

Effects of UV-B Radiation on Near-surface Zooplankton of Puget Sound*

David M. Damkaer¹, Douglas B. Dey¹, Gayle A. Heron¹, and Earl F. Prentice²

¹ University of Washington WB-10, Seattle, WA 98195, USA

² National Marine Fisheries Service/NOAA, Manchester, WA 98353, USA

Summary. An increase in incident solar ultraviolet irradiation, resulting from possible deterioration of the stratospheric ozone layer, would have important biological effects. Though the oceans are relatively opaque to UV radiation, compared to visible light, increases in incident UV may affect organisms living within the first few meters of the sea surface.

Shrimp larvae, crab larvae, and euphausiids were exposed to various low levels of simulated solar UV radiation (UV-B, 290–315 nm) under laboratory conditions. Comparisons between solar and artificial spectra were based on spectroradiometric measurements converted to erythemally effective irradiance. These zooplankton tolerated UV-B irradiance levels up to threshold levels with no significant reduction in survival or developmental rates compared to control organisms. Beyond the threshold levels, activity, development, and survival rapidly declined. The apparent UV thresholds are near present incident UV levels.

Observed survival threshold levels for each experimental group were superimposed on seasonal solar incident UV levels at the experimental site. These threshold levels appeared to be exceeded by median ambient UV levels late in the season of surface occurrence of each species. UV increases resulting from ozone depletion may significantly shorten this season. Although the apparent impact would be lessened by the decrease in UV with depth, irreversible detrimental effects would probably occur before reported survival thresholds were exceeded.

most complex of the environmental issues which are currently perceived as global in scope. There is controversy regarding the magnitude of predicted changes in ozone concentration (Clyne, 1976; Hudson, 1977). Reports emphasize the physico-chemical aspects of stratospheric ozone depletion. They do not deal with the biological significance of the consequent increased UV-B at the earth's surface, primarily because of the relative lack of knowledge of the effects of UV-B on plants and animals. This is especially true with respect to aquatic organisms.

UV-A radiation is not as effective as UV-B radiation in inducing photochemical responses in biological systems. Also, there is great variability in responses to UV-A irradiation, suggesting that these responses cannot be resolved to a few common types. Most of the reactions to UV-A also occur under visible radiation regimes, as well as under UV-B where they are more pronounced and regular. Therefore, UV-A is not a unique nor a very important environmental factor, even though it comprises more than 90% of the total energy of the solar UV spectrum (Caldwell, 1971).

UV-B radiation, in contrast, is readily absorbed by proteins and nucleic acids, and is effective in inducing photochemical reactions in plants and animals (Caldwell, 1971; Giese, 1976). Also, erythema (sunburning) in humans has a UV-B spectral response curve (action spectrum) similar to that of DNA, except that there is a maximum erythemal effect at 297 nm (Koller, 1965). Even though proteins and nucleic acids are commonly involved in biological responses to UV-B, the action spectra for tissues in many organisms may differ because of wavelength-dependent refraction, reflection, or absorption, and hence protection, by outer tissues (Cheng et al., 1978).

There is a common belief that UV light is of no consequence in the ocean; however, the upper few meters of the sea surface receive appreciable UV radiation. Calkins (1975) found that UV-B penetration varied widely at several marine sites, depending on the organic content of the water. The 10% level of incident UV-B irradiation is generally found between 1 and 10 m. Precise information on UV penetration into natural waters is unavailable, although this problem and the associated instrumentation is the subject of other investigations (Smith and Calkins, 1976). The near-surface layer is environmentally important; many zooplankters have their center of abundance there or are found exclusively there for at least a part of their life cycle. Like all organisms faced with UV damage, the near-surface zooplankton might avoid UV through behavior or by screening, or their repair mechanisms could be in equilibrium with the destructive capacity of UV. In either case, the question to be addressed is: what is the tolerance limit for each organism, and might that limit be exceeded by predicted increases in UV irradiation?

Introduction

Ultraviolet radiation in the middle wavelength range 280–315 nm**, denoted as UV-B radiation, has important and practical biological effects (for a review, see Caldwell, 1971). This radiation is of particular interest because it occurs in normal sunlight and would increase if the UV-absorbing stratospheric ozone layer were reduced. Contamination of the ozone layer is among the

Address offprint requests to: Dr. David M. Damkaer, Department of Oceanography, University of Washington WB-10, Seattle WA 98195, USA

* Contribution No. 1107 from the Department of Oceanography, University of Washington, Seattle, WA 98195, USA

** Conventional definitions of ultraviolet (UV) spectral bands are UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (wavelengths shorter than 280 nm).

The broad objectives of the present study are to determine certain responses (general activity, growth rate, and survival) of a variety of common near-surface zooplankton species as functions of UV-B irradiation and exposure times. This report emphasizes the responses of the surface-living larvae of three species of shrimp: *Pandalus danae*, *P. hypsinotus*, and *P. platyceros*. These shrimps include the largest and most important commercially- and recreationally-fished shrimp of the Puget Sound region and Washington State (Magoon, 1974). Data are also included for the responses of the euphausiid *Thysanoessa raschii* and of early and late larval stages of the crabs *Cancer magister* and *C. oregonensis*.

Test organisms were exposed to several levels of artificial polychromatic UV-B irradiation; similar specimens received simultaneous control exposures of artificial visible light and negligible UV. The UV-B spectrum in the treatments was selected to approximate the UV-B wavelength band of sea-level incident solar spectral irradiance under different ozone concentrations.

The specific objectives of these studies were 1) to develop techniques of solar UV-B simulation and measurement, with emphasis on predetermined and reproducible dose rates; 2) to determine UV-B threshold levels (dose rates) for general activity, and to note organism recovery if UV-B is discontinued subsequent to initial effects; 3) to determine UV-B threshold levels for simple survival; 4) to determine, under low UV-B regimes with no significant mortality, if developmental rates are affected; and 5) to monitor ambient incident solar UV-B regime during the natural period of near-surface occurrence, to relate laboratory results to real-time solar UV-B, and to determine if the various species from different seasons also differ in UV sensitivity.

Materials and Methods

The present experiments and measurements were conducted at the National Marine Fisheries Service/NOAA Aquaculture Laboratory at Clam Bay, Manchester, Washington, directly across Puget Sound from Seattle. Seminatural enclosures were established using two 80- \times 250-cm water tables, each divided into 10 troughs of 30-cm depth. Seawater was pumped continuously from the bay; the water was sand-filtered ($\approx 10 \mu\text{m}$) and passed under germicidal UV for partial sterilization, before flowing through the water tables. Within the water table, each trough held five replicate plastic baskets (14 \times 15 \times 12 cm with 1.1-mm mesh size), which contained the experimental animals in a water depth of 8 cm. If required for containment, very small organisms were placed within net liners (110- μm mesh) or in 1,000-ml beakers held by the baskets. Ten specimens were placed in each test container.

Simulation of ambient and enhanced solar irradiance at 290–315 nm was provided by a lamp/filter system similar to that suggested by Sisson and Caldwell (1975). Double-lamp fixtures, each holding one 119-cm Westinghouse[®] FS-40 fluorescent “sun-lamp” and one “cool white” (CW) fluorescent lamp, were fitted with Kodacel[®] TA filters (cellulose triacetate plastic sheets) and positioned above the individual troughs. The cellulose triacetate light filters eliminate wavelengths shorter than 290 nm. The length of the light fixtures exceeded the trough length, so that all organisms were exposed only to the center 2/3 of the lamps, and not to the ends of the lamps where irradiance decreases abruptly. UV-B intensity was adjusted by varying the light-filter thickness (combinations of 5-, 10-, and 20-mil sheets) and the distance between the UV-B source and the water surface. At least one trough, picked at random, held the control organisms, which were irradiated by filtered cool-white fluorescent light only. For maximum

stability of spectrum and intensity, all lamps were preburned for 100 h before use. Light filters were routinely cleaned or changed to maintain initial UV-B intensities. Only the highest UV-B levels produced significant light-filter solarization. The duration of all light exposure was 3 h each day, centered around solar noon. This photoperiod was chosen to simulate solar effective daily doses of UV-B, while retaining a reasonable approximation of solar noon UV-B intensity. A variable intensity was considered impractical, and shorter or longer exposures would have required unrealistically high or low intensities. Experimental UV-B levels were chosen to bracket typical incident noon UV-B, and to approximate the estimated daily UV-B irradiation.

In the earliest experiments, controls with cool-white light had lower mortality than controls with no supplemental light. Possibly this was the result of higher rates of activity and feeding when under visible light stimulus. Therefore, test as well as control organisms received at least some cool-white light in subsequent experiments. It was also believed that the addition of longer wavelength (visible) radiation to the UV stress would better simulate the solar regime, and allow the organism's potential photorepair mechanisms to replace damaged tissues and cells (Caldwell, 1971).

Egg-bearing females of the shrimp *Pandalus danae* and *P. hypsinotus* were collected from Clam Bay, central Puget Sound. Even though the species are found in Puget Sound proper, egg-bearing *P. platyceros* and *Cancer magister*, as sources of larvae for these experiments, were collected from Hood Canal. Females of these shrimp and crab species carry the eggs until hatching; this generally occurs locally from late January through April. *Cancer oregonensis* megalops larvae and the adult euphausiids *Thysanoessa raschii* were collected at mid-day from surface swarms in Clam Bay.

Larval stages of the shrimp were described by Berkeley (1930). Additional details on *P. platyceros* have been documented by Price and Chew (1972). *Cancer magister* larvae were described by Poole (1966). The wild-caught *C. oregonensis* megalops larvae were identified from the descriptions given by Lough (1975), and *Thysanoessa raschii* was identified from the key of Boden et al. (1955).

Female shrimp and crabs, segregated by species, were held in tanks of continuously flowing filtered seawater. The holding tanks were drained and flushed each day so that larvae collected for any particular test were less than 1 day old. Larvae for experiments were removed from the near-surface of the holding tank using a flexible piece of plastic screen or a glass pipette; 10 larvae were counted into a small beaker, counted again, and rinsed into each test container.

Data for “Day 1” are of initial conditions and include only the newly hatched or freshly caught untreated organisms. Each day's light treatments were given simultaneously by automatic timer, after morning counting and other observations. Therefore, the specimens recorded for “Day 2” have received only 1 day's (3 h) UV or cool-white light exposure. The organisms were fed daily, usually on live brine-shrimp nauplii (Forss and Coffin, 1960), and counted daily, recording general behavior and molting frequency, and removing dead organisms and molted integuments.

All spectral irradiance measurements (250–800 nm) were made with an Optronic Laboratories[®] Model 741 spectroradiometer coupled with a Hewlett-Packard[®] 9815A computer for data reduction and digital printout. The low stray-light level with this instrument, essential for accurate spectral measurements over the 250–360-nm wavelength region, is achieved by using a holographic grating monochromator in combination with a filtered solar-blind photomultiplier. The spectroradiometer was periodically recalibrated using a 1,000-W quartz-halogen tungsten coiled-coil filament lamp

of standard spectral irradiance [National Bureau of Standards (NBS)], combined with an Optronics^R Model 83 precision regulated power supply (calibration also traceable to NBS).

Additional UV-B measurements were made using the Robertson-Berger (R-B) Sunburn Ultraviolet Meter (Berger et al., 1975; Billen and Green, 1975), with an excitation spectral response similar to that of the erythema action spectrum (see below).

The spectral irradiance of the fluorescent light sources was measured by aligning the spectroradiometric sensor to the plane of the two lamps in a fixture, at a distance equal to the distance between the lamps and the water surface under experimental conditions. The sensor was aligned vertically below a point 1/3 the distance from the lamp end; this point is representative of the uniform intensity of the middle 2/3 of the lamp.

Ambient incident irradiance was measured by pointing the sensor directly toward the sun; therefore this measurement included sky irradiance.

In general, the actual amount of energy required to produce an effect varies with wavelength, with maximum response occurring at different wavelengths for different effects. The biologically effective UV-B irradiance, as defined in this study, can be characterized in energy terms by the expression:

$$\text{UV-B}_{\text{BE}} = \int_{290 \text{ nm}}^{315 \text{ nm}} \varepsilon_{\lambda} I_{\lambda} d\lambda \quad (1)$$

where ε_{λ} represents the *relative* energy effectiveness for each wavelength as determined by the erythema (sunburning) action spectrum of Green et al. (1974). I_{λ} represents the measured spectral irradiance at any wavelength, λ , in units of energy density flux per wavelength, $\mu\text{W cm}^{-2} \text{ nm}^{-1}$.

An estimate of ε_{λ} can be made directly from the erythema action spectrum, or, as it was done in this study, calculated for each nm wavelength from its analytical representation (Green et al., 1974):

$$\varepsilon_{\lambda} = \frac{\alpha}{1 + e^{(\lambda - \lambda_0)/A}} + \frac{4\alpha' e^{(\lambda - \lambda_0)/A'}}{(1 + e^{(\lambda - \lambda_0)/A'})^2} \quad (2)$$

where $\alpha = 0.04485$, $A = 3.130$, $\lambda_0 = 311.4$, $\alpha' = 0.9949$, $A' = 2.692$, and $\lambda'_0 = 296.5$. For the erythema spectrum, the most effective wavelength has been established at about 297 nm. Once the spectral distribution of radiant energy of any UV source is determined with the spectroradiometer, the total erythemal effectiveness ("biological effectiveness") is calculated by multiplying the observed values of energy in each wavelength region by the corresponding relative effectiveness (ε_{λ}) and summing these values. In this way, the erythemal or biological effectiveness of any spectral distribution of radiant energy (lamps or sun) is expressed as the equivalent amount of energy of wavelength 297 nm that would produce the same biological effect as the measured polychromatic radiation. For the UV-B band, the erythema action spectrum would not give an effective value to wavelengths longer than 311 nm nor shorter than 283 nm (wavelengths shorter than 290 nm are eliminated by the cellulose triacetate filters). The erythema action spectrum reaches a second maximum within the UV-C band, but this is not of practical interest for the present study.

Results

Noon incident solar UV-B intensity was measured at Manchester for nearly two years. For most of the first year, only R-B meter observations were possible; during the second year, both spectro-

radiometric and R-B observations were made. The total irradiance data were converted to biologically effective irradiance. Minimum levels were near zero irradiance, which in the Puget Sound region might occur on any day of the year. With these effective irradiance envelopes, one can estimate the likelihood of particular solar UV-B levels.

Hourly changes in effective irradiance were determined on several days during the two years. The effective daily dose is the area under the curve of these hourly changes. A polynomial equation was empirically derived to estimate the effective daily UV dose from the noon total irradiance, as determined by R-B meter on cloudless days:

$$Y = 14.2x^2 + 8.87x - 1.69 \quad (3)$$

where y represents the effective daily dose (mW-s cm^{-2}) and x represents the noon total irradiance in R-B meter sunburn units. From this relationship, seasonal changes in maximum and median effective daily dose were estimated (Fig. 1). This relationship is not valid on days of variable cloud cover, so that calculated median daily doses are not as accurate as the estimates for maximum daily doses.

Laboratory UV-B levels were selected to approximate incident solar spectral irradiance at present levels and under reduced atmospheric ozone. Only measurements from the R-B meter were available during the earliest experiments. It was subsequently determined that R-B measurements of sun and FS-40 sunlamps can be compared in terms of *total* irradiance within the UV-B band, but because of spectral differences, the *biologically effective* irradiance is not equal. An examination of the UV-B region (Fig. 2) indicates differences near the maximum erythemally effective wavelength of 297 nm. As a result, the *biologically effective* irradiance from the solar sources and from the lamp sources will differ significantly even with equivalent R-B meter values and total irradiance (Fig. 3). This does not diminish the usefulness of the rapid and portable R-B meter; one need only consider the relationships between *effective* irradiance of the separate spectra.

The initial experiments, which equated R-B meter values of sun and sunlamps, resulted in the use of an effective irradiance for sunlamps which was more than twice what it was believed to be (Fig. 3). Therefore, all UV-irradiated organisms in the earliest experiments received fatal doses, evaluated by spectroradiometer after the fact (Figs. 4-5). Experiments with shrimp larvae exposed to lower laboratory UV intensities (Fig. 6) indicate an effective-intensity survival threshold of about $4 \mu\text{W cm}^{-2}$ (297 nm-eq.) – highly significant after 7 days. The thresholds are based on the lowest level of irradiance where statistically significant (exceeding the 95% confidence limits of five replicates) and irreversible effects occur between the controls and the treatments. Below the threshold UV levels, larval stage development did not differ from that of the control organisms.

The first larval stage (zoea) of dungeness crab (*Cancer magister*) demonstrated effects similar to the shrimp larvae under UV stress (Fig. 7). In this case, the threshold lies near $6 \mu\text{W cm}^{-2}$ (297 nm-eq.), with a significant affect on survival appearing in 7 days. In contrast, the second larval stage (megalops) of a closely related species (*C. oregonensis*) exhibited a very high threshold of $12 \mu\text{W cm}^{-2}$ (297 nm-eq.), with effects noted after 20 days (Fig. 8). With the crab larvae, no reduction in development (molting) was noted among the specimens irradiated with subthreshold levels of UV (Fig. 9).

The reaction of euphausiids was similar to that of the dungeness crab larvae. After 7 or 8 days, a significant reduction in survival

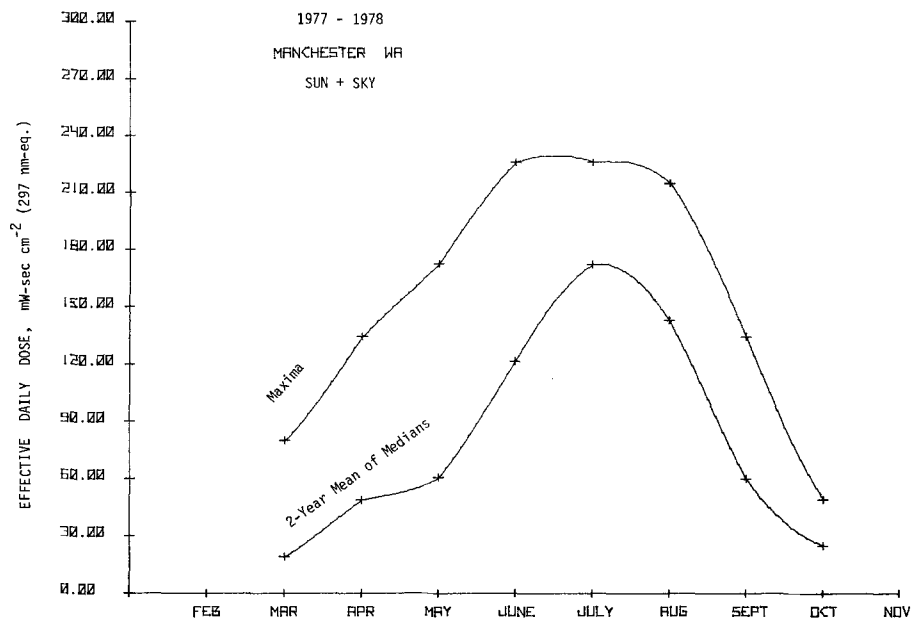


Fig. 1. Effective UV-B solar daily dose; Manchester, Washington, 1977-1978

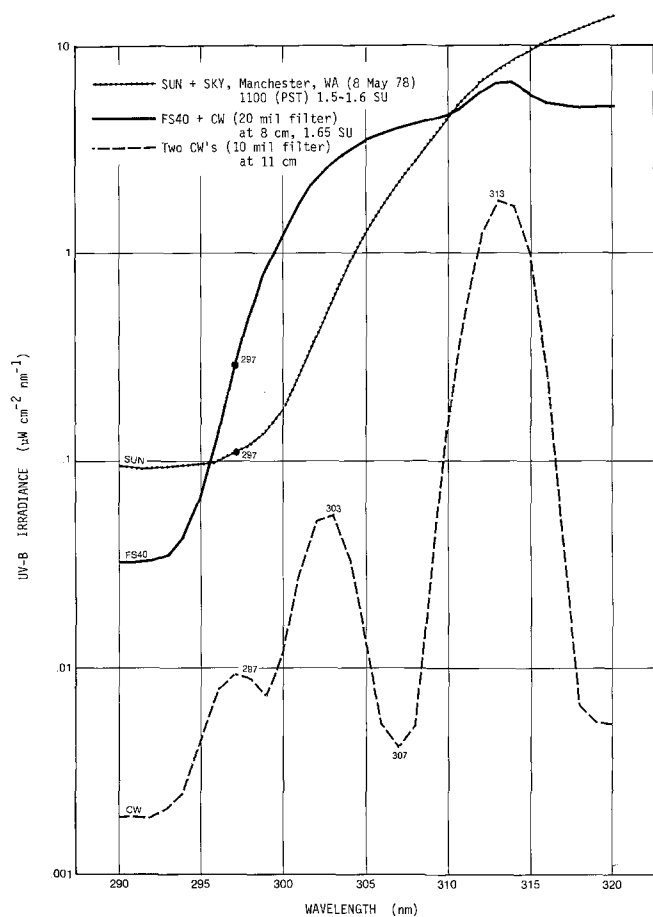


Fig. 2. Spectral irradiance of solar and artificial light sources, 290-320 nm, measured spectroradiometrically

was noted in specimens receiving in excess of $6 \mu\text{W cm}^{-2}$ (297 nm-eq.) effective irradiance (Fig. 10).

The estimated threshold intensities for the principal experimental zooplankton groups, the number of days required for a signifi-

Table 1. Estimated biologically effective UV thresholds for principal experimental zooplankton groups

	Effective irradiance [$\mu\text{W cm}^{-2}$ (297 nm-eq.)]	Effective daily dose ($\text{mW-s cm}^{-2} \text{d}^{-1}$)	Days for significant effect on mortality	Total dose (mW-s cm^{-2})
Shrimp larvae	4	45	8	360
Crab larvae (zoea)	6	65	7	450
Crab larvae (megalops)	12	130	20	2,600
Euphausiids	6	65	7	450

cant survival effect, and the daily and total dose thresholds are shown in Table 1. In these cases the observed main effect was simple survival. The same daily dose threshold values are derived with respect to general activity of the organism, on a scale from 3 to 0 (3 = totally active; 2 = leg movement; 1 = inactive; 0 = dead), but the effect is seen 1 or 2 days earlier. Preliminary experiments suggest that inactive organisms cannot recover even if the UV stress is removed.

Discussion

Qualitatively, the reactions of the zooplankters tested under UV stress are similar. Horizontally trending survival curves represent dose ranges within which the organism can cope with the damage produced. At greater doses, where the survival curve becomes steep, either the repair systems themselves may have become inactivated by the radiation, or the damage to the general tissues is beyond the capacity of the repair systems. There is an insufficient number of experiments to demonstrate reciprocity, but within non-extreme UV levels short exposures of high intensities may result in effects equivalent to those from longer exposures of low inten-

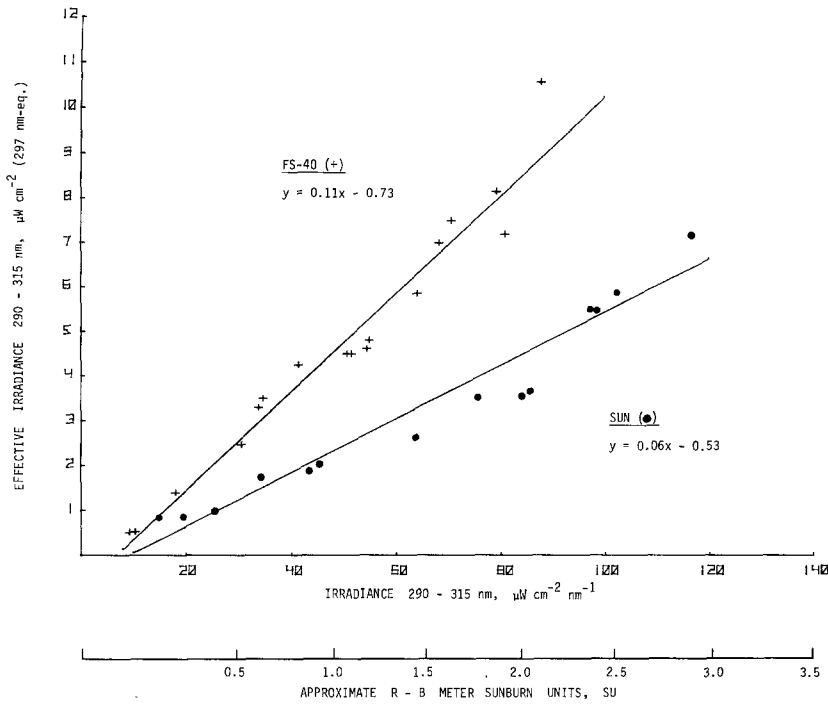


Fig. 3. Relationship between total UV-B irradiance (290–315 nm) and biologically effective UV-B irradiance, for sunlamp and sun + sky

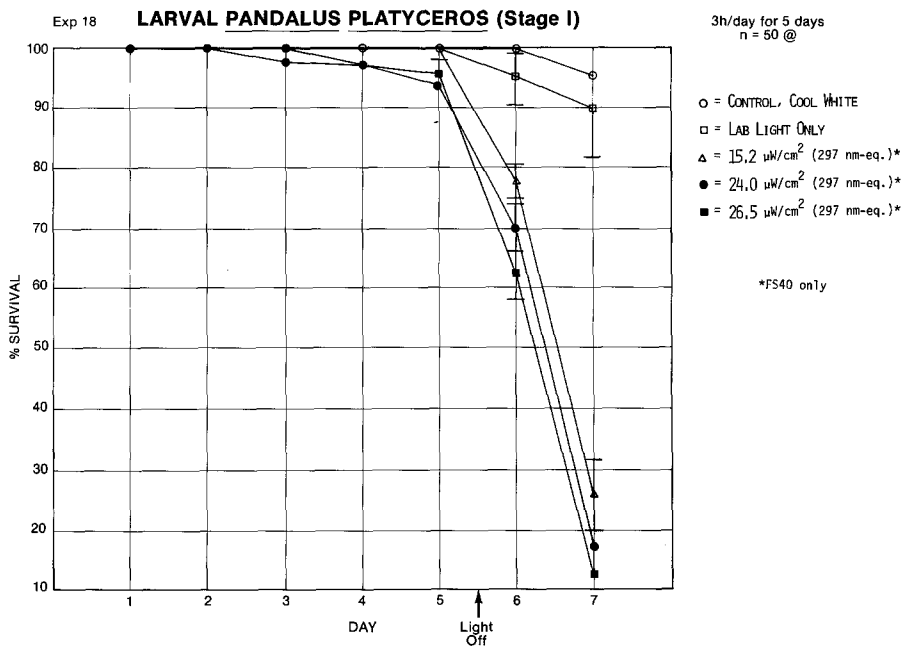


Fig. 4. Percent survival from birth through 7 days of larval *Pandalus platyceros*, at four levels of UV-B radiation. Temperature 8.7–9.0°C. Capped vertical lines represent 95% confidence limits of five replicates

sities. This will be an important concern of future investigations. Data from all of the present shrimp larvae experiments are summarized in Fig. 11, which shows a proposed relationship between total effective dose and survival. Above the 360 mW-s cm⁻² (297 nm-eq.) total effective-dose threshold, there is a rapid increase in mortality. It will be difficult to assign practical and precise threshold values until functionally fatal effects have been clearly defined. It is not necessary to wait until the organism is dead before an irreversible detrimental effect can be established. In this respect, these thresholds are overestimated. On the other hand, this is probably offset by the presently unknown real decrease of UV intensity with depth. Certainly the organisms can adjust

their depths (actively as well as passively) within the near-surface layer. Whether or not they could do so as a response to UV stress is unknown.

A comparison of the effective daily dose UV thresholds (Table 1) with the maximum effective solar daily dose rates for Manchester (Fig. 1) would indicate that the maximum solar levels exceed the sensitivity of all tested organisms. Obviously it is not realistic to compare these threshold values with maximum solar UV levels, since the organisms appear to be continually abundant. To be effective, these threshold levels probably must be exceeded during several consecutive days (Table 1). A more realistic approach would be to compare the threshold levels with median

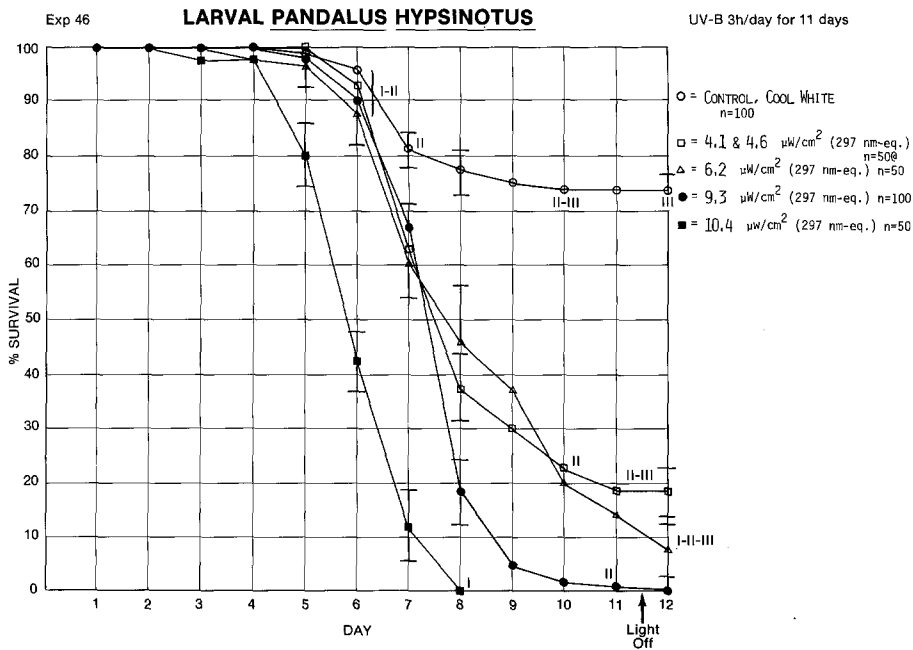


Fig. 5. Percent survival from birth through 12 days of larval *Pandalus hypsinotus*, at five levels of UV-B radiation. Temperature 9.0–10.8° C. Roman numerals indicate larval stages. Capped vertical lines represent 95% confidence limits of five replicates

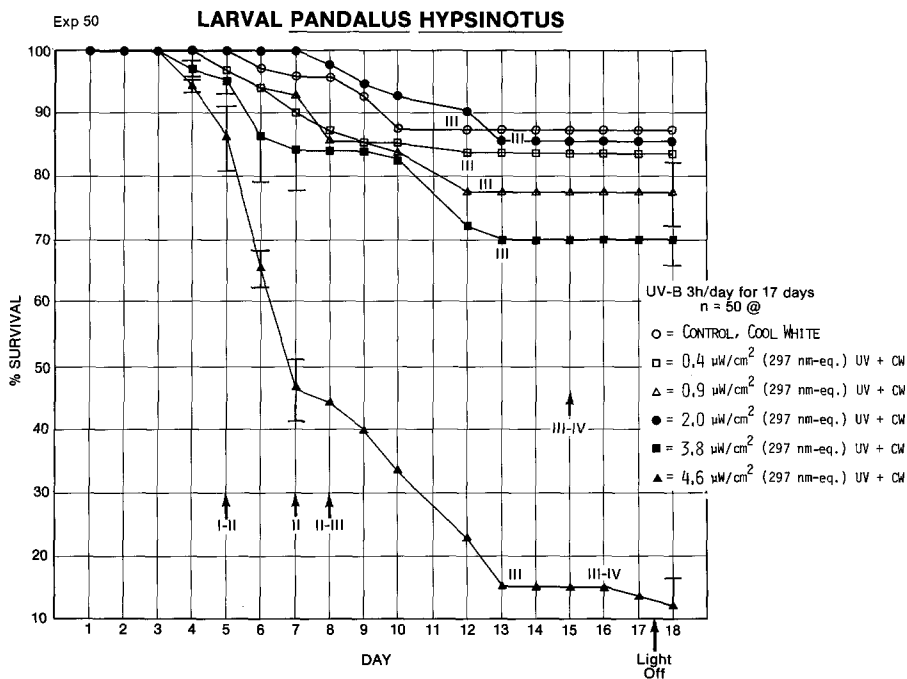


Fig. 6. Percent survival from birth through 18 days of larval *Pandalus hypsinotus*, at six levels of UV-B radiation. Temperature 9.4–11.1° C. Roman numerals indicate larval stages. Capped vertical lines represent 95% confidence limits of five replicates

solar UV levels (Fig. 12). The thresholds for all groups would then appear to be above the present median solar incident UV levels, at least until late in the time span of natural occurrence near the surface. It is possible that UV levels have exerted a considerable influence in the long-term adjustments of these populations to those specific seasons. Of course many other physical as well as biological factors operate concurrently, and the organism's life cycle is a compromise with the total environment. Late in the surface season, it is possible that natural UV levels exert a detrimental effect, particularly on the shrimp larvae, which have a lower *total dose* tolerance than crab larvae.

The subsurface UV values have not yet been determined, because of instrumentation problems; most likely these UV values will be significant through the upper few meters. As stated above, the *in situ* decrease in UV intensities with depth may be offset somewhat by irreversible effects on the zooplankton. The thresholds for irreversible damage appear to be substantially less than those based on absolute survival. This may not be true for UV intensity, but it appears to be the case for *total dose* (i.e., the length of time of exposure to a given intensity is considerably less for probable detrimental sublethal effects than for mortality).

Estimates of effective UV daily doses for Manchester, under

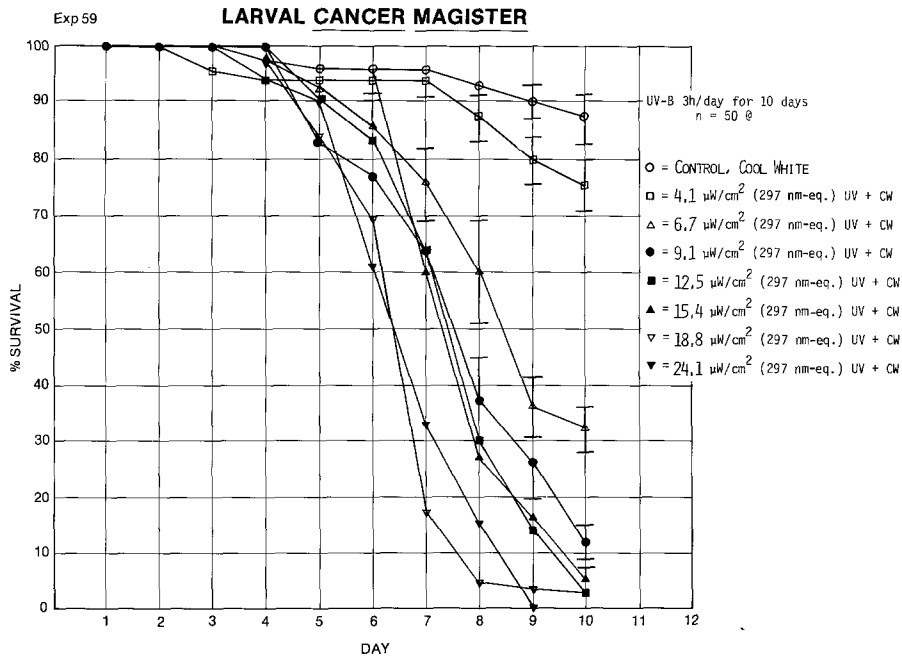


Fig. 7. Percent survival from birth through 10 days of *Cancer magister* larvae (zoaea), at eight levels of UV-B radiation. Temperature 11.4–13.0° C. Capped vertical lines represent 95% confidence limits of five replicates

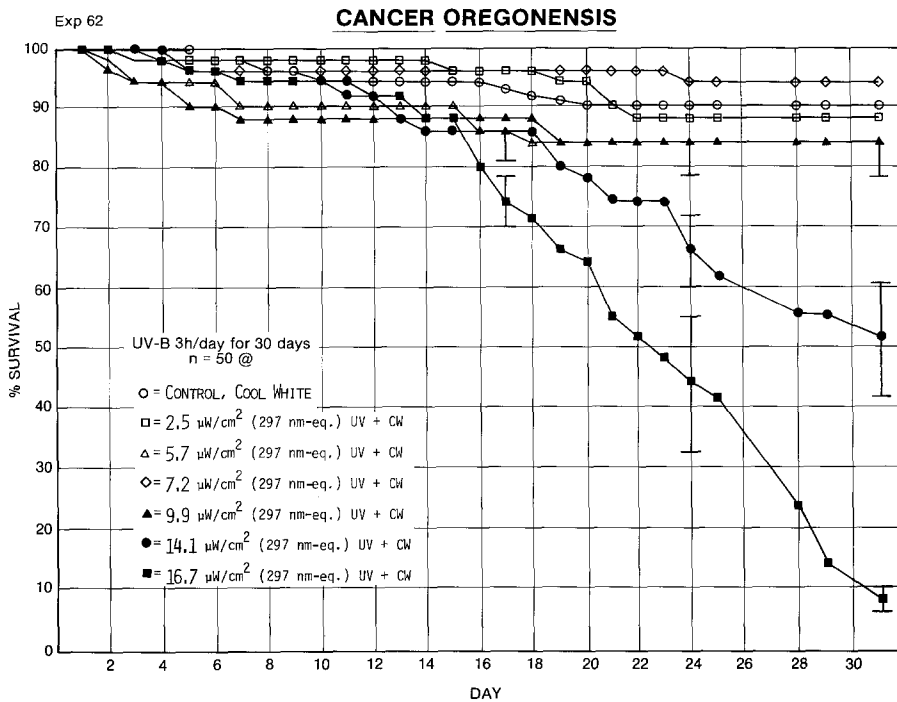


Fig. 8. Percent survival of wild-caught *Cancer oregonensis* larvae (megalops) over 31 days, at seven levels of UV-B radiation. Temperature 11.8–14.5° C. Capped vertical lines represent 95% confidence limits of five replicates

various ozone reductions, are also compared to the UV survival thresholds (Fig. 12). Obviously the probability that UV thresholds will be exceeded will increase with diminishing ozone. However, even with a 40% ozone reduction, there appears to be a “window” of safety at the beginning of each group’s surface season. This season could be significantly shortened by a 20% ozone reduction. Whether or not the populations could endure with a drastically reduced time of near-surface occurrence is not known. Success of any year-class depends on the timing of a great number of other events besides UV levels. Early larvae may do well one

year, whereas only late larvae may survive in a subsequent year. However, an additional stress is not likely to be beneficial.

The composition and intensity of solar UV irradiation to which surface-living zooplankton are actually exposed in the field are of particular interest. The experiments using artificial sources of UV irradiation, comparable to the incident solar UV-B spectrum, could have demonstrated that the zooplankton were essentially indifferent to natural UV levels. However, in each case there were effects to zooplankton following irradiation. These organisms tolerated UV-B irradiance levels up to threshold levels with no signif-

Exp 62

CANCER OREGONENSIS

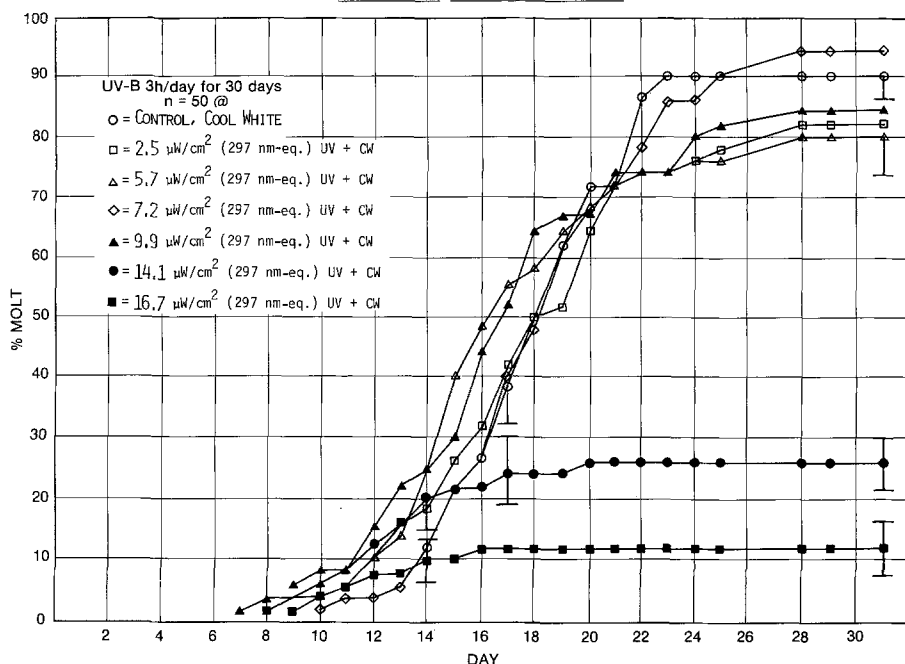


Fig. 9. Percent molt to first crab stage of *Cancer oregonensis* megalops (same experiment as Fig. 8)

Exp 7 **THYSANOESSA RASCHII**

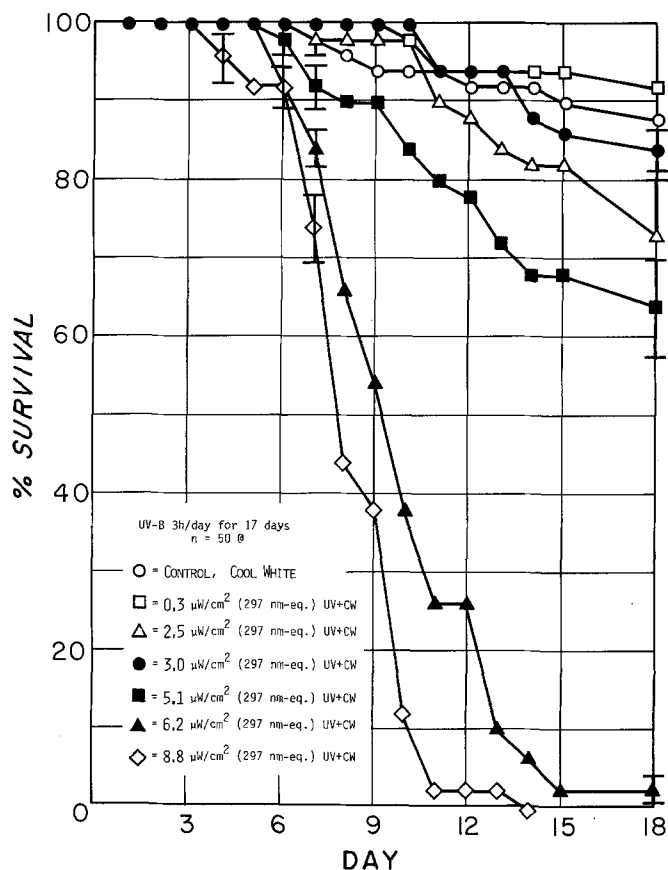


Fig. 10. Percent survival of wild-caught *Thysanoessa raschii* adults over 18 days, at seven levels of UV-B radiation. Temperature 9.1–11.2° C. Capped vertical lines represent 95% confidence limits of five replicates

icant reduction in survival or developmental rates compared to control organisms. That larval stage development appeared to be unaffected below survival threshold UV levels is an important observation, since the ultimate survival of the larvae depends upon their proper and timely development. Beyond the threshold levels, development and survival rapidly declined. The apparent UV thresholds are near present incident UV levels. Nevertheless, the implication of these experiments for zooplankton in nature remains in some doubt because of lack of information on the subsurface UV spectrum, the unknown *in situ* behavior of irradiated zooplankton, and unknown sublethal and pre-lethal effects.

Increases in UV through ozone depletion would apparently create a significant additional stress to the seasonal near-surface stages of these species. It is possible that natural UV levels have had a selective role in the seasonal adaptation of these species. The question remains: how much of their surface-living time could these species forego and still maintain survivor-level populations?

The degree to which other zooplankton groups would be affected by these levels of UV-B irradiation cannot be predicted. Although, in Crustacea, the same basic tissues would likely be involved, and therefore the response would be qualitatively similar, species vary substantially in sensitivity to UV-B radiation. If the *accumulated* level of UV-B radiation is the most important factor in damage, then increased UV through ozone depletion may significantly affect even species that are moderately resistant to short exposures of high UV intensities.

Acknowledgements. This study was supported principally through the Stratospheric Impact Research and Assessment Project of the U.S. Environmental Protection Agency; the authors thank Edward C. DeFabo for his interest and assistance. Our gratitude is also extended to Conrad V.W. Mahnken, National Marine Fisheries Service, for his essential technical and logistic support.

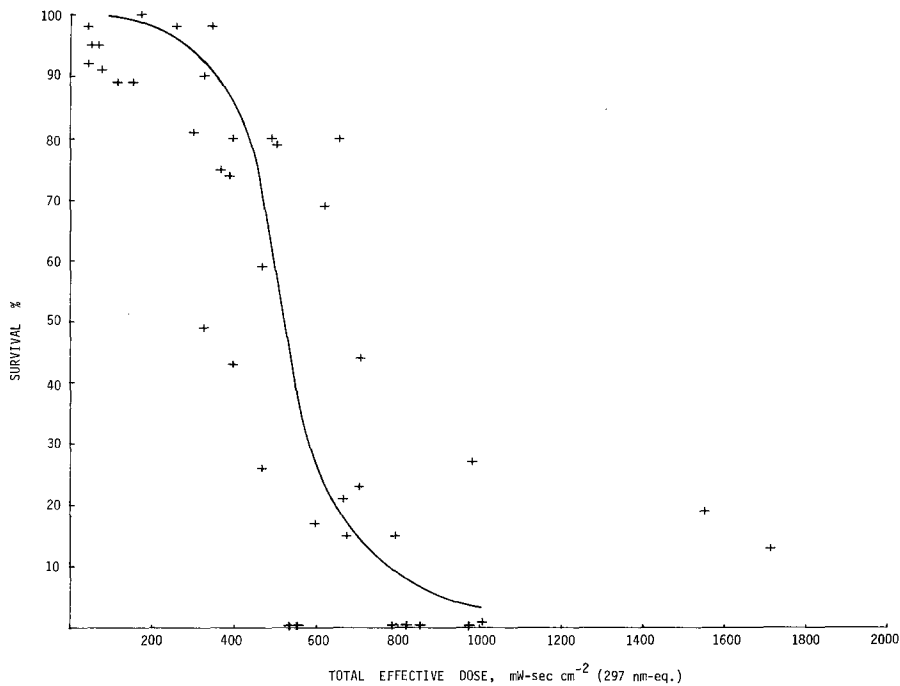


Fig. 11. Proposed relationship between survival of shrimp larvae and total accumulated effective UV-B dose (survival data normalized to non-irradiated deaths)

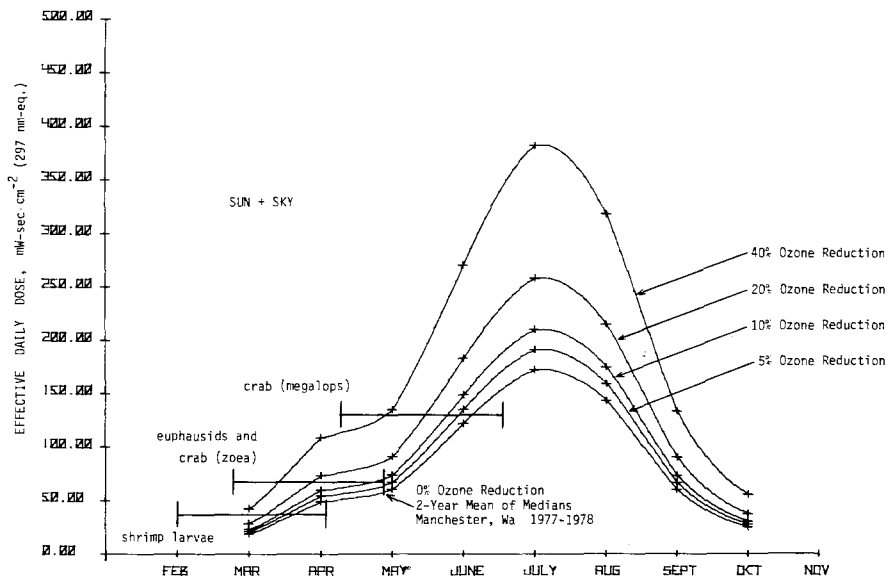


Fig. 12. Estimated effective UV-B solar daily dose at various atmospheric ozone concentrations, based on 2-year mean of medians; Manchester, Washington, 1977-1978. Effective-dose increments are from the erythema-dose/ozone-concentration relationship of Allen and Gausman (1975). Also shown are approximate thresholds of UV-B daily dose for principal experimental zooplankton groups, in natural seasonal position

References

- Allen, L.H., Gausman, H.W.: Penetration of solar ultraviolet radiation into terrestrial plant communities. *Impacts of Climatic Change on the Biosphere, CIAP Monogr.* **5**, 1(2), 78-108 (1975)
- Berger, D., Robertson, D.F., Davies, R.E.: Field measurements of biologically effective UV radiation. *Impacts of Climatic Change on the Biosphere, CIAP Monogr.* **5**, 1(2), 235-264 (1975)
- Berkeley, A.A.: The post-embryonic development of the common pandalids of British Columbia. *Contr. Canadian Biol. Fish., n. ser.*, **6**, 79-114 (1930)
- Billen, D., Green, A.: Comparison of germicidal activity of sunlight with the response of a sunburning meter. *Photochem. Photobiol.* **21**, 449-451 (1975)
- Boden, B.P., Johnson, M.W., Brinton, E.: The Euphausiacea (Crustacea) of the North Pacific. *Bulletin Scripps Inst. Oceanogr.* **6**, 287-400 (1955)
- Caldwell, M.: Solar UV irradiation and the growth and development of higher plants. *Photophysiology* **6**, 131-177 (1971)
- Calkins, J.: Measurements of the penetration of solar UV-B into various natural waters. *Impacts of Climatic Change on the Biosphere, CIAP Monogr.* **5**, 1(2), 267-296 (1975)

- Cheng, L., Douek, M., Goring, D.: UV absorption by gerrid cuticles. *Limnol. Oceanogr.* **23**, 554–556 (1978)
- Clyne, M.: Destruction of stratospheric ozone? *Nature* **263**, 723–726 (1976)
- Forss, C.A., Coffin, H.G.: The use of the brine shrimp nauplii, *Artemia salina*, as food for the laboratory culture of decapods. Walla Walla College Publ. Biol. Sci. **26**, 1–14 (1960)
- Giese, A.C.: Living with our sun's ultraviolet rays, pp. 1–185. New York: Plenum Press 1976
- Green, A., Sawada, T., Shettle, E.: The middle ultraviolet reaching the ground. *Photochem. Photobiol.* **19**, 251–259 (1974)
- Hudson, R.D. (ed.): Chlorofluoromethanes and the stratosphere. NASA Reference Publ. **1010**, 1–266 (1977)
- Koller, L.R.: Ultraviolet radiation. Second edition, pp. 1–312. New York: John Wiley 1965
- Lough, R.: Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969–1971. Unpublished PhD Thesis, pp. 1–299. Oregon State University 1975
- Magoon, C.D.: Shrimp fishing in Washington. Washington State, Dept. Fish., Information Booklet **3**, 1–21 (1974)
- Poole, R.: A description of laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda Brachyura). *Crustaceana* **11**, 83–97 (1966)
- Price, V.A., Chew, K.K.: Laboratory rearing of spot shrimp larvae (*Pandalus platyceros*) and description of stages. *J. Fish. Res. Bd. Canada* **29**, 413–422 (1972)
- Sisson, W.B., Caldwell, M.: Lamp/filter systems for simulation of solar UV irradiance under reduced atmospheric ozone. *Photochem. Photobiol.* **21**, 453–456 (1975)
- Smith, R.C., Calkins, J.: The use of the Robertson meter to measure the penetration of solar middle-ultraviolet radiation (UV-B) into natural waters. *Limnol. Oceanogr.* **21**, 746–749 (1976)

Received September 12, 1979