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Global atmospheric pollution from chlorofluorocarbons has the potential of causing significant reductions in the concentrations of stratospheric ozone. If the production of chlorofluorocarbons were to continue into the future at the rate prevalent in 1977, the steady state reduction in total global ozone could be between five percent to ten percent. This predicted ozone loss would result in an increase in the daily transmission of biologically harmful solar ultraviolet (UV-B, 290-320 nm) radiation. However, there have been relatively few studies concerned with the biological significance of increased UV-B radiation at the earth's surface.

Two different estuarine benthic diatiom assemblages were exposed to solar visible radiation and three levels of simulated solar UV-B radiation. A sunlamp/filter system was used to simulate a natural UV-B spectrum. Artificial substrates colonized by diatoms recruited from Yaquina Estuary and sediment-associated diatoms removed from intertidal sandflats in Yaquina Estuary were the two diatom assemblages examined for UV-B sensitivity. Experiments

were conducted in flow-through microcosms located in a greenhouse at the Oregon State University Marine Science Center in Newport, Oregon. All three experimental UV-B radiation treatments (high, low, control) were present in each microcosm. The artificial substrate assemblages were sampled during the winter and several spring/summer experiments. Sediment community experiments were conducted in the summer. Chlorophyll _a_ concentration, biomass (ash-free dry weight) and primary productivity (radiocarbon uptake) were the parameters measured at each sampling date for the sediment and artificial substrate studies; community composition was determined for diatom assemblages attached to artificial substrates.

A consistent response of the diatom assemblages attached to artificial substrates was an alteration of community structure following four weeks of exposure to UV-B radiation. Analysis of variance of biomass, chlorophyll _a_ and radiocarbon uptake data indicated no significant depression in these parameters by UV-B radiation during each experiment. In fact, in some experiments UV-B radiation appeared to have a beneficial effect. The response of sediment-associated estuarine diatom assemblages to UV-B radiation was different than that observed with the artificial substrate diatom assemblages. There was a significant depression in biomass accumulation following one week of exposure to UV-B radiation and a significant depression in primary productivity following three weeks of exposure to high levels of UV-B radiation.

Response to Ultraviolet (UV-B) Radiation by Attached Assemblages of Estuarine Diatoms

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INTRODUCTION

Recent research has established that atmospheric pollution from chlorofluorocarbons and other gases causes a reduction in the ozone layer by five to ten percent (NAS 1982). As a consequence, an amplification of UV-B radiation (290 - 320 nm) transmitted through the ozone layer is expected. UV-B radiation comprises only a small fraction (less than 1%) of the total solar spectrum, it can have a major impact on biological systems due to its actinic nature. For marine phytoplankton, enhanced UV-B radiation does not only directly affect growth, reproduction, photosynthesis and other metabolic processes but also has an indirect influence on phytoplankton via alteration of the community composition of the ecosystem. However, there have been few studies on the effects of UV-B radiation on marine benthic diatom communities. This may be a serious oversight considering the importance of benthic diatoms in estuarine food webs.

Nearly all of the current information on biological effects of UV-B radiation on plants is based upon controlled environmental studies conducted in growth chambers. In these chambers many environmental variables (temperature, water, nutrients, etc.) are

optimized for plant growth. Such ideal conditions are rarely found in nature. Contributing further to this problem is that the level of photosynthetically active radiation (400-700 nm) in growth chambers is often one-third to one-tenth of natural sunlight. There is some evidence that naturally occurring levels of visible radiation may have an ameliorating effect on UV-B induced damage to plants. This would result in a tendency in these laboratory studies, which used low visible radiation sources, to overestimate the consequences of global ozone depletion on the biosphere.

The goal of this thesis was to measure the response to UV-B radiation by estuarine benthic diatom assemblages under naturally occurring levels of visible radiation. Artificial substrates colonized by diatoms recruited from Yaquina Estuary, Oregon and sediment-associated diatoms removed from intertidal sandflats in Yaquina Estuary were the two different benthic diatom assemblages examined for UV-B sensitivity. Benthic diatom assemblages which inhabit the surface of sediments are often dissimilar in species composition to the epilithic, epiphytic and planktonic diatom assemblages of estuaries. Artificial substrates colonized by estuarine diatoms represent an assemblage comprised of species derived from epilithic, epiphytic and planktonic diatom assemblages in the estuary. The first chapter reports on the response to UV-B radiation by diatom assemblages colonizing artificial substrates. The artificial substrate experiment was repeated at different times in the year to determine if there was a seasonal difference in the response by the benthic diatom assemblages to UV-B radiation. The

second chapter examines the response to UV-B radiation by sediment-associated diatoms. The first chapter can also be viewed as an effort to measure the effect of UV-B radiation on the colonization of new substrates by benthic diatoms. In comparison, the second chapter is an attempt to measure the effect of UV-B radiation on an established, natural community of benthic diatoms.

LITERATURE REVIEW

Environmental photobiology is an area of research which "attempts to examine photobiological processes and their relationships with complete ecosystems" (Seliger 1977). The photobiological process of photosynthesis and its relationship to ultraviolet (UV) radiation and benthic (attached) marine diatoms within estuarine ecosystems is the topic of the following literature review. The first section reviews the role of benthic diatoms in estuaries and the methods employed in sampling and analyzing these microalgal assemblages. The second section reviews the reponse of benthic marine diatom assemblages to their environment, in undisturbed as well as in altered habitats. The final section examines the role of solar ultraviolet radiation in marine ecosystems. Recent data suggest increasing levels of biologically harmful ultraviolet radiation are striking the earth's surface as a result of the photochemical destruction fo the ozone layer in the upper atmosphere by chlorofluorocarbon-based aerosol pollutants. This final section of the review surveys the history of the ozone problem and the potential impact enhanced UV radiation could have on marine benthic diatom assemblages.

Description of and Methods for Analysis of Benthic Diatoms in Estuaries

The word estuary is derived from the Latin word 'aestus', which means tide. The definition most commonly used is "a semi-enclosed

coastal body of water which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage" (Pritchard 1967). Estuaries are common features of coastlines and make up 80% to 90% of North American Atlantic and Gulf coasts and 10% and 20% of the Pacific coast (Emery 1967) but they are uncommon features during most of the earth's history (Russell 1967). They rank high along with tropical rain forests and coral reefs as naturally productive ecosystems (Odum 1972). Their high primary productivity supports large populations of commercially and recreationally important species of fishes and shellfishes for spawning and development during their early life stages. (Hedgpeth 1957; McHugh 1966; Kutkuhn 1966). However, because of the varied and conflicting demands humans place on them, estuaries are of the greatest importance to mankind (Schubel and Hirschberg 1978). Humans are the most estuarine dependent organisms in the biosphere and any shortening in the useful life of an estuary, either through climatic events or poor management, would lead to serious consequences for mankind (Schubel and Hirschberg 1978).

When describing the composition of the plant life in estuaries, it is necessary to distinguish between several terms which often are used (incorrectly) as synonyms for the benthic microalgal component. The term 'periphyton' refers to the attached microalgae. As part of the benthos, the microalgae are also an integral part of attached microcommunities or Aufwuchs. 'Aufwuchs' includes bacteria, yeasts, fungi, protozoans, diatom-microalgae, non-diatom microalgae and

small invertebrates which are firmly attached to a substratum including free-living forms within the mat (Ruttner 1953). The diatom algae are the most common and most often studied component of the Aufwuchs, largely due to their general acceptance as monitors or "indicators" of water quality and environmental change (Weitzel 1979).

There is a variety of terms to describe the diatom flora associated with a specific substrate type. The epilithic flora attached to rock or non-living substrates, the epiphytic flora attached to macrophytes, the unattached epipelic flora of the sediments, and the epipsammic flora attached to sand grains are some of the more common terms (Round 1965). When referring to a collection of co-occurring diatom populations within an area or substrate of interest, the term diatom 'assemblage' has been suggested in lieu of 'community' because little is known about the interrelationships and dependencies among diatom populations and between diatoms and other groups of organisms (McIntire and Moore 1977).

Methods employed in sampling and analyzing periphyton assemblages are numerous. Descriptions of periphytic assemblages have historically taken the form of structural measurements, but more recently there has been a trend toward measurement of functional aspects as well. Simply stated, 'structure' refers to the measurement of abiotic or biotic characteristics at any point in time and 'function' implies measurement of any rate process of the system or its components (Rodgers et al. 1979). Examples of structure include species lists, diversity indices and biomass while examples of

function include species colonization rates, primary productivity and respiratory rates. Structure and function are dual attributes of any system and both should be investigated simultaneously (McIntire and Moore 1977; Cairns 1979).

Taxonomic structure was the earliest method used to define and describe periphyton. Data generated by identification and enumeration of species or types of organisms from assemblages is used differently by each investigator. One approach is to calculate community composition parameters or diversity indices in order to define community structure (Shannon and Weaver 1949; Simpson 1949; McIntosh 1967; Wilhm and Dorris 1968; Hurlbert 1971). These indices provide a means of transforming species list information into one numerical value. For communities of similar sizes and distribution, but comprised of different species, each community will have a similar numerical value of diversity. Measures of similarity, difference and distance provide comparisons of species association between communities and therefore take into consideration the kinds of species present as well as their distribution (MacArthur 1965; McIntosh 1967; Stander 1970). These coefficients are particularly useful in determining the location of discontinuities of species assemblages along environmental gradients (McIntire and Moore 1977).

Besides taxonomic analyses, there are a number of non-taxonomic methods used to analyze and compare the structure of periphyton assemblages. Gravimetric and pigment analyses are two common parameters employed as non-taxonomic structural characteristics. General methods for microalgal biomass measurement are reviewed by

Vollenweider (1969), Strickland and Parsons (1972) and Weitzel (1979).

Unlike pigment (chlorophyll) analyses methods, which express microalgal biomass, gravimetric methods do not distinguish between microflora or microfauna. Biomass expressed as ash-free dry weight represents the organic biological and sediment components of the assemblage or total organic matter concentration of the sample.

Pigment analyses are not without their own problems. Chlorophyll *a* is the most abundant pigment in algal cells but it is at best a rough estimate of biomass because it is a dynamic cellular constituent and can be affected by the algal cell's age and physiological condition (Vollenweider 1969). Non-functional chlorophyll (chlorophyllide) and chlorophyll degradation products (phaeophytin and phaeophorbide) may at times constitute a significant fraction of the chlorophyll and methods have been developed to correct for such bias (Yentsch and Menzel 1963; Lorenzen 1967; Whitney and Darley 1979).

Chlorophyll analyses for estimating the density of benthic microalgae in sediments are generally restricted to the upper centimeter of sediment cores and values range from 10 to 100 mg chl *a* $\cdot$ m^{-2} (Eaton and Moss 1966; Steele and Baird 1968). The amount of chlorophyll in intertidal sediments decreases with water depth and wave action (Fenchel and Staarup 1971; Riznyk and Phinney 1972), however live chlorophyll-bearing micro-algae have been found to a depth of 10 cm (Pamatmat 1968).

In contrast to structural measurements, functional measurements of periphyton assemblages are generally concerned with biochemical rate processes such as photosynthesis and respiration. Very few studies have emphasized taxonomic functional aspects which encompass the study of autecological, population and community dynamics and the influence of environmental factors on species colonization or emigration rates (Patrick 1977; Rodgers et al. 1979).

With regard to measuring primary production, crude rates of community productivity and primary productivity can be obtained from rates of accumulation of biomass and chlorophyll, respectively, on artificial substrates. Oxygen production and radiocarbon uptake are the two most common techniques for measuring primary production.

The light-dark bottle method of measuring oxygen production, pioneered by Gaardner and Gran (1927), provides estimates of gross primary production, respiration and net community production. The limitations and sources of error associated with this technique are discussed by Steemann Nielsen (1958), Strickland (1960) and Vollenweider (1969). Carbon-14 methods are 50 to 100 times more sensitive than dissolved oxygen techniques and provide the only standard method sufficiently sensitive to measure low rates of carbon uptake (Steemann Nielsen 1952). Specific technical problems encountered with carbon-14 methodology are reviewed by Strickland and Parsons (1958), Vollenweider (1969), and Peterson (1980).

Incorporation of radioactive tracers into the organic matter of plants during photosynthesis is used as a measure of the rate of primary production. The most severe shortcoming of this method is

that carbon-14 uptake in the dark bottle is limited to measuring active dark uptake of carbon dioxide plus abiotic formation of labelled particulate carbon. Oxygen uptake in the dark bottle represents respiration in the oxygen method and hence there is no direct estimate of respiration available with the carbon-14 technique (Peterson 1980). The result is uncertainity as to whether the radiocarbon method measures net (total photosynthesis less respiration) or gross (total photosynthesis) primary production or something between the two (Ryther 1954).

An important use or adaptation of the radiocarbon and oxygen techniques is to measure epibenthic production in shallow waters and intertidal sediments. The measurement of epibenthic production presents several problems not encountered in phytoplankton studies, many of which are associated with the algal-substrate relationship. A number of methods involve disturbing the sediment and thereby altering the physical and chemical environment surrounding the cells (Steele and Baird 1968; Hickman 1969; Gargas 1970; Riznyk and Phinney 1972). Where epipelic and epipsammic algal associations occur together, disruption of the sediment is necessary for estimating productivity of each algal assemblage. These are potential rates however and should be coupled with direct, in situ measurements of intact sediments for 'true' benthic productivity estimates (Riznyk and Phinney 1972; Hunding and Hargrave 1973).

Experiments with intact sediment cores revealed production to be approximately 60% lower than when sediments were disturbed (Cadee and Hegeman 1974). Several workers have used radiocarbon to study

in-situ algal production of intact marine sediments (Grontved 1960; Leach 1970; Skauen et al. 1971; Marshall 1973; Van Raalte et al. 1974; Matheke and Horner 1974), and more recently field respirometers in conjunction with intact sediment cores (McIntire and Amspoker 1980; Davis 1982). In almost all methods the algae are submerged when the measurements are made but intertidal sediments are exposed for varying lengths of time each day. Darley et al. (1976) devised a radiocarbon technique measure the productivity of benthic microalgae under exposed conditions. Holmes and Marshall (1982) measured gaseous carbon dioxide exchange from high intertidal estuarine sediments to determine maximal net photosynthetic rates when the sediments were unflooded. Flooding reduced net photosynthetic rates by 48% to 66%.

Estimated annual gross primary production by microalgae on tidal flats ranges from 0 to 325 $gC \cdot m^{-2}$ (Pomeroy 1959; Pamatmat 1968; Riznyk and Phinney 1972; Gallagher and Daiber 1974) and annual net primary production values range from 5 to 188 $gC \cdot m^{-2}$ (Cadee and Hgeman 1977; Davis 1982). Primary production values are dependent on sediment type, season and tidal height with little to no difference in photosynthetic pattern between epipelic and epipsammic cells (Cadee and Hegeman 1974; Colijn and van Buurt 1975). Gross primary production per unit chlorophyll (mg C $\cdot$ mg $chla^{-1}$ $\cdot$ hr^{-1}) was lowest for intact sediment communities (0.1 to 0.7) followed by isolated epipelic and epipsammic diatoms (2.3 to 6.9) from Yaquina Bay, Oregon (Davis 1982). Hickman and Round (1970) and Colijn and Van Buurt (1975) found similar low values for photosynthetic indices

(expressed as mg C fixed· mg chla^{-1} · h^{-1}) of mixed benthic diatom populations inhabiting intact sediment samples. Photosynthetic indices of benthic diatom communities are low in comparison to values for various natural phytoplankton communities which range from 0.1 for phytoplankton from oligotrophic lakes to more than 10.0 for diatom blooms at high temperatures (20° to 25°C, Parsons and Takahashi 1973).

Environmental Features of Estuaries Important to Benthic Diatoms

It is difficult to interpret the response of communities to environmental factors in field studies because several factors will often vary simultaneously. Laboratory model ecosystems or microcosms are an experimental approach to unravel many of the features of in-situ systems and provide a link between the laboratory study of selected species and holistic ecosystem analysis (Menzel 1980). Microcosms retain many of the complexities characteristic of the natural system but differ in that they can be manipulated, replicated and maintained in controlled environmental conditions. There is currently much interest in using microcosms as predictors of the fate and effect of chemical pollutants but they are also useful as models for understanding through exploration and hypothesis testing (Beyers 1963; Leffler 1978).

There are many factors important in the maintenance and distribution of diatoms in marine and estuarine waters. Density-dependent factors or species interaction involve competition or reaction to space limitation, organic excretions and grazing. Grazing pressure affects population size and diversity of periphyton communities. Marine littoral diatoms are the principal food of intertidal gastropods and their grazing strongly limits periphyton standing crop, primary productivity and species composition (Castenholz 1961; Nicotri 1977; Pace et al. 1979; Connor and Edgar 1982). Density-independent factors are environmental factors limiting or essential

which influence diatom development, such as salinity, temperature, nutrients and solar radiation.

In-vitro studies of the growth rates and photosynthesis of benthic diatoms reveals a broad salinity tolerance. The growth rate of mixed populations of sand and mudflat diatoms was evaluated in response to varying salinity (Admiraal 1977a). These estuarine diatoms were tolerant of a wide range of salinities which supports similar observations on benthic salt-marsh diatoms (Williams 1964; Drum and Webber 1966), epilithic diatoms in laboratory microcosms (Martin 1970), and culture studies with benthic diatoms (Medlin and Wilson 1979; Saks 1982). A low salinity (1 ^{o}/oo), but not a high salinity (20 ^{o}/oo), markedly altered the species composition of natural diatom populations cultured in vitro (Admiraal and Peletier 1980). These studies suggest estuarine diatoms may have limited value as indicators of salinity, but salinity may be a factor in determining distribution.

Salinity gradients have been correlated with diatom distribution in several neritic and estuarine areas. Species composition of epilithic flora during the winter was closely related horizontally to salinity gradients in Yaquina Estuary, Oregon. Horizontal discontinuities in the diatom flora occurred at locations where the salinity fluctuated around 5^{o}/oo (McIntire and Overton 1971; McIntire 1973; Moore and McIntire 1977). Epiphytic and sediment-associated assemblages from the same estuary were also correlated with horizontal salinity gradients (Main and McIntire 1974; Amspoker and McIntire 1978). A sharp discontinuity in the sediment flora was

observed where the mean salinity was 5 °/oo. The distributional patterns of seven dominant diatom species on the Eems-Dollard estuarine mudflats were also related to salinity gradients (Admiraal and Peletier 1980).

Temperature is an important environmental variable for benthic diatoms as evidenced by its control on the rate of photosynthesis and growth. Photosynthetic rates roughly increased by about 10% per C° between 4°C and 20°C, with 20°-22°C the optimum temperature for photosynthetic rates by mixed populations of benthic diatoms (Colijn and van Buurt 1975). Admiraal (1977a) found net photosynthesis of cultured benthic diatoms was optimal at 16°C to 25°C and at a light intensity of 2.5 to 5.0 $E \cdot m^{-2} \cdot day^{-1}$. Growth of benthic diatoms in vitro occurs from 4°C to 36°C, which is consistent with the known distribution records. The optimum temperature for growth is similar to or higher than the temperature from where the diatoms were isolated (Admiraal 1977a; Medlin and Wilson 1979). Diatom growth at temperatures higher than those of their natural habitat is not unique and may be a common discrepancy between in vivo and in vitro studies (Smayda 1969; Gessner 1970). Optimum growth rates of benthic diatoms in culture occurs from 16 °C to 25°C (Admiraal 1977a) and temperatures above 36°C stress many marine and estuarine algae and tend to inhibit growth (Saks et al. 1974). Temperature changes have altered the species diversity of benthic diatom assemblages in laboratory microcosms (Berglund 1972).

Nutrient levels also appear to have an effect on the kinds of species of diatoms present. Microalgal growth on sediments is

nutrient-limited only at certain times of the year and in the presence of large populations of the saltmarsh angiosperms (Van Raalte et al. 1976; Welsh 1980). Many species can accumulate large amounts of various nutrients under nutrient-rich conditions and thus are not dependent upon the external medium for some time (Admiraal 1977b).

In experiments with mixed populations of benthic estuarine diatoms in laboratory microcosms, there was no stimulatory effect from added silicate, nitrate, phosphate or wastewater on species composition or density (Admiraal 1978). In a similar field study, where nutrients were applied to the mudflat surface in small constant doses over a short period of time, no change in chlorophyll or diatom community structure was observed (Cardon 1982). Long term phosphorus enrichment of salt marsh sediment caused significant decreases in diatom diversity whereas nitrogen enrichment caused a decrease in the number of species only (Sullivan 1976). A second study using sewage sludge and commercial fertilizers applied to salt marsh sediments also showed a decrease in diatom diversity but did not result in any major change in standing crop (Estrada et al. 1974; Van Raalte et al. 1976).

These findings suggest that high concentrations of micro-nutrients; nitrate, phosphate and silicate are not limiting growth factors for sediment-associated diatoms. This type of diatom assemblage was highly tolerant of short term exposures to organic matter. Continuous exposure had an influence on species compo-

sition, but not on the capacity of the sediment to support diatom growth.

A high concentration of ammonia is a selective factor for diatom populations on mudflats. Addition of ammonia to natural populations of benthic diatoms kept in laboratory cultures either inhibited the growth of all species cultured or promoted growth of certain species (Admiraal 1977b; Admiraal and Peletier 1980). These results corroborate observations on the species composition of mudflat communities related to ammonia concentrations in the sediment (Sullivan 1978).

Sulphates are utilized in the metabolism of diatoms and are one of the required nutrients but sulphides are often toxic. Diatom populations harvested from reduced sediments have the highest sulphide tolerance and this suggests a possible role of free sulphide in the selection and distribution of some diatom species in sediments (Admiraal and Peletier 1979; Admiraal and Peletier 1980).

Light and those factors affecting the availability of light to substrate surfaces are important in regulating benthic diatom photosynthesis, growth and distribution. The effect of light on photosynthesis is usually regarded as the product of light intensity and length of day. The photosynthetic rate of mixed populations of benthic diatoms is saturated by a light intensity around 10,000 to 20,000 lux and at still higher light intensities no photoinhibition is observed (Taylor 1964; Pamatmat 1968; McIntire and Wulff 1969; Cadee and Hegeman 1974; Colijn and van Buurt 1975; Admiraal 1977a). Laboratory studies on intact sediments and isolated epipelic diatoms

from Yaquina Bay, Oregon indicated photosynthesis was light saturated at 200 to 400 $\mu E \cdot m^{-2} \cdot sec^{-1}$ (Davis 1982). Unialgal cultures of benthic diatoms exhibit photoinhibition at higher light intensities but this may reflect pre-culturing at low light intensities and how close the algal species was to their temperature optimum (Colijn and van Buurt 1975). This apparent lack of photoinhibition may be a feature of benthic diatoms which allows them to survive high irradiances on exposed intertidal mudflats (Taylor 1964).

When light is limiting or unavailable, it is possible some diatoms utilize facultative heterotrophic abilities for survival or slow growth (Hellebust and Lewin 1977) There are many facultative, and a few obligate heterotrophic diatom species, and most of these are species of pennate diatoms frequently found in organically enriched benthic environments (Lewin and Lewin 1960).

Photoperiod per se has not been regarded as an important factor of light on photosynthesis and growth. Light intensity 10% to 20% of full sunlight was measured at intertidal sites in Netarts Estuary, Oregon which corresponded to intensities above the level necessary for light saturation of photosynthesis (Davis 1982). Davis concluded photosynthesis was controlled by day length in Netarts Estuary, which has been observed in other estuaries (Cadee and Hegeman 1974; Admiraal and Peletier 1980). Castenholz (1964) showed for two littoral diatoms, Fragilaria striatula and Synedra fasciculata, that growth was day length dependent. Division rates for these two species were significantly lower during short day

periods but Melosira moniliformis and Biddulphia aurita showed little dependence of growth on daylength. Fragilaira grew well under continuous illumination but Biddulphia exhibited some growth inhibition under these conditions.

The vertical distribution of many diatom taxa in estuaries is related to illumination intensity and period of exposure to dessication. Castenholz (1963) demonstrated that directional orientation, and the resulting amount of exposure to direct solar radiation during low tides, was the most important factor determining the upper limits of diatom cover, density and species composition of littoral diatoms on the open coast of Oregon. Differences in species composition of vertically sampled epilithic and epiphytic assemblages from Yaquina Estuary, Oregon, were also closely related to dessication and insolation gradients (McIntire and Overton 1971; McIntire 1973; Main and McIntire 1974). However, differences in composition of Yaquina Estuary sediment-associated assemblages relative to variations in light intensity and intertidal emergence, were not apparent (Amspoker and McIntire 1978). Light intensity also had little to no value in accounting for observed structural differences in edaphic sediment communities of salt marshes (Sullivan 1978).

Ultraviolet radiation has been suggested as one adverse consequence of solar exposure, hence possibly important in determining the magnitude of marine littoral diatom density, species composition and distribution in the environment (Castenholz 1963). However, few investigators have actually measured the comparative

sensitivities of algae to solar ultraviolet radiation (McCleod and MacLachlan 1959; Thomson et al. 1980b; Saks 1982).

Solar Ultraviolet Radiation and Stratospheric Ozone

The ultraviolet portion of the electromagnetic spectrum is sub-divided into three regions: UV-C (40 - 290 nm), UV-B (290 - 320 nm) and UV-A (320 - 400nm). About 7% of the total solar output is ultraviolet radiation but a smaller portion actually penetrates the earth's atmosphere due to a series of stratospheric photochemical reactions involved in the formation and destruction of ozone (Caldwell 1979).

Ozone (O_3) is formed in the presence of a molecular oxygen (O_2), photons ($h\nu_1$) of energy with wavelengths between 40 and 280 nm, and a background molecule M:

$$O_2 + h\nu_1 \xrightarrow[150\ nm\ (max)]{UV\text{-}C} 2\ O^*$$

$$O^* + O_2 + M \longrightarrow O_3 + M$$

and it is dissociated by absorbtion of ultraviolet wavelengths less than 320 nm ($h\nu_2$; Chapman 1930).

$$O_3 + h\nu_2 \xrightarrow{UV\text{-}B,\ UV\text{-}C} O_2 + O^*$$

$$O^* + O_2 \longrightarrow 2O_2$$

The nitrogen cycle is a second method by which ozone is naturally removed from the stratosphere. Nitrous oxide (N_2O) is released to

the atmosphere by dentrifying bacteria found in soils and aquatic systems (Seliger 1977). In the stratosphere nitrous oxide reacts with reactive oxygen (O*) to form nitric oxide (NO) which acts as a catalyst for ozone destruction (Giese 1976).

$$N_2O + O^* \longrightarrow 2\ NO$$

$$NO + O_3 \longrightarrow NO_2 + O_2$$

Without interference, the result of these reactions is an equilibrium amount of ozone averaging 0.32 cm (0.24 - 0.46 cm) at standard pressure and temperature (Environmental Studies Board 1973). Only by altering either the rate of formation or destruction would the level of ozone change. The ultraviolet wavelengths which are most influenced by changes in ozone concentration, 280 -315 nm (UV-B), are also ones effectively absorbed by nucleic acids and proteins (Harm 1979).

Proteins and nucleic acids have absorption maxima at 278 and 260 nm, repsectively (Giese 1968). The absorption of ultraviolet radiation by nucleic acids can lead to cross-linkage of DNA to proteins, chain breaks and more commonly the formation of pyrimidine dimers (Smith 1977). General photochemical reactions of proteins to ultraviolet radiation include changes in solubility, changes in optical and physical properties, sensitivity to denaturation by heat and inactivation of enzymes.

In addition to nucleic acids and proteins, other potential ultraviolet chromophores in plants are abscissic acid, indoleacetic acid, flavoproteins and both forms of phytochrome. Changes in the

normal activity of these chromophores could lead to secondary effects such as changes in membrane permeability and inhibition of photosynthesis and respiration (Caldwell 1981).

There are various repair processes for ultraviolet radiation induced damage to DNA. Photoreactivation (PR) is a molecular repair mechanism for splitting pyrimidine dimers. PR requires the simultaneous or subsequent exposure to longer wavelength radiation (315 - 550 nm) and it has been demonstrated as an effective repair mechanism in algae and higher plants (Halldal and Taube 1972; Caldwell 1981). In contrast to PR, excision repair and post-replication or recombinational repair do not require light for operation. There is one report of excision repair of dimers in algal chloroplast DNA (Small and Greiman 1977).

A photoreactivation mechanism does not appear to participate in the repair of photosynthetic damage but there is evidence that effects of UV-B radiation on plant photosynthesis are dependent on the level of photosynthetically active radiation (400-700 nm). When exposed to UV-B radiation, there is a greater depression in plant photosynthesis under low levels of visible irradiance than under higher levels of visisble irradiance (Sisson and Caldwell 1976; Teramura 1980).

Non-lethal effects of UV-B radiation may be of ecological importance and the assumption has been that there is sufficient stratospheric shielding from ozone to prevent ultraviolet repair mechanisms from being overwhelmed. This assumption was challenged in

the early 1970's when evidence for ozone destruction was first presented.

The development of supersonic transport aircraft (SSTs) was the stimulus for research into the identification of possible ozone depletion catalysts (Johnston 1971; Crutzen 1972). Improvements in predicitive models showed the impact of SSTs on the ozone layer would be limited, but other ozone depletion agents were soon discovered. It was eventually determined that chlorofluorocarbons pose the greatest threat to the ozone layer (NAS 1979). At sea level chlorofluorocarbons (CFC) are chemically inert, insoluble, non-flammable, non-toxic and therefore popular as propellants in aerosols and as refrigerants (Howard and Hanchett 1975). The discovery of CFCs in the upper regions of the atmosphere along with the publication of a catalytic cycle of ozone destruction by free chlorine atoms, resulted in the proposal that photolysis of CFC provided the free chlorine atoms for catalytic destruction of ozone (Lovelock 1971; Stolarski and Cicerone 1974; Molina and Rowland 1974). Once CFCs diffuse into the stratosphere they remain for decades, potentially destroying significant amounts of ozone, until downward diffusion and tropospheric rainout removes the chlorine from the atmosphere.

One theory indicated that changes in the total ozone concentration of 0.15% per year could be expected, if CFC production continued at 1975 levels, with an eventual 2.7% decrease in ozone concentration if all uses of CFCs were totally banned (Tiede et al. 1979). The most recent prediction, based on a 1977 CFC release rate

scenario, is a 5% to 10% reduction in stratospheric ozone (NAS 1982; WMO 1982). The impact of these predictions should be judged along with the knowledge of the natural variation in thickness of the ozone layer and our efforts to curb the production of these chemicals.

The United States has banned the use of CFCs in many products but production outside the United States has increased. If world levels continue to increase to as much as the predicted 57% increase in the next twenty years a depletion greater than 5% - 10% is possible (Maugh 1979). There is also considerable daily and yearly variation for a given locality. The amount of ozone can change up to 10% within a day, 25% between spring and fall and as much as 5% yearly in the course of a decade (NAS 1979). The magnitude of this variation makes cyclical patterns of ozone variation difficult to establish (Cutchis 1974).

Ozone concentration also varies significantly with latitude and longitude (Dütsch 1974; Johnson et al. 1976). Ozone production is greater at the equator compared to polar regions but stratospheric currents transport it away from the equator so that the actual concentration is lowest in this region. In the Northern Hemisphere the total ozone concentration is at a maximum in the spring and a minimum in the fall with the central United States ozone layer varying between 0.28 cm to 0.35 cm (Cutchis 1974). Making accurate continuous measurements of ozone changes as small as 2% to 3% requires carefully calibrated instrumentation maintained over several years. For this reason, baseline values for many localities

at various time of the year have not been possible (Ramanthan 1976). Semi-empirical analytic formulae have been developed for calculating the global UV-B reaching the earth's surface as a function of wavelength, solar angle, aerosol thickness, surface albedo and ozone thickness (Green et al. 1974; Green et al. 1980; Baker et al. 1980).

Even with an awareness of the uncertainities and complexities involved in ozone depletion theory, numerous studies were initiated to explore the biological impact of increased levels of UV-B radiation to the surface of the earth (Environmental Studies Board 1973).

The biological effects of radiation are the consequence of absorption of specific wavelengths by specific molecules within cells and their resultant alteration. However, not all wavelengths of ultraviolet radiation are equally effective in producing biological effects. Action spectra weight each wavelength of radiation according to its effectiveness in producing a specific biological response. Most UV-B action spectra for plant processes (photosynthetic inhibition, inhibition of cell division) are similar in that the biological responsiveness increases with decreasing wavelength. To determine biologically effective irradiances, the spectral irradiance of interest is first weighted by an analytical representation of a chosen action spectrum. The summation over all wavelengths yields the biologically effective irradiance and when summed over time, yields the biologically effective dose (NAS 1979).

There are currently several action spectra in common use (Jones and Kok 1966; Caldwell 1971; Setlow 1974) but the action spectra for

most ultraviolet biological effects are unknown. Setlow's (1974) generalized DNA-damage action spectrum is a combined representation of work with bacteria and viruses. Caldwell (1971) developed a generalized plant action spectrum while the Jones and Kok (1966) action spectrum is based specifically on the photosynthetic inhibition of isolated spinach chloroplasts. Action spectra studies usually employ monochromatic radiation and would not detect synergistic effects of different wavelength regions. There is evidence that synergisms are involved when organisms are exposed to polychromatic sources such as the sun or experimental ultraviolet sources (Elkind et al. 1978).

Fluorescent sunlamps are widely used as a laboratory source or supplement for experimental UV-B exposure of organisms (Sisson and Caldwell 1975). The spectral qualities of radiation from this source are not the same as those of sunlight over the biologically effective wavelengths (280 - 320 nm). There is too little irradiance above 300 nm and possible too much below this wavelength for ozone thicknesses greater than 0.10 atm-cm (NAS 1979). However they have come into common use as UV-B sources because the spectral distribution of a fluorescent inhibition of cell division) are similar in that the biological responsiveness increases with decreasing wavelength. To determine biologically effective irradiances, the spectral irradiance of interest is first weighted by an analytical representation of a chosen action spectrum. The summation over all wavelengths yields the biologically effective irradi-

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The study of UV-B effects on aquatic organisms is complicated by the attenuation of ultraviolet radiation into natural waters. In most experiments only radiation at the water surface is measured. In order to make reliable estimates on the biological effects of UV-B radiation in aquatic ecosystems, accurate data on the penetration of UV-B radiation into natural waters is required (Strickland 1958; Calkins 1975; Lorenzen 1975). The maximum penetration of UV-B occurs in ocean waters having minimum concentrations of chlorophyll and dissolved organic matter (Jerlov 1976). UV-B radiation (eg. 310 nm) is limited to approximately the upper 10% of the euphotic zone for coastal waters before being reduced to 1% of its surface irradiance. This corresponds to roughly the upper 15 m in low organic ocean water and to 1 or 2 m in productive coastal waters (Jerlov 1976). Further analyses by Smith and Baker (1979) have demonstrated that an increase in UV radiation (or dose) at the surface results in a proportional increase in UV radiation (or dose) at all depths.

The attenuation of ultraviolet radiation by natural waters, especially by productive coastal waters, may play an important role in the survival of planktonic plants and animals. For microflora in sandy sediments conditions are much like those of phytoplankton only that the former live in a more light absorbing medium than do the latter. Attenuation coefficients for radiation in sediments depends on grain size and wavelength. Long-waved visible radiation penetrates further than short-wave and fine grained deposits attenuate more than coarse sediments (Gomoiu 1967; Fenchel and Straarup 1971).

Even with the limited penetration of UV-B radiation into natural waters, effects of UV-B radiation on marine phytoplankton primary productivity and growth have been observed by numerous investigators (Steemann Nielsen 1964; Jitts et al. 1976; Lorenzen 1979; Smith et al. 1979; Smith and Baker 1980 a or b; Calkins and Thordardottir 1980; Worrest et al. 1980, Thomson et al. 1980; Wolniakowski 1980; Worrest et al. 1981; and Scott 1982) and reviewed by Worrest (1982). The response by marine phytoplankton to UV-B radiation is variable, but the general trend is a depression of primary production and growth, and an alteration of community structure with increasing UV-B dose. A decrease in quantum efficiency and photoinhibition of photosynthesis has also been observed in macro- and microalgal species upon exposure to ultraviolet radiation (McLeod and Kanwisher 1962; Halldal 1964; Halldal 1967). Marine phytoplankton account for at least 40% of the world primary production (Golley 1972; Lieth and Whittaker 1975) and NAS (1979) has predicted a decrease in production of agricultural and non-agricultural plants as a direct consequence of ozone depletion

In contrast, there have been few studies on the effects of UV-B radiation on marine benthic diatom communities. This may be a serious oversight considering the magnitude of primary production by these primary producers in benthic marine systems. On tidal flats and in shallow-water marine systems, the primary productivity of the benthic or littoral microalgae can exceed that of the phytoplankton (Grontved 1960; Leach 1970) and account for as much as a third of the total annual primary production in these systems (Pomeroy 1959).

Marine benthic diatoms are also important in stabilizing marine sediments and as a carbon source to numerous invertebrates (Holland et al. 1974; Wetzel 1977).

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Response to Ultraviolet (UV-B) Radiation by Estuarine Diatom Assemblages Attached to Artificial Substrates*

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INTRODUCTION

Global atmospheric pollution from halocarbons, particularly chlorofluorocarbons, has the potential of causing significant reductions in the concentration of stratospheric ozone. If the production of chlorofluorocarbons were to continue into the future at a rate prevalent in 1977, the steady-state reduction in total global ozone could be between 5% to 10% (NAS 1982; WMO 1982). A 5% to 10% ozone loss would result at mid-latitudes during the summer in a 13% to 28% increase in the daily transmisson of DNA - damaging ultraviolet radiation in the 290 -320 nm waveband (UV-B radiation (NAS 1982). These predictions of potential ozone depletion have led to numerous studies regarding the possible biological effects of UV-B radiation. Several of these studies indicate that exposure to simulated solar UV-B radiation can have deleterious effects on marine bacteria, phytoplankton and zooplankton (Thomson et al. 1980a; Damkaer et al. 1981; Karanas et al. 1981; Worrest et al. 1981).

Several investigators have measured a depression in marine phytoplankton primary productivity and growth, and an alteration of phytoplankton community structure following exposure to enhanced UV-B radiation (Lorenzen 1979; Calkins and Thordardottir 1980; Smith and Baker 1980; Smith et al. 1980; Thomson et al. 1980b; Worrest et al. 1981). In contrast, there have been relatively few studies on the response of marine benthic diatoms to UV-B radiation. This may be a serious oversight considering the magnitude of primary produc-

tion by marine benthic microflora. In estuaries and coastal wetlands, the epibenthic primary productivity often exceeds that of the phytoplankton and could be an important component of estuarine food webs (Grontved 1960; Leach 1970; Cadee and Hegeman 1974; Matheke and Horner 1974). Benthic diatoms are also a major carbon source for numerous marine and estuarine invertebrates, and their growth on sediment surfaces promotes sediment binding and stabilization (Holland et al. 1974; Wetzel 1977; Frostick and McClave 1979).

In one of the few studies on marine benthic diatoms and ultraviolet radiation, Worrest et al. (1978) quantified changes in biomass and community structure of benthic estuarine diatom assemblages when they were exposed to enhanced UV-B radiation in a laboratory microcosm. In a second laboratory study, Thomson et al. (1980b) measured a depression in the growth rate of a common intertidal epilithic diatom following exposure to enhanced UV-B radiation. However, extrapolating results from these and other similar laboratory studies on UV-B effects to natural systems is controversial.

One reason that extrapolation is dangerous is that exact solar simulation is usually not feasible with the fluorescent sunlamp system which is commonly used to simulate a natural solar UV-B spectrum. The spectral quality of radiation from sunlamps is not the same as that of sunlight over the biologically effective wavelengths (280-320 nm) and biological responses to UV can be very wavelength dependent (NAS 1979). Fluorescent sunlamps also cannot emit the same flux densities of UV-A (320-400 nm) and photosynthet-

ically active radiation (400-700 nm) as the sun. This latter disparity is of particular importance because of one repair process for UV induced damage to nucleic acids which is activated by UV-A and blue light (Caldwell 1981).

Photoreactivation (PR) is a molecular repair system for nucleic acid damage caused by absorption of UV-B and UV-C radiation and requires simultaneous or subsequent exposure to longer wavelength radiation (315 - 559 nm) (Jagger 1964). PR is widespread in the biological kingdom and has been demonstrated to be an effective UV repair mechanism in algae and higher plants (Halldal and Taube 1972; Caldwell 1981). A photoreactivation mechanism does not appear to participate in repair of UV induced photosynthetic damage (Caldwell 1981) but there is some evidence that the effects of UV-B radiation on terrestrial plant photosynthesis are dependent on the level of photosynthetically active radiation. When subjected to UV-B radiation there is a greater depression in terrestrial plant photosynthesis under low levels of visible irradiance than under higher levels of visible irradiance. (Sisson and Caldwell 1976; Teramura et al. 1980).

Nearly all the reports in the literature examining the effects of enhanced UV-B radiation on plant growth and photosynthesis have been conducted in growth facilities where photosynthetically active irradiances were one-tenth to one-third of natural sunlight (Teramura 1982). Naturally occurring levels of visible radiation may have an ameliorating effect on UV-B radiation induced damage. This would result in a tendency in these laboratory studies to

overestimate the consequences of global ozone depletion on the biosphere.

The response of an estuarine assemblage of benthic diatoms to UV-B radiation has been measured under low-levels of visible radiation (Worrest et al. 1978). The purpose of the following study was to measure the response to UV-B radiation by an estuarine assemblage of benthic diatoms under naturally occurring levels of visible radiation. Results from the present study combined with those by Worrest et al. (1978) would indicate whether naturally occurring levels of visible radiation have an ameliorating effect on UV-B radiation induced damage to benthic diatom assemblages.

MATERIALS AND METHODS

The study was repeated four times during the winter, spring and summer of 1981. Experiment I (1 January - 12 February) ran six weeks. Experiments II (29 April - 28 May), III (10 June - 9 July) and IV (13 July - 12 August) were limited to four weeks because of luxuriant, irregular growth beyond a four-week period. Each experiment was conducted using artificial substrates maintained in three replicate microcosms. The microcosms were housed within a greenhouse located at the Oregon State University Marine Science Center in Newport, Oregon (44°37'N).

Each artificial subtrate consisted of a rectangular (30 x 5 cm) piece of Mylar 'D' polyester film (0.13 mm thickness, Du Pont) attached to a matching (30 x 5 cm) polyvinylchloride (PVC) base. The substrates were anchored 2.5 cm (Experiment I) or 10.2 cm (Experiments II, III, IV) apart and 2.5 cm off the bottom of the microcosm using two parallel lengths of 2.5 cm PVC pipe (Figure 1). The depth of the water covering the substrates was 9 cm. The complete assembly of artificial substrates and PVC pipe was centered lengthwise in a microcosm and fastened at each end of the microcosm.

Microcosm A (60 x 187 x 17 cm deep) had a capacity of 137 ℓ while microcosms B and C (50 x 187 x 17 cm deep) each had capacities of 124 ℓ. The microcosms were placed end-to-end along the northern wall of the greenhouse. Seawater entered a microcosm through one vertical inlet located midway along the rear side of the microcosm.

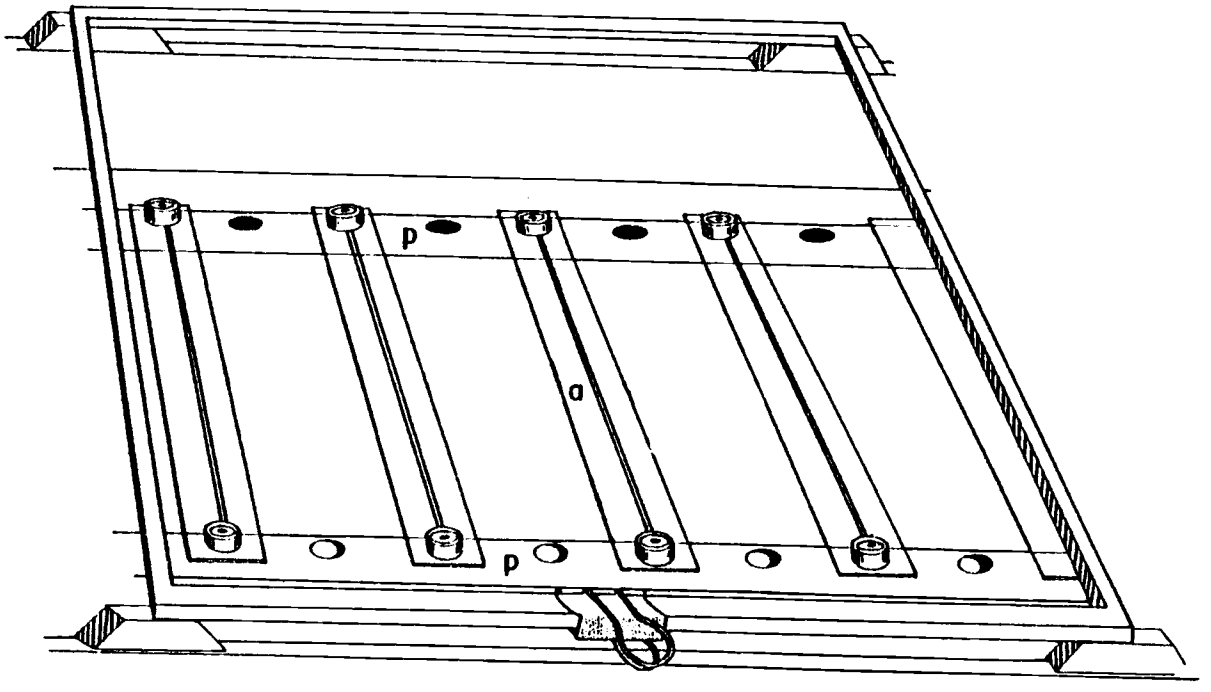

Figure 1: Interior view of a microcosm with the artificial substrates (a) anchored to two parallel lengths of PVC pipe (p) positioned lengthwise along the bottom of the microcosm. For dimension refer to the text.

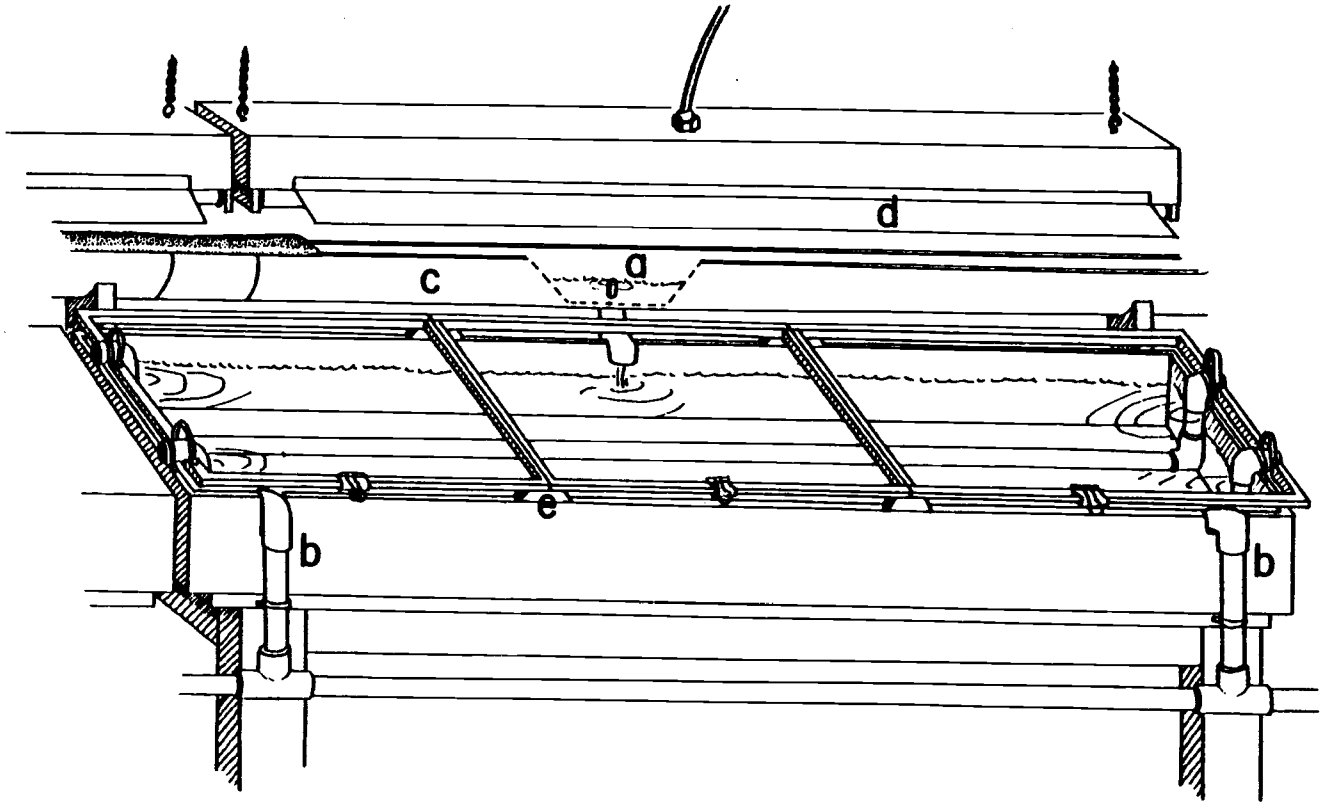

Figure 2: Exterior diagram of one of the three replicate microcosms showing the location of the single inlet (a) and double outlets (b). The inlet was made by drilling a hole into a plastic rain gutter (c) which ran the length of all three microcosms. Sunlamps (d) were positioned overhead and UV filters were clamped onto wooden frames (e).

There were two outlets per microcosm, one at each end opposite the inlet (Figure 2).

Initially, raw seawater from lower Yaquina Bay was pumped continuously through the microcosms. After one to three days the raw seawater was turned off and pathogen-free seawater was used for the remainder of an experiment. Pathogen-free seawater was obtained by first sand-filtering raw seawater followed by exposing the filtered raw seawater to germicidal ultraviolet radiation. The raw seawater provided an initial seed culture while the pathogen-free seawater reduced the introduction of new populations of micro-organisms and prevented the buildup of sediment and macroalgal fragments. Flow rates for raw seawater and pathogen-free seawater were the same in each microcosm during an experiment and ranged from 0.4 ℓ/min to 1.2 ℓ/min.

Water temperature was recorded continuously (Partlow Recording Thermometer, Model RFT) and nutrients (orthophosphorus, reactive silica, nitrite- and nitrate-nitrogen) were monitored weekly in each microcosm. The daily mean temperature of the water during the winter experiment ranged from 10°C to 13°C. In the spring/summer experiments the daily mean temperature of the water ranged from 13°C to 21°C. The temperature in the microcosms was generally higher and the range larger than that measured in lower Yaquina Bay (thermistor sensor, 4.0 m below MLLW) but overlaps did occur between the two temperature ranges. There was less of an overlap between microcosm and Yaquina Bay temperatures during the spring/summer experiments than during the winter experiment (Appendix).

Salinity varied from $10^{o}/oo$ to $30^{o}/oo$ during all experiments. Salinity in lower Yaquina Bay ranges from as low as $8^{o}/oo$ in the winter during high freshwater discharge, to $35^{o}/oo$ in the summer during upwelling.

There were no significant differences in micronutrient levels between microcosms during an experiment (Appendix). However, some nutrient differences existed between experiments. Spring (Experiment II) nitrite-/nitrate-nitrogen levels were significantly higher ($p < .05$) than the levels recorded during the summer experiments. Spring orthophosphorus levels were significantly lower ($p < 0.05$) than the levels of orthophosphorus recorded during the late summer experiment (Experiment IV).

The low-iron glass of the greenhouse (Sunadex, ASG Industries) filtered out most of the solar ultraviolet radiation in the UV-B waveband and absorbed approximately 10% of the natural, visible radiation. Therefore a sunlamp/filter system (Sisson and Caldwell 1975) was used to simulate solar UV-B irradiances for the present study. Each lamp fixture (119 cm) of the sunlamp/filter system held one Westinghouse FS-40 fluorescent "sunlamp" and one "deluxe-white" 40 W fluorescent lamp (Vita-Lite, Duro-Test Corporation). Five lamp fixtures were positioned end-to-end and centered lengthwise above the artificial substrates. All lamps were preburned before use and the duration of sunlamp exposure was 4.0 to 6.0 hours each day, centered around solar noon.

Ultraviolet irradiance at the surface of the microcosms was measured with an Optronic Laboratories Model 742 spectroradiometer

which had been characterized at the U.S. National Bureau of Standards. The spectroradiometer was coupled with a Model 755 data acquisition system for data reduction and digital printout. Supplemental visible irradiance from the fluorescent lamps was measured by a quantum sensor (LI-COR Model LI-192SB; 400 - 700 nm response) and ranged from 0.9 $E \cdot m^{-2} \cdot day^{-1}$ (Experiment I) to 2.5 $E \cdot m^{-2} \cdot day^{-1}$ (Experiments II, III, IV). The total solar irradiance was measured daily with an integrating quantum sensor LI-COR Models LI-550B and LI-190SB; 400 - 700 nm response) and varied widely within each experiment (Figure 3). Total solar irradiance varied between 0.4 and 16.8 $E \cdot m^{-2} \cdot day^{-1}$ during the winter (Experiment I) and in the spring/summer experiments (Experiments II, III, IV) it varied from 10.1 to 45.9 $E \cdot m^{-2} \cdot day^{-1}$. The mean daily total solar illuminance in Experiments I, II, III and IV were 8.5, 26.1, 34.4 and 31.2 $E \cdot m^{-2}$, respectively.

Two UV-B irradiance treatments for each experiment were established by using two different thicknesses of cellulose acetate film (0.13 mm and 0.25 mm) with the lamp fixtures. Cellulose acetate (CA) absorbed wavelengths shorter than 290 nm and transmitted UV-B, UV-A and visible radiation to the surface of the microcosms. The CA was partially photodegraded before use and was changed weekly to compensate for the continued photodegradation that occurs under fluorescent sunlamps. Mylar 'D' (0.18 mm thickness) polyester film, which absorbs UV-B radiation, was used as a control for UV-B effects. Mylar filters were also changed weekly to

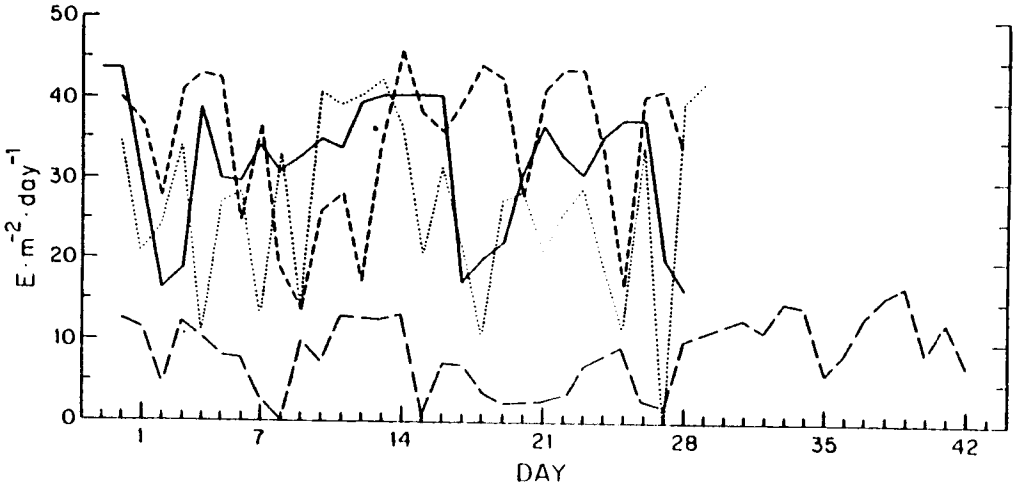

Figure 3: Daily total solar illuminance in the 400 - 700 nm waveband during the period of each experiment. The illuminance was measured with an integrating quantum sensor. Experiment I (— —), Experiment II (....), Experiment III (-----) and Experiment IV (——).

maintain initial irradiance levels. All three UV-B treatments were represented in each of the three microcosms.

The ultraviolet irradiance under the sunlamp/filter system was proportionally greater at the shorter wavelengths in the UV-B waveband if compared to a solar spectrum. Due to this lack of spectral conformity and because not all wavelengths of ultraviolet radiation are equally effective in producing biological effects, it is important to calculate the level of biologically effective UV-B radiation from the sunlamp/filter system and compare it with that from the sun.

Biologically effective UV-B irradiances are obtained through use of weighting functions derived from action spectra. Action spectra weight each wavelength of radiation according to its effectiveness in producing a specific biological response. UV-B action spectra for inhibition of photosynthesis and cell division are similar in that the biological responsiveness increases with decreasing wavelength. To calculate biologically effective UV-B irradiances, the spectral irradiance of interest is first weighted with a particular action spectrum. The summation over all wavelengths yields the biologically effective irradiance; when the irradiance is summed over time, one obtains the biologically effective dose.

Caldwell's (1971) generalized plant action spectrum was used as the basis for simulation of current and enhanced levels of biologically effective UV-B radiation. Worrest et al. (1981) found this weighting function was the best fit of those tested for phyto-

plankton chlorophyll and radiocarbon uptake responses to UV-B radiation. For comparative purposes two other biological weighting functions were considered: an action spectrum for photoinhibition of isolated chloroplasts (Jones and Kok 1966) and a DNA action spectrum (Setlow 1974). The reference wavelengths used in the present study for normalization of the Caldwell (1971), Jones and Kok (1966) and Setlow (1974) weighting functions were the same as those employed by Green and Miller (1975) and Smith and Baker (1979).

Experimental UV-B levels were selected to approximate an incident solar UV-B irradiance at standard (0.32 atm-cm) ozone levels and under reduced atmospheric ozone. The artificial substrates exposed to UV radiation filtered through a 0.25 mm thickness of CA (= LOW) received daily effective doses which simulated predicted incident UV-B levels at 44°37'N latitude for 0.32 cm ozone, 0.0 albedo and 2.0 aerosol scaling factor at sea level (parameters of model described by Green et al. 1980). The daily effective dose under the 0.13 mm thickness of CA (= HIGH) was comparable to a 20-33% reduction in ozone thickness in the model previously described (see 'MODEL' in Table 1).

'LOW' experimental UV-B irradiance levels were the equivalent of the effective UV-B irradiance typically observed at noon near the mid-point date of each experiment. Likewise, the duration of UV-B exposure was chosen to approximate the daily effective UV-B dose observed near the midpoint date of each experiment (Table 1). It was recognized that solar UV-B irradiance has a diel and daily

Table 1. Absolute and biologically weighted UV irradiances and daily doses transmitted by 0.13 mm CA (HIGH), 0.25 mm CA (LOW), and Mylar (CONTROL) filters in each experiment. The absolute and biologically weighted UV irradiances (Solar Noon, Global) and daily doses near the midpoint of each experiment are listed in the table under MODEL. These fluences are from from a computer model based on Green et al. 1980 (R. C. Worrest, personal communication) and correspond to 44.37 °N latitude at sea level. 0.32 atm-cm ozone thickness, 0.0 albedo, and a 2.0 aerosol scaling coefficient (parameters described by Green et al. 1980).

		IRRADIANCE ($mW \cdot m^{-2}$)				DAILY DOSE ($J \cdot m^{-2} \cdot day^{-1}$)			
Experiment	Treatment	DNA	PLANT	PI	ABSOLUTE	DNA	PLANT	PI	ABSOLUTE
I (1 January-12 February)	HIGH	1.0	7.4	282	135	14.3	106.6	4061	1.95×10^3
	LOW	0.5	4.7	204	91	7.6	67.2	2943	1.32×10^3
	CONTROL	*ND	ND	ND	ND	ND	ND	ND	ND
	MODEL	0.3	4.9	2115	611	3.4	66.1	3.95×10^4	9.62×10^3
II (29 April-28 May)	HIGH	17.3	119.9	1000	1511	351.9	2481.9	2.07×10^4	3.13×10^4
	LOW	8.0	66.6	649	951	165.6	1366.2	1.34×10^4	1.97×10^4
	CONTROL	3.8×10^{-3}	13.7×10^{-3}	139	26	0.1	0.3	0.29×10^4	0.05×10^4
	MODEL	3.9	61.8	6672	3179	75.3	1265.7	1.83×10^5	0.05×10^4
III (10 June-9 July)	HIGH	17.0	119.9	1000	1511	367.2	2589.8	3.16×10^4	3.26×10^4
	LOW	8.0	66.6	649	951	172.8	1438.6	1.40×10^4	2.05×10^4
	CONTROL	2.8×10^{-3}	12.7×10^{-3}	139	26	0.1	0.3	0.30×10^4	0.05×10^4
	MODEL	4.5	70.6	7064	3570	90.0	1511.9	2.01×10^5	9.0×10^4
IV (13 July-12 August)	HIGH	17.0	119.9	1000	1511	336.6	2374.0	1.98×10^4	2.99×10^4
	LOW	8.0	66.6	649	951	158.1	1318.7	1.29×10^4	1.88×10^4
	CONTROL	3.8×10^{-3}	13.7×10^{-3}	139	26	0.1	0.3	0.28×10^4	0.05×10^4
	MODEL	4.1	65.0	6834	3286	81.1	1353.7	1.90×10^5	8.10×10^4

* ND = not determined but less than control levels for Experiments II, III, IV.

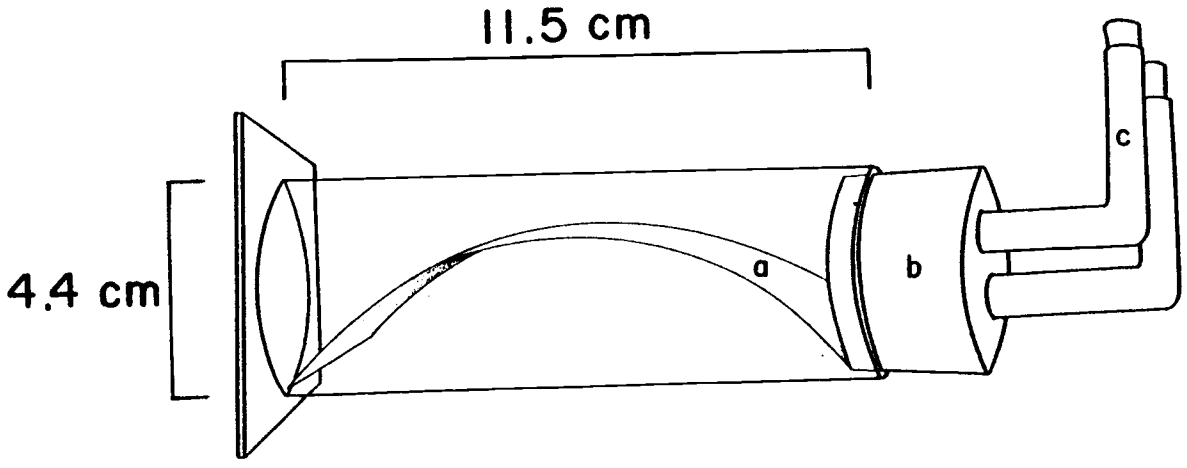

Figure 4: The Vycor glass vessel (125 ml) used for productivity measurements of diatom assemblages attached to artificial substrates. A colonized artificial substrate was sealed in the vessel with a silicone rubber stopper (b) and then filled through a bent glass tube (c).

variance, but a variable experimental UV-B irradiance and variable daily dose were impractical during the course of each experiment in this study.

The artificial substrate diatom assemblages (periphyton) were analyzed at two-week intervals for chlorophyll a, primary productivity (radiocarbon uptake), biomass (ash-free dry weight) and community composition. All four parameters were measured from one substrate, and the measurement of each parameter was based on a 30 cm^2 surface area. There were one or two substrates available per treatment at each sampling date from one microcosm. The artificial substrates were not replaced in the microcosms after they had been removed for sampling.

A Bausch and Lomb Spectronic 70 spectrophotometer with a 1 cm pathlength was used for chlorophyll determinations. The attached periphyton was scraped off the artificial substrate and filtered at 1/6 atm through a magnesium carbonate coated 4.5 cm Whatman GF/C glass filter. The samples were then homogenized in 90% (v/v) analytical grade acetone with a Brinkman Polytron (Model PT 10-35, Brinkman Instruments) for approximately 10 seconds. Extracts were placed on ice and in the dark for 20 minutes before centrifuging (4500 rpm, 12 min) and then measured at 665 nm before and after acidification with 2 drops of 50% (v/v) HCl. Chlorophyll a concentration was calculated according to Lorenzen (1967).

For biomass determinations, the periphyton was scraped off the artificial substrates and desiccated on tared, preashed 4.5 cm Whatman GF/C filters. The filters were next weighed, ashed at 475°C

for 1.5 h, and then weighed again to complete the ash-free dry-weight calculation.

Primary productivity was measured using the traditional carbon-14 light and dark bottle technique (Steemann Nielsen 1952). An undisturbed piece (30 cm^2) of periphyton-covered substrate was incubated in a Vycor (Corning Glass Works) glass vessel (Figure 4, 125 ml). Vycor absorbs and reflects less than 30% of the UV-B radiation. One liter of pathogen-free seawater was inoculated with 20 µCi of ^{14}C-sodium bicarbonate (New England Nuclear) for a final concentration of 0.02 µCi/ml in each vessel. Ten vessels were prepared in this manner for each run: 3 from substrates under 0.25 mm CA (LOW), 3 from under 0.13 mm CA (HIGH), 3 controls (Mylar) and 1 blank (pathogen-free seawater). An eleventh non-labelled substrate was also incubated and later used for a quench curve determination. There was one dark bottle for each UV-B treatment, and dark fixation ranged from 1.7% to 12.0% of the mean light bottle fixation rates. There was no apparent difference in dark uptake between treatments (Appendix).

The vessels were incubated during the experimental UV irradiation period for 3 h (11:00 A.M. - 2:00 P.M.). Each vessel was incubated in the microcosm at its original location to duplicate as closely as possible the radiation regime in which the periphyton developed. Alkalinity was measured during the incubation period with the aid of a YSI salinity meter (Model 33 SCT, Yellow Springs) and an analog pH meter (Model 399A, Orion Research). Total carbon-

ate content was calculated according to Strickland and Parsons (1972).

Following incubation the vessels were returned to the laboratory and kept on ice and in the dark until processed. This method was chosen over the use of fixatives, which are known to cause a loss of ^{14}C-activity from the particulate fraction (Silver and Davall 1978). The labelled periphyton was scraped off the artificial substrate into its Vycor vessel and then mixed gently (30 s) with a glass stirring rod until a nearly uniform suspension was obtained. Each periphyton sample was largely filamentous diatoms which made it difficult to form a completely uniform suspension without disrupting the cells. Triplicate 1 ml aliquants were therefore considered to be a more accurate representation of each periphyton sample. The triplicate 1 ml aliquants of the suspended material were removed from each vessel and membrane filtered separately (0.45 µm porosity, Millipore Corporation) at 1/3 atm vacuum. The membrane filters were next desiccated over indicating silica gel and soda lime and then fumed with concentrated HCl before adding 10 ml of fluor (Ready-Solv HP, Beckman Instruments).

The radioactivity of the samples was determined on a 3-channel liquid scintillation system with Compton external standardization (Beckman LS 8000). The samples were counted for 10 minutes or 10,000 counts. A microdispenser (Drummond Series 200 Dialamatic) was used to dispense ^{14}C-toluene (New England Nuclear) to prepare a quench curve for each radiocarbon experiment. Counting efficiencies

ranged from 46% to 73% (mean 61%), and radiocarbon uptake was calculated according to Strickland and Parsons (1972).

Permanent slides for community structure analysis were first prepared by digesting the material in cold concentrated nitric acid. The cleaned diatom suspensions were then mounted on microscope slides with Hyrax (Custom Research and Development, Inc.) using the procedure outlined in Patrick and Reimer (1966). Samples were taken at each sampling data from each microcosm and then pooled by treatment for community structure analysis. Each slide therefore represented a pooled sample from all microcosms. The prepared slides were examined at 1000x with a Zeiss standard RA microscope. Approximately 500 frustules were counted from each sample. Taxa were identified to species using standard taxonomic references and regional publications (Peragallo and Peragallo 1897-1908; Hustedt 1930; Cupp 1943; Hustedt 1955; Hendey 1964; Patrick and Reimer 1966; Riznyk 1973; Amspoker 1977). To aid in the identification of problematic, usually very small taxa, mounts of cleaned diatom suspension were also examined under a Phillips EM 200 transmission electron microscope (for methodology see Appendix).

Several different species composition parameters and related statistics were calculated for each slide as described in McIntire and Overton (1971). The Information Measure H" (Shannon and Weaver 1949) was calculated for one index of diversity. H" ranges from $\log_2$ S, where S is the total number of species in the sample, if every taxon is equally common, to 0($\log_2$ 1), if all individuals are represented by one taxon. H" is a biased estimator of the popula-

tion value of the diversity (or information) per individual (H'). However, the bias becomes negligible at sample sizes of 500 or more (McIntire and Overton 1971). The variance of H" was calculated according to the formula presented in Pielou (1966). Conditional maximum and minimum values of H" based on the observed number of species in a sample are used to calculate a redundancy index (R'). R' is a useful measure of the relative degree of species dominance in the sample. Values of R' range from 0, when the individuals are equally distributed among the taxa, to 1, when all but one taxon are represented by a single individual. The difference measure (D_{hk}) of MacArthur (1965) was calculated to compare pairs of diatom assemblages. If the two assemblages are identical in species composition and relative abundance, D_{hk} has a minimum of 1, and if the two assemblages possess no taxa in common, D_{hk} has a maximum of 2.

Calculations for analysis of diversity, redundancy and resemblance measures were completed on a Control Data Corporation 170/720 Cyber computer at the Oregon State University Computer Center using the *AIDONE and *AIDN programs. Analysis of variance of biomass, chlorophyll a and radiocarbon uptake was calculated with a PDP 11/70 Digital computer at the Corvallis Environmental Research Laboratory, U.S. Environmental Protection Agency, using the BMDP statistical package.

RESULTS

The dominant diatom taxa sampled during the winter off the artificial substrates were Navicula diserta, Nitzschia fundi and Amphipleura rutilans (Table 2). Melosira nummuloides and Fragilaria striatula var. californica were the predominant diatom taxa found in the spring/summer experiments (Tables 3-5). Matrices of difference (D_{hk}) values, calculated for comparison of the diatom assemblages pooled by experiment, also indicated a seasonal difference in diatom species composition. Because of these seasonal differences, the winter experiment was analyzed separately from the spring/ summer experiments.

In addition to the observed temporal changes in species composition, there were significant temporal changes in biomass, chlorophyll and radiocarbon uptake in almost all experiments (Tables 6 and 7). In general, the trend was an increase in each parameter with time but notable exceptions did occur. There was a significant decrease in biomass from four to six weeks during the winter experiment and no significant change in biomass with time during the late summer experiment (Experiment IV). The spring (Experiment II) and early summer experiments (Experiment III) were characterized by no significant change in radiocarbon uptake with time. During the late summer experiment, (Experiment IV) radiocarbon uptake was significantly lower at four weeks than radiocarbon uptake measured at two weeks.

Daily exposure to enhanced levels of UV-B radiation affected community composition and one or more of the non-taxonomic para-

Table 2: A list of the dominant diatom taxa from Experiment I (1 January - 12 February) and the percentage composition of those species within each assemblage ≥ 5% of the total enumerated per treatment). Treatment HIGH, LOW and CONTROL correspond to 0.13 mm CA, 0.25 mm CA and Mylar filters. Samples were collected after two, four and six weeks of development.

Treatment	Taxon	Percent Composition
HIGH (2 weeks)	Navicula diserta Hust.	22
	Nitzschia subhybrida Hust.	13
	Nitzschia fundi Chol.	11
	Navicula directa W. Smith	7
	Navicula No. 1	5
LOW (2 weeks)	Nitzschia fundi Chol.	22
	Nitzschia subhybrida	14
	Navicula diserta Hust.	15
	Navicula No. 1	7
	Navicula directa W. Smith	6
CONTROL (2 weeks)	Nitzschia fundi Chol.	26
	Navicula diserta Hust.	16
	Mitzschia subhybrida Hust.	10
	Navicula directa W. Smith	5
	Thalassiosira No. 2	5
HIGH (4 weeks)	Navicula diserta Hust.	16
	Navicula directa W. Smith	12
	Navicula tripunctata var. schizonemoides V.H. Patr.	12
	Melosira nummoloides (Dillw.) Ag.	9
	Navicula cryptocephala var. venata (Kutz.) Grun.	7
	Nitzschia fundi Chol.	5
	Berkeleya rutilans (Trent.) Cl.	5
LOW (4 weeks)	Berkeleya rutilans (Trent.) Cl.	36
	Navicula diserta Hust.	9
	Nitzschia subhybrida Hust.	5
	Amphora tenerrima Aleem ex Hust.	5
CONTROL (4 weeks)	Berkeleya rutilans (Trent.) Cl.	23
	Navicula diserta Hust.	15
	Melosira nummoloides (Dillw.) Ag.	9
	Navicula directa W. Smith	7
	Amphora tenerrima Aleem ex Hust.	6

(continued)

Table 2 (continued)

Treatment	Taxon	Percent Composition
HIGH (6 weeks)	Berkeleya rutilans (Trent.) Cl.	56
	Navicula diserta Hust.	10
	Nitzschia fundi Chol.	5
LOW (6 weeks)	Berkeleya rutilans (Trent.) Cl.	30
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	21
	Navicula diserta Hust.	17
	Nitzschia fundi Chol.	8
	Navicula directa W. Smith	5
CONTROL (6 weeks)	Berkeleya rutilans (Trent.) Cl.	62
	Navicula diserta Hust.	11

Table 3: A list of the dominant diatom taxa from Experiment II (29 April - 28 May) and the percentage composition of those species within each assemblage (≧ 5% of the total enumerated per treatment). Treatment HIGH, LOW and CONTROL correspond to 0.13 mm CA, 0.25 mm CA and Mylar filters respectively. Samples were collected after two and four weeks of growth.

Treatment	Taxon	Percent Composition
HIGH (2 weeks)	Fragilaria striatula var. californica Grun.	44
	Cylindrotheca clostserium (Ehr.) Reiman & Lewin	18
	Skeletonema costatum (Grev.) Cl.	9
	Nitzschia fundi Chol.	6
	Navicula diserta Hust.	5
LOW (2 weeks)	Fragilaria striatula var. californica Grun.	50
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	11
	Nitzschia fundi Chol.	7
	Navicula diserta Hust.	6
	Berkeleya rutilans (Trent.) Cl.	6
CONTROL (2 weeks)	Fragilaria striatula var. californica Grun.	54
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	18
	Skeletonema costatum (Grev.) Cl.	10
	Nitzschia fundi Chol.	5
HIGH (4 weeks)	Fragilaria striatula var. californica Grun.	54
	Melosira nummoloides (Dillw.) Ag.	14
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	8
	Navicula ostrearia (Gaillon) Trupin in Bory	5
LOW (4 weeks)	Fragilaria striatula var. californica Grun.	34
	Navicula ostrearia (Gaillon) Turpin in Bory	13
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	8
	Nitzschia longissima var. reversa (Breb.) Grun.	7
	Navicula diserta Hust.	6
CONTROL (4 weeks)	Fragilaria striatula var. californica Grun.	26
	Navicula ostrearia (Gaillon) Turpin in Bory	19
	Nitzschia longissima var. reversa (Breb.) Grun.	9
	Melosira nummoloides (Dillw.) Ag.	9
	Berkeleya rutilans (Trent.) Cl.	5

Table 4: A list of the dominant diatom taxa from Experiment III (10 June - 9 July) and the percentage composition of those species within each assemblage ≧ 5% of the total enumerated per treatment). Treatment HIGH, LOW and CONTROL correspond to 0.13 mm CA, 0.25 mm CA and Mylar filters. Samples were collected after two, and four weeks of growth.

Treatment	Taxon	Percent Composition
HIGH (2 weeks)	Nitzschia americana Hasle	16
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	11
	Berkeleya rutilans (Trent.) Cl.	9
	Melosira nummoloides (Dillw.) Ag.	9
	Nitzschia fundi Chol.	8
	Thalassiosira No. 1	8
	Chaetoceros No. 1	7
	Nitzschia longissima (Breb.) Grun. f. parva	5
	Amphiprora hyalina Eulenstein ex V.H.	5
LOW (2 weeks)	Melosira nummoloides (Dillw.) Ag.	20
	Nitzschia americana Hasle	17
	Thalassiosira No. 1	7
	Nitzschia fundi Chol.	6
	Chaetoceros No. 1	6
	Skeletonema costatum (Grev.) Cl.	5
CONTROL (2 weeks)	Nitzschia americana Hasle	20
	Cylindrotheca closterium (Ehr.) Reiman & Lewin	14
	Thalassiosira No. 1	9
	Nitschia fundi Chol.	6
	Chaetoceros No. 1	6
	Amphiprora hyalina Eulenstein ex V.H.	5
	Melosira nummoloides (Dillw.) Ag.	5
	Nitzschia longissima (Breb.) Grun. f. parva	5
	Skeletonema costatum (Grev.) Cl.	5
HIGH (4 weeks)	Berkeleya rutilans (Trent.) Cl.	35
	Melosira nummoloides (Dillw.) Ag.	31
	Amphiprora hyalina Eulenstein ex V.H.	6
	Amphora micrometra Giffen	5
LOW (4 weeks)	Melosira nummoloides (Dillw.) Ag.	45
	Berkeleya rutilans (Trent.) Cl.	19
	Amphora micrometra Giffen	5

(continued)

Table 4 (continued)

Treatment	Taxon	Percent Composition
CONTROL (4 weeks)	Berkeleya rutilans (Trent.) Cl.	28
	Melosira nummoloides (Dillw.) Ag.	19
	Amphiprora hyalina Eulenstein ex V.H.	7
	Amphora tenrrima Aleem ex Hust.	7
	Bacillaria paxillifer (Mull.) Hendey	7
	Amphora micrometra Giffen	6
	Nitzschia fundi Chol.	5

Table 5: A list of the dominant diatom taxa from Experiment IV (13 July - 12 August) and the percentage composition of those species within each assemblage ≧ 5% of the total enumerated per treatment). Treatment HIGH, LOW and CONTROL correspond to 0.13 mm CA, 0.25 mm CA and Mylar filters respectively. Samples were collected after two and four weeks of growth.

Treatment	Taxon	Percent Composition
HIGH (2 weeks)	Melosira nummoloides (Dillw.) Ag.	23
	Fragilaria striatula var. californica Grun.	21
	Thalassiosira No. 2	16
	Nitzchia fundi Chol.	5
LOW (2 weeks)	Melosira nummoloides (Dillw.) Ag.	34
	Fragilaria striatula var. californica Grun.	21
	Thalassiosira No. 2	8
	Skeletonema costatum (Grev.) Cl.	7
	Nitzschia fundi Chol.	6
CONTROL (2 weeks)	Melosira nummoloides (Dillw.) Ag.	41
	Skeletonema costatum (Grev.) Cl.	11
	Fragilaria striatula var. californica Grun.	10
	Thalassiosira No. 2	8
HIGH (4 weeks)	Melosira nummoloides (Dillw.) Ag.	60
	Fragilaria striatula var. californica Grun.	12
	Amphora micrometra Giffen	5
	Nitzschia fundi Chol.	5
LOW (4 weeks)	Melosira nummoloides (Dillw.) Ag.	51
	Amphora micrometra Giffen	9
	Amphiprora hyalina Eulenstein ex V.H.	5
CONTROL (4 weeks)	Melosira nummoloides (Dillw.) Ag.	38
	Navicula diserta Hust.	9
	Amphora micrometra Giffen	8
	Amphiprora hyalina Eulenstein ex V.H.	8
	Fragilaria striatula var. californica Grun.	7
	Nitzschia fundi Chol.	6
	Berkeleya rutilans (Trent.) Cl.	5

meters in each experiment. Diversity, redundancy and difference values were examined within each experiment for comparisons of the diatom assemblages at each sampling date according to UV-B treatment. There were small differences in these measurements among treatments during the first few weeks of growth. At the end of the each experiment, the highest D_{hk} values were found for comparisons between diatom assemblages collected from HIGH UV-B exposed substrates and those sampled from CONTROL exposed substrates (Table 8 and Table 9).

At the end of the winter experiment, the most diverse diatom assemblage was found on substrates exposed to LOW levels of UV-B radiation and the order of increasing redundancy was LOW - HIGH - CONTROL (Table 10). Species diversity consistently decreased with time under HIGH levels of UV-B radiation in all of the spring/summer experiments. The species composition of the diatom assemblages exposed to UV-B radiation in the spring/summer experiments was characterized by a higher percentage of filamentous and tube-dwelling species if compared to diatom assemblages growing under CONTROL UV-B conditions (Table 5-7). At the end of the spring/summer experiments the order of increasing redundancy was CONTROL - LOW - HIGH (Table 10).

With regard to the non-taxonomic parameters, daily exposure to enhanced UV-B radiation significantly affected biomass (winter and spring), chlorophyll (summer) and radiocarbon uptake (summer) in some experiments (Table 7). The biomass and chlorophyll _a_ responses were an increase in value with increasing UV-B dose. The radio-

Table 6: Biomass (ash-free dry weight), chlorophyll *a* and radiocarbon uptake responses of diatom assemblages to three fluences of UV-B radiation (± SD) in Experiment I (1 January - 12 February), Experiment II (29 April - 28 May), Experiment III (10 June - 9 July) and Experiment IV (13 July - 12 August).

Experiment	Day	Filter	Absolute Fluence (290-320 nm) ($kJ \cdot m^{-2} \cdot day^{-1}$)	Biomass ($gm \cdot m^{-2}$)	Chlorophyll ($mg \cdot m^{-2}$)	Radiocarbon Uptake (mg C fixed $\cdot m^{-2} \cdot h^{-1}$)
I	14 (15 Jan)	0.13 mm CA	1.95	4.00 ± 3.39	12.86 ± 2.32	49.75 ± 1.22
		0.25 mm CA	1.47	5.47 ± 5.02	11.72 ± 2.66	38.83 ± 5.18
		Mylar	ND*	4.85 ± 3.15	12.74 ± 0.46	53.80 ± 1.53
	28 (29 Jan)	0.13 mm CA	1.95	20.17 ± 6.27	41.68 ± 9.48	45.90 ± 3.51
		0.25 mm CA	1.47	10.51 ± 8.49	61.33 ± 10.14	36.98 ± 1.51
		Mylar	ND	4.24 ± 6.64	54.67 ± 21.33	46.24 ± 6.73
	42 (12 Feb)	0.13 mm CA	1.95	5.13 ± 2.95	120.63 ± 70.86	172.57 ± 74.92
		0.25 mm CA	1.47	3.36 ± 0.58	66.00 ± 46.66	144.38 ± 39.13
		Mylar	ND	3.49 ± 1.49	141.17 ±107.78	67.31 ± 11.90
II	14 (14 May)	0.13 mm CA	31.28	3.48 ± 1.49	44.62 ± 21.65	17.03 ± 3.94
		0.25 mm CA	19.69	2.86 ± 1.89	25.75 ± 20.81	25.76 ± 19.59
		Mylar	0.53	2.34 ± 1.29	33.71 ± 23.56	8.59 ± 0.11
	28 (28 May)	0.13 mm CA	31.28	10.56 ± 6.01	22.48 ± 18.90	32.18 ± 0.39
		0.25 mm CA	19.69	7.47 ± 1.75	15.51 ± 6.00	29.08 ± 22.32
		Mylar	0.53	4.68 ± 2.70	13.85 ± 4.37	14.67 ± 8.28
III	14 (25 June)	0.13 mm CA	32.64	2.26 ± 1.12	12.13 ± 4.02	64.45 ± 21.74
		0.25 mm CA	20.54	1.60 ± 0.77	11.52 ± 5.26	23.07 ± 4.76
		Mylar	0.55	2.88 ± 1.82	18.85 ± 4.52	64.76 ± 21.02
	28 (9 July)	0.13 mm CA	32.64	18.25 ± 7.31	86.32 ± 36.40	23.07 ± 4.76
		0.25 mm CA	20.54	13.64 ± 7.08	101.80 ± 33.94	55.33 ± 14.30
		Mylar	0.53	12.50 ± 5.94	74.63 ± 33.25	69.14 ± 29.92
IV	14 (29 July)	0.13 mm CA	29.92	5.64 ± 1.59	38.58 ± 20.08	32.75 ± 0.67
		0.25 mm CA	18.83	11.83 ± 9.60	29.77 ± 17.02	32.65 ± 12.18
		Mylar	0.50	9.30 ± 7.72	18.00 ± 5.12	26.83 ± 10.44
	28 (12 Aug.)	0.13 mm CA	29.92	11.21 ± 4.87	71.10 ± 54.78	18.70 ± 3.75
		0.25 mm CA	18.83	10.17 ± 6.34	59.50 ± 18.68	19.59 ± 6.61
		Mylar	0.50	5.81 ± 2.20	16.98 ± 4.79	12.16 ± 6.47

* ND = not determined but less than 0.05 $kJ\ m^{-2}\ day^{-1}$.

Table 7: Two way analysis of variance of biomass, chlorophyll and radiocarbon uptake comparing UV-B treatment and time of collection. Table values are row and column means and levels of significance for each experiment. All interactions were examined and only two cases were significant.

		UV-B TREATMENT				TIME			
Parameter	Experiment	CONTROL	LOW	HIGH	P-VALUE	2 WEEKS	4 WEEKS	6 WEEKS	P-VALUE
Biomass	I	4.19	6.45	8.82	*	4.70	11.64	4.11	***
	II	3.51	5.16	7.02	*	2.89	7.57	ND†	***
	III	7.69	7.62	10.25	ns	2.24	14.80	ND	***
	IV	7.22	10.91	8.42	ns	8.62	8.70	ND	ns
Chlorophyll	I	69.43	46.35	57.10	ns	12.40	50.58	110.40	***
	II	24.68	20.63	32.54	ns	34.63	17.61	ND	**
	III	56.04	71.71	53.45	ns	14.17	83.52	ND	***
	IV	17.32	49.59	58.09	*	29.76	49.75	ND	***
Radiocarbon	I	55.78	73.39	88.98	ns	55.29	43.75	123.25	***
	II	11.82	27.70	24.60	ns	17.12	25.63	ND	ns
	III	60.56	44.57	66.85	*	50.75	61.50	ND	ns
	IV	19.51	26.12	25.73	ns	30.50	16.58	ND	***

† ND = not determined.
ns ($p > 0.05$) * $p < 0.05$ ** $p < 0.02$ *** $p < 0.005$.

Table 8: Matrices of difference values (D_{hk}) of diatom assemblages collected at two week intervals during Experiments I. The values in the table are (D_{hk}-1) x 10^3.

	HIGH	LOW	CONTROL
		TWO WEEKS	
HIGH		62	70
LOW		---	38
	HIGH	LOW	CONTROL
		FOUR WEEKS	
HIGH		213	128
LOW		---	68
	HIGH	LOW	CONTROL
		SIX WEEKS	
HIGH		103	428
LOW		---	129

Table 9: Matrices of difference values (D_{hk}) of diatom assemblages collected at two week intervals during Experiments II, III and IV. The values in the table are (Dh_k - 1) x 10^3) and compare week-two assemblages (upper right half) and week-four assemblages (lower left half).

Experiment II (29 April - 28 May)			
	HIGH	LOW	CONTROL
HIGH	---	60	35
LOW	126	---	52
CONTROL	141	60	---
Experiment III (10 June - 9 July)			
	HIGH	LOW	CONTROL
HIGH	---	52	39
LOW	52	---	50
CONTROL	73	67	---
Experiment IV (13 July - 12 August)			
	HIGH	LOW	CONTROL
HIGH	---	63	101
LOW	49	---	53
CONTROL	72	45	---

Table 10: The number of individuals (N), number of taxa (S) and expressions of diversity and dominance for diatom assemblages collected from artificial substrates during the winter. The Information Index (H") is expressed as bits per individual and R' is a measure of redundancy. Treatment HIGH, LOW and CONTROL correspond to 0.13 mm CA, 0.25 mm CA and Mylar filters respectively. Variance of H" ranged from 0.0275-0.0230.

Time	Treatment	N	S	H"	R'
EXPERIMENT I (1 January - 12 February)					
2 weeks	HIGH	500	37	2.78	0.267
	LOW	500	38	2.69	0.303
	CONTROL	500	39	2.72	0.303
4 weeks	HIGH	500	34	2.83	0.228
	LOW	500	40	2.66	0.329
	CONTROL	500	35	3.78	0.254
6 weeks	HIGH	500	29	1.91	0.492
	LOW	497	25	2.14	0.373
	CONTROL	500	28	1.67	0.566
EXPERIMENT II (29 April - 28 May)					
2 weeks	HIGH	500	29	2.03	0.452
	LOW	500	30	2.03	0.450
	CONTROL	500	28	1.99	0.457
4 weeks	HIGH	500	24	1.77	0.496
	LOW	501	31	2.45	0.329
	CONTROL	490	27	2.42	0.300
EXPERIMENT III (10 June - 9 July)					
2 weeks	HIGH	500	31	2.80	0.212
	LOW	500	35	2.75	0.264
	CONTROL	500	30	2.77	0.210
4 weeks	HIGH	492	31	2.01	0.475
	LOW	500	27	2.06	0.423
	CONTROL	501	31	2.47	0.320
EXPERIMENT IV (13 July - 12 August)					
2 weeks	HIGH	500	34	2.53	0.326
	LOW	500	32	2.30	0.386
	CONTROL	500	33	2.31	0.392
4 weeks	HIGH	500	26	1.64	0.559
	LOW	498	30	2.10	0.436
	CONTROL	500	33	2.35	0.377

carbon uptake response was more complicated. Radiocarbon uptake under HIGH UV-B radiation and CONTROL was significantly greater than under LOW UV-B radiation in the one summer experiment.

DISCUSSION

Marine algae differ in their tolerance of ultraviolet radiation, some species being sensitive to natural levels of solar ultraviolet radiation. As reviewed by Worrest (1982), the response of marine phytoplankton communities to UV-B radiation is variable, but the general trend is a depression of primary productivity and growth, and an alteration of community structure with increasing UV-B dose. These results have been determined under both field and laboratory conditions. The response of diatom communities in benthic marine systems to UV-B radiation is a depression of growth rate and an alteration of community structure with increasing UV-B dose (Van Dyke and Thomson 1975; Worrest et al. 1978; Thomson et al. 1980b). These are results derived primarily from laboratory microcosms, and have not been corroborated under field conditions. For predicting events in natural ecosystems, the utility of UV-B radiation studies, based on results from laboratory microcosms, is affected by (1) the simplification imposed by the use of microcosms, (2) the attenuation of UV-B radiation in natural waters, and (3) the ratio of photosynthetically active radiation (PAR) to UV-B radiation available to the test organisms. These points will be discussed in further detail in the following paragraphs.

The microcosms in the present study simulated denuded estuarine environments without tidal influence. The success of a particular taxon of diatoms on a substrate depends on its density in the species pool, its ability to attach to the substrate, its tolerance

of the environment, and its ability to compete and reproduce (McIntire and Overton 1971). In natural estuarine ecosystems, benthic diatoms are continuously being replaced by other taxa from the open water or nearby occupied areas. In the present study, recruitment from the inflowing seawater was limited to the first few days in each experiment. Therefore, changes in the abundance of diatom taxa during each experiment was more a result of species interactions and responses to the environment than through invasion by new species from the species pool in Yaquina Estuary.

Although concurrent diatom diversity studies were not conducted in Yaquina Estuary during the present study, field data are available concerning the community properties of littoral diatom assemblages from Yaquina Estuary (McIntire and Overton 1971; Moore and McIntire 1977). Yaquina Bay was the source of seawater for the microcosms. The diatom flora in Yaquina Bay was conspicuously different from other parts of the estuary (Moore and McIntire 1977). The predominant taxa in Yaquina Bay found in these studies on submerged substrates were Synedra fasciculata, Navicula diserta, Melosira nummuloides and Navicula No. 2 during the winter and spring. Fragilaria striatula var. californica, Synedra fasciculata, Navicula diserta and Navicula No. 2 are dominant taxa found during the summer. From a sample size of 500, the number of diatom taxa in Yaquina Bay ranged from 11 to 52 and the species diversity expressed by the Information measure ranged from 0.6 to 4.5 bits/individual depending on the season and intertidal location.

Similar diatom taxa from the above field study and similar values for species composition parameters were also found for the diatom communities which developed on artificial substrates in the present study during both seasons. There was some variation in density and occurrence of specific diatom taxa. The winter diatom assemblage observed by Worrest et al. (1978) on artificial substrates in laboratory microcosms was also recruited from Yaquina Bay. The species composition in their microcosms varied from what has been observed on natural substrates in Yaquina Bay. However, this taxonomic variation may not be great in comparison with natural variabilities between microhabitats within the estuary. It is not clear how the overall variance inherent in the behavior of replicate microcosms should be viewed and few guidelines exist as to how closely and with respect to which parameters a microcosm must follow the natural system to be considered an acceptable model (Pilson and Nixon 1980).

Marine microcosms generally use small volumes of water and would be limited to modeling conditions representative of the first few meters of the sea surface. In comparison to visible radiation, marine waters are relatively opaque to UV radiation except for the upper few meters which can receive appreciable amounts of UV radiation. The penetration of UV-B radiation into the upper few meters of natural waters varies widely depending on the particulate and organic content of the water. Maximum penetration of UV radiation occurs in ocean waters having a minimum concentration of dissolved organic matter. UV-B radiation (e.g., 310 nm) is limited

to approximately the upper 10% of the euphotic zone for coastal waters before being reduced to 1% of its surface irradiance (Jerlov 1976). This corresponds to roughly the upper 15 m in low organic water and 1 or 2 m in productive coastal waters. Smith and Baker (1979) calculated 'lethal doses' of UV radiation on the eggs and larvae of northern anchovy for depths less than about 1.5 m in the clearest waters, less than about 0.7 m in a moderately productive waters, and for depths less than a few decimeters in highly productive water.

In order to fully evaluate the potential harm of present and enhanced solar UV radiation levels, it is necessary to consider how well laboratory microcosms model other physical conditions of the near surface layers of the ocean besides the depth of the attenuating water column. One important environmental parameter to consider is the ratio of photosynthetically active radiation (PAR) to UV-B radiation available to the test organisms.

Previous studies on the effects of UV-B radiation on terrestrial and marine plants were for the most part conducted in growth chambers where the level of PAR was one-tenth to one-third that of natural sunlight (Teramura 1982). Until recently, it was assumed a natural level of PAR was not a critical factor to incorporate into UV-B radiation studies.

However, there is some evidence from terrestrial plant studies that the effects of UV-B radiation on photosynthesis are dependent on the level of photosynthetically active radiation (PAR). In reduced PAR levels UV-B radiation was much more effective in

reducing soybean growth and photosynthesis than in full sunlight (Teramura 1980; Teramura et al. 1980). Although limited in number, these studies indicate there is a substantial interaction between UV-B and PAR and therefore a need to measure PAR when determining the effects of UV-B radiation on plant growth in natural conditions. It is significant to note that almost all published studies on the effects of UV-B radiation on plant growth and photosynthesis have been conducted in growth chambers or greenhouses. The PAR levels in these facilities are at the most 25% to 30% of the mean maximum daily PAR levels naturally occurring in the field (Teramura 1982).

The influence of varying PAR levels on the response of marine organisms to UV-B radiation has yet to be examined. However there does exist complementary pairs of UV-B studies using the same marine organism or community where one study has used low levels of PAR and the second study has used naturally occurring levels of PAR. A rough prediction of the role of PAR on marine organisms under UV-B radiation stress could be made on the basis of the results of these studies.

For example, the impact of UV-B radiation on unialgal laboratory cultures of the marine phytoplankton Dunaliella tertiolecta was a depression in growth rate and radiocarbon uptake after initial exposure to high UV-B fluence levels with recovery in growth rate occurring after 24 hours (Wolniakowski 1980). When exposed to natural levels of PAR, unialgal cultures of Dunaliella tertiolecta again showed a depression in radiocarbon uptake after exposure to UV-B radiation with recovery in growth rate after 48 hours (Scott

1982). The UV-B radiation benthic diatom studies by Van Dyke and Thomson (1975), Worrest et al. (1978) and Thomson et al. (1980b) utilized artificial, low-level visible radiation sources. The microcosms used in the present study to measure the response of benthic diatoms to UV-B radiation were exposed to roughly 90% of the natural visible illuminance.

The results of the study by Worrest et al. (1978) were paired to the present study to determine if naturally occurring levels of PAR have an effect on the response of benthic diatoms to UV-B radiation. Worrest et al. (1978) examined the response of a winter assemblage of benthic diatoms to UV-B radiation under semi-controlled laboratory conditions for 6 weeks. In the study by Worrest et al. (1978), there was a 35% to 40% increase in biologically effective surface UV-B dose from LOW to HIGH UV-B treatments. However, the levels of effective UV-B radiation used were much closer to summer levels typically found off the coast of Oregon, not the winter levels corresponding to when the experiment was conducted. In contrast, the LOW UV-B treatment in the present study was equivalent to an effective UV-B dose found near the midpoint date of each experimental period for the coast of Oregon. During each experiment in the present study there was an average 90% increase in biologically effective surface UV-B dose from LOW to HIGH UV-B treatment.

Despite the above mentioned differences in UV-B irradiance treatments and PAR levels between the two studies, one similar result was observed in the present study and that by Worrest et al.

(1978). The most consistent response by the diatom assemblages to UV-B radiation in both studies was a decrease in species diversity following exposure to enhanced levels of UV-B radiation.

In natural plant communities a change in species composition rather than a decrease in net production might be a more likely result of a decreased ozone layer (Caldwell 1981). The species composition and the pattern of colonization of submerged substrates by diatoms recruited from Yaquina Bay has been described based on a laboratory microcosm study (Berglund 1972). First there was a quick invasion on to the substrates by solitary motile species (Navicula directa, Navicula diserta, Navicula cincta). By the end of the experiment (5 weeks), filamentous and tube-dwelling forms (Fragilaria striatula var. californica, Berkeleya rutilans, and Melosira nummuloides) predominated with motile species interspersed within the mat.

An autecological view of the above filamentous and tube-dwelling taxa, derived from several studies (McIntire and Wulff 1969; Wulff and McIntire 1972; Berglund 1972) was assembled by Moore and McIntire (1977) and is presented in part below. Fragilaria striatula var. californica, B. rutilans and M. nummuloides competed best in the indoor laboratory microcosm at the highest illumination intensity (11,300 lux, McIntire and Wulff 1969). The distribution of these taxa in marine and estuarine environments also suggests a high light intensity requirement. F. striatula var. californica is abundant in the spring and summer on substrates exposed to some desiccation in Yaquina Estuary. Castenholz (1964) showed growth of

this taxon was daylength dependent, preferring long day periods and continuous illumination. Melosira nummuloides and F. striatula var. californica co-occur on the Oregon coast on high intertidal substrates (Castenholz 1963). Wulff and McIntire (1972) found that a sudden unseasonal reduction in salinity or an elevation in water temperature often resulted in dominance by M. nummuloides in a laboratory microcosm. Thomson et al. (1980) isolated M. nummuloides from a laboratory microcosm and measured a depression in growth rate under enhanced UV-B radiation, but low visible illuminances. Berkeleya rutilans is a tube-dwelling diatom whose relative abundance in laboratory studies increases with increasing light intensity (McIntire and Wulff 1969; Wulff and McIntire 1972). Castenholz (1967) and Cox (1977) both suggested B. rutilans requires high light intensity for growth based on its relative low abundance in the winter and limited growth in extremely shaded sites.

With a high light intensity requirement for optimal growth, these filamentous diatom species may exploit sites where growth by other diatom species is restricted by supra-optimal light or by high UV irradiance. There is some evidence for this light competition in some of the experiments in the present study. At the end of the spring/summer experiments, filamentous and tube-dwelling species represented the highest proportion of the species present on the substrates exposed to UV-B radiation. The growth habit of these filamentous, long-chained diatom species is often an overstory or canopy above the diatom mat. This canopy seemed to proliferate with time under UV-B radiation exposure during the spring/summer experi-

ments. It is hypothesized that the canopy effectively shielded the smaller, motile species within the mat from UV-B and visible irradiances. This canopy was inhibiting for the growth of other taxa and resulted in a depression in species diversity of the diatom assemblages exposed to UV-B radiation.

There are several implications of an alteration in the community structure of benthic diatom assemblages. Marine benthic diatoms are an important carbon source for invertebrate grazers and detritus feeders (Wetzel 1977). Benthic algal production, estimated at 20% to 25% of angiosperm production, is the second major primary producer and source of fixed carbon in salt marsh and estuarine ecosystems (Pomeroy 1959; Gallagher and Daiber 1974). Unlike the detrital input from angiosperm production, benthic microalgae represent a seasonally available and readily utilizable source of carbon and nutrients to primary consumers. Diatoms found in the stomach contents of gastropods are primarily motile forms and a shift in community composition to filamentous, non-motile forms could decrease the quantity and quality of food available to these primary consumers (Connor and Edgar 1982).

Nicotri (1977) measured the grazing effects of four Pacific Coast intertidal herbivores on the benthic microflora. He found all four gastropods selectively removed three long-chained diatom species that formed an overstory within the diatom mat: Melosira nummuloides, Melosira moniliformis, and Fragilaria striatula var. california. Two of the three selected diatoms were poorly digested but constituted a significant portion of the grazer diet. Nicotri

suggested that chain morphology, location of such chains in the outer part of the mat, and loose connection of the chains to the substrate facilitated ingestion and availability. The predominance of these chain-forming diatoms under UV-B stress, combined with the preference for chain-forming species by intertidal gastropods, would have drastic effects on microalgal community structure in that the dominant canopy species of the diatom mat would be removed. The removal of this canopy might cause an increase in other diatoms that had been inhibited by the canopy or it might cause an alteration of microclimate that could influence settlement and growth of sporelings (Nicotri 1977).

The effect of UV-B radiation on benthic diatom assemblages may also be measured by examining the response of non-taxonomic criteria to UV-B radiation. It was earlier stated that different UV-B radiation and PAR levels for the present study and the one by Worrest et al. (1978) did result in a similar observation (decreased species diversity). This was not the case with UV-B effects on the nontaxonomic criteria in the two studies.

The decreased species diversity observed in the present study was not accompanied by deleterious effects on biomass and chlorophyll accumulation or by deleterious effects on primary productivity. In fact, chlorophyll _a_ concentration, radiocarbon uptake, and biomass significantly increased following UV-B radiation in some experiments. The depression in biomass and chlorophyll following enhanced UV-B exposure observed by Worrest et al. (1978) occurred after 4-5 weeks of growth. In unialgal cultures of _Thalassiosira_

pseudonana, Geiger et al. (1982) also observed an increase in chlorophyll a concentration as a result of the addition of UV-B radiation to standard culture conditions.

There is some evidence that photosynthesis might be stimulated somewhat by UV radiation, particularly at longer UV wavelengths, since chlorophylls and accessory pigments absorb in the UV-A and UV-B region. Modert et al. (1982) measured the effect of UV-B radiation on the gross primary productivity of natural populations of phytoplankton under naturally occurring levels of visible radiation. It appeared as if these Atlantic Coast lagoonal phytoplankton were able to utilize UV-B and/or UV-A in a beneficial way, up to a threshold level. The increase in productivity for their moderate UV enhanced Vycor-series led them to conclude that UV quanta were being absorbed resulting somehow in increased oxygen production. Worrest (1982) in his review on the impact of UV-B radiation on marine organisms indicated that relative radiocarbon uptake increased at lower UV-B fluence levels for some phytoplankton species. It could be that the threshold levels for inhibition of photosynthesis by UV-B radiation was not reached for the benthic diatoms in the present study or the absorption of UV quanta actually stimulated the growth of certain species. However, according to some investigators, UV-B radiation will only enhance growth of a species as a consequence of improving its competitive circumstance through a detrimental effect of the radiation on its competitor (Fox and Caldwell 1978).

It is uncertain whether the difference between the present study and that of Worrest et al. (1978) is due to immediate repair driven by visible and/or UV-A irradiances. There is also the possibility that benthic diatoms under low visible radiation are morphologically and/or physiologically characteristic of shade adapted plants and therefore have increased UV sensitivity. Even though the two experiments are not directly comparable due to some differences in experimental conditions mentioned earlier, variable results from the two studies points to the need for field validation of conclusions drawn from laboratory studies on UV-B effects on benthic marine plant communities.

Worrest et al. (1978) concluded from their results in the laboratory that the potential adverse effects of increased solar UV-B radiation on benthic diatom communities included decreased community diversity, community structure shifts, and decreased productivity. Decreased community diversity and community structure shifts of benthic diatom communities are also supported by the results of the present study. However, these taxonomic structure changes did not result in a deleterious effect on the primary productivity or biomass and chlorophyll accumulation patterns of the diatom assemblages.

It is difficult to state how UV-B radiation-induced taxonomic changes in benthic diatom communities would affect the energy transfer and stability of higher trophic levels in estuarine ecosystems. If a shift in community structure at the base of marine food chains caused a change in trophodynamics, the resultant impact

would be more significant than the estimated decrease in marine primary productivity from enhanced UV-B radiation (Smith and Baker 1982). This is because of the non-linear nature of trophic relationships in marine food chains (Ryther 1969). If enhanced levels of UV-B radiation produced a change in the number of trophic levels or trophic efficiency, there would be significant change in the output resource of fish production in the sea (Smith and Baker 1982). Future research should focus on seeking answers to trophodynamic questions involving marine primary producers and higher trophic levels before a realistic assessment of enhanced UV-B radiation on benthic marine plant communities can be made.

SUMMARY

Estuarine benthic diatoms grown on artificial substrates were exposed to solar visible radiation and three levels of simulated solar UV-B radiation. The artificial substrates were housed in flow-through microcosms located in a greenhouse at the Oregon State University Marine Science Center in Newport, Oregon. Using a sunlamp/filter system, the UV-B radiation emitted by the sunlamps was shaped by cellulose acetate filters to simulate a natural UV-B spectrum. All three experimental UV-B radiation treatments (high, low, control) were present in each microcosm. The artificial substrates were sampled during one winter and several spring/summer experiments. Chlorophyll *a* concentration, biomass (ash-free dry weight), primary productivity (radiocarbon uptake) and community composition were the parameters measured at each biweekly sampling date.

The response to UV-B radiation by estuarine benthic diatom assemblages, based on a low-light laboratory study on a winter diatom assemblage, was a depression in biomass and chlorophyll accumulation and alteration of community structure (Woorest et al. 1978). Using naturally occurring levels of visible radiation, the response to UV-B radiation by benthic diatom assemblages in all experiments in the present study was also a depression in species diversity following exposure to enhanced UV-B radiation exposure. However, this change in taxonomic structure was not accompanied by a significant depression in chlorophyll *a*, biomass or radiocarbon

uptake. In face, in some experiments UV-B radiation appeared to have a beneficial effect.

The survival and growth of estuarine benthic diatom assemblages on artificial substrates does not appear to be endangered under natural or enhanced levels of UV-B radiation used in the present study. The depression in diatom species diversity indicates some species of benthic diatoms were sensitive to the level of enhanced UV-B radiation used in the present study.

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Response to Ultraviolet (UV-B) Radiation by Sediment-Associated Diatom Assemblages*

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INTRODUCTION

Global atmospheric pollution from halocarbons, particularly chlorofluorocarbons, has the potential of causing significant reductions in the concentration of stratospheric ozone. If the production of chlorofluorocarbons were to continue into the future at a rate prevalent in 1977, the steady-state reduction in total global ozone could be between 5% to 10% (NAS 1982; WMO 1982). A 5% to 10% ozone loss would result at mid-latitudes during the summer in a 13% to 28% increase in the daily transmission of DNA-damaging ultraviolet radiation in the 290-320 nm waveband (UV-B radiation) (NAS 1982). These predictions of potential ozone depletion have led to numerous studies regarding the possible biological effects of UV-B radiation. Several of these studies indicate that exposure to a simulated solar UV-B spectrum can have deleterious effects on marine bacteria, phytoplankton, and zooplankton (Thomson et al. 1980a; Damkaer et al. 1981). Karanas et al. 1981; Worrest et al. 1981a.

With regard to marine phytoplankton, several investigators have measured a depression in phytoplankton primary productivity upon exposure to enhanced UV-B radiation (Lorenzen 1979; Smith and Baker 1980 a,b; Thomson et al. 1980b; Calkins and Thordardottir 1980; Worrest et al. 1981a,b). However, the impact of UV-B radiation on epibenthic microalgal primary productivity is unknown. The epibenthic microalgal flora is composed primarily of epipelic pennate diatoms which inhabit the surface of submerged sediments (Round

1971). In estuaries and coastal wetlands, the epibenthic primary productivity often exceeds that of the phytoplankton and may be an important component of estuarine food webs (Grontved 1960; Leach 1970; Cadée and Hegeman 1974; Matheke and Horner 1974). Marine benthic diatoms are also important in stabilizing sediments and as a carbon source for numerous marine invertebrates (Holland et al. 1974; Wetzel 1977; Frostick and McClave 1979).

The epibenthic (sediment-associated) diatom flora of Yaquina Estuary, Oregon is dissimilar in species compositon to the epilithic, epiphytic and planktonic assemblages of Yaquina Estuary but typical of littoral areas from other parts of the world (McIntire and Overton 1971; Riznyk 1973; Main and McIntire 1974; Karentz and McIntire 1977; Amspoker and McIntire 1978). The impact of UV-B radiation on the phytoplankton and epilithic diatom assemblages of Yaquina Estuary has been the subject of previous studies (Worrest et al. 1978; Worrest et al. 1981a,b). The present study focuses on the primary productivity and biomass response of sediment-associated diatom assemblages from Yaquina Estuary to UV-B radiation.

MATERIALS AND METHODS

Sampling Site Description

The study area was located in lower Yaquina Bay Estuary along the central Oregon coast (44°37'N, Figure 5). The bay is subject to semi-diurnal tides with an average tidal range of 1.67 m. The sampling site was located on intertidal sandflats, 1.0 to 1.1 m above mean lower low water (MLLW), east of the Oregon State University Marine Science Center and within a marine realm of sediment deposition (Kulm and Byrne 1967). The sediment in this area has a mean grain size range of 2.31 - 2.64 Φ and a relatively low percentage of organic carbon (<0.5%, Amspoker and McIntire 1978; Cardon 1982, Davis 1982).

During the summer, lower low tide occurs during the daylight hours and surface sediment temperatures range from 32.5°C in July to a low of 5°C in the winter when exposed at low tide. At high tide sediment and water temperatures are the same and range from a mean of 15°C in the summer to 9°C in the winter (Martin 1970). Salinity in lower Yaquina Bay ranges from a high of 35 °/oo in the summer during upwelling to 8°/oo in the winter during high freshwater runoff (McIntire and Overton 1971). Further details on physical and chemical features of Yaquina Estuary are described by Burt and McAlister (1959), Frolander (1964), and Morgan and Horton (1977).

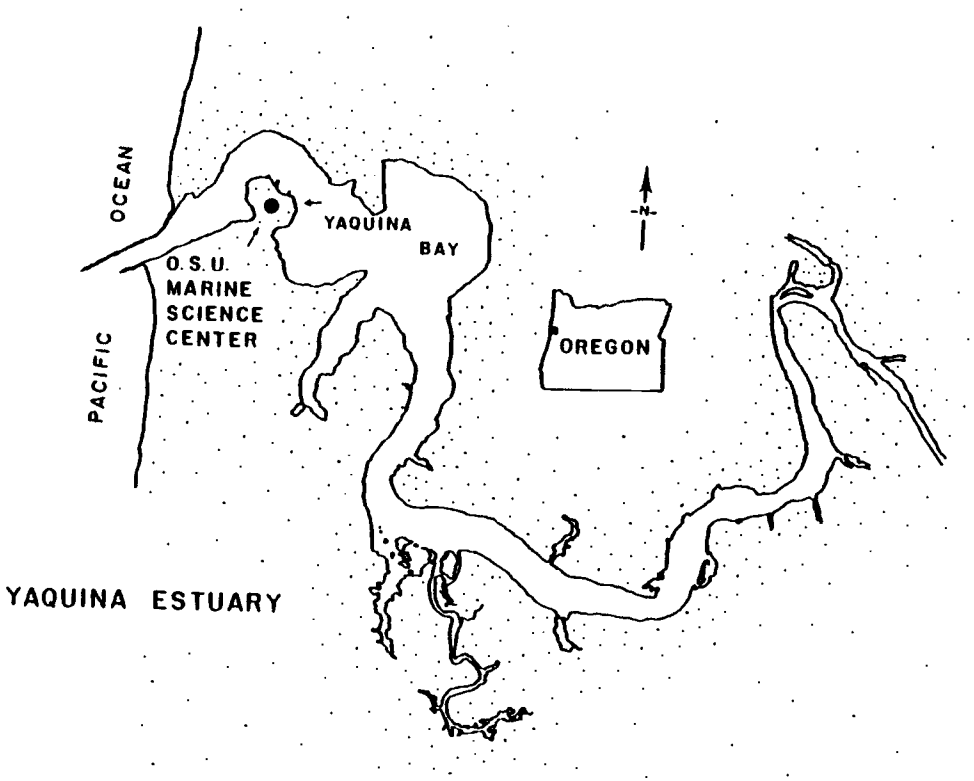

Figure 5: Yaquina Bay and Estuary, indicating the location of the Oregon State University Marine Science Center.

Methods

The response of sediment-associated diatom assemblages to UV-B radiation was measured during the spring (7 May - 27 May, Experiment I) and summer (18 June - 8 July, Experiment II) of 1981. Each experiment was conducted using three replicate microcosms housed within a greenhouse located at the Oregon State University Marine Science Center in Newport, Oregon. Microcosm A (60 x 187 x 17 cm deep) had a capacity of 137 ℓ while microcosms B and C (50 x 187 x 17 cm deep) each had capacities of 124 ℓ. The microcosms were placed end-to-end along the northern wall of the greenhouse. Seawater entered a microcosm through one vertical inlet located midway along the rear side of the microcosm. There were two outlets per microcosm, one at each end opposite the inlet (Figure 6). Pathogen-free seawater was pumped continuously through the microcosms at flow rates ranging from 1.0 ℓ/min to 1.2 ℓ/min. Pathogen-free seawater was obtained by first sand-filtering raw seawater followed by exposing the filtered raw seawater to germicidal ultraviolet radiation. It was used in place of raw seawater to reduce the introduction of new populations of microorganisms and control the buildup of sediment and macroalgal fragments.

Water temperature was recorded continuously (Partlow Recording Thermometer, Model RFT) and nutrients (orthophosphorus, reactive silica, nitrite- and nitrate-nitrogen) were monitored weekly in each microcosm. The daily mean water temperature in the microcosms ranged from 13°C to 21°C (see Appendix). The temperature in the

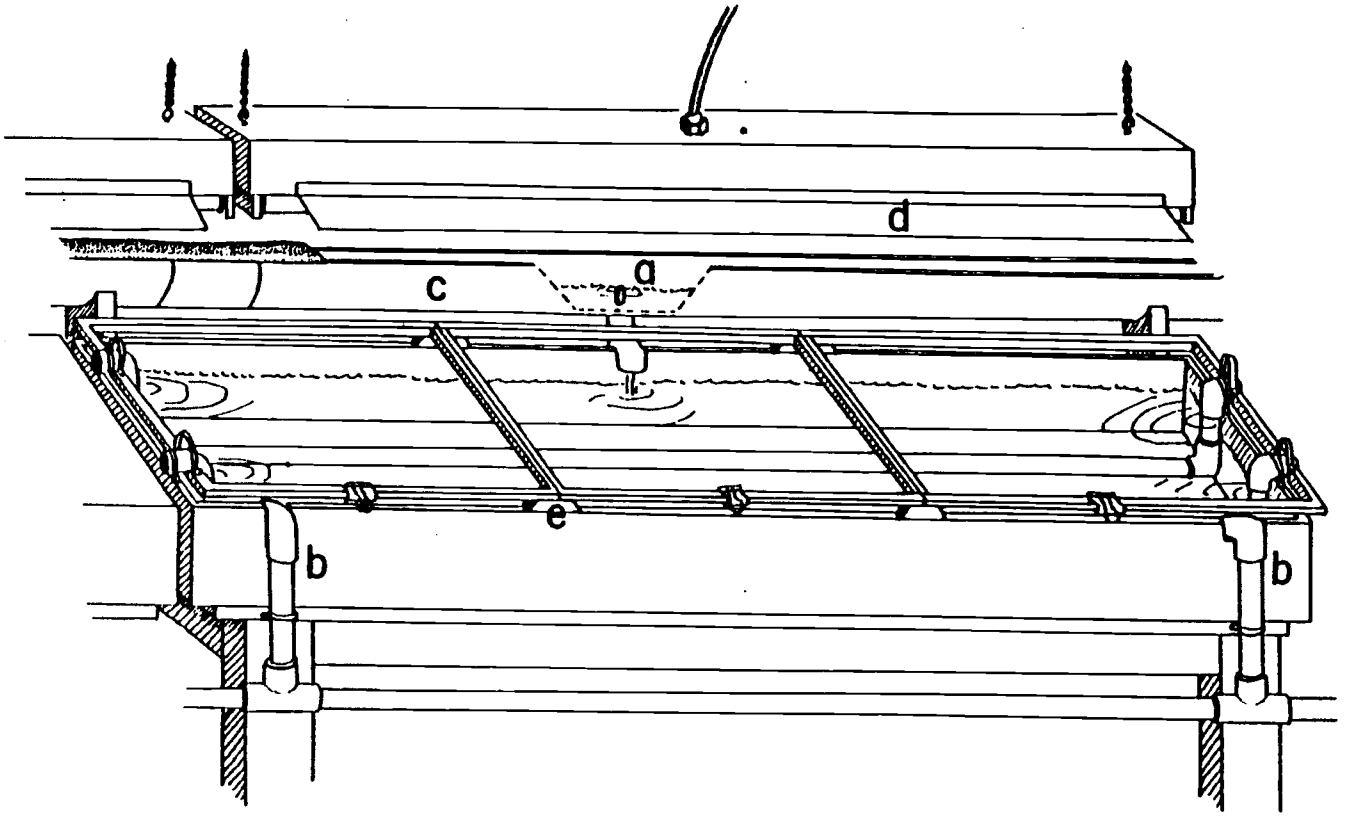

Figure 6: Exterior diagram of one of the three replicate microcosms showing the location of the single inlet (a) and double outlets (b). The inlet was made by drilling a hole into a plastic rain gutter (c) which ran the length of all three microcosms. Sunlamps (d) were positioned overhead and UV filters were clamped onto wooden frames (e).

microcosms was generally higher and the range larger than that measured (thermistor sensor, 4.0 m below MLLW) in lower Yaquina Bay but overlaps did occur between the two temperature ranges. Salinity was measured weekly and varied from 25^{o}/oo to 33 ^{o}/oo during both experiments. There was no significant difference ($p < 0.05$) in micronutrient levels between microcosms during an experiment but some micronutrient differences existed between experiments. Experiment I nitrite/nitrate-nitrogen levels were significantly higher ($p < 0.05$) than the levels recorded during Experiment II.

Intact sediment cores were removed from the sandflats using sections (6.4 x 7.6 cm diameter) of polyvinylchloride (PVC) pipe. One end was beveled to aid penetration into the sediment and also to minimize disturbance of the sediment surface. AMBI® PVC disposable gloves (VWR Scientific) were next slipped over the bottom of each PVC corer to prevent sediment loss out of the corer. The sediment was left 0.5 to 1.0 cm below the rim of the corer. This was a precautionary measure to prevent filamentous diatoms growing on the outside of the corer from invading the sediment surface. The cores were then brought to the greenhouse and placed on the bottom of the microcosm. Microfauna were not removed from the sediment cores and the depth of water over the cores was 9 cm.

The low-iron glass of the greenhouse (Sunadex, ASG Industries) filtered out most of the solar ultraviolet radiation in the UV-B waveband. Therefore a sunlamp/filter system (Sisson and Caldwell 1975) was used to simulate UV-B solar irradiances in the present study. Each lamp fixture (119 cm) of the sunlamp/filter system held

one Westinghouse FS-40 "sunlamp" and one "deluxe-white" 40 W fluorescent lamp (Vita-Lite, Duro-Test Corporation). Five lamp fixtures were positioned end-to-end and centered lengthwise 20.8 cm above the microcosm surface. All lamps were preburned before use and the duration of sunlamp exposure was 5.75 (Experiment I) to 6.00 (Experiment II) hours each day, centered around solar noon.

Ultraviolet irradiance at the surface of the microcosms was measured with an Optronic Laboratories Model 742 spectroradiometer, which had been characterized at the U.S. National Bureau of Standards. The spectroradiometer was coupled with a Model 755 Data Acquisition System for data reduction and digital printout. Supplemental visible irradiance from the fluorescent lamps averaged 2.5 $E \cdot m^{-2} \cdot day^{-1}$ and was measured by a quantum sensor (LI-COR Model LI-192SB; 400 - 700 nm response). The total solar irradiance was measured daily with an integrating quantum sensor (LI-COR Models LI-550B and LI-550B and LI-190SB; 400 - 700 nm response). It varied widely within each experiment around a mean of 26.1 $E \cdot m^{-2} \cdot day^{-1}$ during Experiment I and a mean of 34.4 $E \cdot m^{-2} \cdot day^{-1}$ during Experiment II (Table 11).

The ultraviolet irradiance under the sunlamp/filter system was proportionally greater at the shorter wavelengths in the UV-B waveband when compared to a solar spectrum. Due to this lack of spectral conformity and because not all wavelengths of ultraviolet radiation are equally effective in producing biological effects, it is important to calculate the level of biologically effective UV-B

Table 11: Daily total illuminance solar irradiance (400-700 nm) during each sediment experiment. The irradiance was measured with an integrating quantum sensor (LI-COR Models LI-550B and LI-190SB).

Experiment I	Total Solar Irradiance $E \cdot m^{-2} \cdot day^{-1}$						
Week 1 (07 May - 13 May)	33.4	13.5	40.9	39.2	40.4	42.3	36.8
Week 2 (14 May - 20 May)	20.8	31.5	21.4	10.7	27.2	28.4	21.1
Week 3 (21 May - 28 May)	25.9	28.7	19.2	11.2	34.4	0.3	39.3
Experiment II							
Week 1 (18 June - 24 June)	18.8	14.9	25.9	28.2	16.9	34.6	45.9
Week 2 (25 June - 2 July)	38.1	35.8	38.8	44.2	42.5	27.8	40.7
Week 3 (3 July - 9 July)	43.6	43.6	33.9	16.8	40.0	40.9	34.3

radiation from the sunlamp/filter system and compare it with that from the sun.

Biologically effective UV-B irradiances are obtained through use of weighting functions derived from action spectra. Action spectra weight each wavelength of radiation according to its effectiveness in producing a specific biological response. UV-B action spectra for inhibition of photosynthesis and cell division are similar in that the biological responsiveness increases with decreasing wavelength (Caldwell 1971). To calculate biologically effective irradiances, the spectral irradiance of interest is first weighted with a chosen action spectrum. The summation over all wavelengths yields the biologically effective irradiance; when the irradiance is summed over time, one obtains the biologically effective dose.

Caldwell's (1971) generalized plant action spectrum was used as the basis for simulation of current and enhanced levels of biologically weighted UV-B radiation. Worrest et al. (1981a) found this weighting function was the best fit of those tested for phytoplankton chlorophyll and radiocarbon uptake responses to UV-B radiation. For comparative purposes, two other biological weighting functions were considered: an action spectrum for photoinhibition of isolated chloroplasts (Jones and Kok 1966) and a DNA action spectrum (Setlow 1974). The reference wavelengths used in the present study for normalization of the Caldwell (1971), Jones and Kok (1966), and Setlow (1974) weighting functions were the same as

those employed by Green and Miller (1975) and Smith and Baker (1979).

Experimental UV-B levels were selected to approximate incident solar irradiance at standard (0.32 atm-cm) ozone levels and under reduced atmospheric ozone. The sediment cores exposed to UV radiation filtered through a 0.25 mm thickness of CA (= LOW) received daily effective doses which simulated predicted incident levels at 44°37'N latitude for 0.32 atm-cm ozone, 0.0 albedo, and 2.0 aerosol scaling factor at sea level (parameters of model described by Green et al. 1980). The daily effective dose under the 0.13 mm thickness of CA (= HIGH) was comparable to a 33% (Experiment I) and 28% (Experiment II) reduction in ozone thickness in the model previously described (see 'MODEL' in Table 12).

Solar UV-B irradiance has a diel and daily variance, but a variable irradiance and a variable daily dose were impractical during the course of a particular experiment in this study. 'LOW' experimental UV-B irradiance levels were the equivalent of the effective UV-B irradiance typically observed at nooon near the midpoint date of each experiment. Likewise, the duration of exposure was chose to approximate the daily effective UV-B dose observed near the midpoint date of each experiment (Table 12).

The sediment cores were sampled at one to two week intervals for chlorophyll _a_, biomass (ash-free dry weight) and radiocarbon uptake. For each parameter a smaller PVC corer (5 x 2.5 cm diameter) was used to subsample the main core. These smaller cores were frozen prior to analysis and the top 1 cm removed for chloro-

Table 12: Absolute and biologically weighted UV-B irradiances and daily doses transmitted by 0.13 mm CA (HIGH), 0.25 mm CA (LOW), and Mylar (Control) filters for each experiment. The absolute and biologically weighted UV irradiances (Solar Noon, Global) and daily doses near the midpoint of each experiment are listed in the table under MODEL. These fluences are from a computer model based on Green et al. 1980 (RC Worrest, personal communication) and correspond to 44.37°N latitude at sea level, 0.32 atm-cm ozone thickness, 0.0 albedo, and 2.0 aerosol scaling coefficient (parameters of model described by Green et al. 1980).

		IRRADIANCE ($mW \cdot m^{-2}$)				DAILY DOSE ($J \cdot m^{-2} \cdot day^{-1}$)			
Experiment	Treatment	DNA	PLANT	PI	ABSOLUTE	DNA	PLANT	PI	ABSOLUTE
I	HIGH	17.0	119.9	1000	1511	351.9	2481.9	2.07×10^4	3.13×10^4
(7 May -	LOW	8.0	66.6	649	951	165.6	1366.2	1.34×10^4	1.97×10^4
27 May)	CONTROL	3.8×10^{-3}	13.7×10^{-3}	139	26	0.1	0.3	0.29×10^4	0.05×10^4
	MODEL	3.9	61.8	6672	3179	75.3	1265.7	1.83×10^5	7.71×10^4
II	HIGH	17.0	119.9	1000	1511	367.2	2589.8	2.16×10^4	3.26×10^4
(18 June -	LOW	8.0	66.6	649	951	172.8	1438.6	1.40×10^4	2.05×10^4
8 June)	CONTROL	3.8×10^{-3}	13.7×10^{-3}	139	26	0.1	0.3	0.20×10^4	0.05×10^4
	MODEL	4.5	70.6	7064	3570	90.0	1511.9	2.01×10^5	9.04×10^4

phyll and biomass measurements. The main cores were not replaced in the microcosms after sampling.

A Bausch and Lomb Spectronic 70 spectrophotometer with a 1 cm pathlength was used for chlorophyll determinations. The top 1 cm of sediment was first ground with 10 ml of 90% (v/v) analytical grade acetone and a few drops of saturated magnesium carbonate solution using a mortar and pestle. The chlorophyll extracts were placed on ice and in the dark for 20 - 22 hours before decanting off the supernate. Five milliliters of fresh 90% (v/v) analytical grade acetone was then added to the chlorophyll extract supernate. After centrifugation (4500 rpm, 12 min) the extracts were measured at 665 nm before and after acidification with two drops of 50% (v/v) HCl. Chlorophyll a concentration was calculated according to Lorenzen (1967).

Core biomass samples were placed in tared crucibles and dried for 24 h in a 70°C oven, ashed for 24 h at 450°C and cooled to room temperature in a desiccator. To correct for water of hydration, distilled water was added to the crucibles and the samples were again dried in a 70°C oven for 24 h to obtain a corrected ash-free dry weight.

A modification of the procedure reported in Van Raalte et al. (1974) and Marshall et al. (1973) was used to measure primary productivity of the sediment-associated microflora. Sediment sub-samples were collected from the main core with a corer machined from a 20 cc polyethylene syringe (Stylex, Figure 6). The end was beveled and a drain hole drilled 1 cm from the end. As described in

Marshall et al. (1973), the plunger was above the drain hole while the corer entered the sediment. The plunger was then lowered to cover the drain hole after a desired column of sediment was obtained. One centimeter core sections were obtained in this manner and placed in a polyethylene liquid scintillation vial cap (Whatman), which served as the sediment receptacle during incubation in Vycor (Corning Glass works, 125 ml) glass vessels (Figure 7). The sediment remained intact during radiocarbon uptake as small holes were drilled along the perimeter of the scintillation cap to prevent its dispersal while the incubation vessel was being filled.

One-half liter of pathogen-free seawater was inoculated with 200 μCi of ^{14}C-sodium bicarbonate (New England Nuclear) for a final concentration of 0.4 μCi/ml in each vessel. Ten vessels were prepared in the following manner for each run: 3 from sediments under 0.25 mm CA (LOW), 3 from under 0.13 mm CA (HIGH), 3 controls (Mylar), and 1 blank (pathogen-free seawater). An eleventh non-labelled core was also incubated for quench curve determination. There was generally one dark bottle per run and dark fixation ranged from 1.5% to 6.4% of the mean light bottle fixation rates (see Appendix). There was no apparent difference in dark fixation between treatments.

The Vycor vessels were incubated for 3 h (11:00 A.M. - 2:00 P.M.) during the sunlamp exposure period. Vycor absorbs and reflects less than 30% of the UV-B radiation. Each sediment-containing Vycor vessel was incubated in the microcosm at its original location. Alkalinity was measured during the incubation

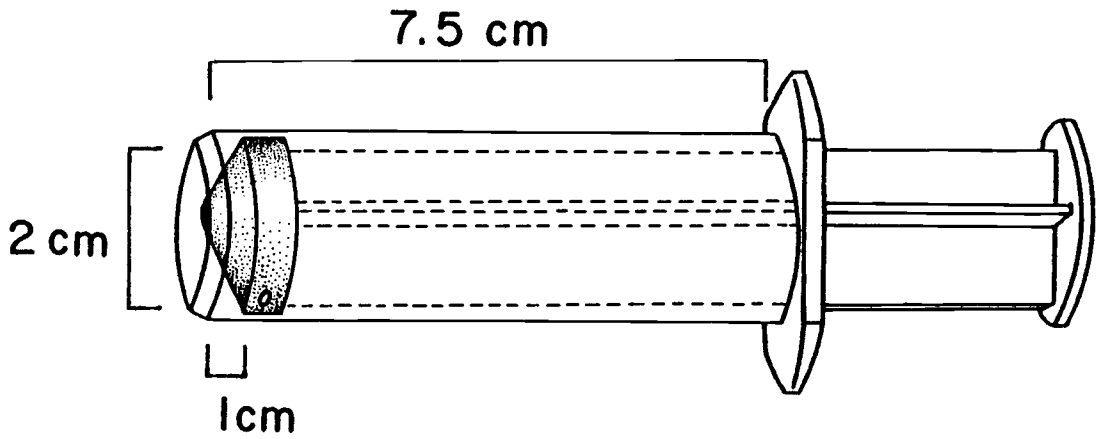

Figure 7 : Modified syringe used in collecting sediment cores for productivity measurements.

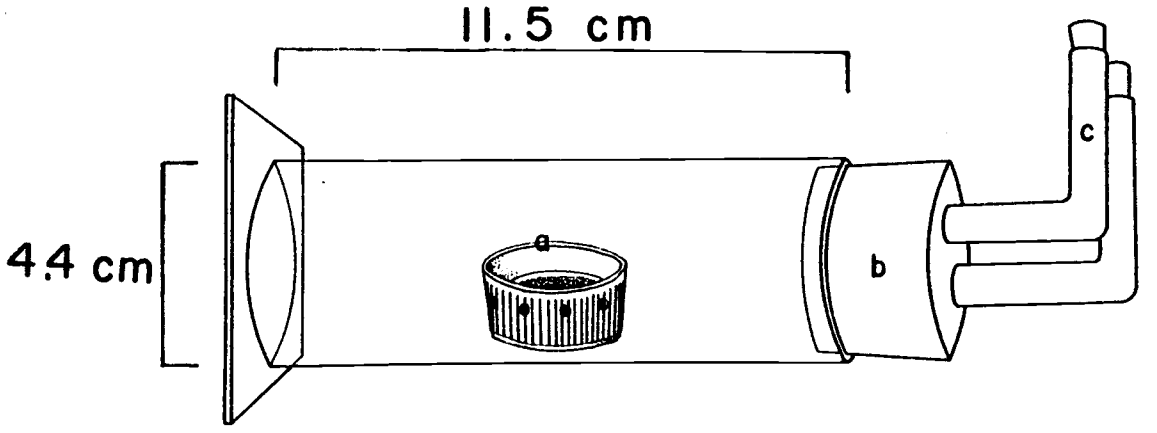

Figure 8; The Vycor glass vessel (125 ml) used for productivity measurements of intact sediment cores. Plastic liquid scintillation caps (a) served as receptacles for the sediment. The vessel was sealed with a silicone rubber stopper (b) and filled through a bent glass tube (c).

period with the aid of a YSI salinity meter (Model 33 SCT, Yellow Springs) and an analog pH meter (Model 399A Orion Research). Total carbonate content was calculated according to Strickland and Parsons (1972).

Following incubation the Vycor vessels were returned to the laboratory and kept on ice and in the dark until processed. No fixatives were used on the sediment. Sediment from the receptacles was removed and membrane filtered (0.45 μm porosity, Millipore) with 50 ml of 2% (v/v) HCl at 1/3 atm vacuum for removal of unassimilated carbon-14. The sediment was then scraped off the filter into an erlenmeyer flask with 10 ml of concentrated HNO_3 and digested overnight. After centrifugation (2400 rpm, 10 min) 1 ml of the supernate was removed and added to 9 ml of 0.75 M Tris buffer. Triplicate one ml aliquants of this preparation were then added to three seperate vials each containing 10 ml aliquants of fluor (Aquasol, Beckman Instruments). The samples were counted on a three-channel liquid scintillation system with Compton external standardization (Beckman LS 8000). A microdispenser (Drummond Series 200 Dialamatic) was used to dispense ^{14}C-toluene (New England Nuclear) to prepare a quench curve for each radiocarbon experiment. Counting efficiencies ranged from 39% to 79% (mean 54%) and radiocarbon uptake was calculated according to Marshall et al. (1973).

Analysis of variance of biomass, chlorophyll *a* and radiocarbon uptake data was calculated with a PDP 11/70 Digital computer at the Corvallis Environmental Research Laboratory.

RESULTS

Analysis of variance indicated there were significant differences ($p < 0.05$) in detrital and microalgal biomass (ash-free dry weight) and radiocarbon uptake associated with the effect of UV-B radiation (Table 13 and Table 14). After one week of exposure to enhanced UV-B radiation, there was a significant decrease in biomass but no significant change in chlorophyll or radiocarbon uptake with UV-B treatment. After three weeks, there was a significantly lower radiocarbon uptake under HIGH UV-B radiation but no significant change in biomass or chlorophyll with UV-B treatment.

With regard to differences in biomass, chlorophyll and radiocarbon uptake associated with the effect of time, analysis of variance indicated significant changes in all three parameters. The general trend was an increase in density of the microflora during Experiment II contrasting with an apparent decrease in microflora density during Experiment I.

Table 13: Biomass (ash-free dry weight), chlorophyll and radiocarbon uptake response of natural assemblages of sediment-associated microflora to three fluences of UV-B radiation (± S.D.). Each experiment ran three weeks.

Experiment	Day	Filter	Absolute Fluence (290-320 nm) ($kJ \cdot m^{-2} \cdot day^{-1}$)	Chlorophyll (mg chl *a* $\cdot m^{-2}$)	Biomass ($gm \cdot m^{-2}$)	Radiocarbon Uptake (mg C fixed $\cdot m^{-2} \cdot h^{-1}$)
I	7 (13 May)	0.13 mm CA	31.28	63.3 ± 5.7	258.2 ± 33.5	21.3 ± 5.9
		0.25 mm CA	19.69	80.0 ± 5.5	248.0 ± 43.7	15.6 ± 3.1
		Mylar	0.53	54.4 ± 1.9	347.8 ± 30.3	22.6 ± 6.9
	14 (20 May)	0.13 mm CA	31.28	119.0 ± 80.5		10.9 ± 7.1
		0.25 mm CA	19.69	183.8 ± 54.8	ND*	7.8 ± 0.1
		Mylar	0.53	105.0 ± 62.5		8.6 ± 4.9
	21 (27 May)	0.13 mm CA	31.28	128.5 ± 40.5	213.3 ± 37.7	6.4 ± 2.2
		0.25 mm CA	19.69	93.7 ± 30.5	230.0 ± 8.8	7.9 ± 2.9
		Mylar	0.53	131.4 ± 17.6	237.3 ± 19.6	3.8 ± 0.8
II	7 (25 June)	0.25 mm CA	32.64	58.4 ± 9.8	222.7 ±95.1	9.1 ± 1.7
		0.13 mm CA	20.54	67.6 ± 23.6	260.1 ± 89.1	7.9 ± 1.2
		Mylar	0.55	49.4 ± 5.5	218.9 ± 73.9	7.0 ± 0.6
	21 (8 July)	0.25 mm CA	32.64	75.8 ± 24.5	252.9 ± 69.5	8.0 ± 2.4
		0.13 mm CA	20.54	115.1 ± 56.8	257.0 ± 57.8	16.4 ± 0.0
		Mylar	0.55	52.7 ± 21.1	268.0 ± 86.8	11.9 ± 1.8

* ND = not determined

Table 14: Two-way analysis of variance of biomass, chlorophyll, and radiocarbon data comparing UV-B treatment and time of collection. Table values are row and column means and levels of significance for each experiment. All interactions were examined and only one case was significant.

		UV-B TREATMENT				TIME			
Parameter	Experiment	CONTROL	LOW	HIGH	P-VALUE	1 WEEK	2 WEEKS	3 WEEKS	P-VALUE
Biomass	I	292.6	239.0	235.8	**	284.7	ND+	226.9	***
	II	243.5	258.6	237.8	ns	233.9	ND	259.3	ns
Chlorophyll	I	108.1	119.1	114.7	ns	65.9	158.9	117.8	***
	II	51.1	91.4	67.1	ns	58.5	ND	81.2	ns
Radiocarbon	I	11.7	10.1	12.8	ns	19.8	9.1	5.7	***
	II	9.9	12.1	8.6	*	8.0	ND	12.1	***

ns ($p > 0.05$) * $p < 0.05$ ** $p < 0.02$ *** $p < 0.005$
+ND = not determined

DISCUSSION

The penetration of UV-B radiation into the upper few meters of natural waters varies widely depending on the organic content of the water. Maximum penetration of UV-B radiation occurs in ocean waters having minimum concentrations of particulate and dissolved organic matter. UV-B radiation (e.g., 310 nm) is limited to approximately the upper 10% of the euphotic zone for coastal waters before being reduced to 1% of its surface irradiance (Jerlov 1976). This corresponds to roughly the upper 15 m in low organic ocean water and 1 or 2 m in productive coastal waters. Smith and Baker (1979) calculated 'lethal doses' of UV radiation on eggs and larvae of northern anchovy for depths less than about 1.5 m in the clearest waters, less than about 0.7 m in moderately productive waters, and for depths less than a few decimeters in highly productive waters.

The attenuation of UV radiation by natural waters, and especially by productive coastal waters, may play an important role in the survival of planktonic marine organisms. However, recent data suggest present levels of solar ultraviolet radiation can depress marine phytoplankton primary productivity and growth in natural waters (Jitts et al. 1976; Lorenzen 1979; Smith and Baker 1980 a,b; Worrest et al. 1981a).

Epibenthic microalgal communities are also important contributors to primary productivity in marine ecosystems. Epibenthic microalgae are primarily epipelic pennate diatoms which inhabit the surface of submerged sediments (Round 1971). However, by virtue of

their location, epibenthic diatoms are susceptible to resuspension in shallow estuarine systems by wind action on the water surface, tidal currents and convective currents (Baille and Welsh 1980). Benthic diatoms have been found in the water column of several subtidal marine systems (Karentz and McIntire 1977; Roman and Tenore 1978). In the water column under these conditions light interactions for benthic diatoms would be similar to what the phytoplankton and near-surface organisms encounter. Thus it would be of interest to consider their sensitivity to ultraviolet radiation not only because of their contribution to primary productivity but also because of their distribution in marine waters.

Except for these periods of resuspension, benthic diatoms are generally in close association with their substrate. As a benthic-dwelling organism, their exposure to light would be quite different in comparison to life in the water column. The vertical distribution of benthic diatoms in marine sediments corresponds to the attenuation of light that occurs in the upper few millimeters of sediments. In sediments, benthic diatoms live in a more light absorbing medium than do phytoplankton. Attenuation coefficients for ultraviolet radiation in sediments have not yet been measured. However, one may predict roughly their magnitude on the basis of careful measurements of photosynthetically active radiation (PAR, 400-700 nm) attenuation coefficients in sediment.

Attenuation coefficients for PAR in sediment depends on the grain size and wavelength. Long wavelengths of PAR penetrate further than short wavelengths and fine grain deposits attenuate

more than coarse sediments (Gomoiu 1967; Fenchel and Straarup 1971; Haardt and Nelson 1980). Davis (1982) measured a reduction of PAR to 1% of surface light intensity at 2.55 mm at sand sites and 1.30 mm at silt sites in Netarts Estuary, Oregon. Investigators from other areas have found the depth of 1% of surface intensity ranging from 0.38 mm to 4.00 mm (Taylor 1964; Riznyk and Phinney 1972, Fenchel and Straarup 1971; Haardt and Nelson 1980).

During periods of tidal emergence, which occurs in Yaquina Estuary in the summer during daylight hours up to 6 hours a day, there is the potential for maximum damage by UV exposure to intertidal organisms. Ultraviolet radiation has been suggested, from results of field experiments, as one adverse feature of solar exposure on benthic marine diatom growth and development, hence possibly an important environmental feature (Castenholz 1963). Studies to date show a depression in marine benthic diatom biomass and growth following exposure to enhanced UV-B radiation in laboratory microcosms.

For example, a significant depression in the growth rate of an epilithic chain-forming marine littoral diatom on agar plates was observed following exposure to UV-B radiation (Thomson et al. 1980b). In a second laboratory study Worrest et al. (1978) measured a depression in estuarine benthic diatom community biomass accumulation, after 4-5 weeks of exposure to enhanced UV-B radiation.

The role of UV radiation on microalgal photosynthesis in situ on exposed sediments is presently unknown, but could be considerable. The primary productivity of intertidal algae under exposed

conditions is equal to or greater than primary productivity when measured under submergence (Johnson et al. 1974; Darley et al. 1976; Quadir et al. 1979). Holmes and Marshall (1982) measured gaseous carbon dioxide exchange from high intertidal estuarine sediments to determine maximum net photosynthetic rates when the sediments were unflooded. Flooding of moist sediments reduced net photosynthetic rates by 48% to 66%.

The depression in primary productivity of benthic diatoms observed in the present study occurred when the sediments were intact and submerged. Cadée and Hegeman (1974) also studied the effect of UV radiation on the primary productivity of submerged benthic microalgae collected from tidal flats. They concluded from incubations with quartz cuettes in full sunlight that ultraviolet radiation had no adverse effects on benthic microalgae inhabitating sediments. However, the present study and Cadée and Hegeman's (1974) study did not consider the influence of diurnal migration activities of sediment-associated diatoms on their measurements. This is an important behavior of sediment-associated diatoms that should be incorporated into experimental design for correct conclusions of the response of this assemblage of microalgae to environmental stress.

The intertidal microalgal flora of intertidal sediments is composed primarily of epipelic, motile and epipsammic, non-motile diatoms (Round 1971). Diurnal vertical movements of the epipelic forms is a well known ecological property of sediment-associated diatom assemblages (Eltringham 1971). Migration upwards to the

surface takes place at low tide if the light intensity exceeds some minimum intensity (McIntire and Moore 1977). On firm sands and muds some species will stay on the surface when the tide comes in if the sea is clear (Harper 1977). Although it is a complex phenomenon, it appears that light rather than tidal cycle is the most important factor for the migration of estuarine diatoms, according to field observations and laboratory studies (Perkins 1960; Round and Palmer 1966; Palmer and Round 1967). These periods of increased motility are not those of maximum photosynthesis as migration upwards takes place around sunrise and migration downwards occurs around sunset. Based on observations of increased densities of mud surface diatoms under red filters as opposed to blue filters (Hopkins 1966), the motility response to light appears to be specifically dependent on wavelength. Epipelic diatoms migrating to the surface of intertidal sediments under enhanced levels of UV-B radiation, and cued to the surface by long wavelengths of visible radiation, might not possess the repair mechanisms for levels of radiation not previously encountered (Conrad 1976).

Macro- or meio-fauna present were not removed from the sediment cores. By allowing grazers to remain in the sediment cores, the potential effects of grazing on the microflora may have overwhelmed the UV-B radiation effects on the sediment microflora community. However, grazing is an important factor determing standing crop, productivity and community structure of benthic diatom assemblages (Nicotri 1977; Pace et al. 1979; Connor and Edgar 1982). The removal of existing grazers or potential microalgal grazers from the

sediments would have created an unnatural sediment community and also altered the physical and chemical integrity of the sediments.

Field and laboratory studies on intertidal sediments from Yaquina Estuary indicated that the removal of infauna allowed the increase of sediment-associated microalgal biomass and production (Davis 1982). This study by Davis was conducted over a 40 day period compared to a 21 day period in the present study. In a study by Admiraal (1978), sediments were removed from intertidal flats and transferred to microcosms. Grazing by ciliates inhabitating the sediments was responsible for a decrease in the density and change in the species composition of the benthic diatom flora. Thus, eliminating the grazing variable might have helped in the interpretation of UV-B radiation effects on benthic microalgae but it would have also reduced the predictability of UV-B radiation effects on natural sediment assemblages.

An alteration in the density of benthic diatoms on marine and estuarine sediments by enhanced UV-B radiation could affect sediment acretion and dispersal patterns in shallow-water marine systems. There is evidence for an association between benthic diatom growth and sediment acretion in estuaries, and benthic microalgal populations have an important role as precursors to salt marsh development (Coles 1979; Frostick and McClave 1979). The mucilaginous secretions by diatoms promotes sediment binding and stabilization of sediments (Holland et al. 1974). Changes in the densities of these mucilage-producing diatom species by UV-B radiation stress could lead to erosion or increased instability of sediment environments.

Future studies should aim toward two goals. One, the study of solar ultraviolet radiation on exposed sediment microalgal assemblages, and a second, whether vertical migration by sediment-associated diatoms to avoid UV radiation is an important mechanism for their protection from high UV levels. It is unknown whether the community structure of sediment-associated diatom assemblages shifts following UV-B radiation exposure. Such a shift could have dramatic effects on other organisms. For example, diatoms found in the stomach contents of marine gastropods are primarily motile forms. A shift in community composition to epipsammic, non-motile forms could decrease the quanity and quality of food available to these primary consumers (Connor and Edgar 1982).

SUMMARY

Intact sediment cores containing epipelic and epipsammic diatoms on the sediment surface were exposed to solar visible radiation and three levels of simulated solar UV-B radiation. The sediment cores were maintained in three flow-through microcosms located in a greenhouse at the Oregon State University Marine Science Center in Newport, Oregon. All three experimental UV-B radiation treatments (high, lowe, control) were present in each microcosm. Using a sunlamp/filter system, the UV-B radiation emitted by the sunlamsp was shaped by cellulose acetate filters to simulate a natural UV-B spectrum. There were two replicate sediment experiments. Each experiment was three weeks in duration and was conducted during the early and late summer. Chlorophyll a concentration, biomass (ash-free dry weight) and primary productivity (radiocarbon uptake) were the parameters measured at weekly sampling date.

The response to UV-B radiation by sediment-associated estuarine diatoms assemblages was a significant depression in biomass following one week of exposure to UV-B radiation. Analysis of variance also showed a significant depression in primary productivity following three weeks of exposure to high levels of UV-B radiation.

A decrease in the density or biomass of benthic diatoms on estuarine sediments by enhanced UV-B radiation could affect sediment dispersal patterns and sediment acretion in shallow-water marine systems. The mucilaginous secretions of certain marine benthic

diatoms aid in the binding of sediment particles. The primary productivity by benthic diatoms contributes a significant amount of carbon into estuarine ecosystems and a depression in this carbon flow would have deleterious effects on higher trophic levels.

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SUMMARY

Global atmospheric pollution from chlorofluorocarbons has the potential of causing significant reductions in the concentration of stratospheric ozone. If the production of chlorofluorocarbons were to continue into the future at the rate prevalent in 1977, the steady state reduction in total global ozone could be between five to ten percent. This predicted ozone loss would result in an increase in the daily transmission of biologically harmful solar ultraviolet (UV-B, 290-320 nm) radiation. However, there have been relatively few studies concerned with the biological significance of increased UV-B radiation to the earth's surface.

Experiments were conducted in flow-through microcosms located in a greenhouse at the Oregon State University Marine Science Center in Newport, Oregon. Two different estuarine diatom assemblages were exposed to solar visible radiation and three levels of simulated solar UV-B radiation in the microcosms. Artificial substrates colonized by diatoms recruited from Yaquina Estuary and sediment-associated diatoms removed from intertidal sandflats in Yaquina Estuary were the two diatom assemblages examined for UV-B radiation sensitivity. A sunlamp/filter system was used to simulate a natural UV-B spectrum and all three experimental UV-B radiation treatments (high, low, control) were present in each microcosm. The artificial substrate assemblages were samples during the winter and several spring/summer experiments. Sediment community experiments were conducted in the summer. Chlorophyll *a* concentration, biomass

(ash-free dry weight) and primary productivity (radiocarbon uptake) were the parameters measured at each sampling date for the sediment and artificial substrate studies; community composition was determined for diatom assemblages attached to artificial substrates.

According to the literature, the response to UV-B radiation by estuarine benthic diatom assemblages, based on a low-light laboratory study, was a depression in biomass and chlorophyll accumulation and a depression in species diversity (Worrest et al. 1978). Using naturally occurring levels of visible radiation, the response to UV-B radiation by diatom assemblages attached to the artificial substrates was also a depression in species diversity following exposure to enhanced UV-B radiation. The depression in diatom species diversity was observed in all experiments. Analysis of variance of biomass, chlorophyll _a_ and radiocarbon uptake data indicated no signficant depression in these non-taxonomic parameters by UV-B radiation during each experiment. In fact, in some experiments UV-B radiation appeared to have a beneficial effect. Based on the taxonomic and non-taxonomic measurements in each experiment, there was no seasonal difference in response to UV-B radiation by diatom assemblages attached to artificial substrates.

The response of sediment-associated estuarine diatom assemblages to UV-B radiation was different than that observed with the artificial substrate diatom assemblages. There was a significant depression in biomass accumulation following one week of exposure to UV-B radiation and a significant depression in primary productivity following three weeks of exposure to high levels of UV-B radiation.

Based on the non-taxonomic parameters measured in both studies, estuarine benthic diatom assemblages associated with sediment surfaces appear to be more sensitive to UV-B radiation than estuarine diatoms attached to artificial substrates.

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APPENDICES

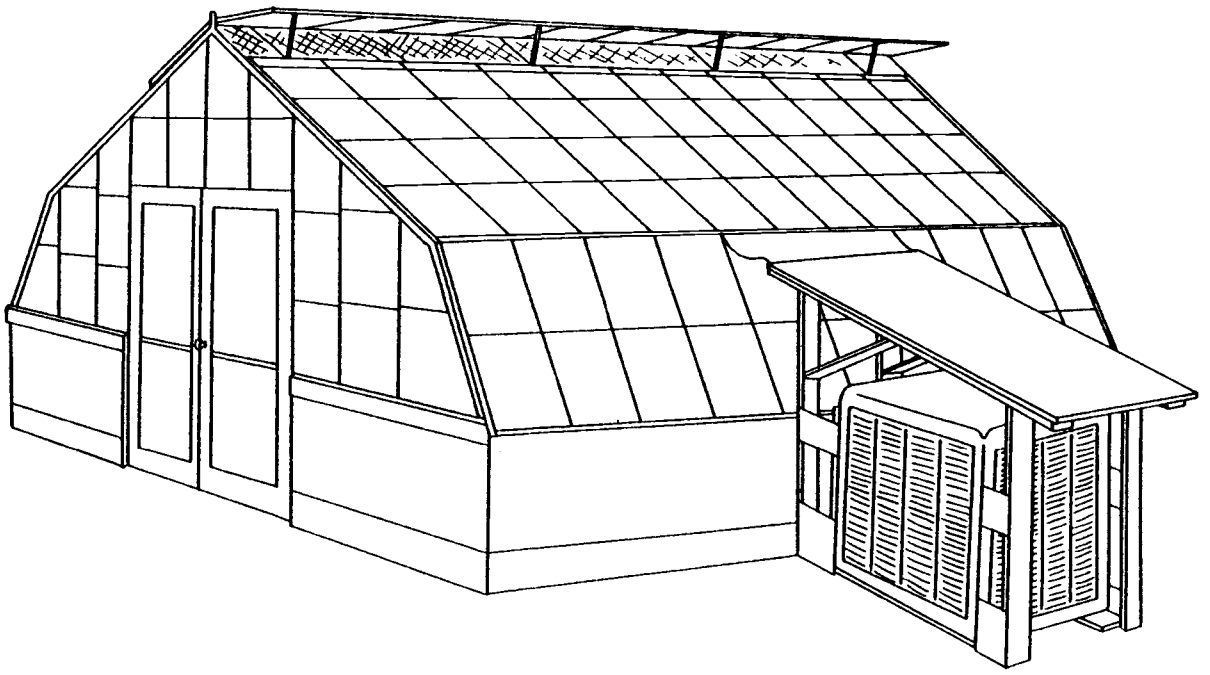

Figure 9: Greenhouse

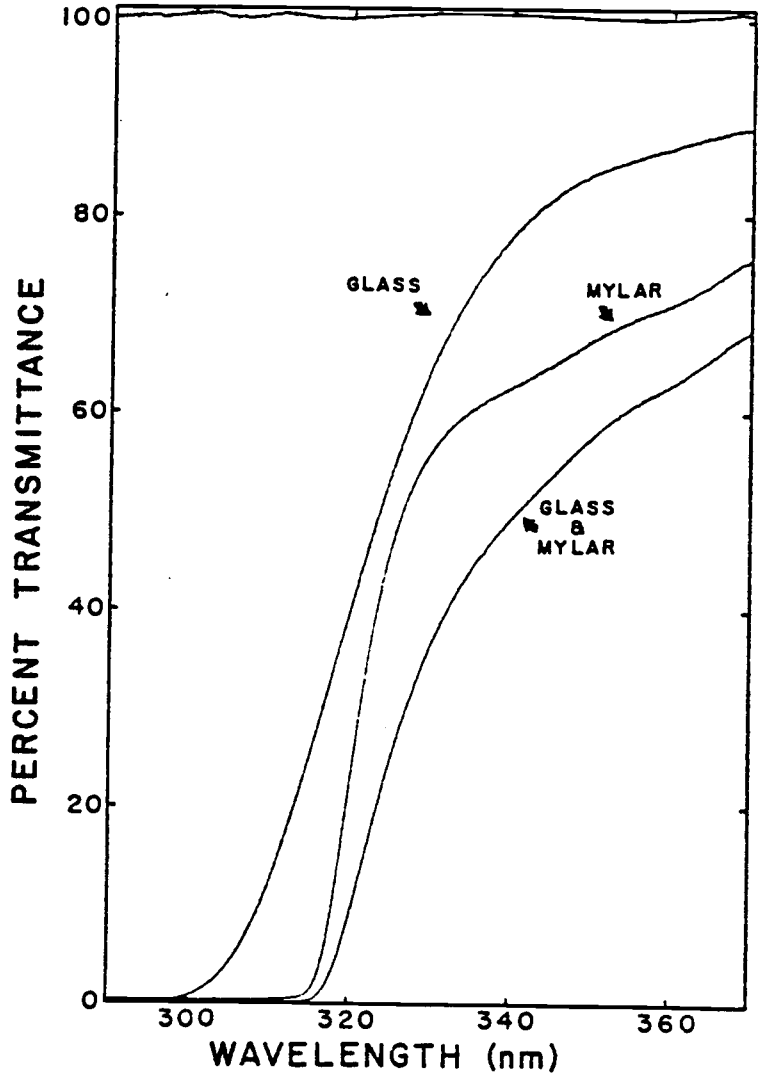

Figure 10: Transmission spectra for a 0.32 cm thickness of Sunadex glass (ASG Industries), a 0.13 mm thickness of Mylar 'D' (Du Pont) and a combination of glass and Mylar as measured with a Shimadzu Recording SPectrophotometer: MPS-50L over a spectral range of 290 - 370 nm.

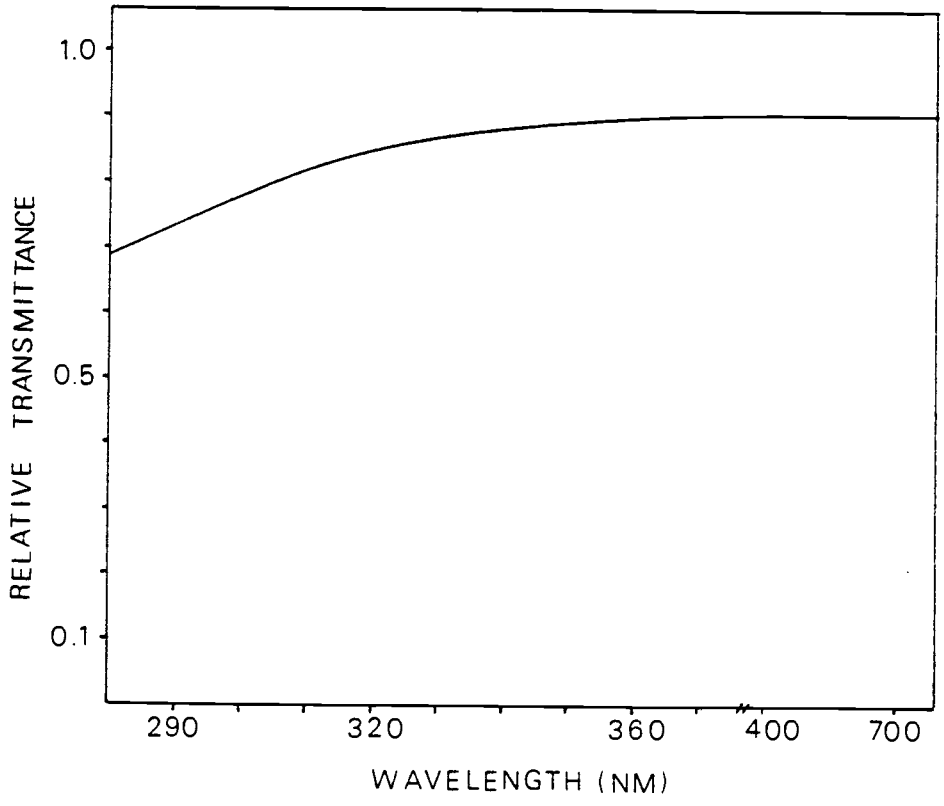

Figure 11: Transmission spectrum for a 2.5 mm thickness of Vycor glass (Corning Glassworks) as measured by a Shimadzu Recording Spectrophotometer : MPS - 50 L over a spectral range of 280 - 700 nm.

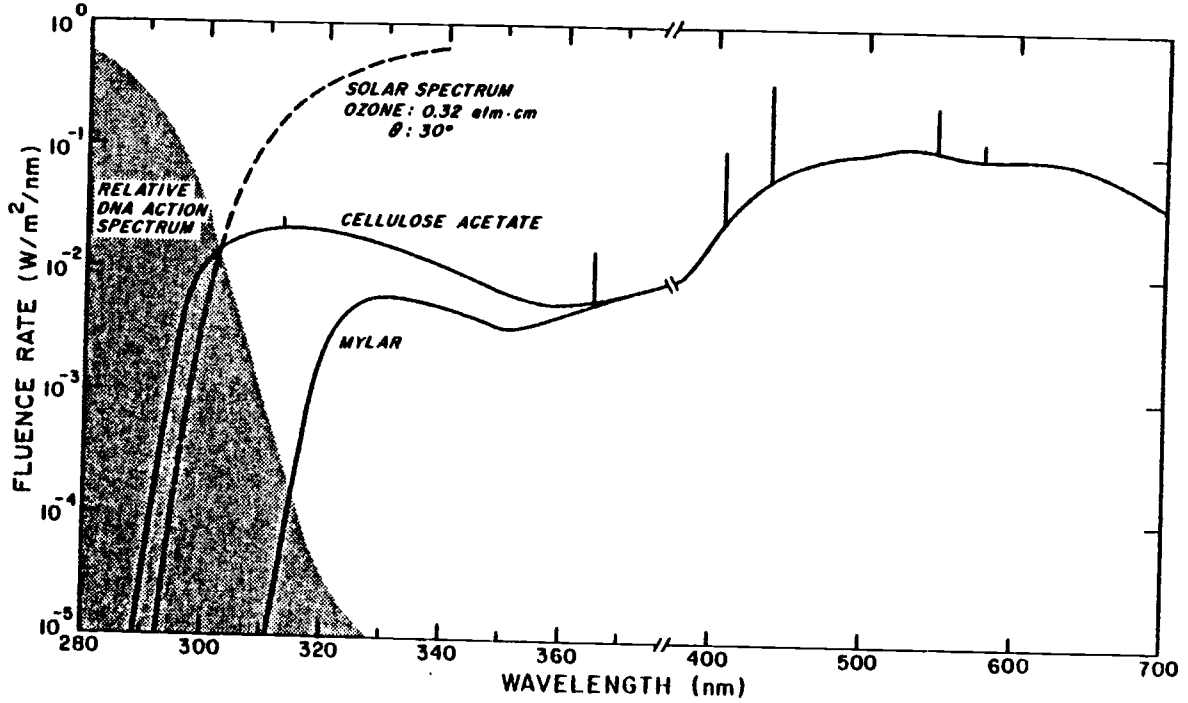

Figure 12: Sample spectra of a deluxe-white fluorescent lamp plus sunlamp/filter system utilizing two different filters: 0.25 mm thickness CA, 0.18 mm thickness Mylar polyester film. The dashed line represents a solar global spectrum as calculated by Green et al. (1974). The shaded area represents an analytical representation of the long-wavelength tail of a DNA action spectrum as calculated by Green and Miller (1975, from Thomson et al. 1980).

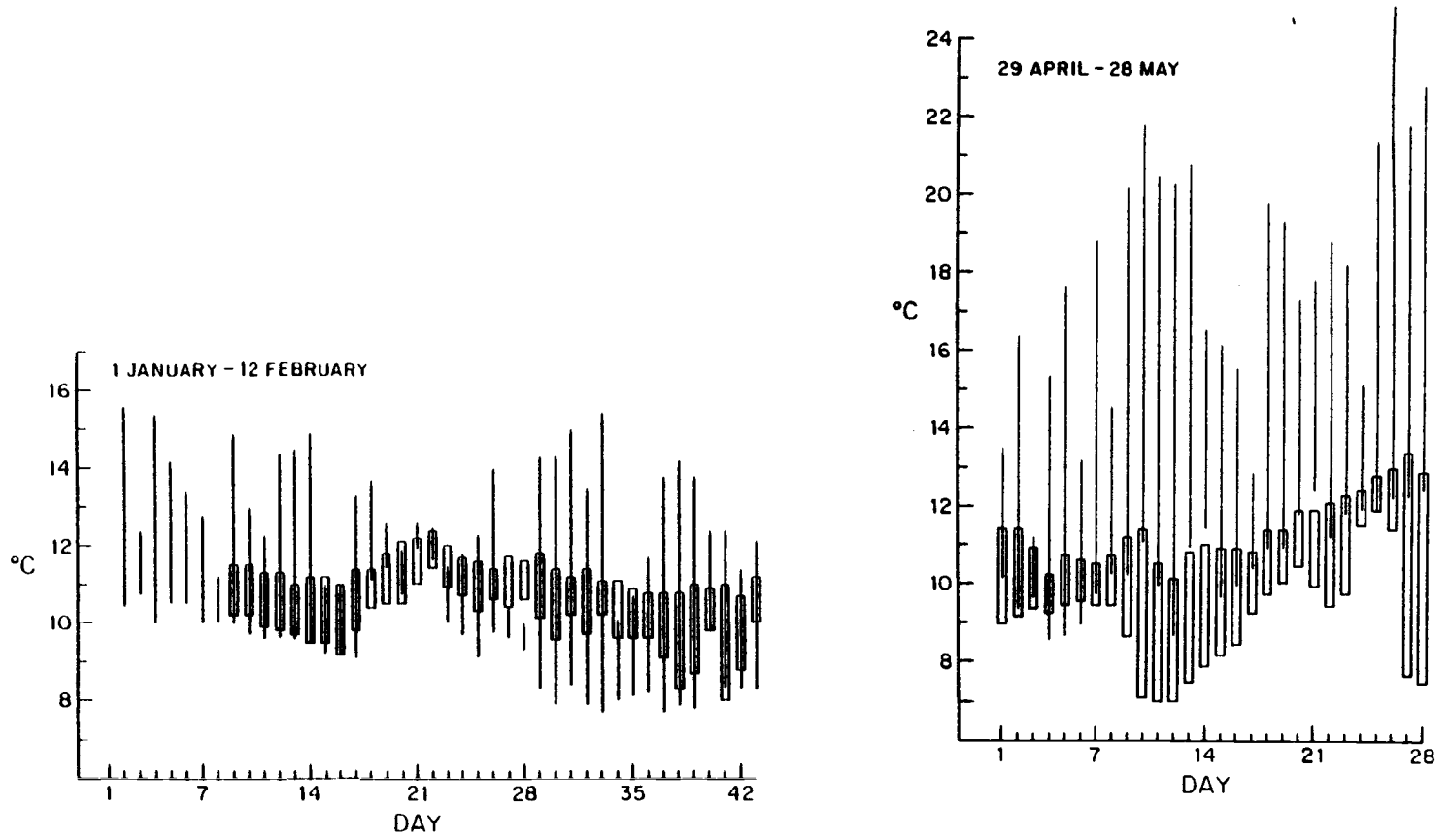

Figure 13. Daily temperature (°C) range for the microcosms (I) and lower Yaquina Bay (□) during artificial substrate experiment I (1 January - 12 February) and experiment II (29 April - 28 May).

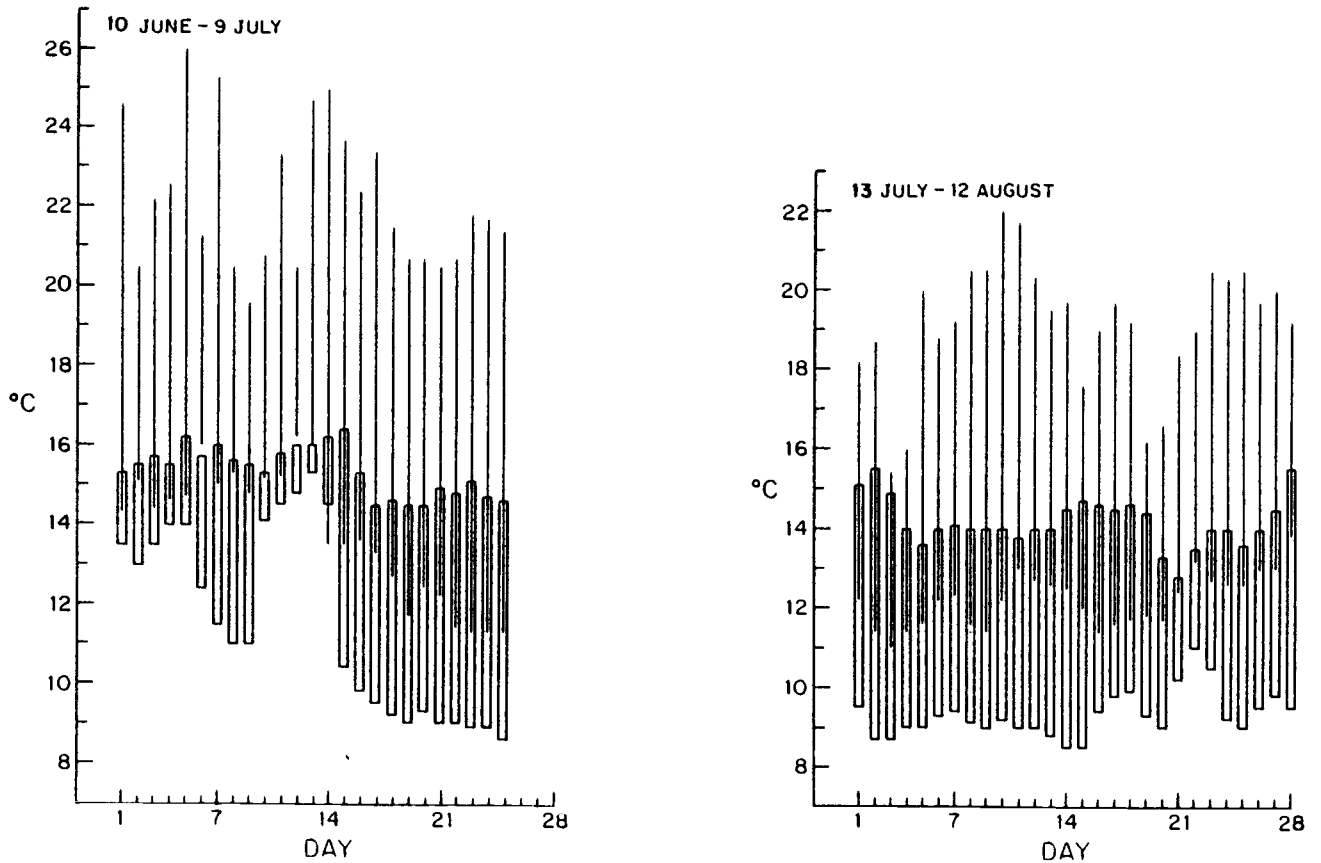

Figure 14: Daily temperature (°C) range for the microcosms (|) and lower Yaquina Bay (□) during the artificial substrate experiment III(10 June - 9 July) and Experiment IV (13 July - 12 August).

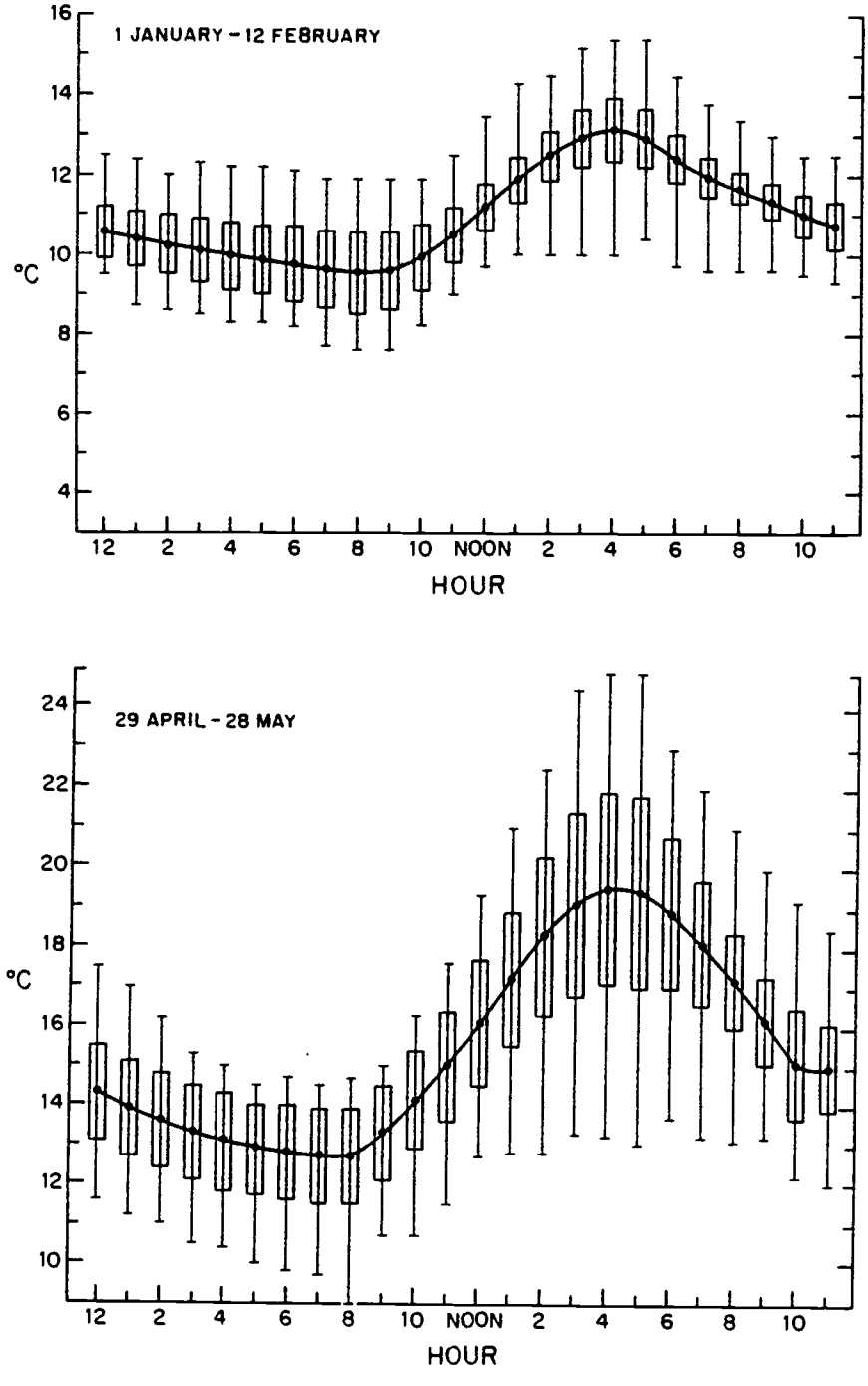

Figure 15 : Diel water temperature (°C) curve for the microcosms during artificial substrate experiments I(1 January-12 February) and experiment II(29 April - 28 May). Mean • SD □ , Range I

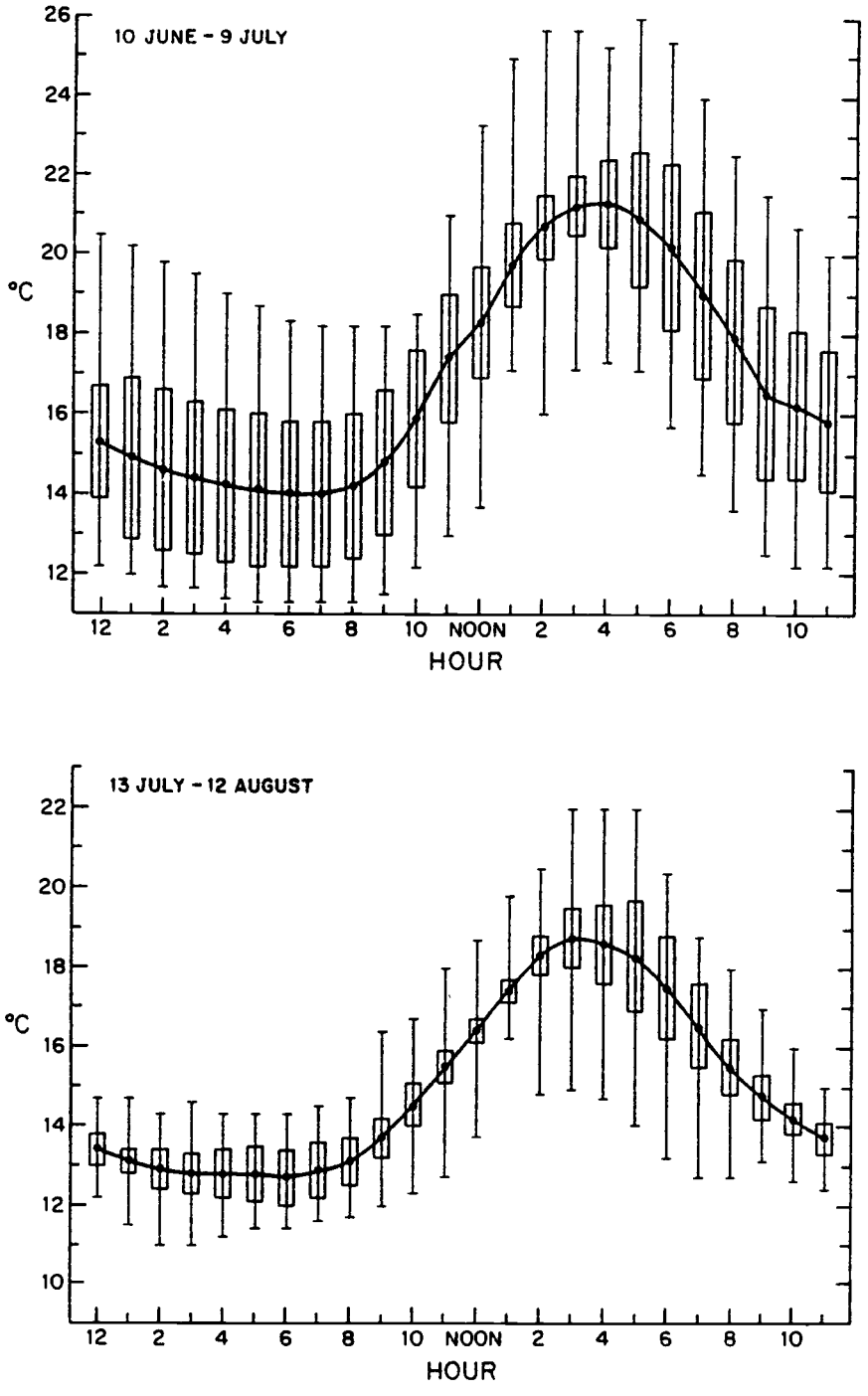

Figure 16: Diel water temperature (°C) curve for the microcosms during artificial substrate experiment III(10 June - 9 July) and experiment IV (13 July - 12 August). Mean • SD □ , Range I

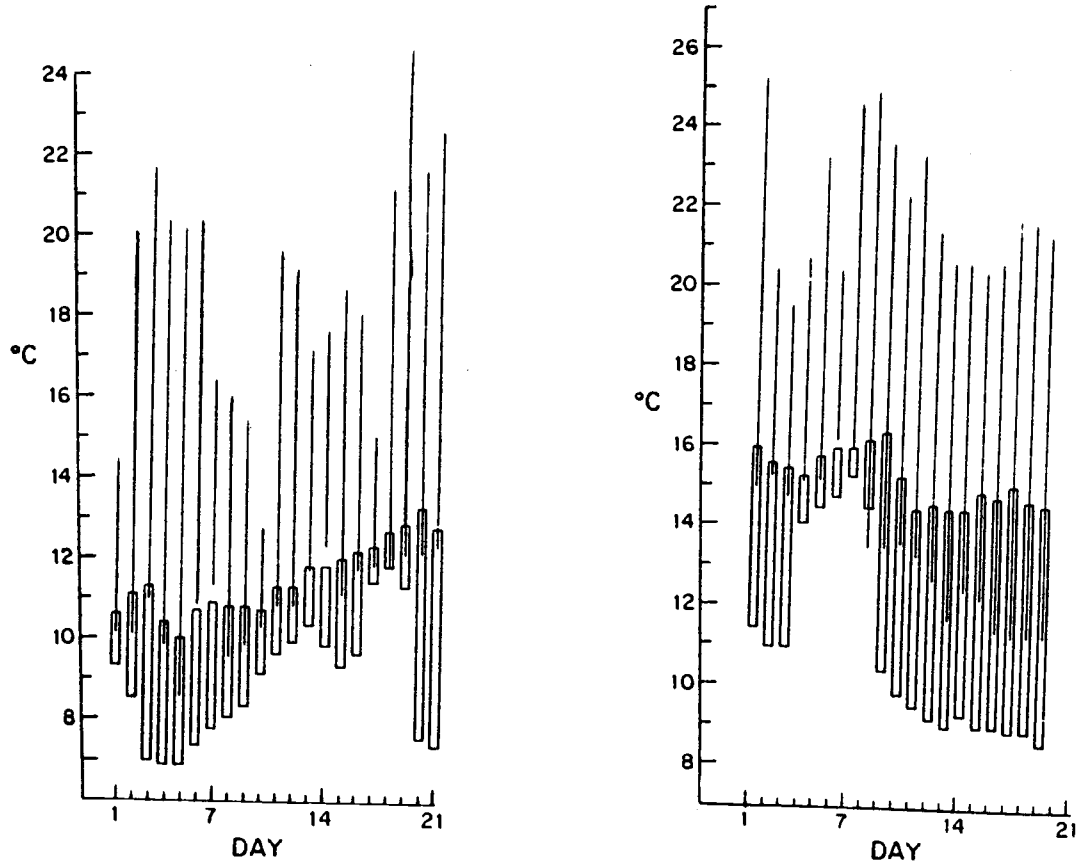

Figure 17: Daily temperature (°C) range for the microcosms (|) and lower Yaquina Bay ([]) during sediment experiment I (left) and II (right).

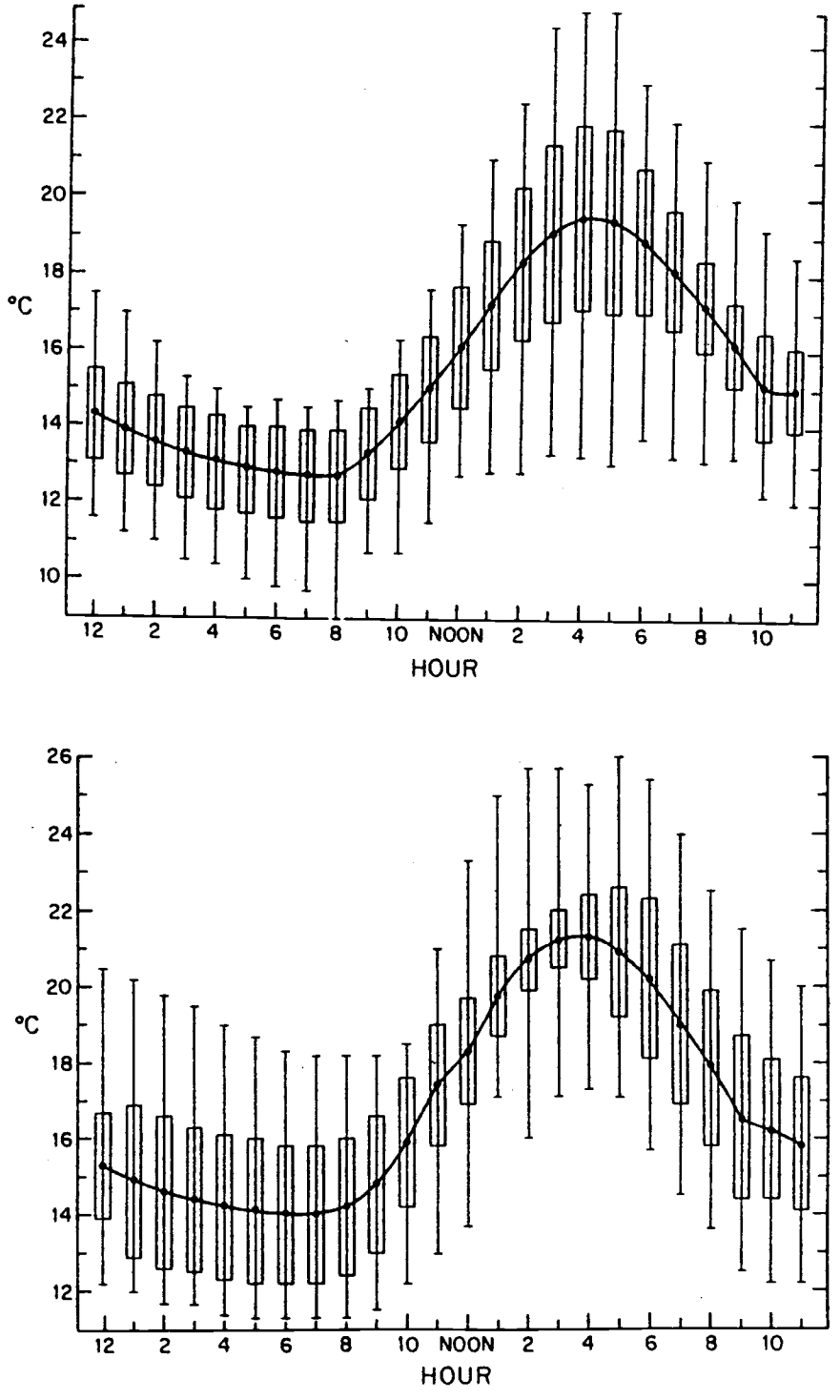

Figure 18: Diel water temperature curves for microcosms during sediment experiment I (upper curve) and II (lower curve).

Table 15 : Concentrations (mg/l) of three micronutrients measured weekly in the microcosms.

Experiment	Date	N	Nitrite/Nitrate-Nitrogen** Mean (± S.D.)	Orthophosphorus* Mean (± S.D.)	Reactive Silica* Mean (± S.D.)
II	29 April*	1	0.07		1.0
	7 May	3	0.07 ± 0.00	± 0.00	1.1 ± 0.2
	13 May	3	0.14 ± 0.04	0.03 ± 0.004	1.5 ± 0.3
	21 May	3	0.04 ± 0.02	0.01 ± 0.001	1.4 ± 0.5
	28 May	3	0.07 ± 0.01	0.02 ± 0.008	1.6 ± 0.2
	Grand Mean	12	0.08 ± 0.04 a***	0.02 ± 0.01 a	1.4 ± 0.3
III	11 June*	1	0.01	0.02	1.0
	18 June	3	0.03 ± 0.01	0.06 ± 0.04	1.2 ± 0.5
	25 June	3	0.07 ± 0.01	0.03 ± 0.005	1.6 ± 0.6
	2 July	2	0.01 ± 0.00	0.01 ± 0.003	0.9 ± 0.2
	9 July	3	0.01 ± 0.003	0.04 ± 0.02	2.3 ± 1.0
	Grand Mean	11	0.06 ± 0.11 b	0.04 ± 0.03	1.6 ± 0.8
IV	13 July*	1	0.04	0.04	1.9
	22 July	3	0.05 ± 0.01	0.03 ± 0.005	1.6 ± 0.4
	30 July	3	0.04 ± 0.02	0.03 ± 0.008	1.1 ± 0.4
	5 August	3	0.01 ± 0.002	0.04 ± 0.02	1.1 ± 1.1
	12 August	3	0.03 ± 0.02	0.02 ± 0.004	1.6 ± 0.2
	Grand Mean	12	0.05 ± 0.02 b	0.03 ± 0.009 b	1.3 ± 0.4

* Day of seeding; not included in grand mean
** Nominal precision for nitrite/nitrate is ± 0.01, orthophosphorus ± 0.05, and reactive silica ± 0.1
*** In the same column, a is significantly different from b ($p < 0.05$)

Table 16: Radiocarbon uptake (mg C · M^{-2} · hr^{-1}) for 'dark' bottles and their percentage uptake compared to 'light' bottles for artificial substrates exposed to three UV-B radiation fluences.

Experiment	Date	TREATMENT		
		HIGH*	LOW*	CONTROL*
I	15 January	0.86 (1.7%)	1.12 (2.9%)	1.78 (3.3%)
	29 January	2.67 (5.8%)	1.71 (4.6%)	1.49 (3.2%)
	12 February	7.33 (4.2%)	5.82 (4.0%)	8.70 (12.0%)
II	14 May	0.60 (3.5%)	0.75 (2.9%)	0.95 (11.0%)
	28 May	0.73 (2.3%)	0.66 (2.3%)	0.99 (6.7%)
III	24 June	2.08 (3.2%)	2.00 (8.7%)	1.56 (2.4%)
	9 July	2.54 (3.7%)	3.23 (5.8%)	2.08 (3.0%)
IV	30 July	0.99 (3.0%)	1.17 (3.6%)	1.42 (5.3%)
	12 August	1.22 (6.5%)	1.21 (6.2%)	0.83 (6.9%)

* HIGH = 0.25 mm CA filter
LOW = 0.13 mm CA filter
CONTROL = Mylar filter

Table 17: Micronutrients (mg/l) as measured weekly in each microcosm.

Experiment	Date	N	Nitrite/Nitrate Nitrogen* Mean (± S.D.)	Ortho-phosphorus* Mean (± S.D.)	Reactive Silica* Mean (± S.D.)
I	07 May	3	0.07 ± 0.00	0.02 ± 0.00	1.1 ± 0.2
	13 May	3	0.14 ± 0.04	0.03 ± 0.004	1.5 ± 0.3
	21 May	3	0.04 ± 0.02	0.01 ± 0.001	1.4 ± 0.5
	28 May	3	0.07 ± 0.01	0.02 ± 0.008	1.6 ± 0.2
	Grand Mean	12	0.08 ± 0.04 a**	0.02 ± 0.01	1.4 ± 0.3
II	18 June	3	0.03 ± 0.01	0.06 ± 0.04	1.2 ± 0.5
	25 June	3	0.07 ± 0.01	0.03 ± 0.005	1.6 ± 0.6
	02 July	2	0.01 ± 0.00	0.01 ± 0.003	0.9 ± 0.2
	09 July	3	0.01 ± 0.003	0.04 ± 0.02	2.3 ± 1.0
	Grand Mean	11	0.06 ± 0.11 b	0.04 ± 0.03	1.6 ± 0.8

* Nominal precision for nitrite/nitrate is 0.01, orthophosphorus 0.05, and reactive silica 0.1.

** In the same column, "a" is significantly different from "b" ($p < 0.05$).

Table 18: Radiocarbon uptake (mg C · m^{-2} · h^{-1}) for 'dark' bottles and their percentage uptake compared to 'light' bottles for intact sediment cores exposed to three UV-B radiation fluences.

		TREATMENT		
Experiment	Date	HIGH*	LOW	CONTROL
I	13 May	1.1 (5.3%)	0.6 (4.0%)	0.3 (1.5%)
	20 May	0.7 (6.4%)	1.6 (2.0%)	2.0 (2.4%)
	27 May	0.2 (3.0%)	0.2 (3.1%)	0.2 (6.3%)
II	25 June	ND**	0.5 (5.8%)	ND
	8 July	ND	0.6 (3.8%)	ND

* HIGH = 0.25 mm CA filter
LOW = 0.13 mm CA filter
CONTROL = Mylar filter
** ND = not determined

APPENDIX III

METHODS FOR CHEMICAL ANALYSIS OF SEAWATER FOR MICRONUTRIENTS

Nitrate + Nitrite-Nitrogen --- Automated Cadmium Reduction Method

A filtered sample is passed through a column containing granulated copper-cadmium to reduce nitrate to nitrite. The nitrite (that originally is present plus reduced nitrate) is determined by diazotizing with sulfanilamide and coupling with N-(1-naphthyl)-ethylenediamine dihydrochloride to form a highly colored azo dye which is measured spectrophotometrically. Separate, rather than combined nitrate-nitrite values, are readily obtained by carrying out the procedure first with, and then without, the initial Cu-Cd reduction technique.

Orthophosphorus --- Automated Molybedenum Blue Method

Ammonium molybdate and antimony potassium tartrate react in an acid medium with dilute solutions of phosphorus to form an antimony-phosphomolybdate complex. This complex is reduced to an intensely blue-colored complex by ascorbic acid. The color is proportional to the phosphorus concentration. Color intensity is measured spectrophotometrically at 880 nm.

Molybadate Reactive Silica --- Automated Heteropoly Blue Method

Ammonium molybdate at pH approximately 1.2 reacts with silica and any phosphate present to produce heteropoly acids.

Oxalic acid is added to destroy the molybdophosphoric acid but not the molybdosilicic acid. The yellow molybdosilicic acid is reduced by means of ascorbic acid to heteropoly blue. The blue color is more intense than the yellow color and provides increased insensitivity. Color intensity is measured spectrophotometrically at 815 nm.

APPENDIX III

ELECTRON MICROSCOPY METHODS

INSTRUMENT: Phillips EM 200 transmission electron microscope

STEPS FOR DEVELOPING EM NEGATIVES (Otho S Litho Film, DuPont):

1) Developer - (D19 - full-strength, 4 min)
2) Stop - acetic acid (50 ml 28% acetic acid and 950 ml water, 30 sec)
3) Fix - 4 min
4) Hypo - 2 min
5) Wash - water (10 min)
6) Photoflo

STEPS FOR DEVELOPING EM PRINTS (Kodak Polycontrast resin-coated F):

1) Developer - Dektol (1:2 stock to water, 1.5 min)
2) Stop - acetic acid (50 ml 28% acetic acid and 950 ml water)
3) Fix - Kodak fixer (full-strength, 5 min)
4) Wash - water (5 to 10 min)
5) Photoflo