance tolerance of an organism may be an effect of wavelength, cumulative dose or the dose-rate of exposure (Whitehead et *al.* 2000).

It is impossible for many organisms to avoid all UVR exposure. As a result, many organisms have evolved combinations of chemical, physical and behavioral defense mechanisms to minimize UVR-induced damage. Many organisms utilize compounds that are photoprotective [e.g., mycosporine-like amino acids (MAAs), fluorescent pigments and melanin] or compounds that are either produced by the organism or acquired through diet that can neutralize toxic photoproducts (e.g. antioxidants and carotenoids). Some organisms simply move (e.g., vertical migration) to minimize exposure to UVR, while other organisms have highly efficient photoenzymatic repair systems. Many organisms incapable of producing UVR-protective compounds may acquire them from their diet or through symbiotic relationships. For example, the symbiotic dinoflagellate *Symbiodinium microadriaticum* synthesizes and transfers MAAs to the tissues of its host, the upside-down jellyfish *Cassiopeia xamachana,* which in part relies on MAAs for photoprotection (Banaszak and Trench 1995).

In order to determine the effect of UVR in the natural environment, UVR exposure treatments should be structured to include the full spectrum of solar irradiance (a polychromatic approach; Caldwell et *al.* 1986, Cullen and Neale 1997). This allows repair responses to counteract any UVR damage as would occur in nature. One basic polychromatic approach is to use presence-absence experiments with treatments that fully allow or prevent organism exposure to full spectrum UVR. In these types of experiments, a screening agent (e.g., a UVR opaque acrylic sheet) is used in 'absence' treatments to prevent UVR exposure and results are compared to a 'presence' treatment using a UVR transparent screen. Results from this type of

presence-absence experiment indicate whether a UVR effect is present at exposures tested, but provide no direct information on organisms' sensitivity to specific wavelengths.

Many biological responses are dependent on spectral composition and interactions among multiple wavelengths. In order to quantitatively relate experimental responses to UVR exposure (or wavelength) it is therefore necessary to apply spectral weighting functions (Cullen and Neale 1997), which describe the relationship between wavelength and the effectiveness of UVR at producing a response (Neale 2000). Biological weighting functions (BWFs) are sets of wavelength-specific weighting coefficients established to represent simultaneous wavelength-dependent effects when using broadband polychromatic approaches (Neale 2000). Using a BWF, biologically effective exposure (measure of UVR dose) can be determined for any type of light source. Net biologically effective exposure is obtained by summing the product of the weighting coefficient, irradiance and bandwidth at each wavelength over the spectrum. The biologically effective exposure can be used to compare responses from exposures with inherently different spectral properties and to determine the effects of varying spectral compositions (e.g., changes in ozone concentration, water depth or clarity, etc.) on organism response. Understanding wavelength-specific responses is necessary to predict consequences of increased UVR exposure and to relate responses among studies with differing spectral irradiance. In aquatic ecosystems, many such studies have focused on primary production.

There have also been several studies on the wavelength dependent effects of UVR on DNA damage and mortality in aquatic animals. These studies examined various transparent life stages of organisms including sea urchin embryos, cod eggs, water fleas and copepods (Kouwenberg et *al.* 1999, Tartarotti et *al.* 2000, Williamson et *al.* 2001, Lesser et *al.* 2006). One important group of transparent organisms for which the effect of spectral variation on UVR effects has not been studied is gelatinous zooplankton including ctenophores.

The lobate ctenophore *Mnemiopsis leidyi* is a highly transparent organism (Johnsen and Widder 2001) found in high UVR tropical waters as well as lower UVR coastal waters. They are found throughout the water column but the amount of time an individual animal spends near the surface versus lower in the water column is unknown. There are inconsistent results from several studies on whether *M. leidyi* exhibits a predictable pattern of directed vertical migration in response to select environmental factors (reviewed in Purcell et *al.* 2001). Only a few members of the phylum Ctenophora have been tested for presence of UVR-absorbing compounds, but none have yielded positive results (Karentz 1991, Banaszak 2003). UVR-transmission scans of individual ctenophores from the Chesapeake Bay show no signs of any photoprotective compound (pers. obs.). There is no information on presence or efficiency of the photorepair system of *M. leidyi*. A potential deficiency in UVR-protective mechanisms could render *M. leidyi* susceptible to deleterious effects from UVR. There is currently no information on the ability of *M. leidyi* to detect, respond to and repair damage from UVR.

Mnemiopsis leidyi is native to estuaries and coasts along the eastern regions of North and South America. They can tolerate a wide range of salinity and dissolved oxygen concentrations but are generally intolerant to temperatures in excess of 30 ^{o}C (Breitburg et *al.* 2003, Purcell et *al.* 2001). Peak *M. leidyi* abundance varies regionally, with temperature, food availability and predators being the most important factors in determining their abundance (Kremer 1994, Purcell and Cowan Jr. 1995). In Chesapeake Bay, *M. leidyi* reaches peak abundances from June through September when UV irradiance is at its annual peak. In more southern latitudes such as Biscayne Bay, Florida, *M. leidyi* abundance peak during fall to winter when UVR is nearing its annual low (Kremer 1994). The ability of *M. leidyi* to inhabit a range of environmental conditions combined with its high reproductive output potential and rapid growth rates has allowed for its rapid and successful invasion of the Black Sea in the early 1980s, and its continual spread to other nearby bodies of water including the Caspian Sea, Sea of Azov, North Sea, and Baltic Sea (Ivanov et *al*. 2000, Boersma et *al*. 2007).

Mnemiopsis leidyi can rapidly increase in size and abundance under favorable conditions. Individual growth and reproductive rates are related to ctenophore size and prey availability. Under favorable conditions, small individuals can double their biomass daily (Reeve et *al*. 1989). *Mnemiopsis leidyi* is a simultaneous hermaphrodite that reaches reproductive maturity around 3 cm in length (Kremer 1976). Mature individuals can release 10,000+ eggs into the water column each night (Kremer 1976). There is a positive relationship between fecundity and ctenophore size for *M. leidyi* (Kremer 1976).

Mnemiopsis leidyi is an important component in the Chesapeake Bay and other coastal and estuarine food webs. They are voracious predators that feed heavily upon zooplankton and ichthyoplankton, including fish and oyster larvae (Nelson 1925, Purcell et. al. 1991, Cowan and Houde 1993). *Mnemiopsis leidyi* has few predators within Chesapeake Bay although the scyphomedusae *Chrysaora quinquecirrha* (the sea nettle) is a dominant predator that can control *M. leidyi* abundances in parts of the mainstem Chesapeake Bay and its tributaries. Because of its importance in estuarine food webs, changes in the abundance of *M. leidyi* have the potential to significantly affect mesozooplankton, oyster, fish and sea nettle populations.

The goal of this study was to examine the effects of current near-surface UVR on growth, reproduction and survival of the ctenophore *M. leidyi* in the Rhode and Patuxent Rivers, subestuaries of Chesapeake Bay. Growth experiments were conducted to test the hypothesis that growth (weight and length) of *M. leidyi* is reduced by exposure to UVR similar to that experienced in near-surface waters of the Rhode River during summer. A negative effect of UVR on growth could potentially prevent smaller *M. leidyi* exposed to high UV irradiance from achieving the minimum reproductive size and could reduce total lifetime egg production for individuals that do reproduce. Reproduction experiments were conducted to test the hypotheses that exposure of *M. leidyi* to UVR similar to that experienced in near surface waters of the Rhode River during summer would result in either a decrease in the number of eggs produced, or possibly, a stress response expressed as an increased number of eggs produced whereby the animal facing imminent death releases maximum gametes.

Reproductive *M. leidyi* might also experience a decrease in size thus reducing either total egg production (as egg production is positively correlated with ctenophore size) or the number of eggs produced per unit *M. leidyi* biomass. Finally, I examined the effects of UVR exposure on the survival of *M. leidyi* and estimated the spectral dependence of the survival response by comparing the survival of ctenophores under different UVR spectral treatments.

Materials and Methods

Preliminary, growth, reproduction and survival experiments

General Experimental Methodology

In order to test the effects of UVR exposure on the growth, reproduction and survival of *Mnemiopsis leidyi*, I conducted three sets of experiments during the summers of 2008 and 2009 as well as a preliminary experiment during 2008 used to determine an appropriate prey density and feeding regime (Table 1). The methodology for each of the experiments was similar; specifics for each experiment type (preliminary, growth, reproduction, survival) follow the general protocol description below. Ctenophores were collected from mesohaline areas of two Chesapeake Bay subestuaries, the Patuxent River (Solomons Island, Maryland) and the Rhode River (Edgewater, Maryland) using a 0.5 cm mesh dip net. Salinity during collections ranged from 7.7 – 12.5.

For all experiments, *M. leidyi* were weighed (to the nearest 0.1 g) and measured (to the nearest 0.1 cm) after four days of UVR exposure. The biometric conversion of *M. leidyi* wet weight to dry weight for salinities of 6 –12 is calculated using the following equation (Nemazie *et al*. 1993; see Purcell *et al*. 2001 for additional salinity regimes):

$$\mathrm{DW} = 0.0095\mathrm{WW} - 0.0014$$

Percent carbon and nitrogen content are calculated as 5.1 % and 1.3 % of the dry weight respectively for salinities of 6 – 12 (Nemazie *et al.* 1993).

For experiments, *M. leidyi* were placed in ten shallow 11 L chambers (43 cm x 28 cm x 12 cm deep) containing 0.5 μm filtered Rhode River water. Chambers were placed either outdoors under ambient solar UVR or in the laboratory under UVR lamps that simulated the spectral composition of noon solar UVR on a summer day. Experimental chambers were fitted with either an Acrylite OP-3 UV resistant (-UVR) or OP-4 UVR transparent (+UVR) acrylic sheet lid. Airlines were placed at the surface of each chamber to gently move water and *Artemia* sp. prey throughout the chamber without damaging *M. leidyi*.

In outdoor experiments (referred to as 'solar' experiments), experimental chambers were placed in a shallow, temperature-controlled (18.0 – 31.5 ^{o}C) water bath for a maximum of 4 d (Fig. 1). The chiller was unable to maintain a constant temperature during hot sunny days therefore ice was added throughout the day to attempt to maintain temperatures within a range of 5 – 7 ^{o}C. Alternatively on cold nights the chiller had difficulty heating the water efficiently to maintain temperatures within a narrow range. Experiments conducted in 2008 had only two treatment levels (-UVR and +UVR). Due to mortality of all animals in +UVR treatments in several late June and early July growth and reproduction experiments in 2009, however, an additional treatment (S+UVR) was added that consisted of a shade cloth placed over a UVR transparent lid, blocking approximately 54% of UVR. The remainder of ambient solar UVR experiments conducted in 2009 therefore included three treatments (-UVR, +UVR, S+UVR) with four control (-UVR) replicates and three replicates each of +UVR and S+UVR treatments.

In indoor laboratory experiments (referred to as 'lamp' experiments), UVR was produced by a bank of Q-Panel UVA-340 lamps. Lamp heights were adjusted to modify the intensity of UVR (i.e. dose rate) so that approximately 12-13 h of UVR exposure day^{-1} generated daily cumulative exposures similar to experiments conducted under ambient solar UVR during late August thru early September 2008 and 2009. The lamp set-up was only used for two reproduction experiments. Experiment duration was 4 d.

Broadband measurements of solar and lamp irradiance for all experiments were made using polysulfone film dosimeters (Dunne 1996). One dosimeter was placed at the bottom center of each of three experimental chambers (one of each treatment) outside of the water bath (temperature does not affect the response of the film to UVR). The film responds to biologically damaging UV-B but does not provide a means to evaluate exposure to the longer, less biologically damaging, UV-A wavelengths. Therefore, while UV-A was not blocked from +UVR treatments and only partially blocked in S+UVR treatments, it was not directly measured.

An initial calibration of the absorbance of dosimeters in air and water was done in comparison to spectral radiometer measurements. Replicate dosimeters placed in black, water filled basins were exposed to solar irradiance for each of five equally progressively longer time increments during a single day. A SERC SR18 spectral UV-B radiometer was located next to the basins to record cumulative spectral irradiance. The optical absorbance at 330 nm of each dosimeter was measured using a Cary 4 dual-beam spectrophotometer subtracting background optical density measured at 400 nm. The average corrected absorbance for replicate calibration

dosimeters was plotted against the corresponding incident cumulative UV-B exposure for each time interval. A saturating exponential curve for the relationship between absorbance and integrated UV-B measured by the SR18 was fitted in Sigma Plot (Jandel Scientific Software) by applying the three parameter exponential rise to a maximum equation: $y = m_1 + m_2(1 - e^{-m_3 x})$. The fitted equation was then rearranged to obtain estimated UV-B exposure from measurements of the absorbance of the dosimeters deployed in experimental treatments. The absorbance measurements were used to calculate UV-B exposures in kJ m^{-2} using the following equation:

$$\text{UVR Exposure} = -\ln(1 - (\text{Abs} - m_1)/m_2))/m_3$$

where Abs equals the absorbance of the dosimeter measured by the spectrophotometer, m_1=0.1267, m_2=0.65801 and m_3=0.056915. The dosimeters were placed at the bottom of the chambers and therefore represent the minimum potential exposure experienced by ctenophores moving throughout the chambers.

Preliminary Feeding Experiments

A preliminary solar UVR growth experiment was conducted in 2008 using a range of *Artemia* sp. densities fed to small (0.7 – 2.2 cm) *M. leidyi* to determine a suitable prey density and feeding regime for later growth experiments. Five prey densities of *Artemia* sp. (10, 40, 120, 200 and 300 *Artemia* sp. L^{-1}) were chosen with one replicate of each in both –UVR and +UVR treatments. Initial weight (to the nearest 0.1 g) and length (to the nearest 0.1 cm) were estimated from 12 randomly selected, similar-sized ctenophores from the same field collection. Each shallow chamber contained six randomly selected *M. leidyi* 0.9 – 1.9 cm in length.

Ctenophores in each chamber were fed the full ration of prey in the morning. Prey densities were monitored and adjusted twice during the day to maintain the designated prey density. After four days of exposure ctenophores were removed from treatments, weighed and measured.

A similar preliminary experiment was conducted in 2008 with large (6.0 - 9.5 cm) *M. leidyi* to determine a suitable feeding regime to test the effect of UVR on *M. leidyi* egg production. For this experiment, five *Artemia* sp. densities (150, 250, 325, 400, 550 *Artemia* sp. L^{-1}) were chosen, with one replicate of each in both –UVR and +UVR treatments. Estimates of initial weights and lengths of individuals were obtained as in the preliminary growth experiment. Additionally, initial egg production was estimated from ten similar sized ctenophores from the same field collection on the evening of collection. Each shallow chamber contained four randomly selected *M. leidyi* 6.6 – 9.5 cm in length. Prey were added to chambers as described above. After four days of solar UVR exposure, *M. leidyi* egg production was estimated by placing individual ctenophores in pitcher sieves fitted with 53 μm mesh bottoms and counting the number of eggs released overnight (modified from Grove and Breitburg 2005). The following morning, ctenophores were removed weighed and measured. Pitchers were individually sieved in order to collect, stain and preserve eggs in a 10% acid Lugol's solution.

Growth Experiments

Three solar growth experiments were conducted in 2009 to test the effects of UVR on growth of small (1.1 – 3.3 cm) *M. leidyi.* Each chamber contained three to four randomly selected *M. leidyi.* The feeding regime for growth experiments was

based on results from the preliminary growth experiment (see above and results). Ctenophores in all UVR treatment chambers (-UVR, +UVR, S+UVR) were fed 300 *Artemia* sp. L^{-1} each morning and a single afternoon addition of 100 – 150 *Artemia* sp. L^{-1}.

Weight (to the nearest 0.1 g) and length (to the nearest 0.1 cm) of experimental *M. leidyi* were measured at the start of each experiment. After four days of UVR exposure (or prior to the fourth day if visual inspection indicated that mortality could be imminent), surviving *M. leidyi* were removed from chambers, and were weighed and measured again (no measurements were obtain from dead ctenophores). It was impossible to track growth of individuals, therefore statistical comparisons used chambers means. All three experiments were conducted similarly with the exception that Experiment 1 was terminated after three days of UVR exposure due to a high mortality rate in the +UVR treatments and seemingly imminent mortality in the S+UVR treatments. The three experiments were analyzed separately because the intensity of daily and cumulative UVR varied among experiments.

Reproduction Experiments

Two reproduction experiments using solar UVR and two reproduction experiments using UV lamps were conducted in 2008 and 2009 to examine the effects of UVR on *M. leidyi* egg production, measured as both the number of eggs released g^{-1} of ctenophore wet weight and total number of eggs released ind^{-1}. Reproduction experiment methods were similar to those for growth experiments except that chambers contained two to four similar-sized ctenophores 4.6 -10.0 cm in length.

Results of the preliminary feeding study indicated that a feeding density of 450 *Artemia* sp. L^{-1} would be sufficient to observe a UVR effect on large *M. leidyi*, if one occurred (see results). In most reproduction experiments, *M. leidyi* in each chamber were, therefore, fed approximately 450 *Artemia* sp. L^{-1} in the morning with an additional 200 *Artemia* sp. L^{-1} in the afternoon. An exception to the feeding regime was the second lamp reproduction experiment (Lamp 2) that examined the interaction between UVR exposure and starvation; for this experiment fed *M. leidyi* received food as described above while starved ctenophores received no food.

For the one solar and two lamp reproduction experiments conducted in 2008, estimates of initial weights (to the nearest 0.1 g) and lengths (to the nearest 0.1 cm) were based on measurements of a subsample of either 10 or 22 (depending on field availability) randomly selected similar-sized ctenophores from the same field collection. For the 2009 solar reproduction experiment (Solar 2), initial weights and lengths of experimental ctenophores were measured as described in growth experiments. A baseline estimate of egg production reflecting field conditions was obtained by conducting egg production assays on similarly-sized ctenophores from the same field collection at the start of each reproduction experiment.

Egg production by individual *M. leidyi* was estimated by placing individual ctenophores in submersed 2 L pitcher sieves fitted with 53 μm mesh bottoms on the evening of the fourth day of UVR exposure at ~17:00, and counting the eggs released overnight. Pitchers were gently lifted from the water at ~08:00 and eggs were gently washed from the sieve bottoms and preserved in 10% acid Lugol's solution. Individual *M. leidyi* were weighed and measured at the end of the assay. All eggs

were counted in samples with approx. ≤ 1,000 eggs; larger samples that appeared to have > 1,000 eggs were subsampled using a Stempel pipette.

Survival Experiments

I conducted four survival experiments specifically to test effects of ambient solar UVR on ctenophore survival and also consider data here from two experiments that had extensive mortality in the + UVR treatments, Growth 1 (referred to as Juvenile 2 in survival experiments) and Reproduction Solar 2 (referred to as Adult 4 in survival experiments). The first survival experiment in 2008 (Juvenile 1 in Table 2) tested juvenile ctenophores at a range of prey densities of *Artemia* sp. (10, 40, 120, 200 and 300 *Artemia* sp. L^{-1}); all other survival experiments used the feeding regime that was selected for the respective ctenophore sizes as described above in growth and reproduction experiments. The experimental design was the same as in solar growth and reproduction experiments. Chambers contained 2 - 6 ctenophores depending on the size and field availability of *M. leidyi*. Experiments lasted for four days unless extensive mortality occurred in UVR exposure treatments prior to the fourth day, in which case the experiment was terminated early. Substantial mortality often occurred after two full days of UVR exposure; all survivorship data were therefore compared using survival to the morning of the third day. Ctenophores were declared dead when either a tissue outline of a carcass remained on the bottom of the chamber or the ctenophore was reduced to an amorphous chunk less than 1/3 of its original size, did not have the characteristic lobate ctenophore shape, had no gut cavity integrated within the remaining tissue, and had little to no movement of the ctenes. The percent

survival for the full duration of each experiment was recorded for all chambers within each UVR treatment (Table 2).

To further investigate the effect of UVR on mortality in *M. leidyi* I compiled survivorship data from all solar experiments (including growth, reproduction and survival) to determine the tolerance of *M. leidyi* to specific features of UVR (e.g. cumulative dose, dose-rate). Because some experiments were terminated before the fourth day, all survivorship data was compared using the two-day percent survival of juvenile and adult ctenophores to mean daily UV-B exposure as described above. The relationship between the two-day percent survival and mean daily UV-B exposure was plotted and fit with a three parameter sigmoidal curve using Sigma Plot (Jandel Scientific Software).

Statistical Analysis

The effect of UVR treatments on the growth, reproduction (eggs produced g^{-1} of ctenophore wet weight and total number of eggs produced ind^{-1}) and survival of *M. leidyi* were each evaluated separately with either analysis of variance (ANOVA) or analysis of covariance (ANCOVA). All data were analyzed with SAS 9.1 (SAS Institute 2002) using Proc Mixed. Data were tested for normality and homogeneity of variances prior to analysis. In 2009 growth and reproduction experiments when initial sizes were available for experimental ctenophores, effects of UVR on weight and length were analyzed using ANCOVA with initial weights or lengths as covariates, otherwise ANOVAs were used to compare treatment mean sizes. Non-significant interactions were removed from the models. In all experiments, t-tests were conducted on the initial ctenophore sizes to verify that there were no significant

differences in starting sizes among UVR treatments. For reproduction experiments, treatment means for eggs released g^{-1} wet weight and total numbers of eggs released ind^{-1} were rank-transformed due to unequal variances among treatments, and analyzed using an ANOVA. One exception was the second lamp experiment where food availability was used as a categorical main effect in the ANOVA. Mean values for growth and reproduction experiments were compared *a posteriori* using Fisher's LSD test ($P < 0.05$). The two-day cumulative percent survival of juvenile and adult ctenophores was compared to mean daily UV-B exposure using ANOVA.

Spectral Response Experiments

Experimental Set-up

In order to test the effects of UVR spectral variation on the survival response of *Mnemiopsis leidyi*, I conducted four experiments in August of 2009 using an outdoor solar photoinhibitron. The photoinhibitron consisted of eight replicate chambers for each of four UVR treatments. Wavelength exposure was manipulated by using Schott longpass cut-off filters with 50% transmission cut-offs at 295, 305, 320 and 370 nm. Post-experimental scans of the filters revealed that the transmission of the 295 was identical to the 305 filters and thus served as additional replicates of the 305 treatment.

Mnemiopsis leidyi were collected using a 0.5 cm mesh dip net from the Patuxent River (Solomons Island, Maryland). Initial weights and lengths of ctenophores were obtained prior to being randomly assigned to treatments. Two *M. leidyi* were placed into each of eight chambers of the solar photoinhibitron. The first

experiment used small (1.2 – 2.4 cm) *M. leidyi*. In this experiment, *M. leidyi* were individually placed into Teflon bottles within the chambers to prevent ctenophores from flowing among and out of the chambers. Subsequent experiments were run with large (5.5 – 11.2 cm) *M. leidyi* placed directly into chambers. Water from the Rhode River (Edgewater, Maryland) was filtered to 0.5 μm and re-circulated through a chiller system to maintain water temperature within 21.7- 27.2 ^{o}C (in one experiment the temperature briefly reached a maximum 33.1 ^{o}C because of restricted water flow and was immediately corrected; Fig. 3). The water inflow rate was adjusted to allow minimal water movement (yet still circulate chilled water) to avoid compressing *M. leidyi* against the opposing wall. Equal prey densities among the chambers could not be guaranteed given the flow-through design of the experimental chambers therefore no food was used during the experiments. Experiments were run for a maximum of four days or until substantial mortality occurred. If *M. leidyi* survived through day four, they were removed from chambers, weighed and measured.

As in the growth, reproduction and survival experiments, polysulfone dosimeters were used to obtain an estimate of broadband UVR exposure within the chambers. Dosimeters could not be placed into the chambers when ctenophores were present because of the potential for shading by the ctenophores. Therefore dosimeters were placed at the bottom of each well for a full day of exposure before ctenophores were added.

To estimate the proportion of incident UVR reaching the bottom of the chambers, the dosimeter exposures for the full spectrum treatments were compared to the incident UV-B exposure measured from the SR18 radiometer located at the

Smithsonian Environmental Research Center, Edgewater, Maryland (also used to calibrate the dosimeters). The proportion of UVR between the measured exposure from the chamber dosimeter and incident radiation was applied to the overall spectrum of UVR exposure (290-400 nm) as determined by a combination of SR18 spectral measurements and radiative transfer modeling performed by the Smithsonian Environmental Research Center's Photobiology and Solar Radiation Lab (Edgewater, Maryland, details in Neale et al. 2005). Spectral transmission scans of the Schott longpass filters and Teflon bottles were also applied to the cumulative experimental exposure for each treatment to estimate the spectral UVR exposure (290-400 nm, 1 nm resolution) within treatment chambers.

Biological Weighting Function

In order to develop a spectrally resolved model of UVR dependent mortality in *M. leidyi*, I developed an exposure response curve and a BWF. Data from the growth, reproduction and survival experiments indicated a threshold exposure for mortality (see results), which suggested an exposure response curve with a threshold (e.g. logit function). A trial model was considered which used the BWF for *Daphnia pulicaria* (Williamson et *al.* 2001). This BWF resulted in inadequate estimations of the predicted versus observed mortality of *M. leidyi*, partly due to the response in the intermediate cutoff (320 nm) treatments (Fig. 3). These results indicated that a *M. leidyi*-specific BWF was required; however, it was not possible to fit both the exposure response function and BWF using the limited number of treatments in the photoinhibitron experiments. I therefore modified the methodology presented in

Williamson et *al.* (2001) to incorporate a logit exposure response curve to calculate weighting coefficients.

The initial objective was to estimate the weighting coefficient for each individual wavelength ($\varepsilon_H(\lambda)$ in $(kJ^{-1}m^{-2})^{-1}$) using Equation 1. In this model, m_1 is equal to the natural logarithm of the weight at 300 nm and m_2 equals the slope of the BWF. The proportionality constant, C, included in this model was set equal to 1. I used the parameters from Williamson et *al.* (2001) for *D. pulicaria* as my initial parameters but subsequently adjusted them based on my model's convergence parameters.

$$\varepsilon_H(\lambda) = C \times (e^{\{-[m_1+m_2(\lambda-300)]\}}) \quad (1)$$

The best fit to the observed responses was determined using a second equation for the biologically effective exposure (H*) which integrates the product of exposure and weighting coefficients over the wavelengths of interest, where H(λ) is the cumulative irradiance exposure at each wavelength. I chose the 290 - 400 nm range to examine the damaging effects specific to UV-A and UV-B.

$$H^* = \sum_{\lambda=290}^{400} \varepsilon_H(\lambda) \times H(\lambda) \times \Delta(\lambda) \quad (2)$$

Once H* was determined, I used a logit function (Eq. 3) to predict mortality in response to the biologically effective exposure where d_1 is a measure of the variability in individual sensitivity of the population.

$$Mortality = \frac{e^{(d_1 \times (H^* - 1))}}{1 + e^{(d_1 \times (H^* - 1))}} \quad (3)$$

The fit of this equation to the data was iteratively improved by adjusting the parameters in Equations 1 and 3 using Marquadt nonlinear least-squares iterations implemented in SAS. In order to fit the full model, the fit included both the photoinhibitron data (to constrain the BWF, Eq. 1) and the solar growth, reproduction and survival experiments (to constrain exposure response, Eq. 3). Standard errors of estimated parameters were obtained from asymptotic variances and covariances. Individual confidence intervals for $\varepsilon_H(\lambda)$ were derived by propagation of errors essentially as described in Williamson et al. (2001).

Results

Preliminary, growth, reproduction and survival experiments

Preliminary Feeding Experiments:

In the 2008 preliminary solar UVR growth experiment to determine a suitable feeding density for a UVR effect on *Mnemiopsis leidyi* growth, the average initial size of ctenophores was 0.34 ± 0.05 g and 1.10 ± 0.07 cm (n=12). The average daily UVR exposure in the +UVR treatment was 29.4 ± 2.8 kJ m^{-2} UV-B day^{-1}(Table 3). There was a wide temperature range during the experiment (Table 4) however only three ctenophores died, each from a different a chamber and treatment.

Final weight and length of ctenophores were significantly affected by both prey density and UVR treatment (Table 5, Fig. 4). The final size difference between -UVR and +UVR treatments tended to increase with increasing prey density. Subsequent growth experiments were run with prey densities of 300 *Artemia* sp. L^{-1} to maximize the potential for detecting a significant effect of UVR treatment on the growth of small ctenophores.

In the 2008 solar reproduction experiment using variable prey densities the average initial size of ctenophores were 29.23 ± 2.72 g and 7.8 ± 0.35 cm (n=10). Final weight and length of ctenophores were significantly affected by UVR treatment but not prey density (Table 5). Ctenophores in +UVR treatments lost weight and shrank in length while in –UVR treatments ctenophores increased in size. The average daily UVR exposure in the +UVR treatment was 23.2 ± 2.8 kJ m^{-2} UV-B

day^{-1} (Table 3). There was a wide temperature range for the experiment (Table 4) however only one ctenophore died.

There was no significant effect of UVR on rank-transformed eggs released g^{-1} ctenophore wet wt. However, there was a significant effect of prey density (Table 5). There were significant effects of both prey density and UVR treatment on the rank-transformed total number of eggs produced ind^{-1} by *M. leidyi* (Table 5, Fig. 5). The results of egg production in –UVR chambers using prey densities of 325 and 550 *Artemia* sp. L^{-1} most closely resembled initial field conditions. Subsequent experiments were therefore run with the average of these prey densities - 450 *Artemia* sp. L^{-1}.

Growth Experiments:

Mnemiopsis leidyi lost weight and shrank in length in all treatments in all three growth experiments, probably because the initial size of ctenophores in these experiments was larger than those in the preliminary growth experiment, and thus the feeding regime chosen may not have been adequate to support positive growth. The initial size of ctenophores averaged 1.8 ± 0.1 g and 2.3 ± 0.8 cm (n=40) in Experiment 1, 2.1 ± 0.2 g and 2.4 ± 0.1 cm (n=30) in Experiment 2 and 1.6 ± 0.2 g and 2.3 ± 0.1 cm (n=30) in Experiment 3. Mean initial sizes (weights and lengths) did not differ significantly among treatments for individual experiments (Table 6). Based on initial measurements, ctenophores in the –UVR treatments lost an average of 24.9 ± 5.6 % of their weight and 16.5 ± 4.5 % of their length (n=40), ctenophores in the +UVR treatments on average lost 43.4 ± 1.2 % of their weight and 27.5 ± 2.5 %

of their length (n=30) and ctenophores in the S+UVR treatments lost 49.2 ± 10.7 % of their weight and 29.8 ± 5.0 % of their length (n=30).

Substantial mortality occurred in UVR exposure treatments in Experiment 1. After three days of UVR exposure, all +UVR ctenophores had died, and S+UVR ctenophores showed signs of impending death. *Mnemiopsis leidyi* comb rows became opaque and lobes appeared shredded in all S+UVR chambers but ctenophores appeared normal (transparent with unshredded lobes) in all –UVR chambers. The experiment was therefore terminated one day early at the end of Day 3. There were no indications of impeding mortality in either Experiment 2 or 3; therefore both experiments ran for the full four days.

The average daily UVR exposure was significantly different among experiments (ANOVA df=2,19, F=12.71, P=0.0003); UVR exposures were highest in Experiment 1 and lowest in Experiment 3 (Table 3). The S+UVR treatment in Experiment 1 had a similar average daily UVR exposure to the +UVR treatment in Experiment 2 and the S+UVR treatment in Experiment 2 had a similar average daily UVR exposure to the +UVR treatment in Experiment 3 (Table 3). Dosimeters confirmed zero UVR exposure in all –UVR treatments. Mean temperatures for the three growth experiments varied by 0.3 ^{o}C (Table 4).

Initial sizes of ctenophores were used as covariates in full statistical models and were retained in final models where the effect of initial size on final size was significant or there was a significant initial size * UVR treatment interaction (P<0.05). Initial ctenophore weight had a significant effect on the final weight of ctenophores in Experiment 3 but not in Experiments 1 or 2. Initial length of

ctenophores had a significant effect on the final length in Experiments 1 and 3 but not in Experiment 2 (Table 7). The interaction between initial length and UVR treatment was significant in Experiment 3 (Table 7).

There were significant UVR effects on both ctenophore weight and length in Experiments 1 and 2 and on ctenophore length in Experiment 3; *M. leidyi* in the –UVR treatment generally lost less weight and shrank less in length than ctenophores exposed to UVR (Table 7; Fig. 6). *A posteriori* Fisher's LSD tests of all pairwise comparisons for each experiment indicated that there were significant differences in final weights and lengths of ctenophores in +UVR treatments and –UVR treatments but no differences in the final weights or lengths of ctenophores in +UVR treatments and S+UVR treatments (Fig. 6).

Reproduction Experiments:

Mortality rates were high in solar +UVR treatments in reproduction experiments. In Solar 1, all four *Mnemiopsis leidyi* from a single +UVR chamber died most likely due to a sharp drop in salinity overnight as a result of heavy rains. The chamber lid was skewed and allowed fresh water into the chamber; the salinity in that particular chamber was 7.0 while the other chambers were 10.7 – 12.1. Three ctenophores from a separate +UVR chamber in the same experiment also died the day after mortality occurred in the chamber with the salinity drop but the cause is uncertain; the single surviving ctenophore from that chamber was excluded from statistics. In Solar 2, there was 100 % mortality in +UVR treatments and also mortality of a total of five ctenophores, each from different chambers, in the S+UVR treatments. No mortality occurred in –UVR chambers in either Solar 1 or Solar 2.

There was no mortality in either lamp experiment. The mean temperature for both solar experiments was similar (Table 4).

Ultraviolet radiation did not affect rank-transformed egg production by surviving *M. leidyi* (Table 8; Fig. 7) as measured by either number of eggs produced g^{-1} ctenophore wet weight or number of eggs produced ind^{-1} in the solar and lamp UVR reproduction experiments. Visual inspection of data suggested a tendency for ctenophores in +UVR treatments to produce more eggs g^{-1}, but $P > 0.10$ for all comparisons of rank-transformed data (Fig. 7). There was also no discernable pattern in the number of eggs produced ind^{-1} (Fig. 7). There was no significant interaction between food availability and UVR treatment in the second lamp reproduction experiment (Lamp 2) that included both starved and fed *M. leidyi* (Table 8; Fig. 7).

Initial reproduction assays were variable; ctenophores produced an average of 8.6 ± 3.5 eggs g^{-1} and 167.7 ± 75.7 total eggs ind^{-1} in Solar 1 (n=10), 35.4 ± 10.2 eggs g^{-1} and 1467.7 ± 452.7 total eggs ind^{-1} in Lamp 1 (n=8) and 46.8 ± 7.6 eggs g^{-1} and 991.6 ± 159.4 total eggs ind^{-1} in Lamp 2 (n=22). Too few ctenophores were collected for Solar 2 to conduct an initial reproduction assay. After four days in experimental chambers, surviving ctenophores in both treatments in Solar 1 produced more total eggs g^{-1} and egg ind^{-1} than in initial reproduction assays. Both treatments in Lamp 1 produced fewer total eggs g^{-1} and eggs $ind^{-1}$and fed treatments in Lamp 2 produced slightly greater eggs g^{-1} and total eggs ind^{-1} while starved ctenophores produced less total eggs g^{-1} and eggs ind^{-1} than ctenophores from the respective initial reproduction assays.

Similar to the growth experiments, all *M. leidyi* lost weight and shrank in length during the reproduction experiments with a consistently greater loss in ctenophore size in +UVR treatments than in -UVR treatments (Table 8). Based on initial measurements, ctenophores in the –UVR treatments lost an average of 4.6 ± 10.1 % of their weight and 4.5 ± 6.7 % of their length (n=80), ctenophores in the +UVR treatments on average lost 22.4 ± 11.5 % of their weight and 17.2 ± 5.3 % of their length (n=49) and ctenophores in the S+UVR treatments lost 62.0 ± 0.0 % of their weight and 37.3 ± 0.0 % of their length (n=12). In all experiments except Lamp 1 there was a significant negative effect of UVR on ctenophore length (Table 8; Fig. 8). There was a significant negative UVR effect on weight of *M. leidyi* in Solar 2 and Lamp 2 and a trend of a negative effect in Solar 1, but no UVR effect on ctenophore weight in Lamp 1 (Table 8; Fig. 8). There was also a significant negative effect of initial weight on the final weight of ctenophores in Solar 2; chambers with larger mean initial weights lost more weight than those with smaller initial weights.

There was no significant difference among the solar and lamp reproduction experiments in the average daily UVR exposure in the surviving UVR exposure treatments (ANOVA df=2,9, F=1.74, P=0.2303; Table 3). The average daily UVR doses for Solar Reproduction 1 and 2 were higher than the average daily UVR doses for all surviving UVR exposure treatments in growth experiments. The UVR dose in the S+UVR treatment for Solar Reproduction Experiment 2 was similar in magnitude to both lamp reproduction experiments, the +UVR treatment in Growth 2 and to the S+UVR treatment in Growth Experiment 1 (Table 3). Dosimeters confirmed zero UVR exposure in –UVR treatments.

Survival Experiments:

Exposure to near-surface solar irradiance with mean daily UVR exposures > 31.0 kJ m^{-2} UV-B day^{-1} resulted in high percentages of mortality of *M. leidyi* (Table 2). The six solar survival experiments resulted in a combined mean of 99.0 ± 1.0 % (n=102) survival in –UVR treatments, 8.8 ± 5.6 % (n=94) survival of ctenophores in +UVR treatments, and 83.4 ± 8.4 % (n=24) survival in the S+UVR treatments. The mean daily UVR exposures for the +UVR treatments of the survival experiments was 31.7 – 41.1 kJ m^{-2} UV-B day^{-1} (Table 2), and all survival experiments had a higher mean daily UVR exposure than all of the surviving treatments in growth and reproduction experiments. Dosimeters confirmed zero UVR exposure in –UVR treatments. T-tests for each experiment confirmed no significant difference ($P > 0.05$) in the size of ctenophores among UVR treatments.

During the summer of 2008 and 2009, two full days of near-surface UVR exposure resulted in a significant decrease (ANOVA df=2,13, F=5.33, P=0.0204) in survival for all experiments (growth, reproduction and survival). Across all solar experiments, survival averaged 99.1 ± 0.6 % (n=196) in –UVR treatments (excluding the mortality attributed to a sharp drop in salinity in a single chamber, see Reproduction experiments), 49.5 ± 14.5 % (n=162) in +UVR treatments, and 91.7 ± 5.9 % (n=42) survival in S+UVR treatments on the morning of Day 3. A comparison of the two-day percent survival of all UVR exposure treatments (+UVR and S+UVR) of juvenile and adult ctenophores from all experiments (including preliminary, growth, reproduction and survival) to mean daily UVR exposure indicated a survival threshold response, with a sharp decline in survival at approximately 31.5 kJ m^{-2}

UV-B day^{-1} and no difference in the response of juvenile and adult life stages (Fig. 9). The response curve yielding the highest R^2 was fit using a three parameter sigmoidal function ($P < 0.0001$). A similar comparison of the four-day percent survival and mean daily UVR exposure (for treatments not terminated in < four days with surviving ctenophores) indicated the threshold to be approximately 33.2 kJ m^{-2} UV-B day^{-1}. An additional comparison was made using the two-day percent survival and the two-day highest hour of UVR irradiance. The response curve was best fit using a four parameter sigmoidal function ($P < 0.0001$) resulting in a threshold around 12.7 kJ m^{-2} UV-B $hour^{-1}$ (Fig. 10).

Spectral Response Experiments

The combined results from the solar photoinhibitron experiments suggest that spectral variation of UVR has a significant effect (ANOVA, df=2,11, F=16.98, P=0.0004) on the percent survival of *Mnemiopsis leidyi*. The percent survival progressively decreased as shorter wavelength irradiance was included; the 370 treatment had 100.0 ± 6.2 % (n=16) survival, followed by the 320 treatment with 50.0 ± 14.4 % (n=16) survival and the 295/305 treatment with 12.5 ± 8.5 % (n=24) survival.

The mortality and cumulative irradiance data from the solar photoinhibitron, growth, reproduction and survival experiments were used to fit the BWF parameters resulting in values of -3.0415 ± 0.1861 for m_1 (the natural log of the weight at 300 nm), 0.1142 ± 0.0081 for m_2 (the spectral slope of the BWF) and 15.95 ± 7.87 for d_1 (the measure of variability of individual sensitivity). The BWF model for *M. leidyi* was fit with an R^2 value 0.74, P<0.0001 (Fig. 11). Applying the BWF obtained to

spectral exposure produces a spectrum of biologically effective exposure per wavelength (H*(λ)), from this it was possible to determine the range of most damaging wavelengths to *M. leidyi*. The range corresponds to the region where the H*(λ) was greater than 50% of the effective exposure peak response, in this case 307-330 nm (Fig. 12). In comparing the BWF for *M. leidyi* to that published in Williamson et *al.* (2001) for *Daphnia pulicaria*, my model revealed that the response for *M. leidyi* is essentially the same as for *D. pulicaria* for much of the UVR spectrum (Fig. 11).

The overall fit of the BWF model for *M. leidyi* is shown by comparing predictions to observed mortality in the photoinhibitron, growth, reproduction (solar and lamp) and survival experiments (Fig. 13). The relationship between two-day H* and cumulative experimental mortality suggests that the logistical response model is an acceptable predictor (R^2=0.73, P<0.0001) of the effects of UVR on mortality. The model is defined so that the threshold (50% mortality) of biologically effective exposure that *M. leidyi* can tolerate in a two-day period is at H*= 1.0 (Fig. 13).

Discussions and Conclusions

Results under ambient solar UVR conditions indicate that summertime solar UVR exposure equivalent to average conditions within the top 0.5 m of the water column of the Rhode River has both lethal and sub-lethal deleterious effects on *Mnemiopsis leidyi* individuals. Exposure to Rhode River near-surface summertime solar UVR significantly decreased size and increased mortality of ctenophores, but did not significantly affect egg production.

Except in preliminary experiments, experimental chambers designed to permit UVR exposure did not result in ctenophore growth, even in –UVR control treatments, but the loss in ctenophore weight and length was consistently greater in solar UVR exposure treatments than in controls for both growth and reproduction experiments. Because *M. leidyi* individuals I tested shrank in body size during all solar experiments, my results may reflect the impacts of the combined stresses of UVR exposure and an insufficient feeding regime. However, preliminary experiments in which growth did occur yielded a similar pattern.

Mnemiopsis leidyi also did not achieve positive growth in indoor laboratory experiments. Although ctenophore gut cavities contained food throughout the day, growth was negative in all growth and reproduction experiments. This negative growth in growth experiments may have been due to an inadequate feeding regime as the size of the ctenophores used in the preliminary growth experiment to determine an appropriate feeding regime for subsequent experiments were much smaller than those used in later experiments. There was also negative growth in the reproduction

experiments but positive grown seen in ctenophores in the –UVR treatment in the preliminary experiment; the size of ctenophores used in the preliminary reproduction experiment was similar to the later reproduction experiments but ctenophores were fed only twice day^{-1} and the second feeding was not adjusted for prey depletion. The shallow (12 cm) dimensions of the chambers used to control UVR exposure may also have impeded growth. Even with airlines at the surface, chambers did not provide natural water circulation and may have inhibited the ability of *M. leidyi* to capture sufficient prey.

There was a negative effect of UVR exposure on ctenophore size in only one of the two reproduction experiments using lamp-produced UVR (Lamp 2). This effect of lamp-produced UVR on size occurred under similar cumulative UVR exposures to solar UVR exposures that also negatively affected ctenophore size. The spectral composition of the UVA-340 lamps closely mimics summer noontime solar radiation, so I do not believe that spectral qualities of the lamps were responsible for differences in experiments using ambient solar and lamp produced UVR. Instead an important difference may be that the UVR dose rate output of the lamps is constant during exposure, whereas the spectral composition and intensity of solar UVR varies throughout the day and the dose rate is not constant (Fig. 14). There was no UVR effect on ctenophore size in Lamp Experiment 1 which had a higher average daily exposure to UVR than Solar Growth Experiment 2 where a UVR effect on size was observed in both +UVR and S+UVR treatments. These results may indicate that *M. leidyi* is less sensitive to the cumulative daily UVR dose and more susceptible to

exposure to specific wavelengths, the dose-rate of exposure, the peak intensity of daily UVR, or a combination of these factors.

I found no significant effect of UVR on egg production either as eggs g^{-1} of ctenophore wet weight or total eggs produced ind^{-1}. It would be reasonable to expect that an organism that is sensitive to UVR, has both ovaries and testes near the surface of a transparent body, and gametes that are released into the environment may experience direct damage to gonads or alter its reproductive effort during stressful periods of high UVR. *Mnemiopsis leidyi* has a high and rapid capacity to repair physical damage (Coonfield 1936). In addition, reproduction occurs overnight and eggs hatch before the daily peak in UVR. One possible explanation for this strategy is that it ensures that organs exposed to UVR have time to be repaired before releasing gametes and that the gametes themselves are protected from UVR exposure. Another alternative may be that UVR exposure necessary to reduce egg production may be nearly equivalent to lethal exposures.

Because the energy required for egg production in *M. leidyi* is very low (Reeve et al., 1989), natural selection may not favor shifting energy allocation away from reproduction in response to damage from UVR or similar stressors. If investment in reproduction is small compared to the energy required for tissue repair, individuals may not gain a lifetime fitness advantage from altering reproductive output in favor of somatic repair, assuming minimal or no damage to the functionality of the reproductive organs has occurred. Furthermore, if damage sustained to reproductive organs can be rapidly repaired before reproduction occurs, there may be no benefit to reducing reproductive output even in the presence of damage to gonads.

Organism response and tolerance to UVR varies among species and life stages, and can be dependent on spectral composition (Vincent and Neale 2000). Data from the growth, reproduction and survival experiments suggest that the tolerance threshold of *M. leidyi* does not differ with post-larval ctenophore size. The results from applying the BWF to the photoinhibitron, growth, reproduction and survival experiment data to calculate net biologically effective exposure suggested that *M. leidyi* is tolerant of a biologically effective exposure of about 1.0 within a two day period but does not indicate whether the threshold is due to the cumulative biologically effective exposure of 1.0 over a two day period or whether the threshold is due to a single high day of biologically effective exposure. From these results it is uncertain whether reciprocity holds (i.e. the response to a dose of UVR being independent of the dose rate). Reciprocity in *M. leidyi* needs to be further examined before these results can be applied to other scenarios. Regardless of whether the BWF is determined to be applicable to other conditions (i.e., if reciprocity holds), its implications on sensitivity may still provide insights and explanations into some of the behavioral ecology and trade-offs of *M. leidyi* in response to UVR.

An organisms' position in the water column is key in determining the amount of UVR exposure and subsequent damage. An organism that spends much of its time at the water's surface during periods of high UVR is more likely to suffer harmful consequences than an identical organism that spends its time at depth. The outdoor growth, reproduction and survival experiments and the solar photoinhibitron experiments were performed under natural solar irradiance and their subsequent exposures are representative of average summertime UVR conditions within the top

0.5 m of the Rhode River. *Mnemiopsis leidyi* is found throughout the water column and not strictly limited to surface waters, therefore the exposures experienced in these experiments are not representative of typical exposures for ctenophores that move throughout the water column.

Organisms generally move throughout the water column for reasons such as pursuing prey, following the thermocline, halocline or pycnocline, or in response to UVR. *Mnemiopsis leidyi* is typically described as being found throughout the water column and have not been shown to exhibit a predictable pattern of diel migration. However, fine-scale diel variations in vertical distributions relative to UVR penetration have not been examined. Costello and Mianzan (2003) observed distinct aggregations of *M. leidyi* both in surface and near bottom waters off the coast of Argentina. They were unable to attribute the aggregations to a specific environmental variable. *Mnemiopsis leidyi* tend to avoid rough surface waters created by high winds. It is unknown, however, whether they will also avoid surface waters during periods of high UVR. If *M. leidyi* does have the ability to detect and respond to UVR then it seems reasonable they would seek refuge at depths during periods of intense UVR.

Some organisms also move vertically during the daytime to avoid visual predation. In Chesapeake Bay, the main predators of *M. leidyi* are the sea nettle *Chrysaora quinquecirrha* and the ctenophore *Beroe beroe*. Neither *C. quinquecirrha* nor *B. beroe* are visual predators and therefore whether *M. leidyi* is UVR-transparent as a method of camouflage is likely irrelevant in reducing its predation by these predators. This suggests that the risk of visual predation would not be a reason to

favor absence of photoprotective compounds as a UVR-defense strategy. Photoprotective compounds are also costly to produce and may not offer enough protection against the most biologically damaging wavelengths specific to *M. leidyi*. For example, the majority of known mycosporine-like amino acids absorb maximally in the 320-360 nm range, which covers a only a portion of the wavelength range (307 - 330 nm) that appears to be the most harmful to *M. leidyi.*

Mnemiopsis leidyi is a voracious predator that does not appear to greatly discriminate in prey selection (Purcell et *al.* 2001). *Mnemiopsis leidyi* are not visual predators and forage with their oral cavity open and lobes extended to capture prey. Transparency to UVR as well as transparency in general may allow *M. leidyi* to avoid detection from potential prey when feeding. Several species of zooplankton have been shown to have UVR photoreceptors and thus may depend on UVR for vision (Leech and Johnsen 2003). If *M. leidyi* were to employ photoprotective compounds blocking UVR they would be visible to prey species with UV-vision and thus potentially reduce capture and feeding rates.

An organisms' sensitivity to UVR may affect its seasonality in regions with high incident UVR and penetration. In Chesapeake Bay which is at 38 ^{o}N latitude and has turbid water and, in recent decades in Narragansett Bay farther to the north, *M. leidyi* reaches peak abundances from June through September when UV irradiance is at its annual peak (Kremer 1994, Sullivan *et al*. 2001). In some more southern latitudes such as southern Florida (25 ^{o}N), however, *M. leidyi* peaks in eutrophic and clear, subtropical waters during fall to spring when UVR is well below its annual peak (Kremer 1994, Breitburg *et al*. unpublished data). It is possible that latitudinal

variation in incident UVR contributes to latitudinal variation in peak *M. leidyi* abundance. *Mnemiopsis leidyi* in Chesapeake Bay may be able to withstand the peak surface UVR (which this study suggests can be lethal) solely by seeking depth refuge. This is possible in highly eutrophic waters where high abundances of dissolved organic matter and particulates block UVR penetration from sub-surface waters, while ctenophores in clear shallow (< 5 m) waters may have no refuge and therefore peak during low UVR periods. Breitburg *et al*. (unpublished data) found that *M. leidyi* densities in the St. Lucie River (Fort Pierce, Florida) tended to be higher during peak UV periods from May- June than in the adjacent, clearer Indian River Lagoon. An alternative explanation for the ability of *M. leidyi* to inhabit and thrive in high-UVR clear tropical waters may be that the photoprotective strategies or photorepair systems of populations of *M. leidyi* differ latitudinally and ctenophores from high-UVR oligotrophic and tropical waters may utilize superior photoprotective mechanisms, have a more efficient repair system, or may have higher tolerance to UVR. The damage caused by UVR is not dependent on temperature. However, the rate of photorepair and other repair mechanisms increases with increasing temperatures (Williamson et *al*. 2002, Häder et *al*. 2007). These may be key points that should be further examined to better understand the continued existence of the UVR-sensitive *M. leidyi* in clear tropical waters where incident UVR and UVR penetration are high.

In aquatic ecosystems, incident UV-B will increase due to ozone depletion but more importantly, efforts to improve water quality in eutrophic coastal regions by reducing runoff and nutrient loading will likely lead to reduced CDOM and increased

amounts and penetration of UV-B into the water column (Molot et *al.* 2004). If a reduction in particulates and CDOM were to occur, *M. leidyi* could be at increased risk for UVR damage at deeper depths, and in some cases where the water is very shallow, *M. leidyi* may not find a depth refuge from UVR exposure. However, *M. leidyi* has been observed in early June, near the annual peak in irradiance in shallow (> 3 m) clear tropical waters off Carrie Bow Cay, Belize where there is no refuge from UVR (pers. obs.).

UVR exposure could also affect natural populations by delaying or preventing affected individuals from reaching the minimum size for reproduction. Reduced growth rates leading to overall smaller sizes of individuals therefore have the potential to decrease the lifetime fitness of individual ctenophores as well as population growth rates. Although I did not detect a reduction in egg production in my experiments, longer duration exposures might result in sufficiently reduced sizes of reproductive individuals to generate an effect in the number of eggs produced ind^{-1} because egg production is positively correlated with ctenophore size. Consequences of increased UVR penetration could therefore include reduced population sizes of *M. leidyi* and resulting changes to coastal and estuarine food webs including increases in zooplankton and ichthyoplankton populations and decreases in sea nettle and Beroe populations in Chesapeake Bay.

There is much still unknown about the behavior and physiology of *M. leidyi*, especially in response to UVR. The results from these experiments indicate that at current conditions in the Rhode River, *M. leidyi* is at risk for damage from UVR exposure within the top 0.5 m of the water column. The solar photoinhibitron

experiments and the determination of the BWF and biologically effective exposure suggest that *M. leidyi* are most sensitive (i.e. have the lowest tolerance) to the high-energy, shorter UV-B wavelengths. One of the caveats of the experiments is that these mortality results would be anticipated if *M. leidyi* were confined to the upper 0.5 m of the water column or should conditions within the Rhode River change allowing increased UVR exposures similar to these experimental exposures at greater depths. However, these results cannot yet be applied to other situations until the concept of reciprocity in *M. leidyi* is more closely examined. This information may still provide additional insight into understanding the behavior of *M. leidyi*. In addition to examining reciprocity, another interesting course of study would be to investigate the behavioral responses of *M. leidyi* to UVR and examine differences in physiological and behavioral responses in populations that differ latitudinally and from waters with different eutrophic states.

Table 1. Summary of experiments conducted in 2008 and 2009 with associated types and treatments.

Experiment Type	Treatments	Number of Experiments		Notes
		2008	2009	
Preliminary	+UVR, -UVR	2	0	Variable prey densities (one growth, one reproduction).
Growth	+UVR, -UVR, S+UVR	0	3	Mortality of all +UVR in first experiment.
Reproduction	+UVR, -UVR	3	0	One solar and two lamp experiments.
Reproduction	+UVR, -UVR, S+UVR	0	1	Solar.
Survival	+UVR, -UVR, S+UVR	0	6	Four solar survival experiments. Data also from one growth and one reproduction experiment.

Table 2. Mean size and daily UVR exposure (± 1 SE) with corresponding results for the duration of the experiments on the cumulative survival of juvenile (< 3 cm) and adult (> 3 cm) *M. leidyi* in UVR treatments (n/a= not applicable).

		Mean Daily UVR (kJ m^{-2} UV-B day^{-1})		% Survival		
Experiment	Size (cm)	+UVR	S+UVR	+UVR	S+UVR	-UVR
Juvenile 1	1.4 ± 0.1	32.0 ± 3.2	n/a	26.7	n/a	100.0
Juvenile 2	2.3 ± 0.1	41.1 ± 2.6	21.7 ± 4.5	0.0	91.7	93.8
Adult 1	5.8 ± 0.2	35.0 ± 7.2	n/a	26.0	n/a	100.0
Adult 2	6.1 ± 0.2	35.3 ± 3.3	n/a	0.0	n/a	100.0
Adult 3	7.6 ± 0.1	40.0 ± 6.3	n/a	0.0	n/a	100.0
Adult 4	5.8 ± 0.1	31.7 ± 7.4	20.3 ± 2.6	0.0	75.0	100.0

Table 3. Mean daily solar UVR exposure (± SE) for growth and reproduction experiments (n/a= not applicable).

	Mean Daily UVR (kJ m^{-2} UV-B day^{-1})	
Experiment	+UVR	S+UVR
Preliminary Feeding (Growth)	29.4 ± 2.8	n/a
Preliminary Feeding (Repro)	23.2 ± 2.8	n/a
Growth 1	41.1 ± 2.6	21.7 ± 0.8
Growth 2	23.1 ± 1.5	13.8 ± 0.9
Growth 3	14.0 ± 3.0	9.0 ± 1.9
Reproduction Solar 1	26.2 ± 3.0	n/a
Reproduction Solar 2	35.0 ± 5.4	20.3 ± 2.6
Reproduction Lamp 1	19.8 ± 2.3	n/a
Reproduction Lamp 2	21.3 ± 2.3	n/a

Table 4. Mean (± 1 SE), minimum and maximum recorded temperature measurements for all solar experiments.

	Temperature (^{o}C)		
Experiment	Mean	Minimum	Maximum
Preliminary Growth	24.6 ± 0.2	19.7	31.5
Preliminary Reproduction	23.2 ± 0.3	19.5	29.0
Growth 1	23.6 ± 0.1	21.2	27.8
Growth 2	23.7 ± 0.1	18.0	26.8
Growth 3	23.4 ± 0.1	21.3	27.1
Solar Reproduction 1	23.9 ± 0.3	19.4	27.4
Solar Reproduction 2	25.2 ± 0.1	24.1	27.4

Table 5. Statistical results from preliminary feeding experiments. Final models were run as ANCOVA using Type III SS. Non-significant results in parenthesis were excluded from the final model.

Measure	df	F	*P*
Growth Experiment			
Weight			
UVR treatment	1,7	7.51	0.0289
Prey Density	1,7	17.27	0.0043
(UV treatment x Prey Density	1,6	4.66	0.0742)
Length			
UVR treatment	1,7	6.17	0.0419
Prey Density	1,7	20.86	0.0026
(UV treatment x Prey Density	1,6	1.30	0.2970)
Reproduction Experiment			
Egg Production (eggs g^{-1}) rank-transformed			
UVR treatment	1,7	2.63	0.1490
Prey Density	1,7	8.29	0.0237
(UV treatment x Prey Density	1,6	0.10	0.7639)
Egg Production (total eggs) rank-transformed			
UVR treatment	1,7	9.64	0.0172
Prey Density	1,7	10.89	0.0131
(UV treatment x Prey Density	1,6	0.22	0.6551)
Weight			
UVR treatment	1,7	19.82	0.0030
Prey Density	1,7	0.13	0.7309
(UV treatment x Prey Density	1,6	0.40	0.5518)
Length			
UVR treatment	1,7	26.92	0.0013
Prey Density	1,7	0.37	0.5646
(UV treatment x Prey Density	1,6	0.19	0.6785)

Table 6. Statistical results for initial size (weight and length) comparisons of *M. leidyi* by treatment for individual growth experiment. Models were analyzed as ANOVA's using Type III SS.

Source	df	F	*P*
Initial weights			
Growth 1	2,27	0.41	0.6674
Growth 2	2,27	0.23	0.7964
Growth 3	2,27	0.01	0.9932
Initial lengths			
Growth 1	2,27	0.39	0.6788
Growth 2	2,27	0.45	0.6415
Growth 3	2,27	0.05	0.9556

Table 7. Statistical results for growth experiments examining effects of UVR on growth (weight and length) of *M. leidyi*. Final weight model for Experiments 1 and final weight and length models for Experiment 2 were analyzed as ANOVA's using Type III SS. Final length model for Experiment 1 and final weight and length models for Experiment 3 were analyzed as ANCOVA's using Type III SS. Results in parenthesis were excluded from the final model.

Source	df	F	*P*
Growth 1			
Weight			
UVR treatment	1,5	21.18	0.0058
(Initial Weight	1,4	0.06	0.8192)
(Initial weight x UVR treatment	1,3	0.80	0.4364)
Length			
UVR treatment	1,3	52.81	0.0054
Initial length	1,3	21.10	0.0194
(Initial length x UVR treatment	1,2	0.00	0.9711)
Growth 2			
Weight			
UVR treatment	2,7	5.80	0.0327
(Initial weight	1,6	0.47	0.5202)
(Initial weight x UVR treatment	2,4	1.05	0.4307)
Length			
UVR treatment	2,7	6.94	0.0218
(Initial length	1,6	0.15	0.7116)
(Initial length x UVR treatment	2,4	0.02	0.9823)
Growth 3			
Weight			
UVR treatment	2,4	4.22	0.1033
Initial weight	1,4	49.01	0.0022
Initial weight x UVR treatment	2,4	8.59	0.0357
Length			
UVR treatment	2,6	7.93	0.0207
Initial length	1,6	6.55	0.0430
(Initial length x UVR treatment	2,4	0.65	0.5709)

Table 8. Reproduction experiments. Statistical results for the effect of UVR on rank-transformed egg production and size (weight and length) of *M. leidyi*. Models of egg production were analyzed in Solar 1, Solar 2 and Lamp 1 using ANOVA with Type III SS; the final model in Lamp 2 was analyzed using ANCOVA with Type III SS. Ctenophore size was analyzed as ANOVA using Type III SS in Solar 1 and Lamp 1 while the final model in Solar 2 and Lamp 2 were analyzed as ANCOVA using Type III SS.

Source	df	F	*P*
Reproduction Solar 1			
Eggs g^{-1} rank-transformed	1,6	1.11	0.3336
Total eggs rank-transformed	1,6	0.52	0.4991
Weight	1,6	5.38	0.0595
Length	1,6	13.42	0.0105
Reproduction Solar 2			
Eggs			
Eggs g^{-1} rank-transformed	1,5	0.11	0.7575
Total eggs rank-transformed	1,5	0.02	0.8940
Weight			
UV treatment (on final weight)	1,4	145.89	0.0003
Initial weight	1,4	79.97	0.0009
(Initial weight x UV treatment	1,3	0.70	0.4651)
Length			
UV treatment (on final length)	1,4	10.14	0.0334
Initial length	1,4	2.31	0.2032
(Initial length x UV treatment	1,3	0.16	0.7121)
Reproduction Lamp 1			
Eggs g^{-1} rank-transformed	1,8	0.87	0.3780
Total eggs rank-transformed	1,4	2.07	0.2233
Weight	1,8	0.26	0.6238
Length	1,4	0.84	0.4102
Reproduction Lamp 2			
Eggs g^{-1} rank-transformed			
UVR treatment	1,9	0.92	0.3632
Food availability	1,9	14.68	0.0040
(Food availability x UVR treatment	1,8	0.49	0.5053)

Total eggs rank-transformed			
UVR treatment	1,9	0.84	0.3823
Food availability	1,9	30.38	0.0004
(Food availability x UVR treatment	1,8	0.35	0.5716)
Weight			
UVR treatment	1,9	5.42	0.0449
Food availability	1,9	1.94	0.1970
(UVR treatment x food availability	1,8	0.66	0.4391)
Length			
UVR treatment	1,9	18.09	0.0021
Food availability	1,9	4.22	0.0701
(UVR treatment x food availability	1,8	0.73	0.4174)

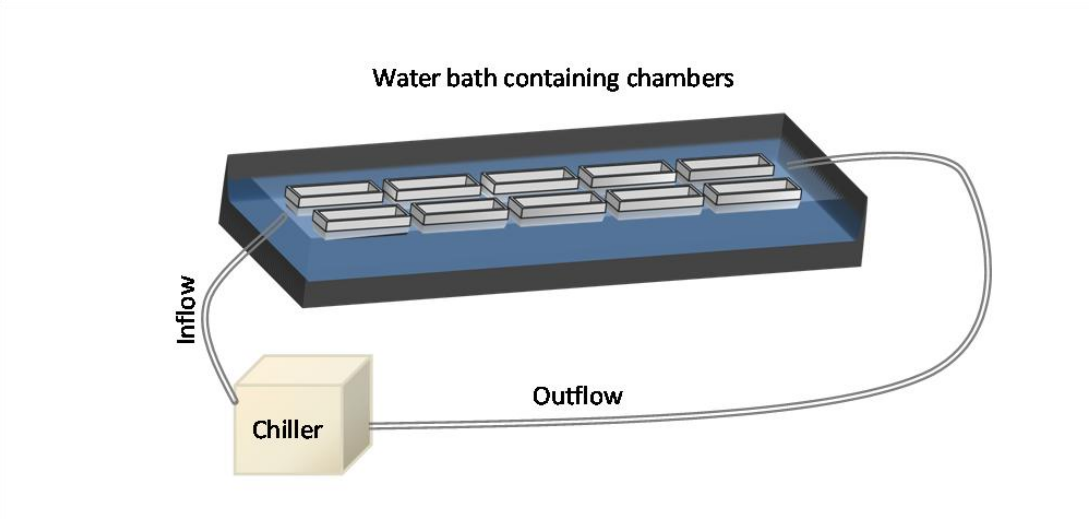

Figure 1. Experimental design for all outdoor growth, reproduction and survival experiments under ambient solar set-up. Closed-system with water re-circulated through a chiller to maintain temperatures within experimental chambers.

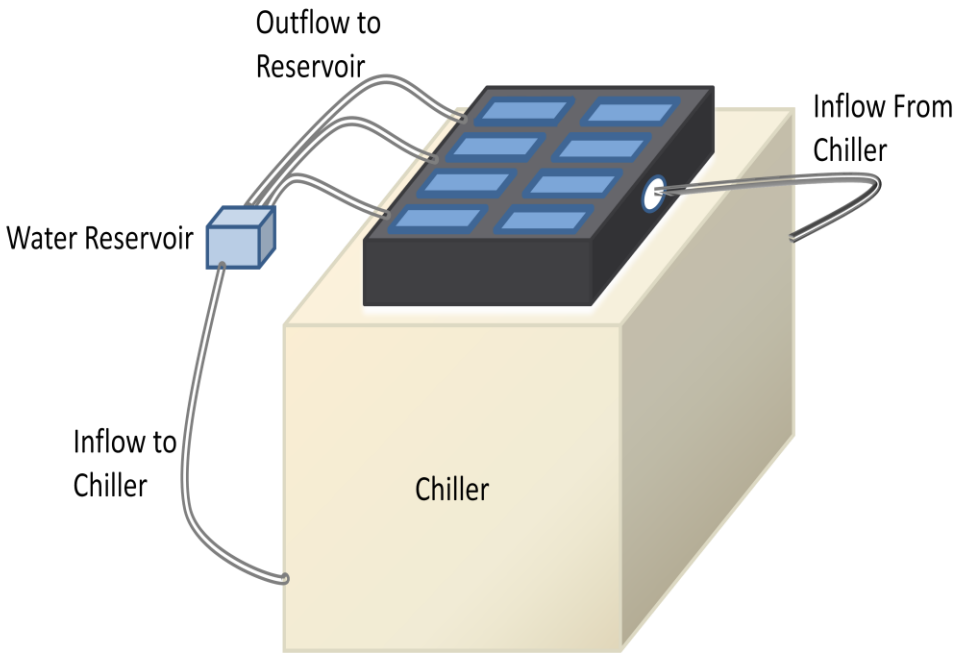

Figure 2. Experimental design for the solar photoinhibitron experiments used to determine the biological weighting function. Closed-system with water re-circulated through a chiller to maintain temperatures within experimental chambers.

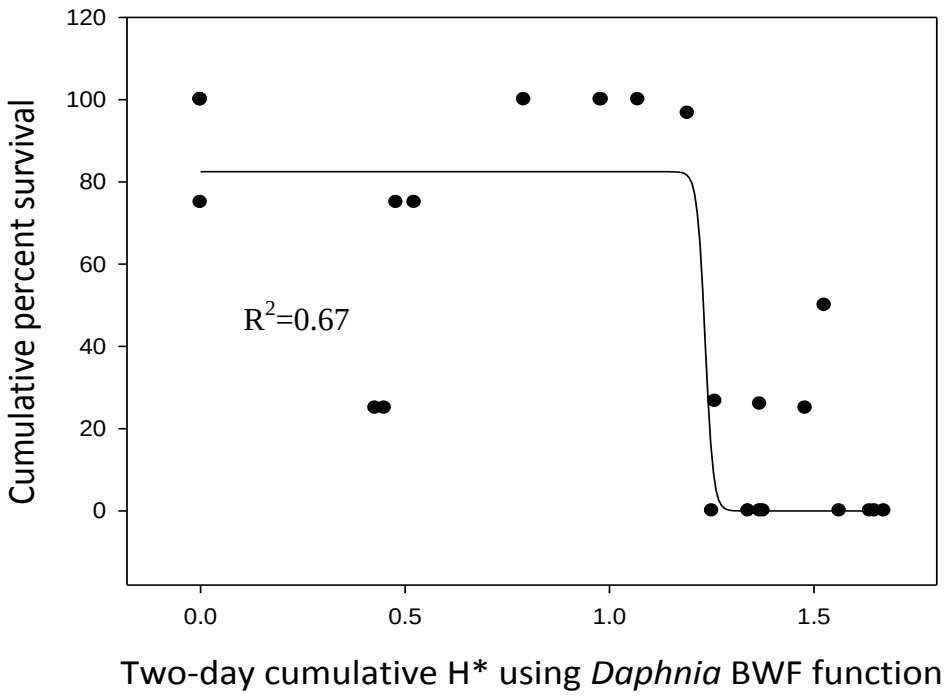

Figure 3. The threshold response curve relating cumulative percent survival in photoinhibitron, growth, reproduction and survival experiments to two-day cumulative biologically effective exposure (H*) using the *Daphnia pulicaria* biological weighting function.

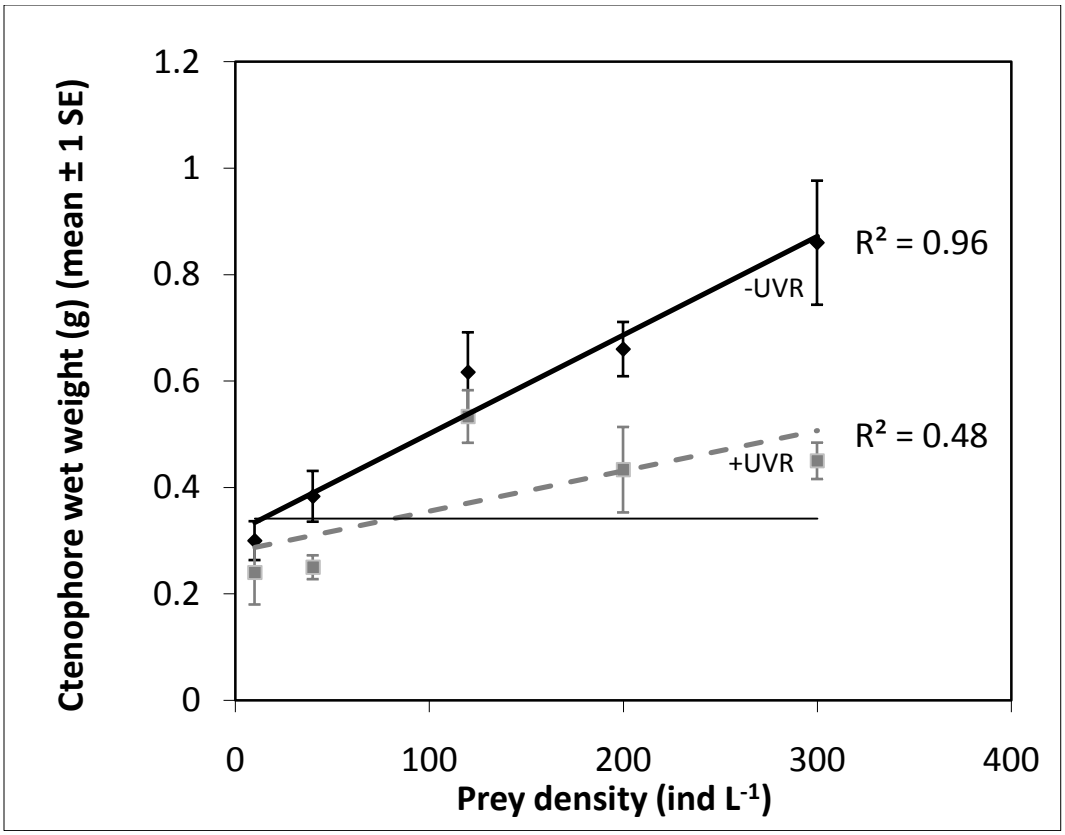

Figure 4. Preliminary growth experiment; mean final wet weight (g) comparisons of juvenile *M. leidyi* in +UVR (grey line) and -UVR (black line) treatments. Thin solid line represents estimate of initial weight. The R^2 values represent the linear fit for +UVR and –UVR treatments with *P*-values of 0.1980 and 0.0035 respectively. 1g *M. leidyi* WW = 0.0081 g DW, 0.0004 g C, 0.0001 g N (Nemazie *et al.* 1993).

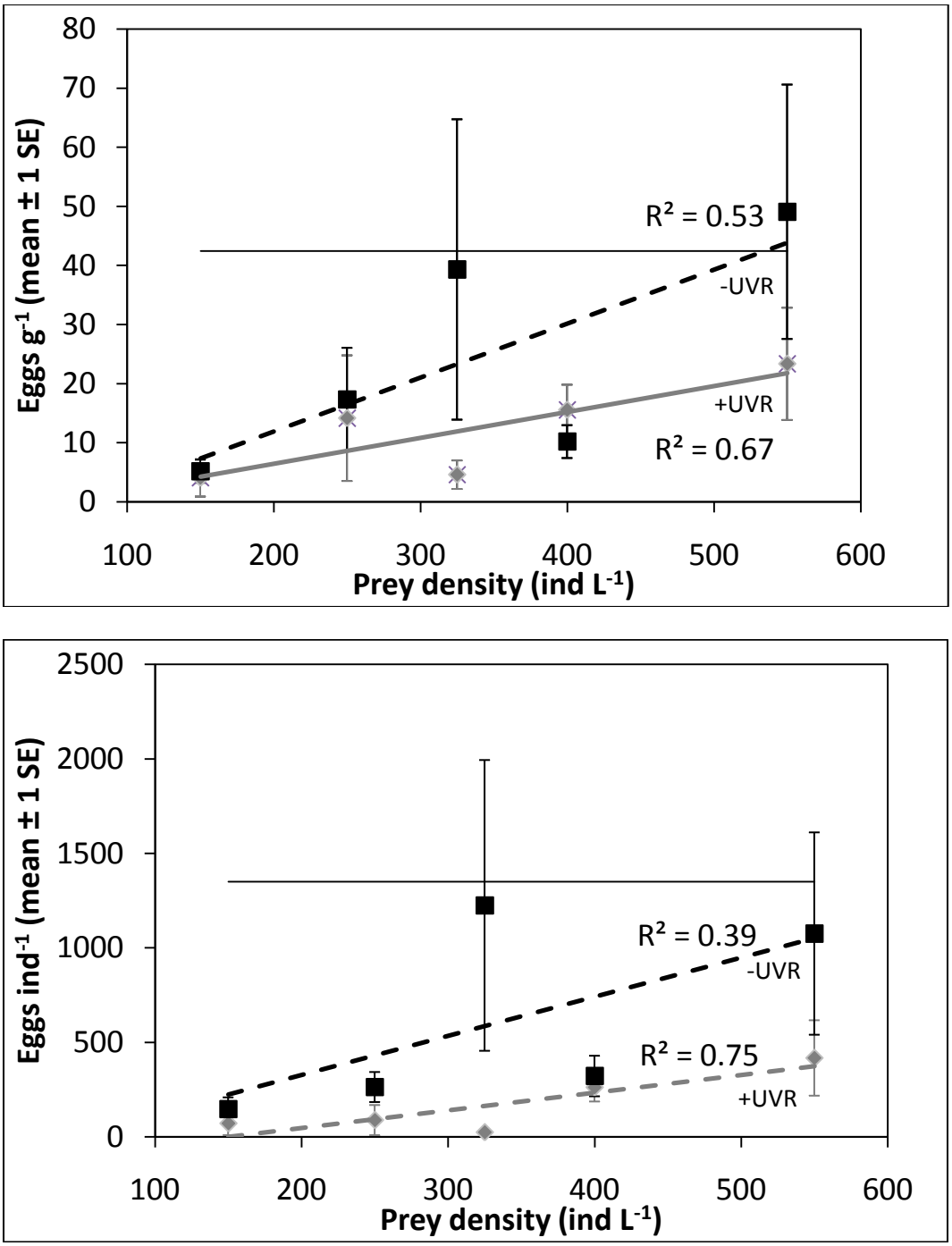

Figure 5. Preliminary reproduction experiment; comparison of mean eggs produced g^{-1} of ctenophore wet weight (top) and mean total eggs produced ind^{-1} (bottom) in +UVR (grey line) and -UVR (black line) treatments. Thin solid line represents estimate of initial egg production. The R^2 values represent the linear fit for +UVR and –UVR treatments with *P*-values of 0.0899 and 0.1652 for mean eggs g^{-1} and 0.0590 and 0.2608 for mean total eggs respectively.

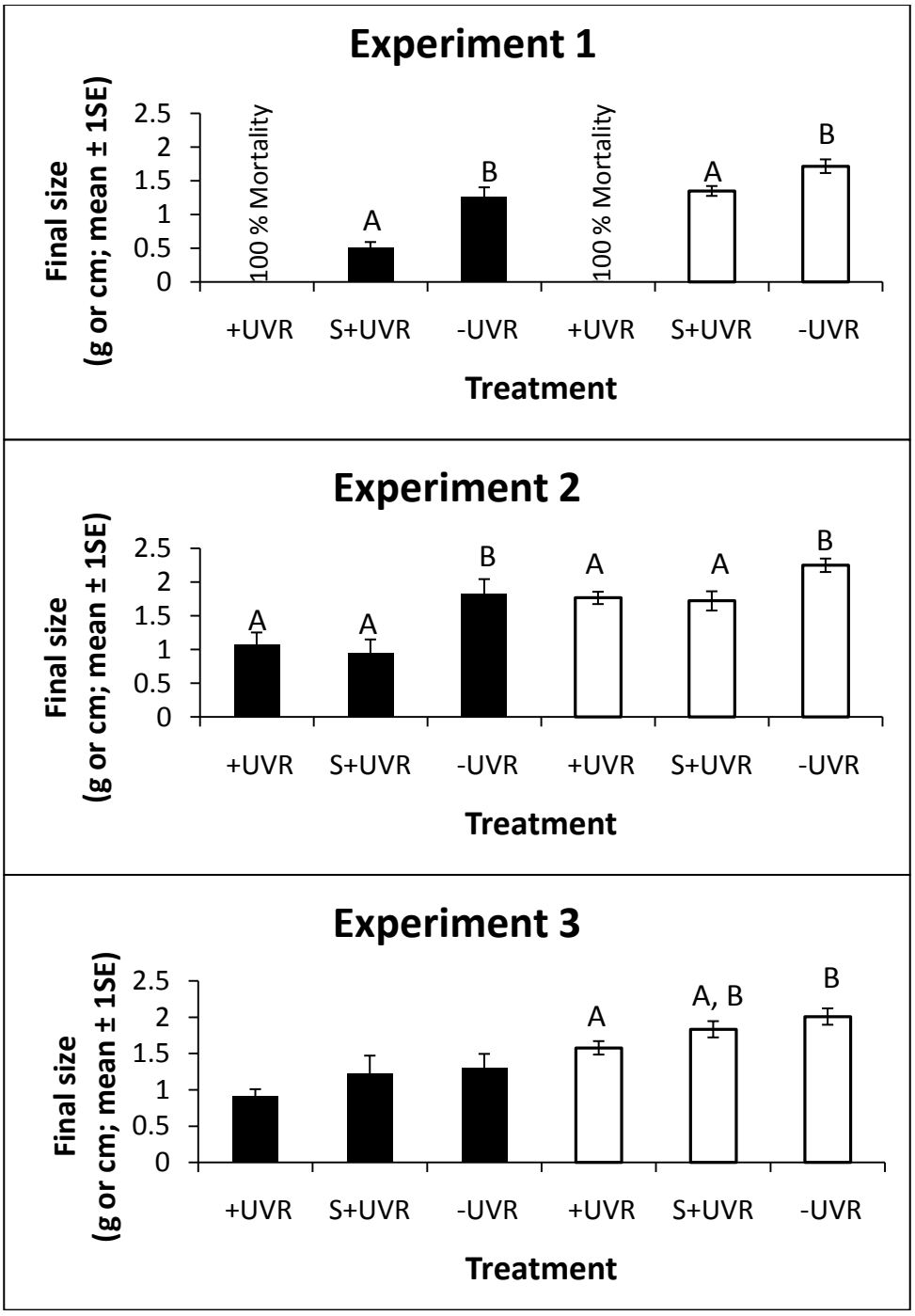

Figure 6. Mean final wet weight (black bars) and length (open bars) comparisons of small *M. leidyi* in growth experiments. Letters represent results of *a posteriori* Fisher's LSD test on all pairwise comparisons. Different letters represent significant differences between treatments $P < 0.05$. No pairwise comparisons were performed on the weights in Experiment 3 due to a significant interaction between initial weight and UVR treatment.

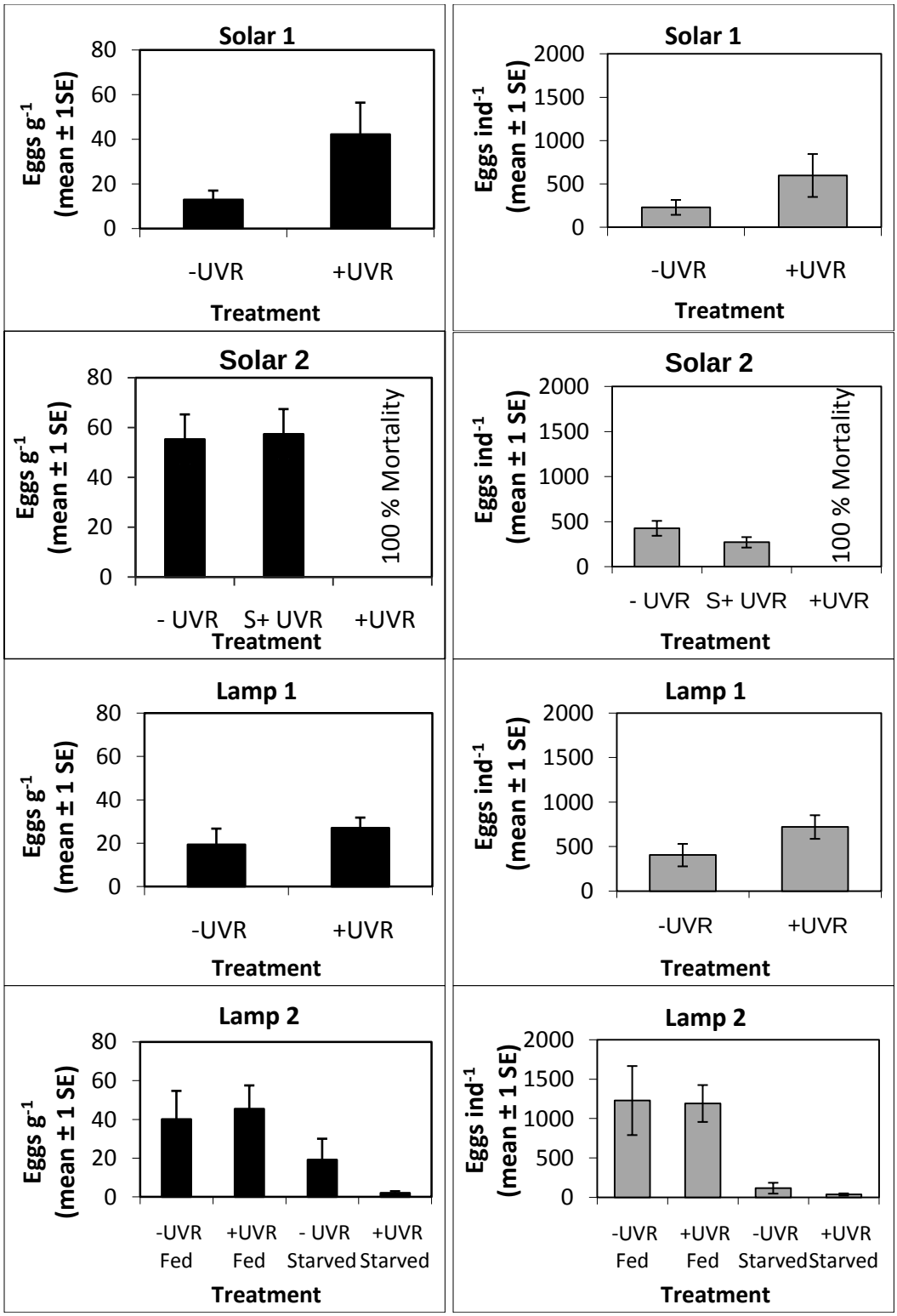

Figure 7. Mean number of eggs produced g^{-1} ctenophore wet weight (black, left) and mean total number of eggs produced ind^{-1} (grey, right) in reproduction experiments under solar and lamp-produced UVR.

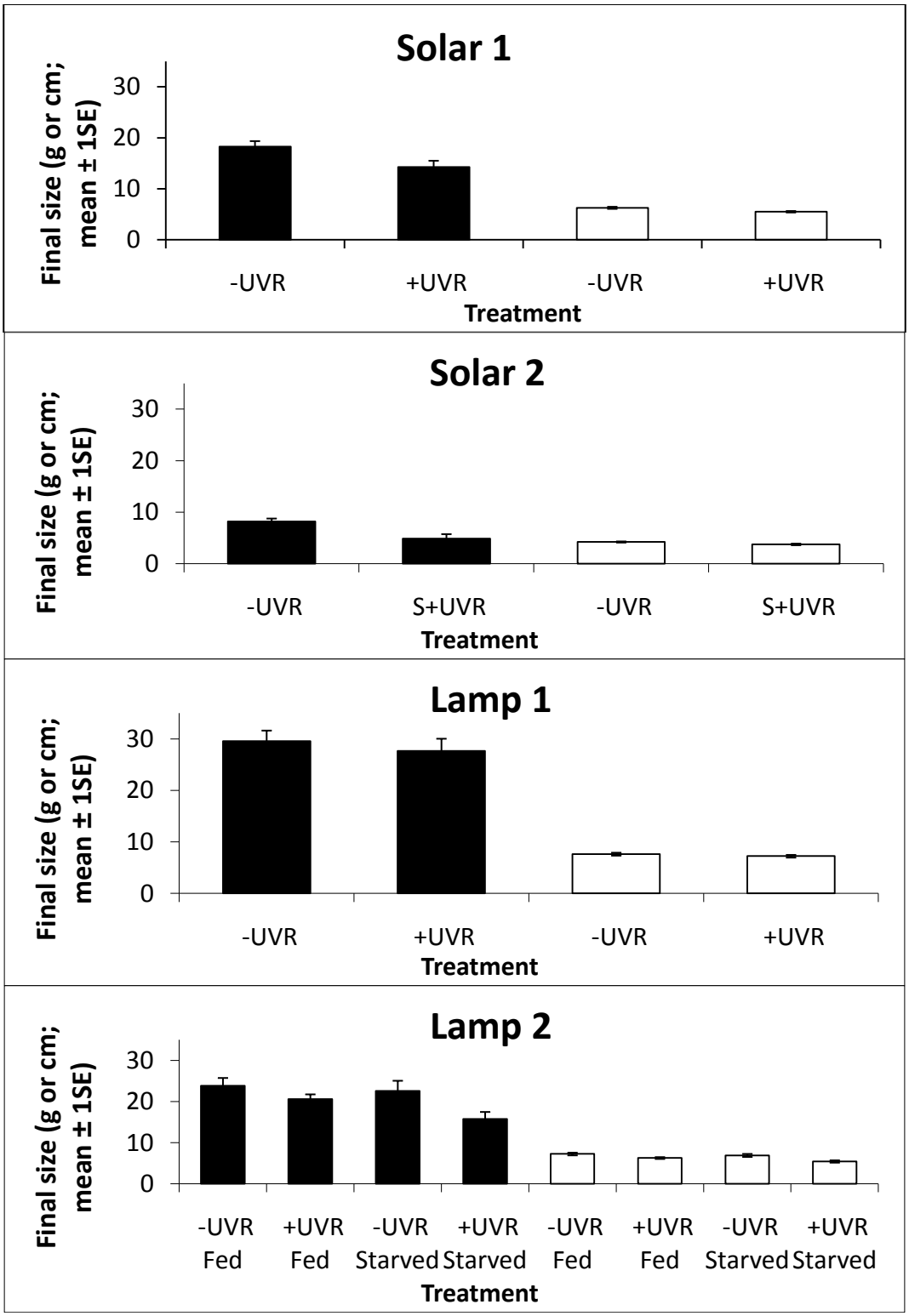

Figure 8. Mean final wet weight (black bars) and length (open bars) of *M. leidyi* in reproduction experiments.

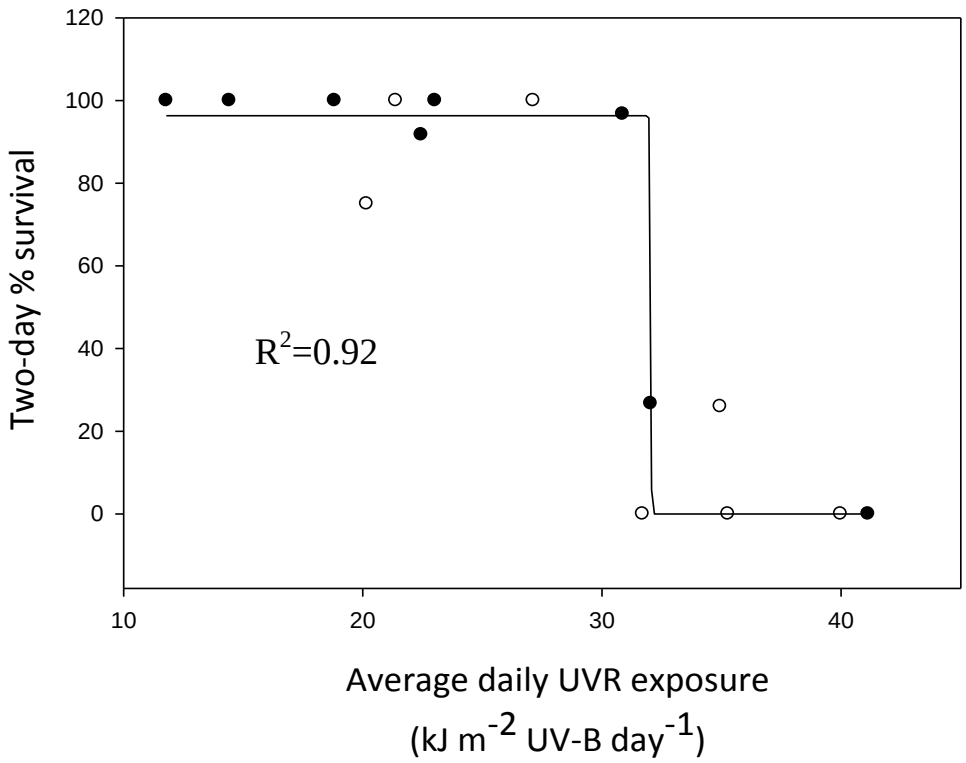

Figure 9. Two day survival curve in response to average daily UV-B exposure for UVR exposure treatments for all growth, reproduction and survival experiments. Black circles represent experiments with juvenile ctenophores (< 3 cm), white circles represent experiments with adult ctenophores (> 3 cm).

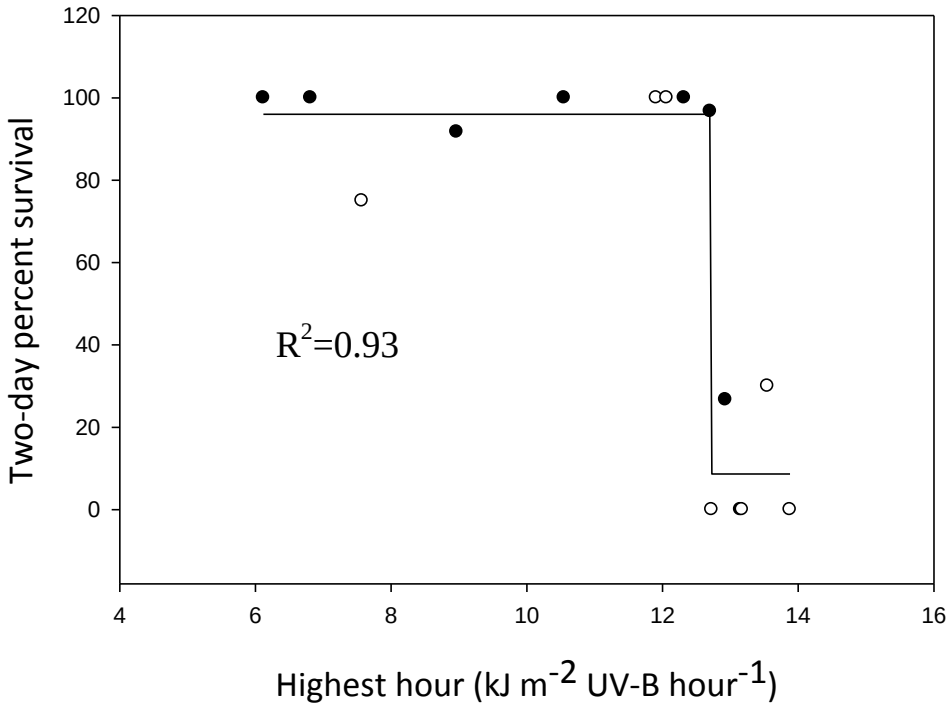

Figure 10. Two day survival curve in response to the two day highest hour of UV irradiance for UVR exposure treatments for all growth, reproduction and survival experiments. Black circles represent experiments with juvenile ctenophores (< 3 cm), white circles represent experiments with adult ctenophores (> 3 cm).

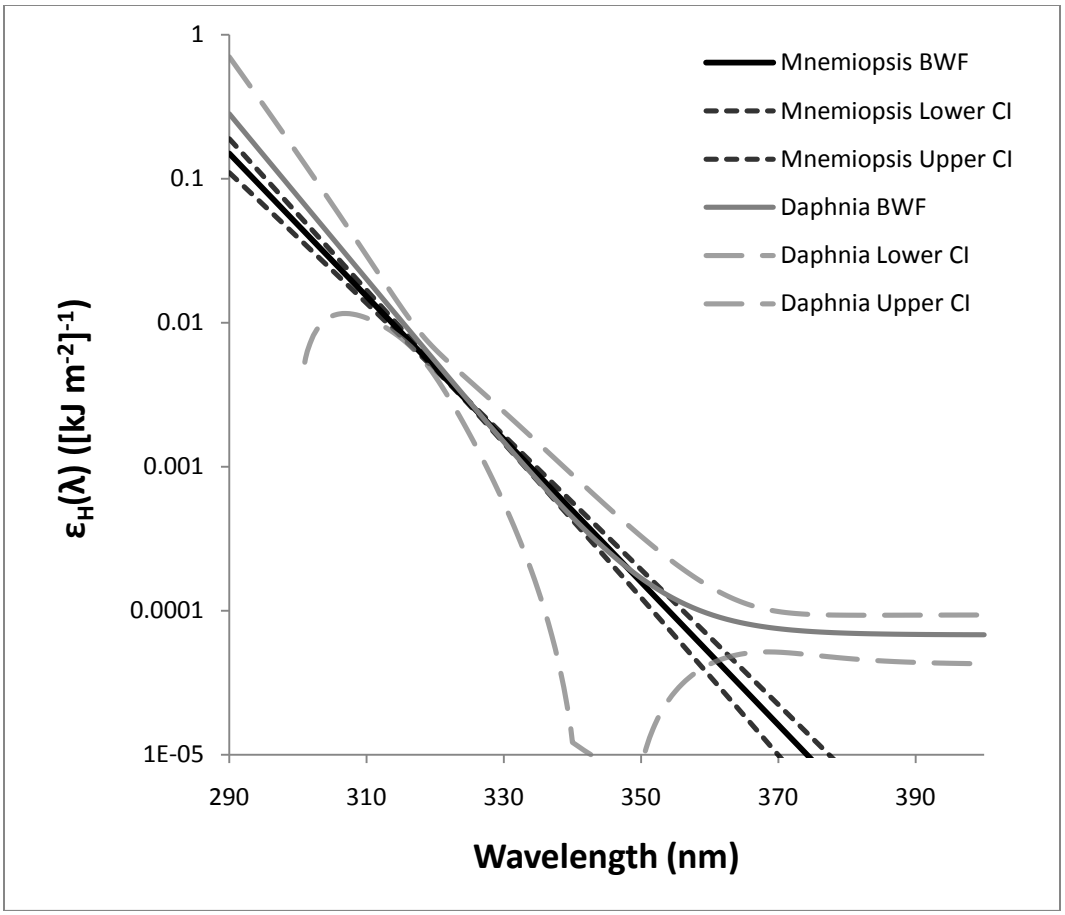

Figure 11. The biological weighting functions for *Mnemiopsis leidyi* and *Daphnia pulicaria* (Williamson et *al.* 2001) with 95 % confidence intervals.

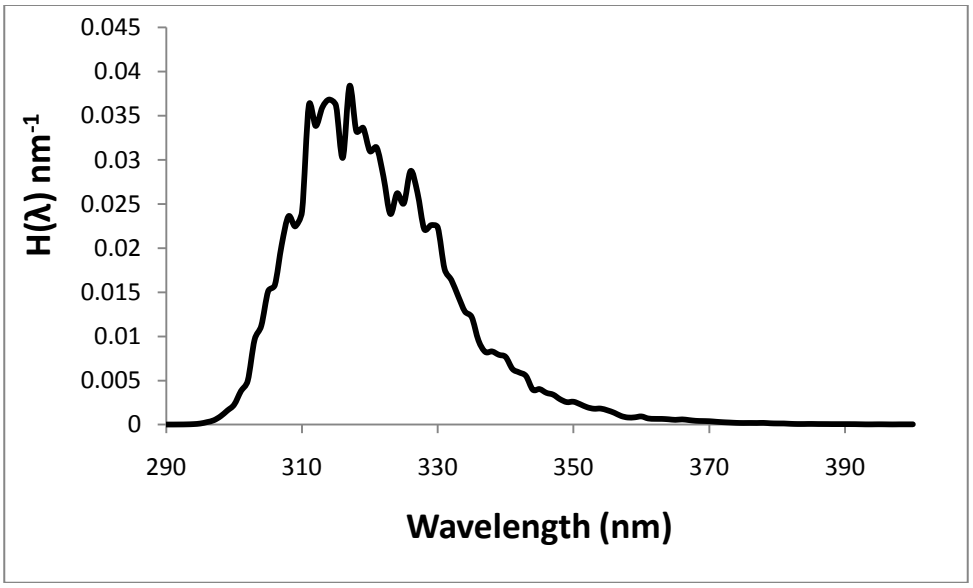

Figure 12. The mean weighted cumulative irradiance exposure for individual wavelengths from the solar photoinhibitron experiments.

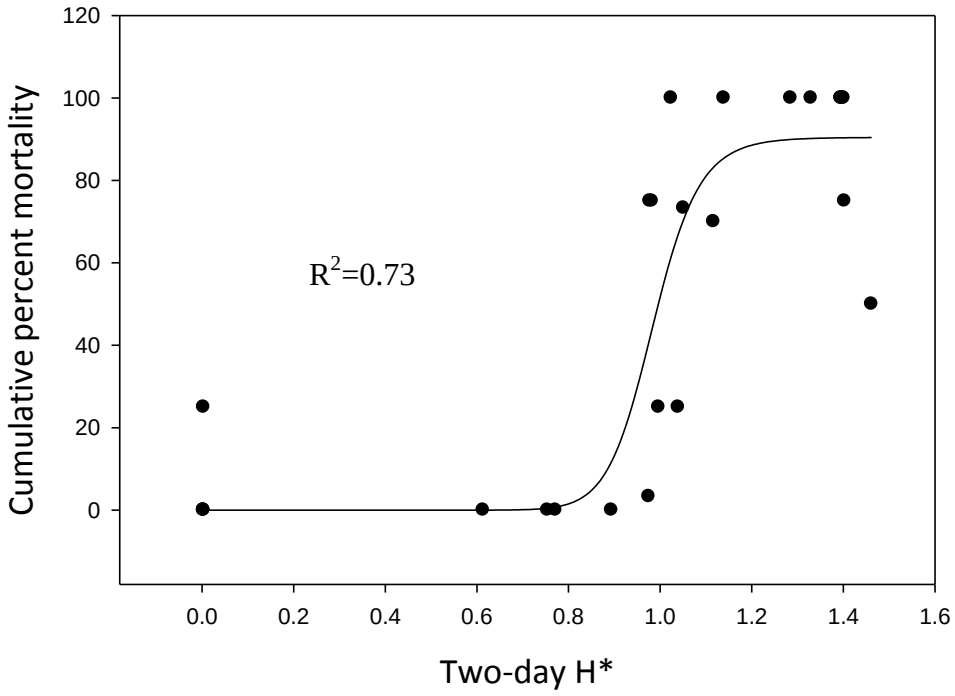

Figure 13. The threshold response curve relating cumulative experimental mortality in photoinhibitron, growth, reproduction and survival experiments to two-day cumulative biologically effective exposure (H*).

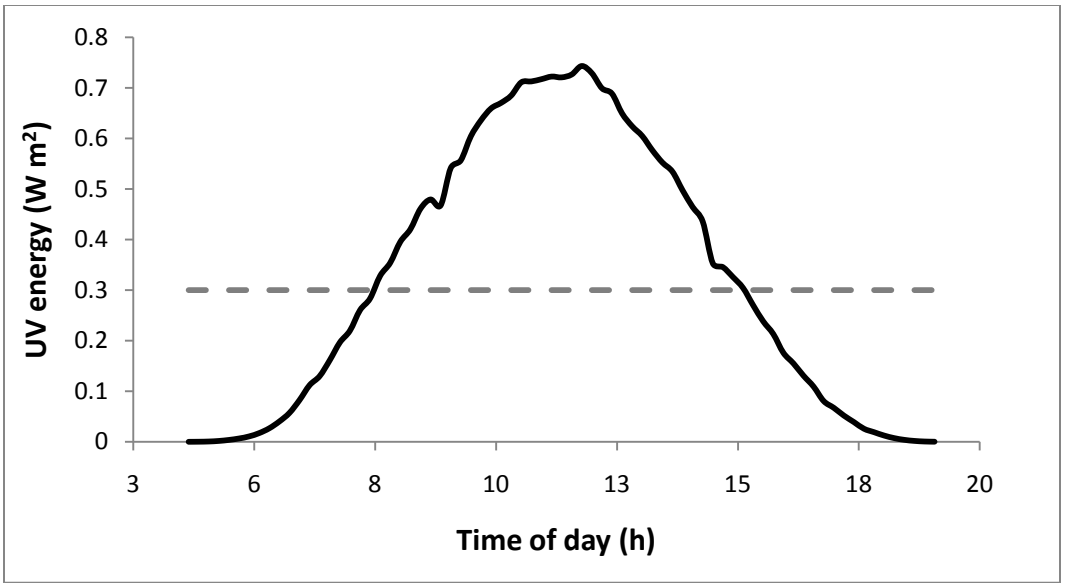

Figure 14. Solar and lamp UV energy comparison. Dashed line represents output from the UV lamps; solid line represents solar energy from a typical clear summer day (Data from July 28, 2009).

Bibliography

Banaszak, A.T. 2003. Photoprotective physiological and biochemical responses of aquatic organisms. In: Helbling, E.W., and Zagarese, H. (eds.) *UV effects in aquatic organisms and ecosystems,* The Royal Society of Chemistry, Cambridge, pp 329–356.

Banaszak, A.T., and Trench, R.K. 1995. Effects of ultraviolet (UV) radiation on marine microalgal-invertebrate symbioses. II. The synthesis of mycosporine-like amino acids in response to exposure to UV in *Anthopleura elegantissima* and *Cassiopeia xamachana*. J Exp Mar Biol Ecol, 194:233-250.

Blaustein, A.R., Hoffman, P.D., Hokit, D.G., Kiesecker, J.M., Walls, S.C. and Hays, J.B. 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? Proc. Natl. Acad. Sci. U. S. A., 91: 1791-1795.

Boersma, M., Malzahn, A.M., Greve, W. and Javidpour, J. 2007. The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. Helgol Mar Res, 61: 153-155.

Breitburg, D.L., Adamack, A., Rose, K.A., Kolesar, S.E., Decker, M.B., Purcell, J.E., Keister, J.E. and Cowan, J.H. Jr. 2003. The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. Estuaries, 26: 280-297.

Buma, A.G.J., Boelen, P. and Jeffery, W.H. 2003. UVR-induced DNA damage in aquatic organisms. In: Helbling, E.W., and Zagarese, H. (eds.) *UV effects in aquatic organisms and ecosystems,* The Royal Society of Chemistry, Cambridge, pp 291–327.

Caldwell, M.M., Camp, L.B., Warner, C.W. and Flint, S.D. 1986. Action spectra and their key role in assessing biological consequences of solar UV-B radiation change. In: Worrest, R.C., Caldwell, M.M. (eds.) *Stratospheric Ozone Reduction, Solar Ultraviolet Radiation and Plant Life*, Springer, New York, pp 87-111.

Coonfield, B.R. 1936. Regeneration in *Mnemiopsis leidyi*, Agassiz. Biol Bull (Woods Hole), 71 (3): 421-428.

Costello, J.H. and Mianzan, H.H. 2003. Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? J Plankton Res, 25:455-459.

Cowan Jr., J.H. and Houde, E.D. 1993. Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Mar Ecol Prog Ser, 95: 55-65.

Cullen, J.J. and Neale, P.J. 1997. Biological weighting functions for describing the effects of ultraviolet radiation on aquatic systems. In: Häder, D.-P. (Ed.) *The effects of ozone depletion on aquatic ecosystems*. R.G. Landes Company, 97-118.

Dunne, R.P. 1999. Polysulphone film as an underwater dosimeter for solar ultraviolet-B radiation in tropical latitudes. Mar Ecol Prog Ser, 189: 53-63.

Fischer, J.M., Fields, P.A., Pryzbylkowski, P.G., Nicolai, J.L. and Neale, P.J. 2006. Sublethal exposure to UV radiation affects respiration rates of the freshwater cladoceran *Daphnia Catawba*. Photochemistry and Photobiology, 82: 547-550.

Grad, G., Williamson, C.E. and Karapelou, D.M. 2001. Zooplankton survival and reproduction responses to damaging ultraviolet radiation: A test of reciprocity and photoenzymatic repair. Limnol Oceanogr, 46: 584-591.

Grove, M. and Breitburg, D.L. 2005. Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. Mar Ecol Prog Ser, 301: 185-198.

Häder, D.-P., Kumar, H.D., Smith, R.C. and Worrest, R.C. 2007. Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. Photochemical and Photobiological Sciences, 6: 267-285.

Ivanov, V.P, Kamakin, A.M., Ushivtzev, V.B., Shiganova, T., Zhukova, O., Aladin, N., Wilson, S.I., Harbison, G.R. and Dumont, H.J. 2000. Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). Biological Invasions, 2: 255-258.

Johnsen, S. and Widder, E.A. 2001. Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. Mar Biol, 138: 717-730.

Karanas, J.J., Worrest, R.C. and Van Dyke, H. 1981. Impact of UV-B radiation on the fecundity of the copepod *Acartia clausii*. Mar Biol, 65: 125-133.

Karentz, D., McEuen, F.S., Land, M.C. and Dunlap, W.C. 1991. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. Mar Biol, 108: 157-166.

Kouwenberg, J.H.M., Browman, H.I., Cullen, J.J., Davis, R.F., St-Pierre, J.-F. and Runge, J.A. 1999. Biological weighting of ultraviolet (280-400 nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. Mar Biol, 134: 269-284.

Kremer, P. 1976. Population dynamics and ecological energetic of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley, M.L. (ed.) *Estuarine Processes*, Academic Press, New York, 1:197-215.

Kremer, P. 1994. Patterns of abundance for *Mnemiopsis* in U.S. coastal waters: a comparative overview. ICES J Mar Sci, 51:347-354.

Leech, D.M. and Johnsen, S. 2003. Behavioral responses – UVR avoidance and vision. In: Helbling, E.W and Zagarese, H. (eds.) *UV Effects in Aquatic Organisms and Ecosystems*, The Royal Society of Chemistry, Cambridge, 455-481.

Leech, D.M., Williamson, C.E., Moeller, R.E. and Hargreaves, B.R. 2005. Effects of ultraviolet radiation on the seasonal vertical distribution of zooplankton: a database analysis. Arch Hydrobiol, 162: 445-464.

Lesser, M.P., Barry, T.M., Lamare, M.D. and Barker, M.F. 2006. Biological weighting functions for DNA damage in sea urchin embryos exposed to ultraviolet radiation. J Exp Mar Biol Ecol, 328: 10-21.

Molot, L.A., Keller, W., Leavitt, P.R., Robarts, R.D., Waiser, M.J., Arts, M.T., Clair, T.A., Pienitz, R., Yan, N.D., McNicol, D.K., Prairie, Y.T., Dillon, P.J., Macrae, M., Bello, R., Nordin, R.N., Curtis, P.J., Smol, J.P. and Douglas, M.S.V. 2004. Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters. Can J Fish Aquat Sci, 61: 2511-2521.

Mostajir, B., Demers, S., de Mora, S., Belzile, C., Chanut, J., Gosselin, M., Roy, S., Zulema Villegas, P., Fauchot, J. and Bouchard, J. 1999. Experimental test of the effect of ultraviolet-B radiation in a planktonic community. Limnol Oceanogr, 44(3): 586-596.

Neale, P.J. 2000. Spectral weighting functions for quantifying the effects of UV radiation in marine ecosystems. In: de Mora, S. J., Demers, S. & Vernet, M. (eds.) *The effects of UV radiation in the marine environment*, Cambridge Univ. Press, Cambridge, 72-100.

Neale, P., Goodrich, R. and Brinley, W. 2005. The Smithsonian-NIST-USDA-FPL Network for Monitoring Solar Ultraviolet Irradiance: Comparison of Radiometer Measurements and Radiative Transfer Model Calculations. In:

Martin, J. W., Ryntz, R. A. & Dickie, R. A. (eds.) *Service Life Prediction: Challenging the Status Quo*. Federation of Societies for Coatings Technology, Blue Bell, PA, pp. 159-70.

Nelson, T.C. 1925. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. Biol Bull (Woods Hole), 48:92-111.

Nemazie, D.A., Purcell, J.E. and Gilbert, P.M. 1993. Ammonium excretion by gelatinous zooplankton and their contributions to the ammonium requirements of microzooplankton in Chesapeake Bay. Mar Biol, 116: 451-458.

Palen, W. J., Williamson, C. E., Clauser, A. A. and Schindler, D. E. 2005. Impact of UV-B exposure on amphibian embryos: linking species physiology and oviposition behavior. Proc R Soc Lond B, 272: 1227-1234.

Purcell, J.E. and Cowan Jr., J.H. 1995. Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. Mar Ecol Prog Ser, 129: 63-70.

Purcell, J.E., Cresswell, F.P., Cargo, D.G. and Kennedy, V.S. 1991. Differential ingestion and digestion by the scyphozoan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*. Biol Bull (Woods Hole), 180: 103-111.

Purcell, J.E., Shiganova, T.A., Decker, M.B. and Houde, E.D. 2001. The ctenophore *Mnemiopsis leidyi* in native and exotic habitats: U.S. estuaries *versus* the Black Sea basin. Hydrobiologia (Dev Hydrobiol 155), 451: 145-176.

Reeve, M.R., Syms, M.A. and Kremer, P. 1989. Growth dynamics of a ctenophore (*Mnemiopsis)* in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth and assimilation efficiency. J Plankton Res, 11: 535-552.

Speakman, J. 1997. Factors influence the daily energy expenditure of small mammals. Proceedings of the Nutrition Society, 56: 1119-1136.

Sullivan, B.K. Van Keuren, D. and Clancy, M. 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. Hydrobiologia (Dev Hydrobiol 155), 451: 113-120.

Tartarotti, B., Cravero, W. and Zagarese, H.E. 2000. Biological weighting function for the mortality of *Boeckella gracilipes* (Copepods, Crustacea) derived from experiments with natural solar radiation. Photochemistry and Photobiology, 72: 314-319.

Tedetti, M. and Sempéré, R. 2006. Penetration of Ultraviolet Radiation in the Marine Environment. A Review. Photochemistry and Photobiology, 82: 389-397.

Vincent, W. F. and Neale, P. J. 2000. Mechanisms of UV damage in aquatic organisms. In: de Mora, S. J., Demers, S. & Vernet, M. (eds.) *The effects of UV radiation on marine ecosystems,* Cambridge Univ. Press, Cambridge, 149-176.

Whitehead, R.F., de Mora, S.J. and Demers, S. 2000. Enhanced UV radiation – a new problem for the marine environment. In: de Mora, S. J., Demers, S. & Vernet, M. (eds.) *The effects of UV radiation on marine ecosystems,* Cambridge Univ. Press, Cambridge, 1-34.

Williamson, C.E., Metgar, S.L., Lovera, P.A. and Moeller, R.E. 1997. Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens*. Ecological Applications, 7: 1017-1023.

Williamson, C. E., Neale, P. J., Grad, G., De Lange, H. J. and Hargreaves, B. R. 2001. Beneficial and detrimental effects of UV on aquatic organisms: Implications of spectral variation. Ecological Applications, 11: 1843-1857.

Williamson, C.E., Zagarese, H.E., Schulze, P.C., Hargreaves, B.R. and Seva, J. 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. J Plankton Res, 16: 205-218.

Zagarese, H. E. and Williamson, C.E. 2001. The implications of solar ultraviolet radiation exposure for fish and fisheries. Fish and Fisheries, 2: 250-260.