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EFFECTS OF SOLAR ULTRAVIOLET RADIATION ON STREAM ECOSYSTEMS AND THEIR APPLICATION TO FORESTRY PRACTICES IN BRITISH COLUMBIA

by

David John Kelly ©

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

in

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Department of Biological Sciences

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"Eventually all things merge into one, and a river runs through it.
The river was cut from the worlds great flood,
and runs over the rocks from the basement of time.
On some of the rocks are timeless raindrops,
under the rocks are the words, and some of the words are theirs.
I am haunted by waters."

– Norman Maclean, 1989 [1]

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[1] Norman Maclean, 1989. A River Runs Through It. University of Chicago Press.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Effects of solar ultraviolet radiation on stream ecosystems and their application to forestry practices in British Columbia" submitted by David John Kelly in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the field of Environmental Biology and Ecology.

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ABSTRACT

Clear-cut logging, and removal of riparian canopy, can result in considerable increases in solar ultraviolet radiation (UVR, 280-400 nm) flux to streams, and may increase the exposure of aquatic organisms to UVR by altering the export of dissolved organic matter (DOM) from the terrestrial catchment. Riparian buffer strips have been adopted to mitigate the effects of canopy removal, however, the width and composition of prescribed buffer strips can vary, and provide variable shading to the stream. Experiments were performed along coastal streams in British Columbia to examine the effects of UVR from canopy removal on stream algal, invertebrate, and fish communities. I performed in-stream and mesocosm experiments that manipulated the exposure of stream biota to UVR by using solar exclusion filters which removed all, or portions of, incident UVR.

Increased solar UVR exposure to streams either from direct canopy removal or declines in DOM significantly decreased total invertebrate biomass and community diversity, particularly during low-flow summer months. Increased UVR exposure affected riverine food-webs in a complex manner, clearly altering community interactive processes such as herbivory. Increases in UVR exposure had even greater effects on communities when they occurred in combination with increased water temperature. The effects of UVR on benthic food-webs varied across the spectrum, with UVA (320-400 nm) predominantly inhibiting benthic algae, and UVB (280-320 nm) having the most pronounced effects on invertebrates. No significant effects of UVR on benthic communities occurred under old-growth canopies, which had significantly more diverse invertebrate assemblages. Attenuation of UVR by dissolved organic matter was important for protecting organisms from inhibitory effects of UVR, with concentrations between 2-5 mg/L DOM in a critical concentration range for biological effects. Juvenile coho salmon that live in these coastal systems avoided high intensities of solar UVA in

experimental enclosures, suggesting that UVR may influence microhabitat selection by salmonids.

These results demonstrate that increases in solar UVR exposure to streams from clear-cutting, either by directly removing riparian canopy or changing DOM, has severe effects on the productivity, diversity, and functioning of coastal stream ecosystems.

PREFACE TO THE THESIS

The structure of my dissertation is in paper format, as outlined by the faculty of graduate studies and research, and is presented as four manuscripts (Chapters 2 - 5). An introductory chapter (Chapter 1) is intended to provide background on the field of research, state my research objectives, and outline my experiments. A general conclusions chapter (Chapter 6) is also provided to summarize conclusions drawn from all components of my research, and to propose future directions of research in the field. As with most scientific endeavors, my studies required collaboration with several individuals. In recognition of their contribution, I have cited the manuscripts now published or submitted for publication in the scientific literature, including their co-authors.

Chapter 2:

David J. Kelly, John J. Clare and Max L. Bothwell. 2001. Attenuation of solar ultraviolet radiation by dissolved organic matter alters benthic colonization patterns in streams. *Journal of the North American Benthological Society* **20**: 96-108.

Chapter 3:

David J. Kelly, Max L. Bothwell, and David W. Schindler. Effects of variable solar ultraviolet radiation exposure on stream communities: control by the riparian canopy. Submitted to *Ecology.*

Chapter 4:

David J. Kelly, Max L. Bothwell,and David W. Schindler. Effects of synergistic increases in solar ultraviolet radiation and temperature from clear-cut logging on benthic communities in a British Columbia coastal stream. Submitted to *Nature.*

Chapter 5:

David J. Kelly, and Max L. Bothwell. Solar ultraviolet radiation affects microhabitat selection by juvenile coho salmon (*Oncorhynchus kisutch*). Submitted to the *Canadian Journal of Fisheries and Aquatic Sciences.*

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1. GENERAL INTRODUCTION

Solar ultraviolet radiation (UVR, 280-400 nm) is increasingly cited as an important factor affecting freshwater systems (reviewed by Williamson et al. 1995). UVR has been demonstrated to affect benthic community metabolism (McNamara and Hill 2000, Watkins et al. 2001), community composition and succession (Bothwell et al. 1993, Kiffney et al. 1997, Vinebrooke and Leavitt 1999), trophic dynamics (Bothwell et al. 1994, Kelly et al. 2001), and behaviour (Kiffney et al. 1997b, Donahue and Schindler 1998, Clare et al. 2001). UVR also has negative effects on higher trophic levels, with documented impairment of both fish (Siebeck et al. 1994) and amphibian species (Blaustein et al. 1995, 1997). Clear-cut logging, and removal of riparian canopy can result in large increases in solar flux to the streams (Holtby et al. 1988, Hetrick et al. 1998, Clare 2000). Logging may also increase UVR exposure to the streambed by altering the export of dissolved organic matter (DOM) (Hobbie and Likens 1973, Meyer and Tate 1983), the principle attenuator of UVR in oligotrophic fresh waters (Scully and Lean 1994). I examined the effects of increased ultraviolet radiation exposure resulting from riparian canopy removal by logging activities on aquatic communities in streams on Vancouver Island, BC. The principle objectives of my research were:

1) To examine how UVR attenuation by dissolved organic matter affects colonization patterns of benthic communities
2) To examine how the riparian canopy mediates effects of UVR on benthic communities
3) To examine how synergistic increases in UVR and water temperature from clear-cut logging affect benthic communities
4) To examine how UVR affects microhabitat selection by stream reared juvenile coho salmon

Review of the Effects of Ultraviolet Radiation on Stream Ecosystems

Interest in the effects of solar ultraviolet radiation has increased since the discovery of springtime reductions in stratospheric ozone in the polar vortex over Antarctica (Solomon 1988, Madronich 1994), and more recently in the northern hemisphere (Hansen and Chipperfield 1998), resulting in an estimated 20% increase in DNA damaging UVB (280-320 nm) per decade at mid-temperate latitudes (Madronich 1992, Kerr and McElroy

1993, Kerr 1995). Factors that affect the penetration of UVR into the water column can contribute to increased UVR exposure to aquatic environments, in addition to current trends in stratospheric ozone depletion (Williamson et al. 1996, Schindler 1998). For example, decreases in coloured DOM (CDOM), caused by localized acidification and climate warming resulted in considerably larger increases in the exposure of northern boreal lake communities to UVR than increases in ground-level solar radiation flux from ozone depletion (Schindler et al. 1996, Yan et al. 1996, Donahue et al. 1998). Thus, other human activities may have a greater effect on UVR exposure to freshwater ecosystems than stratospheric ozone depletion alone.

Factors affecting UVR penetration to aquatic systems

The variability of UVR fluxes to both the earth's surface and stream-bottom, and their potential effects on aquatic communities have not been examined closely. Fluxes to the earth's surface are affected by latitude, altitude, cloud cover, solar angle, stratospheric atmospheric conditions and shading by the terrestrial riparian canopy (Kirk 1983, Smith 1989, Blumthaler at al. 1992). Penetration of UVR to the stream-bottom is controlled mainly by CDOM (measured by dissolved organic carbon [DOC]), although other factors such as albedo of the water surface, turbidity, plankton (near lake outflows) and macrophyte productivity may also influence UVR penetration (Kirk 1994, Scully and Lean 1994, Hill et al. 1997, Laurion et al. 2000). In the clearest waters, UVR may penetrate up to 20 m (Smith and Baker 1980, Vincent et al. 1998), while in humic freshwater lakes, UVR may be completely attenuated within the first few centimetres of the water column (Cooper and Lean 1989, Scully and Lean 1994). DOM is also highly variable in both its chemical structure and optical properties (Scully and Lean 1994, Morris et al. 1995, Arts et al. 2000), largely determined by whether it was generated from within the aquatic system (autochthonous) or from outside decomposing terrestrial vegetation (allochthonous) (McKnight et al. 1997). Allochthonous DOM, which typically composes the larger fraction of riverine DOM (McDowell and Fisher 1976), tends to be more refractory and more important for UVR attenuation than autochthonous fractions (Green and Blough 1994). However, in-stream physical, chemical and biological processes such as flocculation (Naiman and Sedell 1979), bacterial metabolism (Meyer et al. 1987, Wetzel et al., 1995), photochemical bleaching (Cooper et al. 1994, Molot and Dillon 1997, Bertilsson and Tranvik 2000), pH (Donahue et al. 1998), binding to metals and contaminants (Winner and Owen 1991), autotrophic production (Wetzel and Manny 1971), and shredder CPOM processing (Meyer and O'Hop 1983) may all affect the transport, quantity, and quality (optical characteristics) of DOM, and in turn the penetration of UVR into the waterbody. Therefore, DOM may interact both chemically and physically to affect aquatic communities (Vinebrooke and Leavitt 1998, Kelly et al. 2001).

Effects of UVR on aquatic biota

Effects of UVR occur primarily through damage of cellular macromolecules such as nucleic acids and proteins which absorb high energy UV photons. Damage may occur either directly from the de-stabilizing or breakdown of the molecules, or from production of intermediate reactive oxygen species (ROS) such as superoxides and hydroxl radicals (Vincent and Neale 2000). For aquatic organisms, the main forms of damage to cells occur from damaged DNA, pigments, and photosystem reaction centres (Karentz et al. 1994). Cellular mechanisms have evolved to reduce or repair damage from UVR. These protective mechanisms can reduce UV-damage by absorbing incident UVR, repairing damaged macromolecules such as DNA, or by antioxidant quenching agents such as carotenoids that reduce damage from ROS (Vincent et al. 2000). UVR absorbing pigments that have been isolated from aquatic organisms including mycosporine like amino acids (MAAs) (Carreto et al. 1990, Garcia-Pichel 1994) and the sheath pigment in cyanobacteria, scytonemin (Garcia Pichel and Castenholz 1991, Leavitt et al. 1997).

UVR has complex effects on cellular processes, species succession and population dynamics in aquatic ecosystems (reviewed by Karentz et al. 1994, and Häder et al. 1998). UVR inhibits algal photosynthesis in both planktonic (Cullen and Lesser 1991, Smith et al. 1992, Vincent and Roy, 1993, Moeller 1994) and attached algal communities (McNamara and Hill 2000, Watkins et al. 2001), potentially causing depressions of autotrophic biomass (Worrest et al. 1981, Vinebrooke and Leavitt 1996, 1999, Kiffney at al. 1997a, Xenopoulos et al. 2000, Kelly et al. 2001). A wide range of sensitivities to UVR exist among algal taxa (Jokiel and York 1984), due to differences in photoprotective pigments (Carreto et al. 1990, Karentz at al. 1994, Leavitt et al. 1997, Sommaruga and Garcia-Pichel 1999), morphological differences such as cell size or cell wall thickness (Karentz et al. 1991, Bothwell et al. 1993, Garcia-Pichel 1994, Hessen et al. 1997) or photorepair capacity (Vincent et al. 1993, Wilson and Greenberg 1993, Sommaruga and Buma 2000). Differential sensitivities to UVR have been shown to affect succession of communities during some long-term experiments (Worrest et al. 1981, Bothwell et al. 1993, Vinebrooke and Leavitt 1999), although this is not universal (see DeNicola and Hoagland 1996, Hill et al. 1997).

UVR also inhibits pelagic (Williamson et al. 1994, Vinebrooke and Leavitt 1999) and benthic aquatic invertebrates (Bothwell at al. 1994, Kiffney et al. 1997a, Kelly et al. 2001), with evidence for differential sensitivities between taxa (Ringelberg et al. 1984, Hessen 1993, McNamara and Hill 1999). Invertebrates may respond to UVB by vertically migrating (Siebeck and Bohm 1994, Williamson et al. 1994) or drifting (Kiffney at al. 1997b, Donahue and Schindler 1998). UVR can also negatively affect freshwater vertebrates (reviewed by Siebeck et al. 1994). Impairment of both fish and amphibian species have been documented, and include effects of UVB on egg survival (Blaustein et al. 1995, Williamson et al. 1997), larval development (Hunter et al. 1979, Blaustein et al. 1997), skin lesions (Little and Fabacher 1994, Bullock and Coutts 1985), respiratory control (Freitag et al. 1998), immune system function (Salo et al. 1998), and behaviour (Kelly and Bothwell 2001).

UVR can also inhibit aquatic biota indirectly through the production of reactive byproducts such as superoxides, hydrogen peroxide and hydroxyl radicals in the photochemical breakdown of DOM (Cooper et al. 1988, Cooper and Lean 1989). The effects of superoxides and hydrogen peroxide on biota have been documented in laboratory studies, and include inhibitory effects on dark reaction processes of photosynthesis and bacterial protein synthesis (Takabe et al. 1980, Fridovich 1986, Xenopoulos and Bird 1997). However, on an ecological level, production of hydrogen peroxide has not been examined in rivers, and only assumptions as to its potential toxicity to biological communities have been made in lakes (Karentz et al. 1994, Scully et al. 1995, Scully and Lean 1996).

Effects of UVR on community dynamics

UVR can affect community interactive processes such as herbivory and predation, complicating the ability to predict the inhibitory effects of UVR at single trophic levels (Williamson et al. 1995). For example, suppression of grazers by UVR can indirectly increase algal accrual to a greater extent than direct photoinhibition of UVR on algal production (Bothwell et al. 1994, Kelly et al. 2001). Alternatively, suppression of algal production by UVR, and the promotion of the growth of larger thick-walled, less edible taxa (Garcia-Pichel 1994, Van Donk and Hessen 1995) could potentially reduce the availability of food resources to herbivores. The availability of consumers to predators may also be affected by both changes in pigmentation and vertical migration of prey species, as well as by food availability and quality to consumers. Small invertebrate taxa may also utilize epilithic standing crops as a protective canopy against high UVR exposure (Clare et al. 2001). Inhibitory effects of UVR are also highly wavelength specific (Cullen et al. 1992). For instance, UVA (320-400 nm) is predominantly responsible for algal inhibition (Bühlmann et al. 1987, Milot-Roy and Vincent 1994), while benthic invertebrates are more sensitive to UVB (Bothwell at al. 1994, Kiffney at al. 1997a, 1997b).

Effects of Clear-cut Logging on UVR Exposure to Streams in British Columbia

Riparian canopy removal effects on UVR exposure to streams

Ecological patterns and processes in streams are intimately linked to the surrounding terrestrial ecosystem (Vannote et al. 1980). Riparian zones surrounding streams are transitional interfaces between aquatic and terrestrial systems that mediate inputs of energy and yield allochthonous materials to streams (Gregory et al. 1991). Alteration of the riparian canopy can increase solar exposure and autotrophic production in streams (Stockner and Shortreed 1976, Hetrick et al. 1998), which are often limited by light (Hill and Knight 1988, DeNicola et al. 1992). Riparian buffer strips have been adopted by managers to mitigate the effects of clear-cut logging on stream environments (Barton et al. 1985, Osbourne and Koviak 1993, Naiman et al. 2000). The width and vegetative composition of the buffer strip can vary considerably depending upon the management goals (Gregory et al. 1991), and result in variable cover to the stream. In British Columbia, prescribed riparian management areas (RMAs) are designated by the Forestry Practices Code (British Columbia Ministry of Forests 1995), which allows for varying widths (0-100 m) and harvesting within RMAs, and can provide variable amounts of shading to the stream. For example, Clare (2000) observed approximately an 8.3 fold increase in light exposure to a British Columbia central-interior stream following timber harvesting with a 20 m riparian management zone. The effects of increases in UVR flux from reduction in riparian cover on stream ecosystems have not been documented, and are important for the management of riparian areas.

Indirect effects of clear-cutting on UVR exposure of streams

Physical and chemical changes to streams following logging have been studied extensively, and include alterations to flow regime (Lisle 1982), substrate composition (Lisle 1982, Garman & Moring 1991), suspended and dissolved matter (Hobbie and

Likens 1973, Borman et al. 1974, Meyer and Tate 1983, Lowe et al. 1986, Heede 1991), sediment transport (Lisle 1982, Heede 1991), thermal regime (Brown and Krygier 1970, Lynch et al. 1984, Holtby 1988, Hetrick et al. 1998), riparian cover (Carlson et al. 1990, Ryan & Grant 1991), and channel width (Lisle 1982, Heede 1991, Ryan & Grant 1991). These disturbances generally result in streams with higher peak flows, wider channels, shallower pools, higher dissolved and particulate matter, and larger thermal variability, often occurring for several kilometres downstream of the cut area (Ryan and Grant 1991). Several of these alterations to stream morphology allow a greater amount of solar radiation to reach the streambed, thereby enhancing increases in UVR exposure to the stream from canopy removal.

Clear-cut logging may also increase the exposure of steams to UVR indirectly by altering the concentration of DOM in streams (Hobbie and Likens 1973, Meyer and Tate 1983). Changes to the terrestrial vegetation, evapotranspiration, and runoff following logging are intimately linked with terrestrial carbon cycling within the catchment (Meyer and Tate 1983), thereby altering the export of DOM. The long-term effects of logging on DOM export are still relatively unknown, and can be influenced by a combination of biogeographical parameters of the watershed such as slope, catchment area, precipitation, temperature, as well as vegetation and soil parameters (Meyer and Tate 1983, Engstrom 1987, Rasmussen et al. 1989, Curtis and Schindler 1997). The few investigations into changes in DOM export following timber harvesting have produced conflicting results, and were highly influenced by regional specific parameters. For instance, Hobbie and Likens (1973) observed small increases in DOM export following logging in Hubbard Brook. Alternatively, Meyer and Tate (1983) observed lower DOM concentrations and reduced DOC export following logging in Coweeta Basin, North Carolina, attributed to lower leaf litter input by the regenerating forest. Tate and Meyer (1988) also observed decreasing DOM export with forest succession in Coweeta. Both Moore (1987) and Collier et al. (1989) observed variable changes in DOC export following logging in adjacent watersheds of western New Zealand, linked to differences in hydrologic conditions, watershed morphology, drainage, and soil types. Long-term changes in DOM export following logging in watersheds of British Columbia have yet to be documented.

Effects of clear-cut logging on stream communities

Physical and chemical alterations to streams following logging have caused variable changes to resident biological communities. Increases in autotrophic biomass production following the removal of riparian canopy have been observed fairly consistently, predominantly due to increased light (Stockner and Shortreed 1976, Murphy and Hall 1981, Lowe at al. 1986, Robinson and Rushforth 1987, Hetrick et al. 1998). Changes to invertebrate production and community composition have been more variable (Murphy et al. 1981). For instance, Garman & Moring (1991) found that physical conditions following logging favoured a shift from heterotrophic to autotrophic dominance attributed to increased stream temperature and reduced coarse particulate organic matter as a food source to benthic invertebrates. Conversely, Newbold et al. (1980) and Carlson et al. (1990) found that benthic invertebrate (heterotrophic) populations increased by as much as 107% following logging. Although increased light exposure following logging is consistently cited as an important factor affecting aquatic communities, it has normally been related to stream temperature (Lynch et al. 1984, Hotlby 1988, Hetrick et al. 1998) rather than potential effects of UVR.

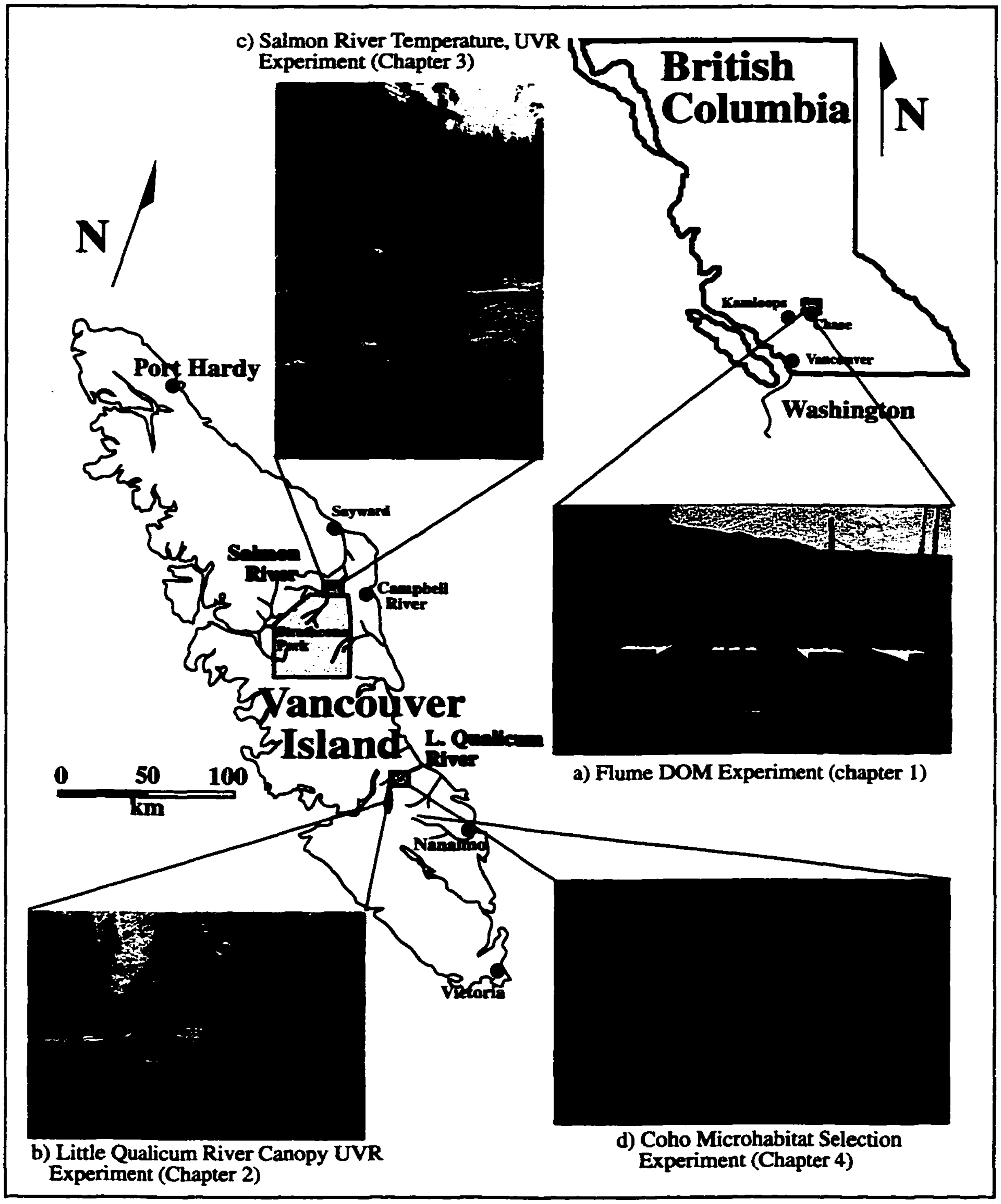
Juvenile salmonids also prefer stream habitats with high cover (Lister and Genoe 1970, Platts and Nelson 1989, Heggenes et al. 1991). However, logging can result in greater production of juvenile salmonids (Hawkins et al. 1983, Keith et al. 1998). Several lines of evidence suggest that salmonids can compensate for adverse affects of large-scale habitat alteration through microhabitat selection and use of in-stream cover and large debris (Dolloff 1987, Shirvell 1990, Bugert et al. 1991). Use of cover by juvenile salmonids has been assumed to be for predator avoidance (Dill and Fraser 1984, Faush 1993). However, the ability of juvenile salmonids to visually detect long-wave UVR (λ_{max}= 360-370 nm) (Hawryshyn et al. 1990, Novales-Flamarique et al. 1992) suggests that salmonids select light environments for other purposes, such as UVR avoidance. No published works have examined the effects of increased UVR exposure from canopy removal on salmonid habitat use.

Study Outline

Research was conducted at three locations in British Columbia (Fig. 1.1). Both in-stream and mesocosm experiments were performed. In-stream experiments were conducted in both the Little Qualicum River on the southeastern portion of Vancouver Island, and in the Salmon River located along the central-east coast of the island. Both watersheds have undergone considerable logging. Forests are comprised partially of old-growth, with varying age stands of regenerating second-growth. Canopies are dominated by Western Hemlock (*Tsuga heterophylla*), Western Red Cedar (*Thuja plicata*), Subalpine Fir (*Abies lasiocarpa*), Douglas Fir (*Pseudotsuga menziesii*), Red Alder (*Alnus rubra*), and Bigleaf Maple (*Acer macrophyllum*), which provide considerable shading to the streams. Environment Canada's Experimental Troughs Apparatus (EXTRA) on the South Thompson River, BC, was used for a DOM-mediated UVR exposure mesocosm experiment. I manipulated UVR exposure to the streambed by suspending large (≈ 2 m^2) filters immediately above the water surface which selectively removed portions of UVA and/or UVB while not significantly altering visible light (PAR). Site specific details of the three study locations , methods, and discussion of experimental results for individual experiments are provided in Chapters 2 - 5.

My first experiment (Chapter 2) at EXTRA examined the sensitivity of algal and invertebrate assemblages to variable UVR by using DOM (in water filters) as a spectrally selective UVR filter. This approach is different from previous field investigations, which have examined UVR effects on biota in either the presence or absence of UVA and/or UVB (Bothwell et al. 1993, 1994, DeNicola & Hoagland 1996, Vinebrooke & Leavitt 1996, 1999, Hill et al. 1997, Kiffney et al. 1997a, 1997b). Our approach also isolated the effect of the UVR attenuation by DOM from the potential confounding chemical and biological influences of DOM on biofilm communities. These experimental results provide insight into what systems may be potentially sensitive to effects from UVR based on DOM and water-column transparency.

My second experiment (Chapter 3) examined the effects of UVR on stream communities under varying solar exposure mediated by the riparian canopy. I examined the effect of both UVA and UVB radiation on benthic algal and invertebrates along several reaches of a fourth order coastal stream (Little Qualicum River) varying in riparian canopy cover. I hypothesized that effects of UVR on benthic communities would increase with increased solar exposure, and that changes in UVB:UVA:PAR under different


c) Salmon River Temperature, UVR Experiment (Chapter 3)

a) Flume DOM Experiment (chapter 1)

b) Little Qualicum River Canopy UVR Experiment (Chapter 2)

d) Coho Microhabitat Selection Experiment (Chapter 4)

Figure 1.1. Locations of the study areas in British Columbia for the (a) DOM mediated UVR exposure experiment at Environment Canada's Experimental Troughs Apparatus (EXTRA), (b) canopy mediated UVR exposure experiment on the Little Qualicum River, (c) Salmon River sysnergistic temperature/UVR experiment, and (d) Qualicum Channels coho microhabitat selection experiment.

canopies would contribute to differential effects of UVR on the various trophic levels. Direct effects of UVR on algal communities were examined in an adjacent open-canopied channel with reduced grazers.

In my third experiment (Chapter 4) I examined the direct and synergistic effects of increased UVR and temperature on stream benthic communities along a large (3.2 km) clear-cut in the Salmon River, BC. Past investigators attributed community shifts from increased solar exposure following clear-cut logging mainly to increases in stream temperature (Murphy and Hall 1981, Robinson and Rushforth 1987, Nelson and Platts and Nelson 1989). They did not consider the effects of increased UVR. I examined the effect of UVA and UVB on benthic communities at three sites along a thermal gradient created by the large clear-cut, immediately upstream of the cut (-UVR / -T), at the upstream margin of the clear-cut (+UVR / -T), and ≈3.2 km downstream along the clear-cut (+UVR / +T). My results thus differentiate between the effects of increases in temperature and UVR exposure on stream communities, and their interactions with nutrient and DOC inputs along clear-cuts.

In my last experiment (Chapter 5) I examined the influence of UVR on microhabitat selection by juvenile coho salmon (*Oncorhychus kisutch*), using in-stream experimental enclosures. No investigations have addressed the potential for UVR avoidance to be a factor in microhabitat selection by salmonids. Experimental trials were performed on newly emerged coho fry (May 1997) and juvenile coho two months after emergence (July 1997). I hypothesized that coho would be most sensitive to UVR upon initial exposure to sunlight. Trials were also performed under different cloud-cover conditions to assess if UVR responses vary under different ambient solar intensity. Results from these trials provide insight into potential effects of increased UVR exposure from canopy removal on salmonid habitat.

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2. ATTENUATION OF SOLAR ULTRAVIOLET RADIATION BY DISSOLVED ORGANIC MATTER ALTERS BENTHIC COLONIZATION PATTERNS IN STREAMS

Introduction

The role of dissolved organic matter (DOM) in attenuating solar ultraviolet radiation (UVR, 280 - 400 nm) is of critical importance in mediating the exposure of freshwater communities to harmful UVR (Scully and Lean 1994, Williamson et al. 1996). Present-day intensities of UVR reaching the earth's surface can inhibit algal and invertebrate communities in oceans, lakes, and rivers (see review by Häder et al. 1998). These findings have raised concerns about future increases in UVR since the discovery of seasonal declines in stratospheric ozone over southern polar regions (Farman et al. 1985, Madronich 1994), and more recently at northern polar and temperate latitudes (Kerr and McElroy 1993). Studies on ecosystem effects of UVR have predominantly focused on marine systems (Karentz et al. 1991, Smith et al. 1992). In contrast to the relatively high UVR-transparency of open ocean water, penetration of UVR into freshwater systems can be strongly attenuated by DOM (Scully and Lean 1994, Williamson et al. 1996). Freshwater systems low in DOM (e.g., alpine and polar lakes) can allow UVR to penetrate to depths up to 10 m, whereas high-DOM humic lakes attenuate UVR in the initial few centimetres of the water column (Scully and Lean 1994, Morris et al. 1995). Decreases in DOM can result from several factors within the terrestrial catchment, including drought and acid deposition (Yan et al. 1996, Schindler et al. 1997), and may have a far greater effect than increases in ambient UVR from atmospheric change (Schindler et al. 1996).

DOM consists of a mixture of organic molecules that influence ecosystem processes through a variety of physical and chemical pathways (see review by Thomas 1997). Absorption of solar radiation by DOM is greatest at shorter wavelengths of UVR (Kirk 1994, Scully and Lean 1994). The efficiency of DOM in attenuating UVR can vary widely, and depends upon whether the DOM is of autochthonous or allochthonous origin (McKnight et al. 1997). Terrestrially derived allochthonous DOM has a greater chromophoric DOM (CDOM) content than DOM derived within aquatic systems and absorbs UVR to a greater degree (Green and Blough 1994). Photochemical degradation (photobleaching) of CDOM reduces its efficiency to attenuate UVR (Lindell et al. 1995, Molot and Dillon 1997), which can increase UVR transparency in waterbodies over seasonal time scales (De Haan 1993, Morris and Hargreaves 1997). Photobleaching of CDOM also produces reactive by-products such as H_2O_2, which are potentially damaging to aquatic communities (Cooper and Lean 1992). Furthermore, DOM can augment microbial productivity by acting as a source of C and/or inorganic nutrients following photolysis (Meyer et al. 1987, Wetzel et al. 1995), or can inhibit microbial productivity by forming complexes with bioavailable nutrients and iron (Stewart and Wetzel 1981).

Inhibitory effects of UVR on freshwater biota have been well documented (see review by Karentz et al. 1994), and include changes in primary productivity (Bothwell et al. 1993, Rader and Belish 1997), secondary productivity (Bothwell et al. 1994, Kiffney et al. 1997a), and community composition (Bothwell et. al. 1994). Photodamaging effects of UVR are wavelength specific (Cullen et al. 1992). Near-ultraviolet (UVA, 320 - 400 nm) wavelengths are often the dominant contributor to photoinhibition of algae (Bühlmann et al. 1987, Kim and Wantanable 1993, Milot-Roy and Vincent 1994,), whereas suppression of invertebrates is more a function of mid-ultraviolet radiation (UVB, 280 - 320 nm)(Bothwell et al. 1994, Kiffney et al. 1997a). Greater attenuation of shorter than longer waveband UVR by colored DOM compounds increases the ratio of UVA to UVB with depth, complicating the ability to predict which trophic levels may be most affected by UVR. Increasing UVA:UVB may also enhance DNA dark-repair mechanisms in algae by increasing the relative proportion of long-wave UVA that acts to induce these processes, while reducing photodamaging short-wave UVA and UVB (Karentz et al. 1991).

I examined the sensitivity of algal and invertebrate assemblages to a range of UVR intensities by using DOM as a spectrally selective UVR filter. This approach is different from previous field investigations, which have examined UVR effects on biota in either the presence or absence of UVA and/or UVB (Bothwell et al. 1993, 1994, DeNicola & Hoagland 1996, Vinebrooke & Leavitt 1996, 1999, Hill et al. 1997, Kiffney et al. 1997a, 1997b). I used water filters constructed of UVR-transparent plastic containing different concentrations of DOM as irradiance filters placed above shallow flow-through flumes. Although a few studies have examined how DOM affects aquatic communities through UVR attenuation (Moeller 1994, Vinebrooke and Leavitt 1998), they have been unable to separate the UVR attenuating effects from secondary chemical effects. This approach isolated the effect of the UVR attenuation by DOM from the potential confounding chemical and biological influences of DOM on biofilm communities. These experimental results also provide insight into what natural systems may be potentially sensitive to biological effects from UVR, based on DOM and water-column transparency.

Methods

Experimental apparatus

The experiment was conducted between 28 July and 28 August 1996 at Environment Canada's experimental troughs apparatus (EXTRA) located on the South Thompson River, British Columbia (Bothwell 1988, 1992). A large industrial pump delivered water from the adjacent South Thompson River to a large head tank (4000 L) which was then diverted to 12 replicate stream flumes (2m long, 19 cm wide). Approximately 50 L/min of unfiltered river water was continuously discharged through each flume at a flow of 50 cm/s at a depth of 1 cm. Sheets of open-celled Styrofoam-DB (Flora Craft Inc., Pomona, California) provided a substratum for colonization by algal and invertebrate assemblages.

Sealed water filters (50 x 22 x 7 cm) constructed of UVR-transparent plastic (OP4 acrylic sheets; 4.7 mm thick; 70 - 90% transmittance of UVB and UVA) were placed above each flume (Fig. 2.1). The water filters were filled to 7 cm depth with DOM solutions containing either 0, 2, 5 or 8 mg/L of chemical-grade, dried humic acid (Sigma-Aldrich Canada Ltd., Oakville, Ontario) dissolved in distilled water. Sigma-Aldrich humic acid (derived from dried peat) is 39.8% C by mass, therefore DOM concentrations were roughly equivalent to 0, 0.8, 2.0, and 3.2 mg/L of dissolved organic carbon (DOC). However, because the DOM I used was composed primarily of high molecular weight CDOM, absorption in the UV range was 2 to 4 times higher per unit C than DOM in most natural fresh waters (Chin et al. 1994).

Experimental approach

The experiment was initiated when styrofoam substrata were placed in each of the 12 flumes, and DOM water filters were placed over the upstream portion of each flume. DOM treatments were run in triplicate (i.e., 4 treatments x 3 replicates), and solutions were renewed every 72 hours to minimize the changes in attenuation from photobleaching. Lotic assemblages were allowed to colonize from the river water.

Irradiance measurements

Light transmission of the four DOM water filters and changes caused by CDOM

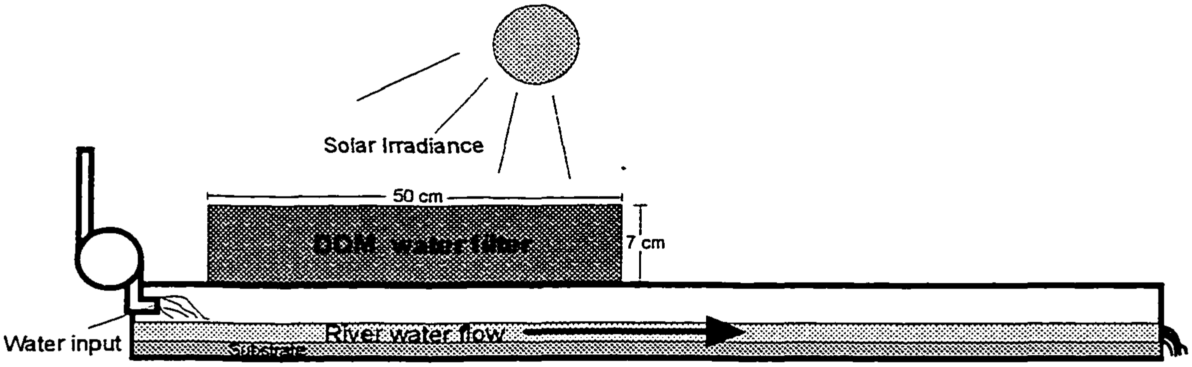

Figure 2.1. Diagram of the dissolved organic matter (DOM) water filter placed over an experimental flume.

photobleaching were measured in a 72-h experimental trial. Each of the solutions (0, 2, 5, and 8 mg/L Sigma-Aldrich humic acid) was placed in individual 2-cm diameter quartz tubes and incubated in natural sunlight for 72 h. Five millilitre samples were withdrawn after 0, 24, 48, and 72 h of exposure, and spectral scans of the absorbance of DOM solutions were made between 280 and 700 nm using a Cary 50 (Varian Instruments, Walnut Creek, California) scanning spectrophotometer equipped with a 2-cm quartz cuvette. Light transmission by the DOM water filters over the 7 cm depth was calculated from this, incorporating absorbance by the plexiglas frame. Hourly integrated ambient solar irradiance between 280 and 700 nm was also recorded during the 72-h incubation period using a Licor LI 1000 data logger equipped with a quantum cosine photosynthetically active radiation (PAR) sensor (Licor Instruments, Lincoln, Nebraska) and broadband UVA and UVB sensors (BW20, Vital Technologies, Toronto, Ontario).

During the colonization experiment, PAR flux densities at EXTRA were recorded hourly, and then converted to total daily solar energy (E $m^{-2} d^{-1}$) by summing over the 24-h period. Total daily UVA and UVB at EXTRA during this time were predicted from the measured PAR values, and equations calculated from linear regressions of daily PAR to daily UVA (UVA [kJ $m^{-2} d^{-1}$] = 17.953 PAR [mol $m^{-2} d^{-1}$] + 179.046, $R^2 = 0.858$) and daily UVB (UVB [kJ $m^{-2} d^{-1}$] = 0.981 PAR [mol $m^{-2} d^{-1}$] + 8.298, $R^2 = 0.838$) measured at EXTRA in four previous summers (1991 - 1994) (Bothwell et al. 1993, 1994). UVB was measured (in 1991, 1993, and 1994) with a Brewer ozone spectrophotometer (Sci-Tec Instruments, Saskatoon, Saskatchewan), UVA was measured (in 1992) with an OL-752 spectroradiometer (Optronics Laboratories, Orlando), and PAR was measured (in all years) with a Licor quantum cosine sensor. Instruments were calibrated with an external lamp from NIST (US National Institute of Standards). Hourly scans were made with the Brewer at 0.5-nm intervals between 290 and 320 nm during daylight periods, and recorded in W $m^{-2} nm^{-1}$. Hourly scans were made with the OL-752 at 2-nm intervals between 290 and 700 nm during daylight periods, and recorded in W $m^{-2} nm^{-1}$. Solar photon flux densities were integrated over the spectral range and summed over the entire daylight period for calculation of daily solar PAR, UVA, and UVB energy in kJ $m^{-2} d^{-1}$. Daily PAR energy during the colonization experiment was converted from mol $m^{-2} d^{-1}$ to kJ $m^{-2} d^{-1}$ (PAR [kJ $m^{-2} d^{-1}$] = 159.45 PAR [mol $m^{-2} d^{-1}$] + 557.23, $R^2 = 0.926$) for comparative purposes by the regressing daily PAR measured by the Licor quantum cosine sensor against the OL-752 spectroradiometer.

Algal and invertebrate assemblages

Community response to DOM mediated UVR exposure was measured by chlorophyll [a] and invertebrate assemblage composition over the 31-d period. Chlorophyll samples were collected every three days, starting on day 9, by taking triplicate 5 cm^2 cores from the Styrofoam substratum (Bothwell 1988). Cores were frozen immediately following sampling and stored in the dark until analysis. Chlorophyll was extracted in the dark in 10-mL tubes with 90% ethanol at 78°C as outlined by Nusch (1980). Pigment extracts were analyzed fluorometrically using a Turner Designs model 10au fluorometer.

On days 10, 21, and 31, the invertebrate assemblage was sampled by removing a section (190 cm^2) of the substratum. Adhering invertebrates were removed by physically agitating the sample in 70% ethanol or by removing individual invertebrates with forceps. Invertebrates were preserved in 70% ethanol until analysis. Samples were diluted to 500 mL in a 1-L Imhoff cone, and five 50-mL subsamples for enumeration were removed while air was bubbled through the cone to homogenize the sample (Wrona et al. 1982). A minimum of three subsamples was enumerated, or enough subsamples to count 100 individuals of the most numerous taxa. Invertebrates were identified to family level using Merritt and Cummins (1996). Family-level taxonomic resolution was chosen because in previous experiments at EXTRA, the two dominant families were each predominantly composed of a single species (*Cricotopus bicintus*, Chironomidae; *Simulium vittatum*, Simuliidae) (Bothwell et al. 1994).

Statistical analyses

Repeated measures (RM) statistical tests were used for all analyses (SPSS for Macintosh, Version 6.1, SPSS Inc., Chicago, Illinois). A RM-ANOVA was used to test for the effects of DOM treatment, time, and their interaction on chlorophyll concentration. A RM-MANOVA was used to test the effects of DOM treatment, time, and their interaction on invertebrate assemblage composition. Because of their low abundance (<1% of the total abundance), Trichoptera, Plecoptera, and Hydracarina taxa were omitted from the statistical analysis. Invertebrate data were log transformed (log [n+1]) to attain homogeneity of variances (Zar 1984).

Results

Irradiance

Transmission of UVB, UVA, and PAR through the DOM solutions decreased with increasing concentration, with attenuation strongest at the shorter UV wavelengths (Fig. 2.2). The 8 mg/L treatment allowed transmission of only small portions of UVB (12%) and UVA (34%), whereas PAR transmission was considerably higher (82%) (Table 2.1). UVB and UVA attenuation rapidly decreased with decreasing DOM concentration, with only a small reduction in UVB (73%), UVA (89%), and PAR (94%) transmittance by the 0 mg/L (distilled water) treatment (Fig 2.2), primarily because of attenuation by the walls of the plexiglas water filter. Small changes in the optical transmittance of DOM from photobleaching were observed over 72 h (Table 2.1). Photobleaching increased with both increasing DOM concentration and with decreasing wavelength, and occurred mainly in the initial 48 h of exposure. The 8 mg/L DOM water filter transmitted 6.9% more UVB (78.8% change from time 0 hrs), 13.1% more UVA, and 7.2% more PAR following 72 h of exposure to sunlight, at mean daily solar irradiances of 46.7 kJ $m^{-2} d^{-1}$ UVB, 913.81 kJ $m^{-2} d^{-1}$ UVA, and 11960 kJ $m^{-2} d^{-1}$ PAR.

Daily PAR levels at EXTRA ranged between 3100 and 11,500 kJ $m^{-2} d^{-1}$ (mean 7876 kJ $m^{-2} d^{-1}$) (Fig. 3). Predicted daily UVB radiation was between 21 and 54 kJ $m^{-2} d^{-1}$ (mean 43.84 kJ $m^{-2} d^{-1}$), and predicted UVA radiation ranged between 432 and 1147 kJ $m^{-2} d^{-1}$ (Fig. 2.3). Using the mean transmittance of the DOM water filters, mean daily exposures of flume communities to UVB were calculated to be 5.4, 11.8, 23.8, and 32.4 kJ $m^{-2} d^{-1}$, and for UVA were 284, 444, 639, and 739 kJ $m^{-2} d^{-1}$ for the 8, 5, 2, and 0 mg/L treatments, respectively.

Algal abundance

Periphyton standing crop, inferred from chlorophyll concentration, differed significantly between DOM mediated light treatments over the course of the colonization experiment (RM-ANOVA, $F = 6.11, p = 0.018$) (Fig. 2.4). The algal biomass for all treatments was generally low, and appeared to be primarily diatomaceous. Temporal patterns in chlorophyll concentration under the 5 and 8 mg/L DOM treatments were similar, as were patterns in the 0 and 2 mg/L treatments. Chlorophyll biomass was greater under the 5 and 8 mg/L treatments over the first 14 d of colonization. However, by day 20, chlorophyll biomass peaked in the 5 (10.6 mg/m^2) and 8 mg/L (5.3 mg/m^2) treatment and then

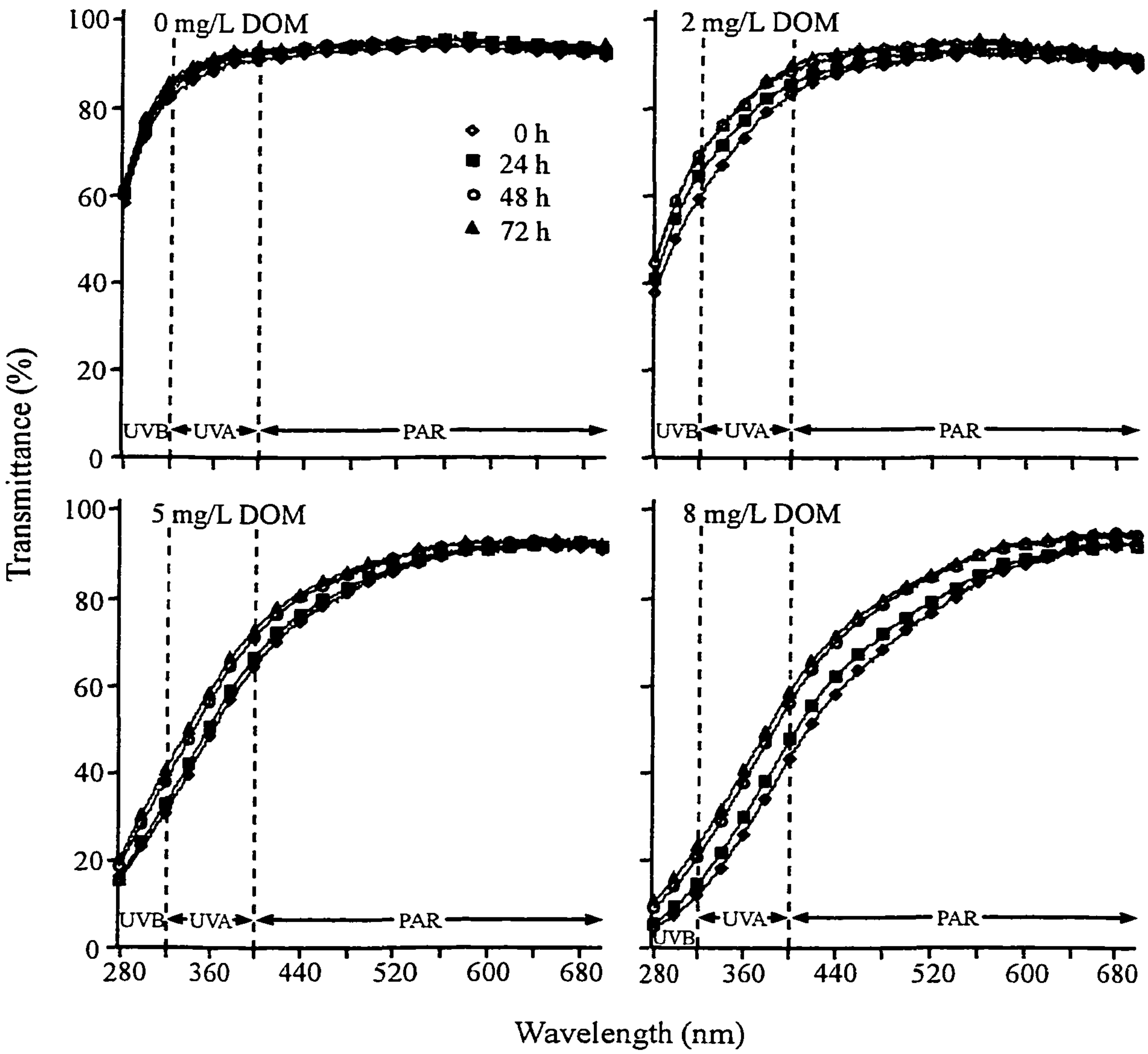

Figure 2.2. Spectral transmission of the four dissolved organic matter (DOM) water filters following 0, 24, 48, and 72 h of exposure to ambient sunlight. Percent changes in transmission of photosynthetically active radiation (PAR), near -ultraviolet (UVA) and mid-ultraviolet (UVB) radiation are reported in Table 2.1.

Table 2.1. Changes in light transmittance due to photobleaching of the four dissolved organic matter (DOM) water filters during 72-h exposure to full spectrum natural sunlight. Mean solar irradiances during the trial were 46.7 kJ m^{-2} d^{-1} UVB, 913.81 kJ m^{-2} d^{-1} UVA, and 11960 kJ m^{-2} d^{-1} photosynthetically active radiation (PAR, 400 - 700 nm). UVB = mid-ultraviolet radiation (280 - 320 nm) and UVA = near-ultraviolet radiation (320 - 400 nm).

DOM treatment (mg/L)	Time (h)	Transmittance (%) UVB	UVA	PAR
0	0	71.93	87.57	92.74
	24	73.36	88.94	93.98
	48	74.63	89.65	93.99
	72	75.89	90.37	94.01
	Mean	73.95	89.13	93.68
2	0	49.08	72.23	89.99
	24	53.59	76.09	91.07
	48	57.58	79.99	92.61
	72	57.64	80.16	93.12
	Mean	54.47	77.11	91.70
5	0	23.42	48.70	85.84
	24	24.61	50.80	86.51
	48	28.84	56.21	88.56
	72	30.89	58.51	89.01
	Mean	26.94	53.55	87.48
8	0	8.76	27.58	76.22
	24	10.16	30.91	78.15
	48	14.03	38.17	82.92
	72	15.67	40.70	83.43
	Mean	12.15	34.34	80.19

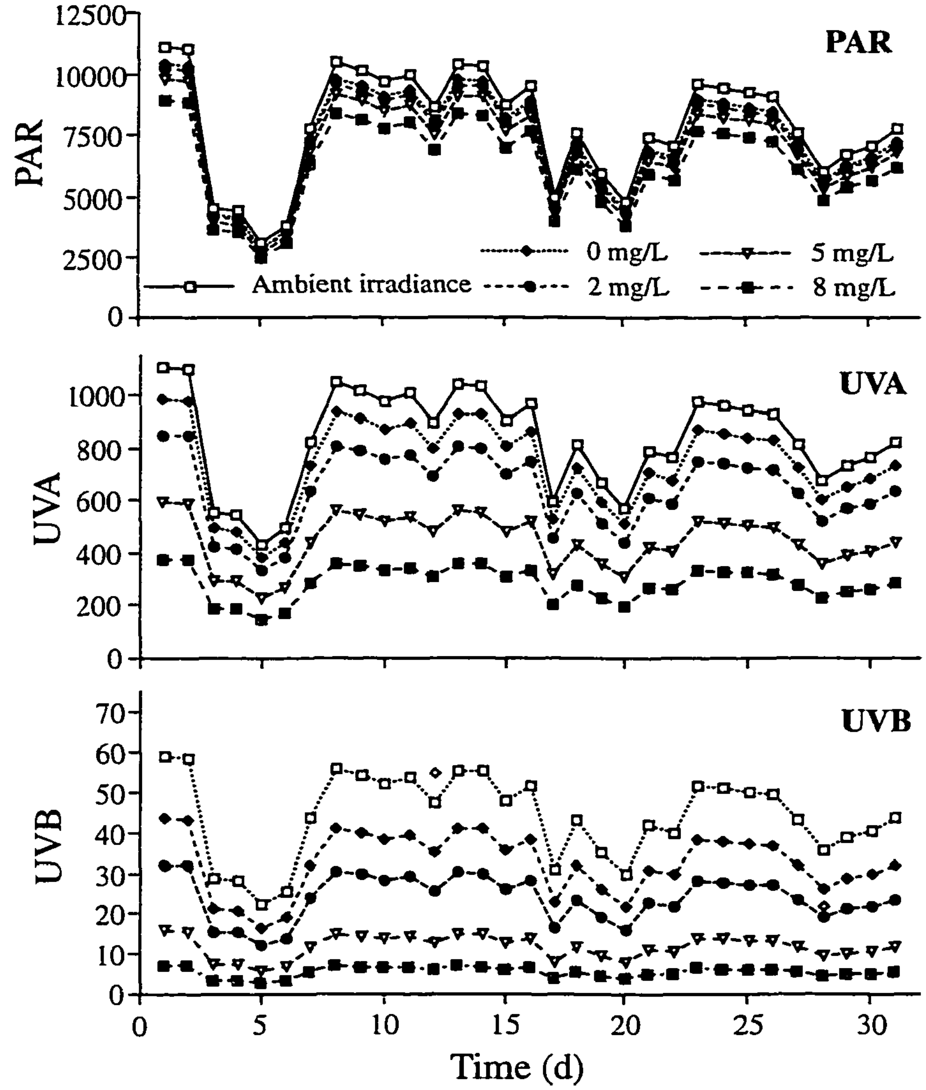

Figure 2.3. Estimated flux of photosynthetically active radiation (PAR), near-ultraviolet (UVA) and mid-ultraviolet (UVB) radiation (kJ m^{-2} d^{-1}) for the four dissolved organic matter (DOM) water filters during the 31-d colonization experiment in August 1996. Daily UVA and UVB were calculated from PAR recorded at the site and linear regression equations of PAR to UVA and UVB from previous experiments at the site (Bothwell et al. 1993, 1994).

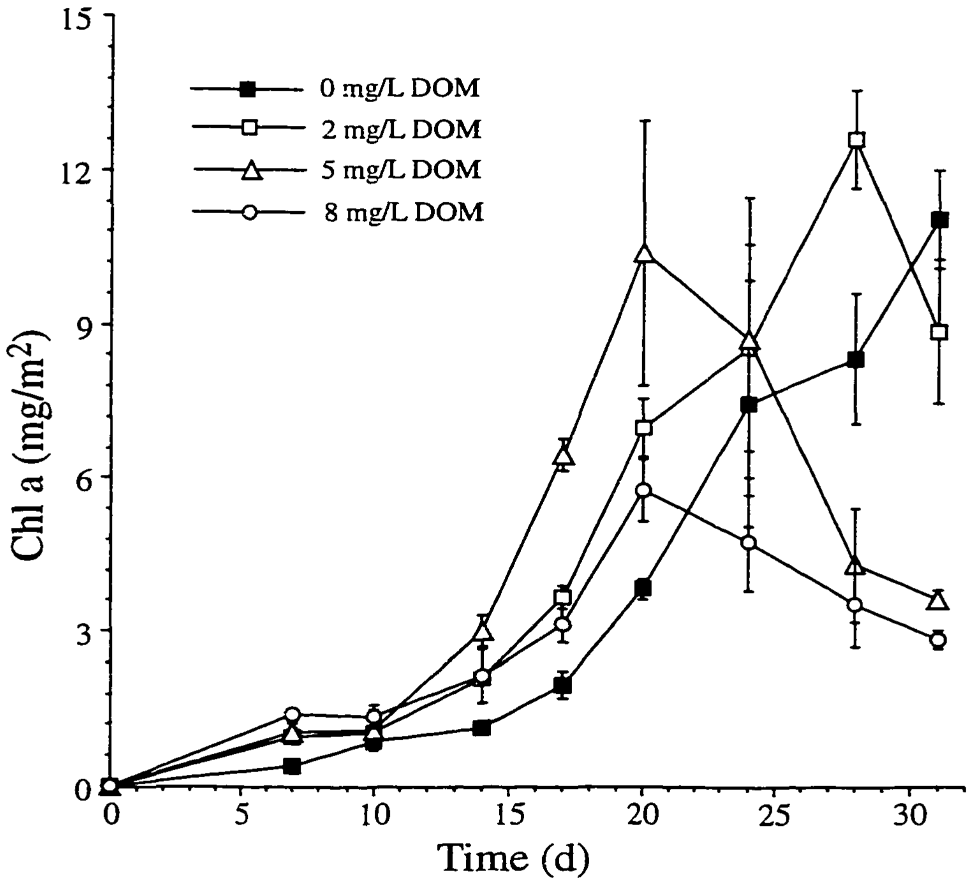

Figure 2.4. Chlorophyll (Chl) *a* concentration (mean ± 1 SD, n = 3) during the 31-d colonization experiment under the four dissolved organic matter (DOM) water filter treatments.

steadily declined until the end of the experiment. In contrast, chlorophyll biomass in the 0 and 2 mg/L treatments increased continuously over the course of the experiment, with concentrations surpassing those of the 5 and 8 mg/L treatments following day 24. The reversal in chlorophyll trends over the colonization period was highlighted by the RM-ANOVA, which showed significant effects of both time ($F = 31.8$, $p < 0.001$) and the interaction between time and DOM treatment ($F = 5.7$, $p < 0.001$). By the end of the trial, chlorophyll in the 0 mg/L (11.2 mg/m^2) and 2 mg/L (9.1 mg/m^2) treatments were significantly greater (Student-Newman-Keuls test [SNK], $p < 0.05$) than both the 5 mg/L (3.8 mg/m^2) and 8 mg/L (3.1 mg/m^2) treatments.

Benthic invertebrate assemblage abundance

Increasing DOM resulted in significantly increased invertebrate abundance for nearly all taxa (Table 2.2, Fig. 2.5). As with trends for chlorophyll, effects of the DOM light manipulations on benthic invertebrate abundance were similar for the 5 and 8 mg/L treatments and for 0 and 2 mg/L treatments. Total invertebrate abundance was significantly higher under 5 and 8 mg/L DOM treatments than under 0 and 2 mg/L treatments (Fig. 2.5a, SNK, $p < 0.05$), with differences diverging over time (time x DOM interaction, $p < 0.005$). At the end of the experiment, invertebrate abundances were ≈200% greater under 5 (mean 2.8/cm^2) and 8 mg/L (mean 3.1/cm^2) DOM than under 0 (1.1/cm^2) and 2 mg/L (1.6/cm^2) DOM treatments. The difference in total invertebrates was driven mainly by chironomids, which composed at least 60% of the total invertebrate abundance (Fig. 2.5b). Throughout the experiment, chironomid abundances were 200 to 300% greater in 5 and 8 mg/L DOM flumes than in 0 and 2 mg/L flumes (SNK, $p < 0.05$). Chironomids were also 51% more abundant in 2 versus 0 mg/L DOM treatments (SNK, p

Table 2.2. Repeated measures MANOVA results of the effects of dissolved organic matter (DOM) mediated light treatments on the abundances of total invertebrates, Chironomidae, Simuliidae, and Naididae. Reported are univariate F statistics (F), multivariate Hotellings F statistic (H-F), p values (p) and degrees freedom (df).

		Total inv.		Chironomidae		Simuliidae		Naididae		MANOVA	
Source	df	F	p	F	p	F	p	F	p	H-F	p
DOM	3	188.0	<0.001	136.8	<0.001	26.3	<0.001	12.2	0.0023	26.4	<0.001
Time	2	4.3	<0.001	357.7	<0.001	18.2	<0.001	212.4	<0.001	61.6	<0.001
Time x DOM	6	0.33	0.004	8.8	<0.001	4.8	0.0052	3.3	0.0254	7.9	<0.001

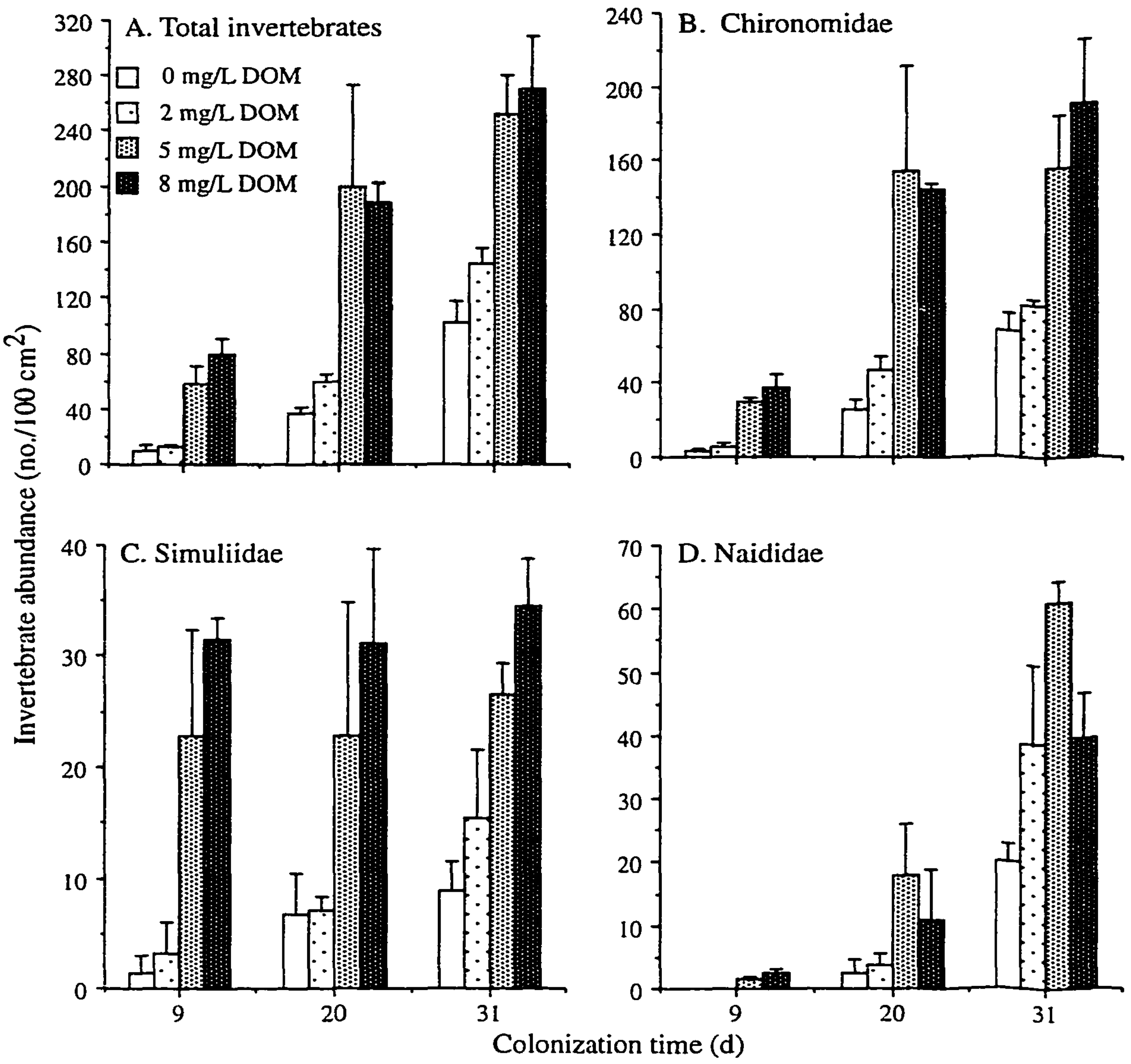

Figure 2.5. Mean abundance (mean + 1 SD, n = 3) of total invertebrates (a), Chironomidae (b), Simuliidae (c), and Naididae (d) under the 4 dissolved organic matter (DOM) water filter treatments over 31 d.

< 0.05), although this was the only invertebrate group to show significant differences between these 2 treatments. Abundances of simuliids (Fig. 5c, SNK, $p < 0.05$) and oligochaetes (Fig. 5d, SNK, $p < 0.05$) were also significantly higher under 5 and 8 mg/L DOM treatments than under 0 and 2 mg/L DOM treatments, although the magnitudes of the differences were less pronounced than for chironomids.

Discussion

DOM effects on UVR and benthic colonization

My results showed that attenuation of UVR by DOM strongly influenced the colonization dynamics and trophic interactions of algal and invertebrate assemblages in shallow lotic ecosystems. My findings also suggest the existence of a threshold UVR exposure range. Increasing mean daily UVB from 11.8 to 23.8 kJ $m^{-2}d^{-1}$ (27 to 55% ambient) and UVA from 444 to 640 kJ $m^{-2}d^{-1}$ significantly decreased the abundance of colonizing invertebrates and increased algal biomass accrual predominantly through its effects on grazers. This intensity of UVR appears to be a threshold range for colonization dynamics because no significant impacts were seen leading up to this level, however, once this range was exceeded biological effects were consistently apparent. This threshold range occurred in my experiment between 2 and 5 mg/L DOM, or expressed in units of C, between 0.8 and 2 mg/L DOC. However, Chin et al. (1994) reported that Sigma-Aldrich humic acid had a 2 to 4-fold greater absorption in the UV range (per unit C) than DOM present in natural waters because of its high specific CDOM content. This high UVR absorption by the DOM used in my experiment threfore tends to offset the difference between the units of DOM I reported, and units of DOC more commonly reported in the literature.

Algal reponse to UVR attenuation by DOM

Bothwell et al. (1994) demonstrated that ambient intensities of UVR can result in more rapid algal biomass accrual when compared to UV-shielded communities because of a concurrent reduction in grazing invertebrates. Findings of my experiment corroborates those of Bothwell et al. (1994), that although direct inhibitory effects of UVR on algal accrual are most prevalent in early stages of colonization when grazer abundances are low, UVR inhibitory effects on grazers in later succession communities have an overriding effect on algal accrual. Under lower UVR exposures (5 and 8 mg/L DOM), algal biomass declined by >40% between days 20 and 31 of the experiment, coinciding with the highest abundances of grazing chironomids. In contrast, under high UVR exposure (0 and 2 mg/L DOM) during the same period (day 20 - 31), algal biomass continually increased with significantly lower abundances of chironomids. Under lower grazing pressure (0 and 2 mg/L DOM), the direct inhibitory effect of UVR on algal accrual was apparent throughout the experiment. The decline in algal biomass that occurred under the 2 mg/L treatment between days 28 and 31 was likely a result of sloughing because the algal biofilms were at their highest densities, flow velocities were supercritical, and grazer abundances were low.

Previous field experiments have confirmed the direct inhibitory effects of ambient UV radiation on benthic algal accrual first reported by Bothwell et al. (1993). Typically, algal biomass is reduced by 30 to 50% over colonization periods >25 d (Vinebrooke and Leavitt 1996, 1999, Kiffney et al. 1997a, Rader and Belish 1997, Francoer and Lowe 1998). I observed even greater effects of inhibition by ambient UVR on algal accrual, with ≈60% less chlorophyll under my highest UVR exposure (0 mg/L compared to 8 mg/L DOM) after 14 d. I believe that this response in chlorophyll was reflective of the patterns in algal cell growth that occurred in my experiment. Although the chlorophyll content of algal cells (i.e., chlorophyll:biovolume) has been shown to change under different UVR (El-Sayed et al. 1990) and PAR intensities (Perry et al. 1981, Falkowski and LaRoche 1991), previous field investigations at EXTRA reported a strong correlation between trends in chlorophyll concentration and total algal cell biovolume under similar manipulations of PAR and UVR intensity (Bothwell et al. 1993).

DOM attenuation of UVR in my experiment increased the ratio of UVA:UVB by almost 300% at the highest (8 mg/L) concentration, with an even greater increase in the proportion of long-wavelength UVA. Increasing DOM concentration should decrease photoinhibitory effects on algae by reducing the flux of more photodamaging short-waveband UVR (Cullen and Lesser 1991, Karentz et al. 1994) to photoreactivating long-wavelength UVA (Quesada et al. 1995). Nevertheless, I observed lower rates of chlorophyll accumulation under 8 mg/L DOM compared to 5 mg/L, despite the lower UVR exposure and higher UVA:UVB ratio in the 8 mg/L treatment. Reduced levels of PAR in the 8 mg/L treatment may have contributed to lowered photosynthetic rates and algal growth, although this scenario is unlikely because previous investigations at EXTRA observed light saturation of photosynthesis at intensities below those present under the 8 mg/L treatment during my experiment (Jasper and Bothwell 1986). Higher invertebrate abundances (≈30%) in the 8 versus 5 mg/L treatment during the early stages of the experiment may have also contributed to the lower accrual rates under the 8 mg/L treatment through increased grazing. Aside from the lower chlorophyll accrual under the 8 mg/L treatment, photoinhibition for the other 3 treatments was characteristic of both UVR exposure and UVA:UVB ratios.

Invertebrate response to UVR attenuaton by DOM

Similar sensitivities to UVR were observed for all invertebrate taxa colonizing flumes, although only a small number of taxa was involved. Several other field investigations observed inhibition of stream invertebrates by UVR (Bothwell et al. 1994, Kiffney at al. 1997a, 1997b, Donahue and Schindler 1998). However, variable sensitivity among different taxa has generally been reported (Kiffney et al. 1997a, 1997b, Vinebrooke and Leavitt 1998, 1999). For instance, Kiffney et al. (1997a) observed that, although most taxa increased in response to the screening of UVB, some taxa (e.g., Heptageniidae and Glossosomatidae) increased more when UVA was additionally removed. Vinebrooke and Leavitt (1999) and Hurtubise and Havel (1998) observed differential sensitivities among lentic zooplankton taxa, presumably linked with differences in pigment composition or behavioral adaptations. In my experiment the sharp threshold response in invertebrate colonization that occurred between the 2 and 5 mg/L DOM was most obvious for grazers (chironomids), but also for filter feeders (Simuliidae) and detritivores (Naididae). Encased invertebrate taxa such as trichopterans and gastropods are considered to be less sensitive to UVR (Hill et al. 1997), but I observed similar responses to UVR by both chironomids encased in sand-grain-matrix tubes and other noncased taxa (i.e., simuliid larvae, naidids). A sand case would provide considerable shading to the chironomid larvae, except for the head and parts of the thorax, which would extend from the case during movement. Physical features such as pigmentation, body armor, and body-cases may be protective adaptations against UVR exposure, however, my results suggest caution in generalizing UVR sensitivity based on these features.

Some investigators have reported no negative effects of UVR on natural stream invertebrate communities (DeNicola and Hoagland 1996, Hill et al. 1997). My finding that effects of UVR only occurred at low DOM concentrations (<5 mg/L) in shallow depths (7 cm) suggests that in some other studies where no UVR effects were reported , attenuation by DOM in the water column may have already decreased UVR intensity below a critical level. Investigations reporting no effects of UVR on invertebrate communities typically come from deeper streams (mean depths >20 cm, >3 times the depth of the water filters), with DOC concentrations equivalent to my 2 to 5 mg/L DOM treatments (or ≈1 - 2 mg/L CDOC)(DeNicola and Hoagland 1996, Hill et al. 1997). For example, Kiffney et al. (1997a) did not observe significant photoinhibitory effects of UVR on benthic invertebrate colonization until after 30 d, when water depth had dropped from 40 to 10 cm, and UVR absorbance (at 254 nm) had decreased by 30%. My results indicate that daily UVR exposures in the range of 20 kJ $m^{-2} d^{-1}$ UVB (50% ambient) and 700 kJ $m^{-2} d^{-1}$ UVA (60% ambient) may be ecologically significant for UVR effects on stream invertebrates at equivalent northern latitudes.

Implications of UVR attenuation by DOM in freshwater systems

This experiment demonstrates the potential for DOM to influence benthic colonization through its influence on UVR. A high degree of variability in DOM concentration exists for freshwater systems, which can result in considerable changes in UVR exposure to resident aquatic biota over relatively small temporal and spatial scales. For example, Morris and Hargreaves (1997) observed a 39 to 81% spring - summer decline in epilimnetic UVR attenuation in lakes from photochemical degradation of DOM. Photochemical bleaching of the DOM solutions used in these trials resulted in increased light transmission of 6.9% UVB and 13.1% UVA over a 72-h period. Changes in water transparency to UVR because of CDOM photobleaching could be an important seasonal mechanism regulating benthic community productivity and composition, especially if increased penetration allows UVR exposure to exceed the threshold values I observed. Over longer time scales, anthropogenic activities linked to climate warming and acid deposition result in large changes to DOM export and UVR transparency of several watersheds in North America (Schindler et al. 1996, Yan et al. 1997). Schindler at al. (1996) observed 15 to 20% decreases in DOM because of climate warming over a 20 year period in the Experimental Lakes Area (ELA), resulting in increases in UVR penetrance from 22 to 63%. In addition, DOM decreased by nearly 80% in acidified lakes at the ELA, resulting in a >400% increase in UVR exposure (Schindler et al. 1996). Long-term declines in CDOM could have pronounced effects on benthic communities from increased UVR exposure, most notably in shallow-water systems that already have relatively low DOM concentrations. These results demonstrate that the changes in UVR exposure from even small decreases in DOM could result in dramatic changes in resident aquatic communities. I predict that streams with DOM concentrations <5 mg/L DOM could be particularly sensitive to UVR and potentially most negatively affected by future increases in UVR exposure as a result of ozone depletion or DOM decreases.

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3. EFFECTS OF VARIABLE SOLAR ULTRAVIOLET RADIATION EXPOSURE TO STREAM COMMUNITIES: CONTROL BY THE RIPARIAN CANOPY

Introduction

Riparian canopies affect the functioning of aquatic ecosystems (Hynes 1975, Vannote et al. 1980) by controlling inputs of solar energy and contributing allochthonous materials to waterbodies (Gregory 1991, Naiman and Decamps 1997). They also protect aquatic biota from exposure to harmful ultraviolet radiation (UVR, 280 – 400 nm), now recognized to be an important component shaping freshwater communities (reviewed by Williamson 1995, Hader et al. 1998). Management of riparian zones has been the subject of extensive research (Osbourne and Koviak 1993, Naiman et al. 2000), due in part to the heavy pressure of land-use practices along riparian corridors (Allan et al. 1997). Alteration of the riparian canopy through land-use activities such as logging and urban development, or through natural disturbance processes such as fires, wind, and floods, can result in large increases in sunlight exposure to the waterbodies. Canopy removal can also alter the export of dissolved organic matter (DOM) (Hobbie and Likens 1973, Meyer and Tate 1983, Hill 2000), the principle UVR attenuator in oligotrophic freshwaters (Scully and Lean 1994). I studied the effects of the riparian canopy on stream exposure to UVR and the resulting effects on benthic communities in a clear coastal stream located on Vancouver Island, British Columbia.

Natural intensities of UVR have been shown to be detrimental to benthic algae (Bothwell et al. 1993, Vinebrooke and Leavitt 1996, 1999, Kiffney et al. 1997a, McNamara and Hill 2000, Watkins et al. In press) and invertebrates (Bothwell at al. 1994, Kiffney et al. 1997a, 1997b, Donahue and Schindler 1998, Kelly et al. 2001), and can alter the composition of benthic communities (Bothwell et al. 1993, Kiffney et al. 1997a, Vinebrooke and Leavitt 1999). Increases in UVR exposure can cause significant changes in benthic communities (Rader and Belish 1997), with large differences in the sensitivity of organisms to UVR (Karentz et al. 1991, Bothwell et al. 1993, McNamara and Hill 1999, Sommaruga and Buma 2000). Photoinhibitory effects of UVR are wavelength dependent (Cullen et al. 1992), and can affect components of benthic food-webs differently (Bothwell et al. 1994, Vinebrooke and Leavitt 1999), thereby influencing herbivory and predation (Bothwell et al. 1994, Hessen et al. 1997, Kelly et al. 2001). Changes to the relative intensities of UVB and UVA to photosynthetically active radiation (PAR, 400

– 700 nm) from alteration of the riparian canopy complicates the ability to predict which trophic levels might be affected, and the interactions between these effects.

Removal of the riparian canopy has been shown to result in considerable changes to resident biological communities (Shortreed and Stockner 1983, Robinson and Rushforth 1987, Garman & Moring 1991, Hetrick et al. 1998a, b). Although increased autotrophic production is generally seen following alteration of the riparian canopy (Shortreed and Stockner 1983, Robinson and Rushforth 1987), effects on invertebrate production have been variable (Murphy and Hall 1981), either decreasing in response to reduced availability of coarse particulate organic matter (CPOM) resources (Garman & Moring 1991), or increasing due to greater production of algae as a food source (Newbold et al. 1980, Hetrick et al. 1998b). The magnitude of these community responses are strongly influenced by the extent of the canopy removal, type of catchment vegetation, and volume of the stream (Murphy and Hall 1981). Riparian buffer strips have been adopted to mitigate the effects of canopy removal (Gregory et al. 1991, Osborne and Kovacic 1993), however, the width and composition of prescribed buffer strips can vary considerably, and provide variable protection to the stream from harmful UVR. Although some studies have examined the effects of increased sunlight intensity on stream communities following canopy removal (Shortreed and Stockner 1983, DeNicola et al 1992, Robinson and Rushforth 1987), none have specifically examined the effects of increased UVR.

I examined the effect of UVA and UVB radiation on stream communities under varying degrees riparian canopy shading along several reaches of a fourth order coastal stream (Little Qualicum River, Vancouver Island, British Columbia). I hypothesized that the effects of UVR on benthic communities would increase with less canopy cover, and that little or no effect of UVR would occur in highly shaded stream reaches. I also hypothesized that changes in UVB:UVA:PAR under reduced canopies would contribute to differential effects of UVR on the various trophic levels of the benthic community. The direct effects of UVR on algal communities were also tested by reducing grazers in an adjacent open-canopied man-made channel.

Methods

Study Site

Experiments were conducted during the summers of 1995 and 1996 along a 3 km section of the Little Qualicum River (49°17' N, 124°35' W), and an adjacent spawning channel diverted from the river (Fig. 3.1). The study site on the Little Qualicum River is a medium-sized (fourth order) stream located approximately 15-18 km downstream from Cameron Lake. The Little Qualicum River catchment (135 km^2) is located on the central-eastern Nanaimo lowlands of Vancouver Island, British Columbia within Pacific Coastal Ecoregion. Forests in the watershed are predominantly mature second growth, although clearings from logging, residential development, and farming occur along the river, as well as some areas of intact old-growth forest, resulting in variable amounts of shading to the stream. The adjacent man-made spawning channel has no riparian canopy. Riparian forests are dominated by western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). Substrata in both the river and spawning channel are composed mainly of cobble (5 cm - 15 cm) and gravel (2 mm - 5 cm), with a matrix of sand (64 µm - 2 mm), and silt (<64 µm). Peak flows occur in November (≈15 m^3/s), declining to summer base-flows (≈2 m^3/s) by July through September. Approximately 0.7 m^3/s of the river flow is diverted into the spawning channel year round. During base-flow, the river and channel at my study site had mean widths of 22 m and 7.6 m, respectively, and mean depths of 0.47 m and 0.25 m, respectively. During the summers of 1995 and 1996, river water had a circumneutral pH (6.9-8.0), a conductivity of 92 µS/cm, an alkalinity of 43 mg $CaCO_3$/L, and low nutrient concentrations (≤ 0.02 mg/L NO_3, ≤ 0.01 mg/L TP) (Table 3.1). Water transparency to UVR was high, with a mean DOC concentration of 1.3 mg/L in both summers.

Table 3.1. Water chemistry parameters for Little Qualicum River during the 1995 and 1996 experimental trials.

	1995		1996	
Parameter	**Mean**	**SD**	**Mean**	**SD**
pH	7.2	0.3	7.8	0.3
Conductivity (µS/cm)	93.3	0.1	91	0.5
Alaklinity (mg $CaCO_3$/L)	40.3	1.3	45.9	0.2
Hardness (Ca+Mg mg/L)	49.1	1.6	42.7	1.1
Nitrate (NO_3 mg/L)	<0.02	0.0	0.011	0.007
Total Nitrogen (mg/L)	0.093	0.010	0.063	0.011
SRP (mg/L)	0.008	0.001	0.002	0.001
Total Phosphorus (mg/L)	0.01	0.007	0.006	0.001
Silica (SiO_2 mg/L)	7.9	7.5	7.2	0.5
DOC (mg/L)	1.3	0.7	1.3	0.5

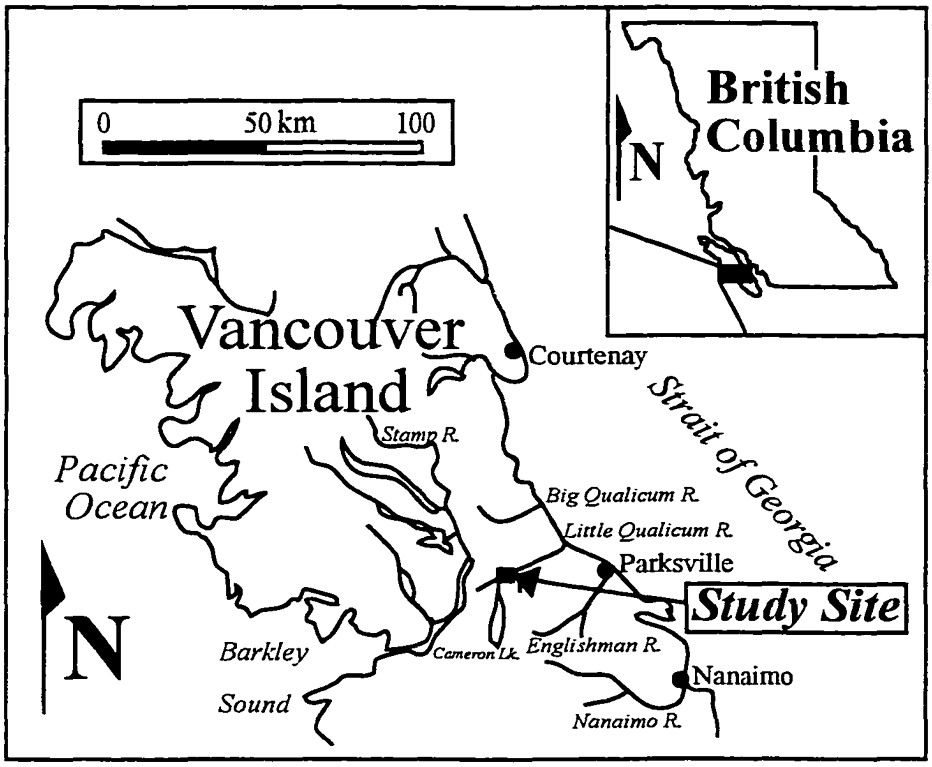

Figure 3.1. The location of the study site on the Little Qualicum River and the adjacent salmon spawning channel.

Variable riparian canopy experiment

The influence of riparian canopy shading on UVR effects to stream communities was assessed in a 91-d experimental trial in the main-stem of the Little Qualicum River between May 18 and August 17, 1996. A 3x3 factorial experiment considered three canopy treatments (no canopy, intermediate canopy, and intact canopy) and three radiation treatments (PAR+UVA+UVB [control], PAR+UVA, and PAR). Site characteristics that influenced light exposure to the stream, including channel aspect, channel width, riparian height, riparian width, and canopy composition are described in Table 3.2. Overhead canopy cover at the three sites was quantified using a spherical canopy densitometer (Lemmon 1957). Canopy coverages were 0% under no canopy, 33% under intermediate canopy, and 90% under full canopy. Radiation treatments were applied to an ≈4 m^2 mid-channel section in triplicate at each site in a 3x3 randomized block design to control for small-scale variations in light exposure, water depth, and water velocity. Radiation treatments were established by suspending large area (≈2 m^2) plastic filters immediately (≈3 cm) above the water surface. The filters used were, for PAR, UF4 plexiglas sheets (Rohm and Hass; 6.4 mm thick; 50% transmission at 398 nm), for PAR+UVA, Mylar-D (Du Pont; 0.1 mm thick, 50% transmission at 318 nm), and for PAR+UVA+UVB, OP4 acrylic sheets (CYRO; 4.7 mm thick; 70-90% transmittance throughout the UVB and UVA) (Fig. 3.2). Filters were placed over shallow riffle zones of approximately equal water depth and velocity. Mean water depth and velocity at the beginning of the experiment were 0.39 m and 0.38 m/s, respectively.

Grazer-reduced experiment

The direct effect of UVR on epilithon colonization was investigated under reduced grazing pressure in a 70-d experimental trail in an open (non-canopied) section of the

Table 3.2. Riparian characteristics of three sites on the Little Qualicum River varying in riparian canopy cover.

Site	Aspect	Channel width (m)	Canopy cover	* Riparian Depth (m)	* Riparian Height (m)	Riparian Composition**
No Canopy	211°	25	0%	0 W, 50 E	0 W, 5 E	100% RA
Intermediate Canopy	283°	24	33%	25 S, 50 N	15 S, 17 N 5% BLM, 5% DF	75% RA, 15% WRC,
Full Canopy	201°	21	90%	500 W, 150 E	20 W, 30 E	50% RA, 30 WRC 10% BLM, 10% DF

** RA = Red Alder WRC = Western Red Cedar BLM = Bigleaf Maple DF = Douglas Fir

* The side of the stream channel that the riparian corridor ocurrs; E = esat, W = west, N = north, S = South

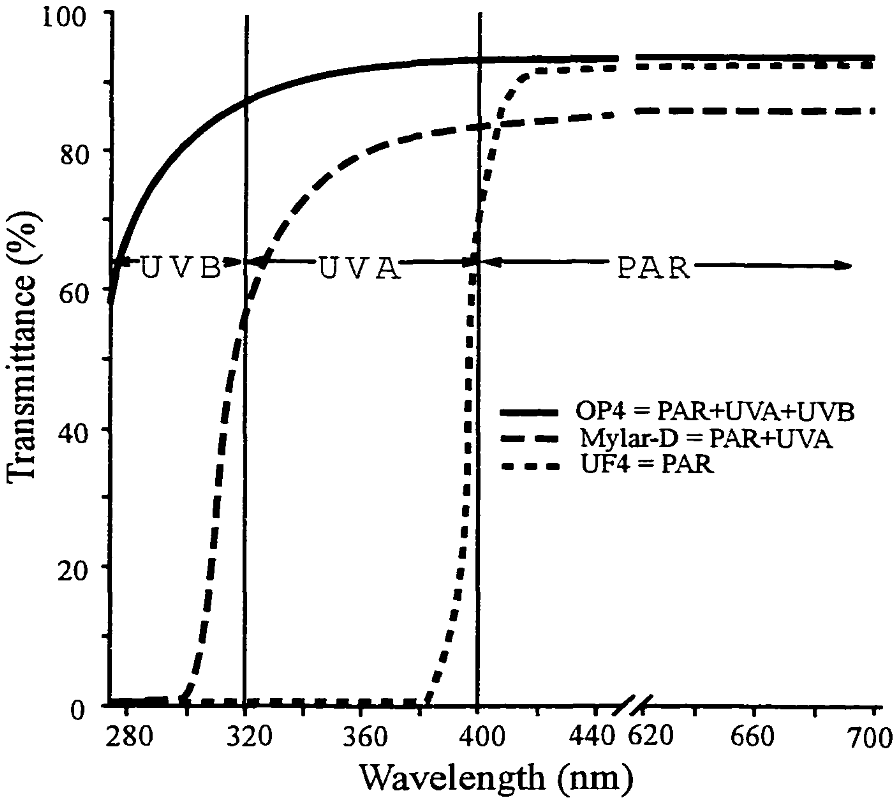

Figure 3.2. Transmittance properties of the three plastic filters used in the experimental trials, OP4 plexiglass, Mylar-D and UF4 plexiglass, through the UVB (280-320 nm), UVA (320-400 nm), and PAR (400-700 nm) spectral ranges.

Little Qualicum River spawning channel between June 20 and August 29, 1995. Prior to the initiation of the experiment the Department of Fisheries and Oceans cleaned the spawning channel to remove sand, silt and organic detritus in order to improve hatching success of chum salmon eggs. A bulldozer was used to turn over the top 0.6 m of substrata, working downstream for the entire length of the channel (4.1 km). Re-suspended sand, silt, and benthic material were then diverted from the channel (by pump) through a settling field before re-entering the main-stem of the river. In 1992 seventy metric tonnes of material were removed from the channel (Mundie and Crabtree 1997). The effects of the channel cleaning procedure on the benthic community has been previously investigated and shown to depress invertebrate biomass for several weeks (Mundie and Crabtree 1997). Hence minimal epilithic or invertebrate communities were established in the channel at the initiation of my experiment. The three light treatments described above (PAR, PAR+UVA and PAR+UVA+UVB) were applied in triplicate. Filters were placed randomly in line (due to a narrower channel) along a 20 m homogenous section of the channel.

Physical variables

PAR was measured continuously at the mid-point of the radiation treatments of each site with a Licor (Lincoln, NE) LI100 data logger and a LI190SA quantum cosine sensor. Ambient UVB radiation was estimated from UVB measured at the meteorological station operated by Environment Canada on Saturna Island, located approximately 32 km southwest from the study location. UVB flux was recorded with a Brewer Ozone Spectrophotometer (Sci-Tec Instruments, Saskatoon, Saskatchewan, Canada) at hourly intervals during daylight periods. Readings were made at 0.5 nm intervals between 280 and 320 nm, and integrated over the UVB spectral range to determine hourly UVB.

Total daily intensities of above canopy PAR and regional UVB were similar in both the 1995 and 1996 experimental trials (Fig. 3.3). In 1995, total daily PAR ranged between 7.8 and 60.6 E m^{-2} d^{-1} (mean 40.6 E m^{-2} d^{-1}), and in 1996 PAR intensities ranged between 12.3 and 57.1 E m^{-2} d^{-1} (mean 40.4 E m^{-2} d^{-1}). Similarly, mean total daily UVB estimated from Saturna Island differed only marginally between years (0.145 E m^{-2} d^{-1} in 1995 versus 0.150 E m^{-2} d^{-1} in 1996). Total daily PAR was significantly correlated with UVB at Saturna Island over the two years of data ($r^2 = 0.548$, $p < 0.001$).

Interception of solar radiation by the riparian canopy at each site (intact, intermediate and no canopy) was quantified during a two-week period in August 1997 with an

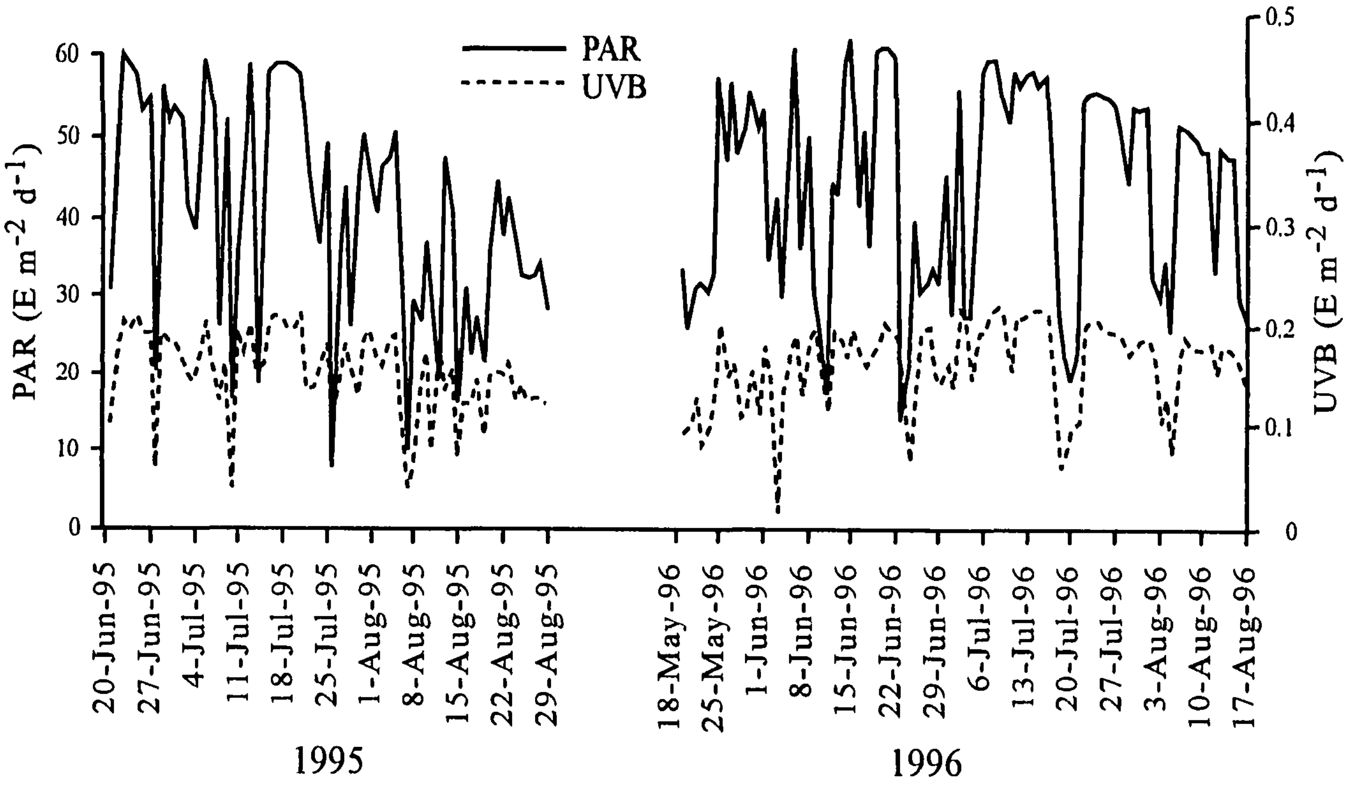

Figure 3.3. Above canopy daily PAR irradiance at the study site during the 1995 and 1996 experimental trials, and daily UVB irradiance measured at Saturna Island meteorological station, located approximately 35 km distance from the site.

Optronics OL-754 Spectroradiometer (Optronics Laboratories, Orlando, FL). Hourly scans of irradiance between 290 and 700 nm were recorded during daylight hours at 2 nm intervals (in W m^{-2} nm^{-1}) over three days at each site. Measurements were collected from the mid-point of the radiation pannels at each site, and therfore respresent exposure at that point location. It was assumed that the site with no riparian canopy received 100% of the above-canopy irradiance. The proportion of ambient irradiance between 290 and 700 nm transmitted through the canopy at the two canopied sites was calculated from the mean total daily irradiance (at each wavelength) over the three days.

Light attenuation by the river water during the experimental trials was quantified by river-water measurements of absorbance between 280 and 700 nm (at 0.5 nm intervals) using a Cary 50 (Varian Instruments, Walnut Creek, California, USA) scanning spectrophotometer equipped with a 2 cm quartz cuvette. Water samples for absorbance measurements were collected at the same times as biological samples, and were filtered with a 0.4 μm filter and refrigerated until analysis. Transmittance over the water column was extrapolated from absorbance measurements over the 2 cm cuvette path-length. Particulate material in the water column was very low during the experimental period and probably contributed only slightly to light scattering, however, my estimates of water column transmittance would have been slight over-estimates of the actual exposure. Total daily irradiance between 280 and 700 nm downwelling to the streambed was calculated by multiplying the water column transmittance (over the mean site water depth) by the mean total daily irradiance at the site.

Other physical variables were collected throughout the experiment. Mean daily water temperature ranged between 14.6 and 20.2 °C (mean 16.1 °C) during the 1995 trial (Table 3.3). The temperature range was slightly larger (12.9 - 20.1 °C) during 1996. No significant differences in water temperature were found between sites (RM-ANOVA, p = 0.842). Water velocities decreased over experimental trials as discharge fell, although the decrease was considerably less in the channel because the flow was controlled. Mean velocity in the channel was 0.56 m/s (range 0.62 - 0.46 m/s), while river velocity averaged 0.27 m/s (range 0.44 - 0.14 m/s). There were no significant differences in current velocities between the different canopied river sites (RM-ANOVA, p = 0.0791).

Response variables

A mixture of air-dried gravel and cobble in 0.092 m^{-2} in screened bottomed colonization trays (L = 30.3 cm; W = 30.3 cm; H = 3.0 cm) served as substrata for colonization by the benthic community under the UVR filters. Trays were dug into the channel substrata to allow for uninterrupted flow over the stream-bottom, and were placed >30 cm from the edge of the UVR filters to ensure exposure to the intended radiation treatment. Individual trays were collected from underneath all of the UV-filters starting on day 28 at three week intervals (i.e., day 28, 49, 70 and 91) during the 1996 canopy experiment, and at two week intervals (i.e., day 28, 42, 56, and 70) during the 1995 grazer-reduced experiment.

Epilithic community: Samples were collected for chlorophyll, algal elemental composition (C, H, N), and algal taxonomy. Chlorophyll samples were collected in triplicate by taking 4.9 cm^{-2} scrapings (using a hard bristle brush) from randomly selected rocks and filtered onto Whatman GFC filter papers. Filters were frozen and stored in the dark until analysis. Single 4.92 cm^{-2} scrapings were collected for epilithic HCN content and frozen in vials until analysis. Algal taxonomic composition samples were collected by pooling three 4.92 cm^{-2} scrapings, and preserving with Lugol's solution until analysis.

Chlorophyll was analysed fluorometrically using a Turner Designs model 10au fluorometer. Chlorophyll was extracted in the dark in 10 ml tubes of 90% ethanol at 78°C for five minutes, following the procedure outlined by Nusch (1980). Epilithic C was quantified by CHN analysis with a Control Equipment Corporation 440 Elemental Analyzer. Frozen algal samples were filtered onto pre-combusted, pre-weighed Whatman GFF filter papers, and dried overnight at 60°C in a drying oven.

Algal species composition was quantified for the grazer-reduced experiment by light microscopy techniques. Random fields were enumerated from a sub-sample plated on to a hemacytometer counting chamber (1000x magnification) until at least 300 live cells were counted. Taxonomic identifications were done to species level for diatoms, and to genus for chlorophytes and cyanophytes using dichotomous keys (Patrick and Reimer 1966, 1975, Prescott 1976). Identification of diatoms was aided by examining sub-samples cleaned in boiling 30% hydrogen peroxide and mounted in hyrax. Diatoms identified in fresh samples were then matched to those identified in mounted samples. Biovolumes of individual species were estimated from the average dimensions of 10 - 15 individual cells, and converted to biovolume using Hamilton's (1990) computer program.

Benthic invertebrate community: Benthic invertebrates were collected for taxonomic identification from the remaining substrata washed through a 125 μm mesh sieve. All organisms retained on the sieve were preserved in 70% ethanol until analysis. Invertebrates were enumerated with keys by Merritt and Cummins (1996) and Clifford (1991).

Insects were identified to the genus, except Diptera, which were identified to family. Non-insect taxa (e.g., Hydrozoa, Hydracarina, Crustacea, Oligochaeta, and Hirudinea) were identified to order. All invertebrates retained by a 2 mm mesh were enumerated, but smaller invertebrates were sub-sampled. Those passing through the sieve (125 µm ≤ 2 mm) were diluted to 1 L in an Imhoff cone, and five 50 ml sub-samples collected while air was bubbled through the cone to homogenize the sample (Wrona et al. 1982). Invertebrates were counted in a minimum of three sub-samples, or until at least 100 individuals of the most abundant taxa were counted. Biomass of invertebrate taxa was calculated from mean dry weights of at least 5-20 individuals from both the coarse (> 2mm) and fine (125 µm ≤ 2 mm) fractions at each site for each sampling time. Specimens were dried in alluminum foil weighing boats overnight at 60 °C and weighed using a Cahn electrobalance accurate to 0.1 mg. Mean mass of each taxon was multiplied by abundance to determine the total biomass. The reported invertebrate biomass does not include the fraction that was soluble in alcohol (i.e., lipids) due to their preservation in ethanol.

Statistical analyses

Results from the grazer-reduced experiment were analysed separately from the canopy experiment because of the prior manipulation of the benthic community. Because we expected differential effects of our UVR treatments on benthic communities under each canopy type in the variable riparian canopy experimental trial, we examined the effects of canopy and UVR separately. Effects of canopy type on the response variables was conducted only considering the full spectrum radiation treatments (i.e., PAR+UVA+UVB). Effects of UVR on the response variables was conducted independently under each canopy type.

One-way repeated measures analysis of variance (RM-ANOVA) tests were used to test for the effect of canopy type (considering only PAR+UVA+UVB treatments) and UVR treatment (at each site) on chlorophyll a, epilithic carbon, total invertebrate biomass, and invertebrate diversity. Repeated measures multivariate analysis of variance (RM-MANOVA) tests were used to test for the effect of UVR treatment on benthic algal biovolumes of the major algal divisions (i.e., chlorophytes, diatoms, and cyanophytes), and species composition (five most abundant species by biovolume over the four sampling days [*Didymosphenia geminata, Epithemia hyndmanii, Oedogonium spp., Spirogyra spp.*, and *Cladophora spp.*]) in the grazer-reduced experiment. RM-MANOVAs were used to test for the effect of canopy type (only PAR+UVA+UVB treatments) and UVR treatment (at each site) on benthic invertebrate groups in the variable riparian canopy trial. Insects were grouped by order (Mayflies, Stoneflies, Caddisflies, Dipterans), and all other invertebrates (other) were combined as a single group (Coleoptera, Hydrozoa, Hydrachnidia, Crustacea, Oligochaeta, and Hirudinea) for the analysis.

Statistical analysis of the data was completed on Log (n+1) transformed data when necessary to meet homogeneity of variance or normality assumptions. For RM-MANOVAs, both multivariate and univariate test results are reported. Univariate tests represent the equivalent RM-ANOVA of the particular variable (i.e., group or species). Student-Newman-Keuls *post-hoc* tests were performed on univariate RM-ANOVAs. All analyses were conducted using SPSS (v 6.1, 1995, SPSS Inc.) or SuperANOVA (v 1.11, 1991, Abacus Concepts Inc.) statistical packages.

Results

Irradiance

Interception of light by the riparian canopy was variable over daylight hours as the sun traversed the sky (Fig. 3.4). The intermediate canopy shaded the river predominantly in the hour before (13:00 in August), and in the two hours following (14:00-15:00) solar noon . The full canopy provided considerable shading to the river throughout the day, except around solar noon (13:00 - 14:00) when 95% of the total daily solar energy was transmitted.

The spectral composition of solar energy transmitted by the two canopy types also differed (Fig. 3.5). The proportion of total daily irradiance transmitted by the intermediate canopy increased with decreasing wavelength, while the full canopy transmitted a higher proportion of longer-wave radiation. During daylight hours, the intermediate canopy transmitted approximately 51% PAR (mean 4960 kJ m^{-2} d^{-1}), 62% UVA (mean 533 kJ m^{-2} d^{-1}), and 70% UVB (mean 28.4 kJ m^{-2} d^{-1}), while the full canopy transmitted 17% PAR (mean 2650 kJ m^{-2} d^{-1}), 13% UVA (mean 154 kJ m^{-2} d^{-1}), and 11% UVB (mean 7.1 kJ m^{-2} d^{-1}) (Fig. 3.5).

In the river channel, total daily exposure of the streambed to irradiance increased during the summer due to simultaneous decreases in water depth and DOC concentration (Table 3.3). The magnitude of the increase in irradiance was much larger in 1996 because of greater declines in water level in the river, with an average decline of 46% (0.18 m)

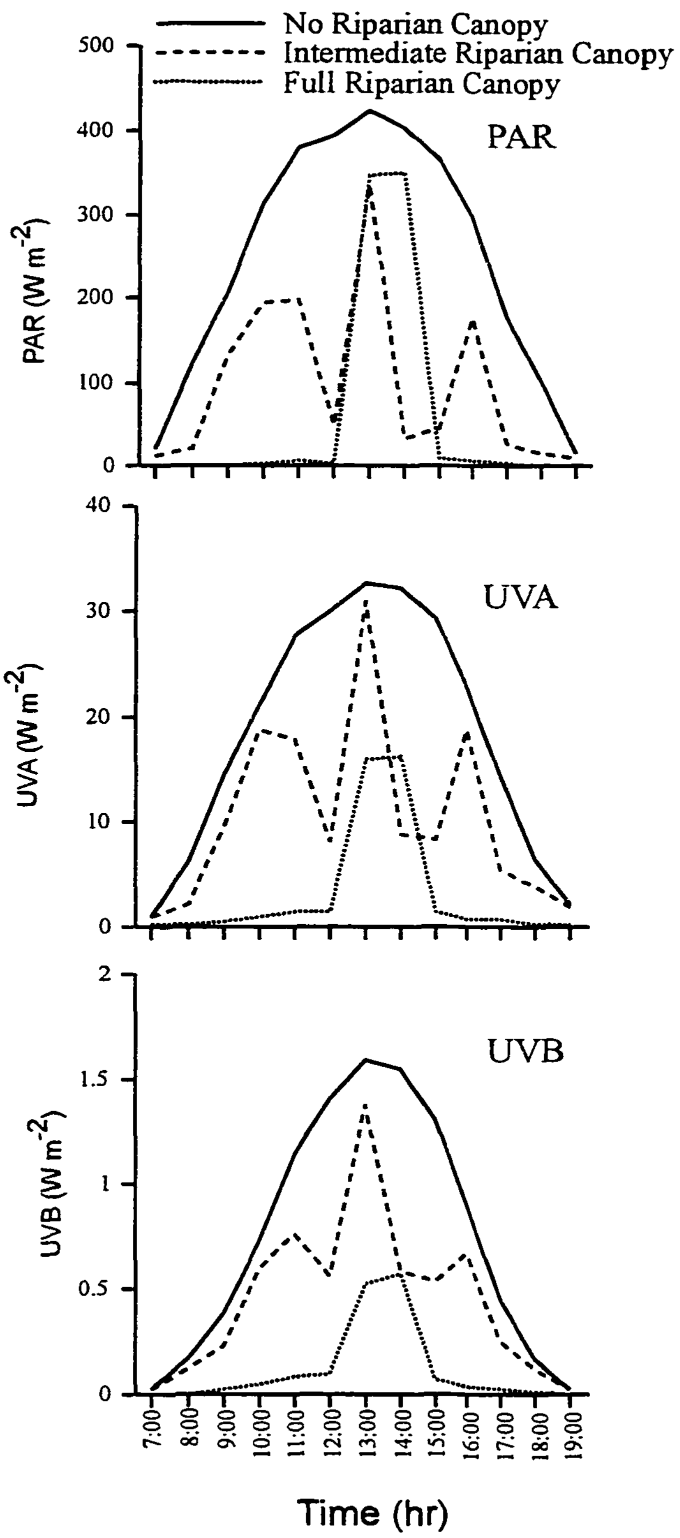

Figure 3.4. Daytime stream-surface PAR, UVA and UVB irradiance at three sites varying in riparian canopy cover on the Little Qualicum River.

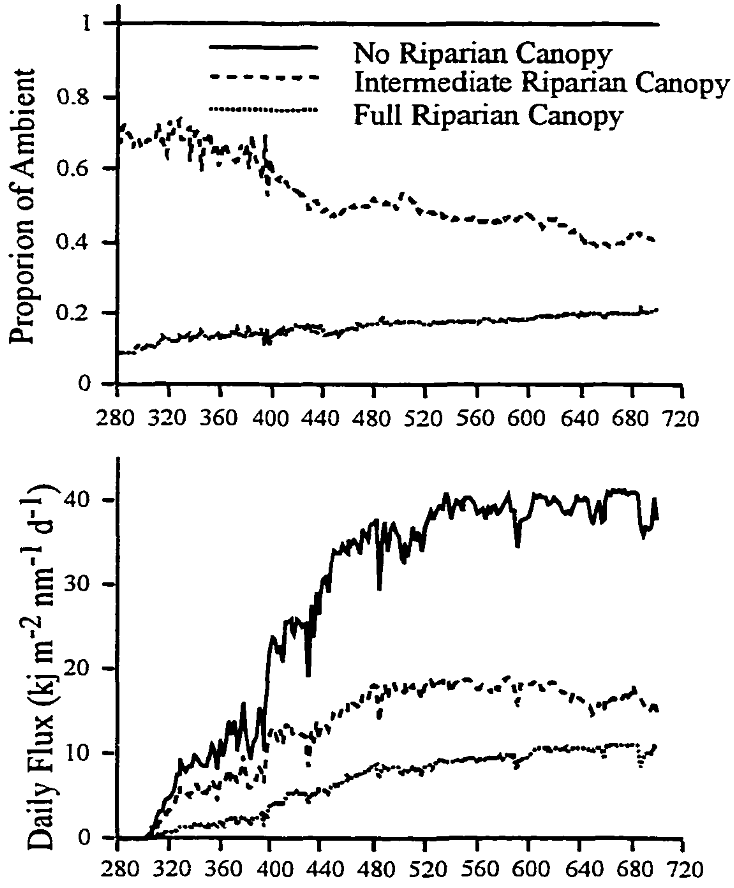

Figure 3.5. The total daily proportion of above canopy irradiance, and total daily energy of downwelling irradiance to the stream-surface at three sites on the Little Qualicum River varying in the amount riparian canopy cover.

Table 3.3. Dissolved organic carbon, water depth, velocity, temperature, and light exposure to the streambed (expressed as the proportion of above canopy irradiance) during 1995 and 1996 experimental trials at four sites on the Little Qualicum River varying in riparian canopy cover.

1996-Experimental Trial	Week 0	Week 7	Week 10	Week 13
DOC (mg/L)	1.87	1.63	0.93	0.87
Full riparian Canopy (90% cover)				
Mean Depth (m)	0.36	0.34	0.26	0.20
Water Velocity (m/s)	0.34	0.32	0.23	0.18
Mean Daily T (°C)	-	14.9	18.3	16.2
PAR Transmittance (%)	18.4	22.0	22.4	23.2
UVA Transmittance (%)	4.08	6.53	6.98	11.0
UVB Transmittance (%)	0.71	1.56	2.74	5.07
Intermediate riparian Canopy (33% cover)				
Mean Depth (m)	0.42	0.38	0.30	0.24
Water Velocity (m/s)	0.44	0.35	0.21	0.14
Mean Daily T (°C)	-	15.0	19.2	16.3
PAR Transmittance (%)	32.4	40.0	40.6	42.6
UVA Transmittance (%)	10.9	18.6	19.1	32.3
UVB Transmittance (%)	1.63	3.90	6.85	13.5
No riparian Canopy (0% cover)				
Mean Depth (m)	0.38	0.32	0.24	0.18
Water Velocity (m/s)	0.37	0.33	0.19	0.17
Mean Daily T (°C)	-	15.2	19.4	16.4
PAR Transmittance (%)	73.7	89.1	90.5	94.6
UVA Transmittance (%)	21.3	34.8	36.8	59.2
UVB Transmittance (%)	3.74	8.43	14.8	28.0

1995-Reduced Grazer Trial	Week 0	Week 4	Week 7	Week 10
No riparian Canopy (0% cover)				
DOC (mg/L)	2.0	2.1	<1.0	<1.0
Mean Depth (m)	0.27	0.26	0.25	0.23
Water Velocity (m/s)	0.62	0.62	0.55	0.46
Mean Daily T (°C)	14.8	16.3	17.1	15.8
PAR Transmittance (%)	84.4	83.2	91.3	92.8
UVA Transmittance (%)	35.9	36.4	42.1	47.1
UVB Transmittance (%)	10.4	10.6	15.2	19.6

over the 91-d trial. During this time, DOC concentration also decreased from 1.87 mg/L to 0.87 mg/L. As a result, under no canopy, transmission of PAR, UVA and UVB to the streambed increased from 74, 21 and 4% of ambient irradiance, respectively, to 95, 59 and 28%, respectively, over the 91 d.

In contrast, stable water levels in the spawning channel limited increases in total daily irradiance exposures over the 70-d grazer-reduced trial, with PAR, UVA, and UVB increasing from 84, 35, and 10% of ambient irradiance, respectively, to 93, 47 and 20%, respectively. The more modest increases in solar exposure resulted from DOC declining from 2.1 to < 1 mg/L over the 70 d.

Epilithic Algal Biomass

Canopy Effects: Reduction in riparian canopy cover caused significantly higher accrual of both chl *a* and epilithic C (Fig. 3.6, Table 3.4). Chl *a* and C biomass increased over time under all canopy treatments ($p < 0.002$), although rates of accrual were higher under reduced canopies. Under full spectrum sunlight (i.e., PAR+UVA+UVB), mean chl *a* was 14% higher (8.76 mg/m^2) under no canopy (Student Newman Keuls [SNK], $p < 0.05$), and 39% higher (9.37 mg/m^2) under an intermediate canopy (SNK, $p < 0.05$), than under a full canopy (6.75 mg/m^2) (Fig. 3.6). This trend was even more pronounced for epilithic C, which was 186% and 211% higher under open and intermediate canopies (SNK, $p < 0.05$), respectively, than under a full canopy (Fig. 3.6). Grazer reduction resulted in the highest accrual of both chl *a* and C. Mean chl *a* was 350% higher (21.0 mg/m^2) than under a full canopy, and more than double the non-canopied site where grazers were not altered.

UVR Effects: Differential effects of the UVR treatments on chl *a* and C accrual were observed under each canopy type (Fig. 3.6). Under a full canopy, there were no effects of UVR on either chl *a* or epilithic C accrual (Table 3.4). Under intermediate canopy, chl *a* was more than 82% higher under PAR+UVA and PAR+UVA+UVB treatments (SNK, $p < 0.05$) than under the PAR by the end of the experiment. Conversely, with no canopy, both chl *a* and epilithic C were at least 20% higher under PAR (SNK, $p < 0.05$) than under both PAR+UVA and PAR+UVA+UVB by the end of the experiment. This difference was even greater in the grazer-reduced experiment (Table 3.4), where mean chl *a* and C were 32% and 66% higher, respectively, under the PAR than under both UVR exposed treatments after 70 d (SNK, $p < 0.05$).

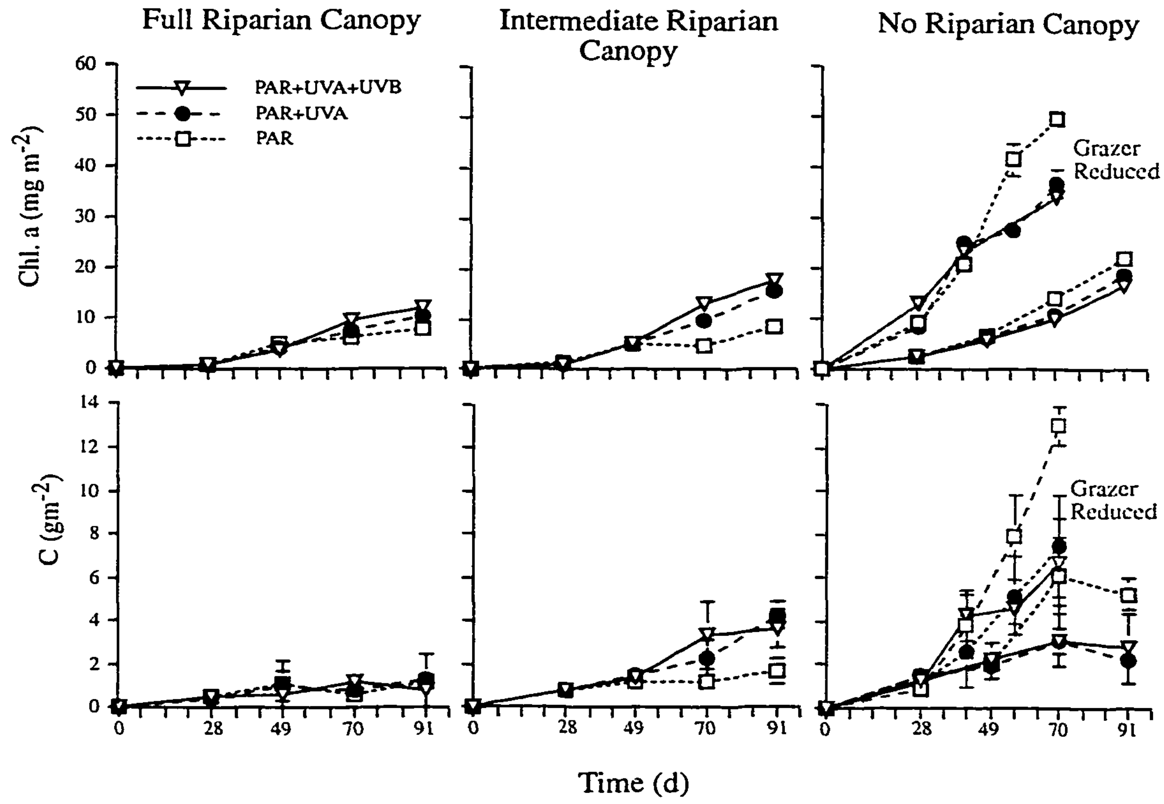

Figure 3.6. Epilithic chlorophyll (Chl) *a* and C biomass under different UVR exposures at four sites on the Little Qualicum River varying in the amount of riparian canopy cover. Grazers were reduced at one of the two locations (Qualicum Channels) with no riparian canopy. Values represent mean chlorophyll (n = 3) ± 1 SE.

Table 3.4. Results of the RM-ANOVAs of the effects of canopy cover (Canopy) and ultraviolet radiation (UVR) on chlorophyll (chl a) and epilithic C accrual for the variable riparian canopy experiment and the grazer reduced experiment in the Littlle Qualicum River. Mean (n=3) chl a values were used for each treatment replicate. Data reprted are *F* statistics and *p* values.

		Chl *a*		Epilithic C	
Source	df	*F*	*p*	*F*	*p*
Canopy	2	6.61	0.030	18.33	0.003
UVR - Full Canopy	2	1.64	0.271	0.17	0.846
UVR - Int. Canopy	2	25.32	0.001	7.00	0.027
UVR - No Canopy	2	7.79	0.021	22.14	0.002
UVR - Grazer Reduced	2	9.15	0.015	5.44	0.045
Time (all factors)	3	>25.06	<0.001	>7.39	<0.002
Time x Canopy	6	1.79	0.157	1.49	0.238
Time x UVR - Full Canopy	6	0.83	0.566	2.67	0.050
Time x UVR - Int. Canopy	6	5.41	0.002	4.54	0.006
Time x UVR - No Canopy	6	10.42	0.001	3.03	0.031
Time x UVR - Grazer Reduced	6	4.69	0.004	8.58	<0.001

Epilithic Algal Composition

Trends in total epilithic algal biovolume during the grazer-reduced experiment were similar to those for chlorophyll (Fig. 3.7). Up to Day 42, total epilithic algal biovolume was slightly lower when exposed to PAR alone. By Day 56 and thereafter, biovolume was at least 45% higher under PAR alone than under UVR exposed treatments (SNK, $p <$ 0.05). Similarly, biovolumes of the major algal taxonomic divisions (i.e., Chlorophyta, Bacillariophyta, and Cyanobacteria) were generally higher under PAR alone than either of the UVR treatments (Table 3.5). Differences among treatments diverged over time (Fig. 3.7). Diatoms were most abundant early in the experiment (Day 28), dominated by *Synedra ulna* (>28%), *Epithemia hyndmanii* (>11%), *Fragilaria crotonensis* (>9%) and *Didymosphenia geminata*_(>4%)(Table 3.6). However, after Day 28 the chlorophytes *Spirogyra spp.*, *Cladophora* spp., and *Oedogonium* spp. dominated, together comprising at least 75% of the total biovolume until the end of the experiment. Aside from the successional changes in algal species over time (Time, $p < 0.0001$), there were no differences in the species composition of epilithon between the UVR treatments (Table 3.5). There were also no differences in the species diversity between treatments over the course of the experiment (Table 3.5). Shannon-Wiener indices ranged between 0.996 and 1.171 (Table 3.6).

Benthic Invertebrate Community

Canopy effects: The riparian canopy significantly affected the biomass of colonizing invertebrates, community composition, and diversity, although these effects varied over time (Table 3.7, Fig. 3.8). Under full and intermediate canopies, total invertebrate biomass generally increased over time, with peak biomass observed at the end of the experi-

Table 3.5. Statistical results of the effects of ultraviolet radiation (UVR) on the biovolume of the major algal divisions of the epilithic community in the reduced grazer trial in Qualicum Channels. Reported are the results from univariate ANOVA tests of the major algal divisions, the combined biovolume (Total), community diversity, and the multivariate test (MANOVA) incorporating all three algal divisions. Data given are *F* statistics and *p* values for univariate tests, and Hottelings (H) *F* statistic for the multivariate test.

		Greens		Diatoms		Cyanobacteria		Total		MANOVA		Diversity	
Source	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*H-F*	*p*	*F*	*p*
UVR	2	16.50	0.004	0.75	0.510	19.00	0.003	60.38	0.001	11.45	0.010	0.21	0.931
Time	3	145.1	0.001	14.42	0.001	9.84	0.001	479.9	0.001	229.7	0.001	1.32	0.751
UVR x Time	6	10.02	0.001	0.99	0.459	1.91	0.134	22.40	0.001	8.75	0.001	0.621	0.856

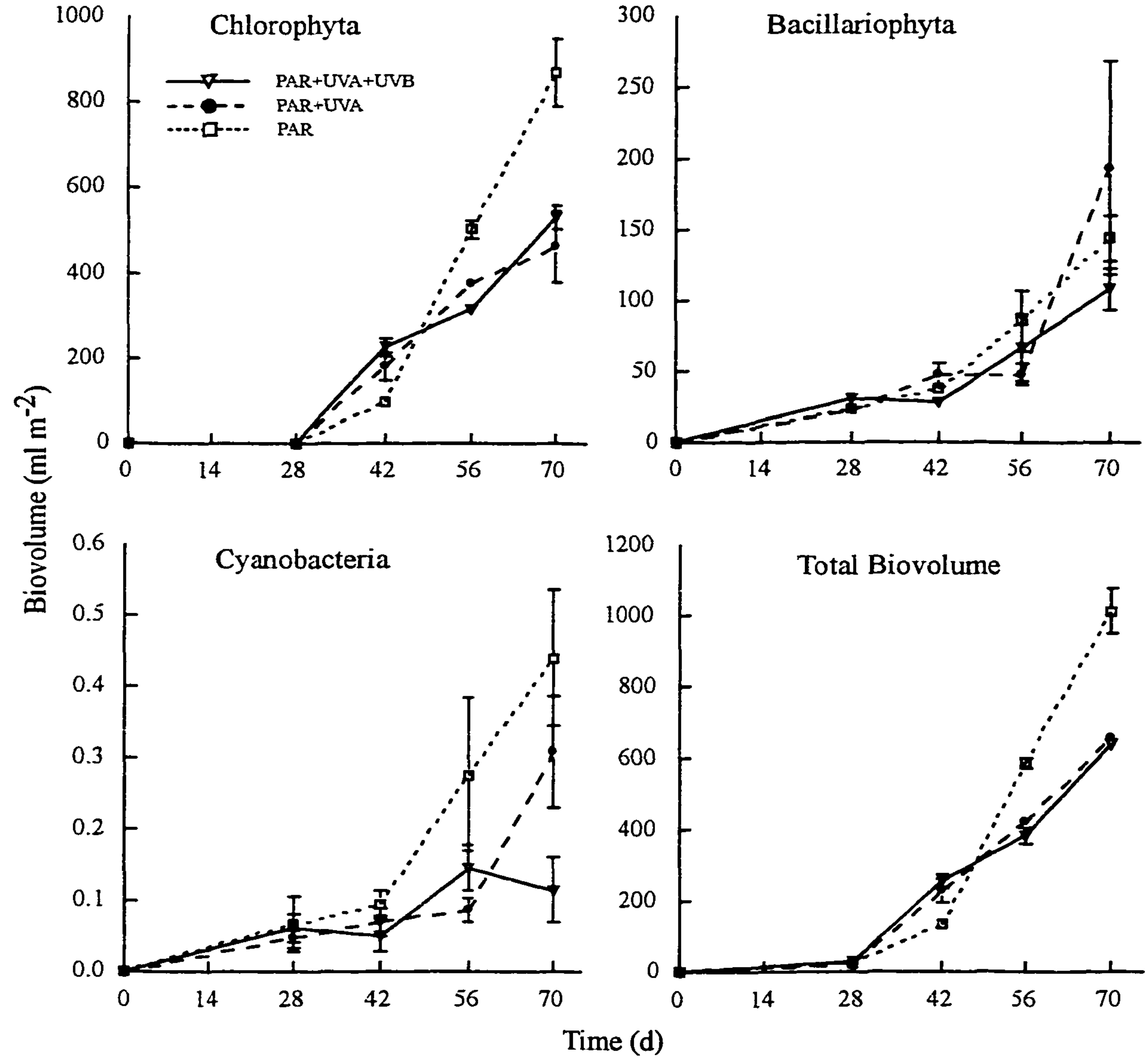

Figure 3.7. Biovolume of the major algal divisions under variable UVR exposure (no riparian canopy cover) in the 1995 reduced grazer experimental trial. Values represent mean biovolume (n=3) of live cells ± 1 SD.

Table 3.6. Percent composition (by volume) of the dominant epilithon species present (≥2% of total biovolume), and Shannon-Wiener (H') diversity of the epilithic community under variable UVR exposures (no riparian cover) during the reduced grazer trial in Qualicum Channels. Shown are the mean values (n=3) ± 1 SD.

		PAR+UVA+UVB	PAR+UVA	PAR
Day	**Species**	**% Vol.**	**% Vol.**	**% Vol.**
28	*Synedra ulna*	35.6 ± 4.8	41.9 ± 11.4	28.3 ± 6.8
	Epithemia hyndmanii	17.0 ± 6.5	11.6 ± 10.8	18.9 ± 4.1
	Didymosphenia geminata	11.7 ± 1.3	5.1 ± 8.9	4.6 ± 7.9
	Fragilaria crotonensis	9.7 ± 3.6	9.9 ± 3.4	13.7 ± 5.5
	Diatoma vulgare	5.1 ± 2.3	4.1 ± 1.2	4.3 ± 3.9
	Amphipleura pelluicida	3.8 ± 2.2	3.4 ± 3.0	4.42.1
	Cymbella minuata	2.2 ± 0.1	3.0 ± 1.5	3.0 ± 1.4
	Achnanthes minutissima	2.0 ± 0.3	2.1 ± 0.7	2.9 ± 0.7
	Diversity (H')	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01
42	*Spirogyra sp.*	42.7 ± 4.8	43.1 ± 19.8	42.2 ± 36.6
	Cladophora sp.	26.8 ± 6.0	21.9 ± 19.3	24.3 ± 42.1
	Oedogonium sp.	19.2 ± 10.9	13.7 ± 11.2	3.9 ± 1.9
	Synedra ulna	3.7 ± 1.0	4.0 ± 1.9	10.2 ± 1.8
	Didymosphenia geminata	2.7 ± 1.7	8.8 ± 2.7	2.1 ± 1.8
	Epithemia hyndmanii	np	3.4 ± 2.0	np
	Cocconeis placentula	np	np	2.4 ± 1.3
	Fragilaria crotonensis	np	np	2.1 ± 0.8
	Diversity (H')	1.0 ± 0.02	1.1 ± 0.01	1.0 ± 0.01
56	*Spirogyra sp.*	51.1 ± 11.4	47.2 ± 6.0	46.6 ± 9.6
	Cladophora sp.	23.6 ± 26.6	38.5 ± 7.3	8.0 ± 13.8
	Oedogonium sp.	8.2 ± 7.9	2.7 ± 0.9	30.4 ± 5.8
	Didymosphenia geminata	6.2 ± 6.0	5.0 ± 3.2	5.7 ± 2.6
	Epithemia hyndmanii	3.9 ± 1.5	2.0 ± 0.2	4.8 ± 1.2
	Synedra ulna	3.7 ± 2.2	np	np
	Diversity (H')	1.0 ± 0.03	1.1 ± 0.01	1.0±0.03
70	*Spirogyra sp.*	32.3 ± 6.4	24.0 ± 8.2	13.5 ± 11.7
	Cladophora sp.	25.2 ± 25.9	35.7 ± 15.2	38.5 ± 18.6
	Oedogonium sp.	25.1 ± 16.7	10.4 ± 15.1	33.2 ± 30.0
	Didymosphenia geminata	8.3 ± 2.9	9.6 ± 3.8	4.9 ± 2.6
	Epithemia hyndmanii	4.4 ± 2.3	8.0 ± 3.1	4.0 ± 3.5
	Synedra ulna	2.0 ± 0.4	2.2 ± 0.8	np
	Diversity (H')	1.1 ± 0.02	1.0 ± 0.01	1.0 ± 0.06

np - Not Present at ≥ 2% of the total biovolume

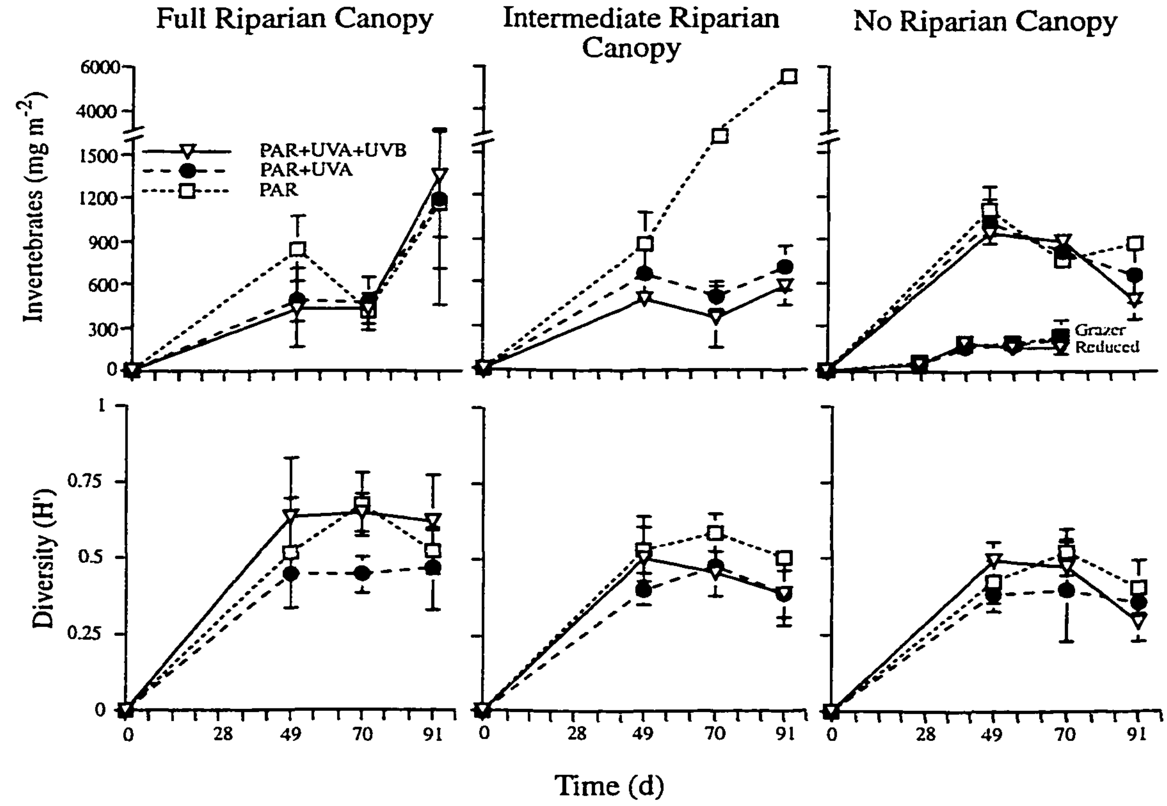

Figure 3.8. Total invertebrate biomass and Shannon-Wiener Diversity (H ± 1 SD) of benthic invertebrates under variable UVR exposures at four sites on the Little Qualicum River with variable amounts of riparian canopy cover. Colonizing invertebrates were reduced (grazer reduced) at one of the two locations with no riparian canopy cover. Values represent mean biomass ± 1 SD.

Table 3.7. Results of the RM-ANOVAs of the effects of ultraviolet radiation (UVR) and riparian canopy cover (Canopy) on the biomass of the major invertebrate orders, total invertebrates, and diversity for the variable riparian canopy trial in the Little Qualicum River. Reported are the results from univariate tests of the four major orders (mayflies, stoneflies, caddisflies,and dipterans), a combined group of all other invertebrate taxa (Other= Copepoda, Cladocera, Hydracarina, Nematoda, Oligochaeta, and Ostracoda), total invertebrate biomass (Total) and Shannon-Wiener community diversity. Also resported is the multivariate test incorporating all five sub-groupings of invertebrates (MANOVA). Data given are *F* statistics and *p* values for univariate tests, and Hoteeling (H) *F* statistic for the multivariate test.

		Mayflies		Stoneflies		Caddisflies		Dipterans		Other		Total		MANOVA		Diversity	
Source	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	P-*F*	*p*	*F*	*p*
Canopy	2	14.60	0.005	13.74	0.006	0.95	0.437	55.12	0.001	0.66	0.549	3.69	0.079	24.12	0.050	5.74	0.041
UVR- Full Canopy	2	0.07	0.934	0.92	0.447	2.28	0.183	0.67	0.544	0.05	0.955	1.40	0.317	1.34	0.412	3.36	0.105
UVR - Int. Canopy	2	4.22	0.072	2.68	0.147	11.39	0.003	11.40	0.009	1.21	0.361	63.88	0.001	5.79	0.016	4.58	0.062
UVR - No Canopy	2	0.13	0.878	2.38	0.173	1.00	0.421	1.15	0.378	1.98	0.217	2.93	0.129	1.67	0.273	2.23	0.188
Time - All Factors	3	>15.1	<0.01	>0.6	<0.53	>1.5	<0.24	>1.1	<0.41	>0.4	<0.77	>12.2	<0.01	>7.6	<0.01	>0.8	<0.46
Time x Canopy	6	23.82	0.001	2.94	0.066	2.49	0.099	5.64	0.009	2.90	0.068	14.78	0.001	6.69	0.001	1.26	0.338
Time x UVR - Full Canopy	6	0.95	0.467	1.61	0.234	0.14	0.963	1.08	0.407	0.46	0.767	1.15	0.378	0.73	0.762	0.76	0.569
Time x UVR - Int. Canopy	6	0.95	0.468	0.56	0.693	3.21	0.052	2.22	0.127	0.77	0.560	20.68	0.001	1.23	0.275	0.76	0.570
Time x UVR - No Canopy	6	7.15	0.035	0.71	0.603	3.18	0.053	3.19	0.053	2.37	0.111	4.20	0.024	2.89	0.002	1.13	0.386

ment. In contrast, with no canopy, peak invertebrate biomass occurred by Day 49, then steadily declined until the end of the experiment. Under full spectrum sunlight, final invertebrate biomass at the full canopied site was 235% and 277% higher, respectively, than those of the of the intermediate and open canopied sites (SNK, $p < 0.05$). Shannon-Weiner diversity of invertebrate communities was on average 21% higher under full canopy (SNK, $p < 0.05$), than under either of the reduced canopies (Fig. 3.8).

Canopy significantly affected the composition of invertebrate communities (Table 3.7). Mayflies, initially abundant under all canopy treatments, decreased considerably over time under both the intermediate and open canopies (Fig. 3.9). Under full canopy mayfly biomass increased continuously. By the end of the experiment it was at least double those under the other two canopy types (SNK, $p < 0.05$). This was particularly apparent for *Cymigula* spp. (Heptageniidae) and *Baetis* spp. (Baetidae), which were at least four times higher under the full canopy by the end of the experiment (Table 3.8). Similarly, stonefly biomass was at least 150% higher under the full canopy than under the other two canopy types by the end of the experiment (SNK, $p < 0.05$). In contrast, dipteran biomass increased with reduction of the canopy (Table 3.7), and was generally twice as high under no riparian canopy than under a full canopy (SNK, $p < 0.05$). There were no differences in caddisfly biomass between canopy types under full spectrum sunlight (Table 3.7), although this group was extremely responsive to UVR under reduced canopies. A small number of non-insect taxa colonized our experimental substrata (i.e., Copepoda, Cladocera, Nematoda and Ostracoda), however only oligochaetes and Hydracarina (mites) were present at $\geq 1\%$ of the total biomass (Table 3.8). There were no significant differences in these taxa between canopy types (Table 3.7).

UVR effects: The response of benthic invertebrates to the UVR treatments varied with canopy type (Table 3.7, Fig. 3.9). Under full canopy, UVR had no effects on either total invertebrate biomass, community diversity, or any invertebrate groups (Table 3.7).

The greatest effect of UVR on benthic invertebrates was observed under the intermediate canopy (Table 3.7), predominantly in response to the combined removal of UVA+UVB (SNK, $p < 0.05$). Differences between UVR treatments increased over time (Table 3.7), coincident with large increases in UVR exposure to the streambed. Total invertebrate biomass was at least double for PAR treatments under intermediate canopy than any other canopy-treatment combinations (Fig. 3.8). Diversity at this site was also higher under PAR treatments (SNK, $p < 0.05$) compared to UVR exposed treatments.

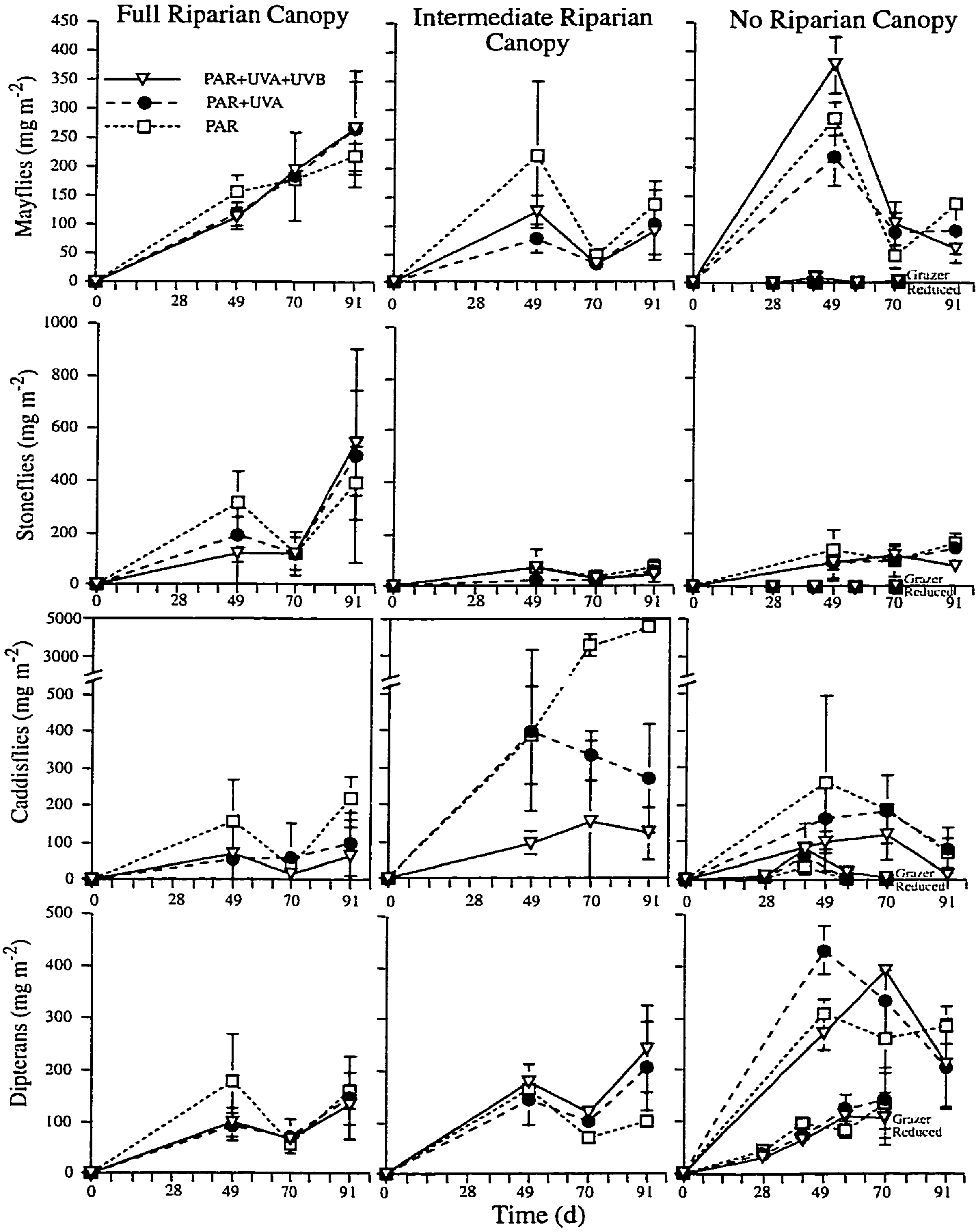

Figure 3.9. Biomass of the dominant invertebrate orders under variable UVR at four sites on the Little Qualicum River differing in the amount of riparian canopy cover. Invertebrates were reduced (grazer reduced) at one of the two no riparian canopy sites. Values represent mean biomass (n=3) ± 1 SD.

Table 3.8. Mean final (day 91, n=3) biomass of benthic invertebrate taxa under different UVR exposures at three sites on the Little Qualicum River varying in riparian canopy cover. The reported taxa represent ≥1% of the total invertebrate biomass for at least one of the treatment/canopy combinations (np = not present). Feeding guilds are classified according to Merrit and Cummins (1995) and include collector gatherers (CG), scrapers (SC), shredders (SH) and predators (PR).

		Full Canopy			**Intermediate Canopy**			**No Canopy**		
	Feeding	PAR+UVA +UVB	PAR+UVA	PAR	PAR+UVA +UVB	PAR+UVA	PAR	PAR+UVA +UVB	PAR+UVA	PAR
Taxa	Guild	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}	mg m^{-2}
Ephemeroptera										
Baetis sp.	CG	76.0	86.7	78.0	21.8	13.9	20.4	22.1	28.2	50.7
Caudatella sp.	CG	30.1	32.5	24.3	10.2	2.4	3.5	21.3	30.8	57.0
Cymigula sp.	SC	97.1	49.0	37.0	8.4	0.6	20.8	7.6	6.5	9.6
Rithrogena sp.	SC	10.7	19.3	8.1	0.6	0.1	5.4	0.1	3.0	1.7
Paraleptophlebia sp.	CG	50.0	76.0	72.1	47.6	82.0	82.8	4.5	15.6	12.0
Plecoptera										
Amphinemura sp.	SH	54.0	29.3	27.0	6.6	10.2	11.9	24.2	25.8	39.0
Calineuria sp	PR	38.9	72.8	35.2	np	np	np	np	29.7	np
Isoperla sp.	PR	21.8	19.6	28.6	11.4	3.9	7.2	21.9	30.0	50.1
Sweltsa sp.	PR	431.3	372.2	300.0	27.4	45.2	56.7	32.6	61.0	80.7
Tricoptera										
Dicosmoecus sp.	SC	42.0	84.0	209.9	94.3	235.9	4906	np	46.2	np
Hydroptila sp.	CG	1.7	3.6	2.1	10.4	7.9	1.0	24.3	5.1	11.4
Rhyacophila sp.	PR	21.9	7.52	7.3	14.6	21.9	np	8.6	25.7	60.1
Coleoptra										
Zaitzevia sp.	SC	2.4	4.2	2.9	5.9	1.0	4.0	2.3	3.6	6.2
Diptera										
Hexatoma sp.	PR	25.9	26.4	27.1	27.3	9.5	3.6	6.6	4.6	4.1
Chironomidae	CG	107.3	120.9	133.4	213.8	199.2	98.4	206.5	201.5	282.2
Oligochaeta	CG	2.4	5.8	2.5	14.8	11.9	8.0	13.6	13.9	21.5
Hydracarina	PR	23.0	21.5	21.2	37.0	26.9	18.3	7.0	21.0	27.7
Total Invertebrates		1354	1193	1154	576	702	5262	488	660	870

Caddisflies were the most responsive group to UVR screening ($p = 0.029$). For instance, final biomass of *Dicosmoecus* spp. (Limnephillidae) under PAR was nearly 5000 mg/m^2 (Table 3.8), more than 40 times the caddisfly biomass under PAR+UVA+UVB and 15 times that under PAR+UVA at this site. Mayflies and stoneflies were also on average 76% and 51% higher, respectively, under PAR than either UVR exposed treatments, although these differences were non-significant (Table 3.7). In contrast, dipterans at the site were higher under UVR exposed treatments than PAR (SNK, $p < 0.05$).

In the absence of a riparian canopy there were no overall effects of UVR treatments on invertebrate biomass (Table 3.7). As at the intermediate canopy site, responses to UVR treatments diverged over time as streambed UVR exposure increased. Final invertebrate biomass under PAR was at least 50% higher than PAR+UVA and PAR+UVA+UVB treatments (Table 3.8), although this was not significant. The final biomasses of mayflies, stoneflies and caddisflies under PAR and PAR+UVA treatments were at least 113% and 50% greater, respectively, than under the full spectrum sunlight. Treatment effects were observed for several taxa, including *Caudatella* spp. (Heptagenidae), *Amphinemura* spp. (Nemouridae) and *Sweltsa* spp. (Chloroperlidae), and *Rhyacophila* spp. (Rhyacophillidae) which were nearly double the biomass under the PAR than PAR+UVA+UVB (Table 3.8). By contrast, the biomass of dipterans and other invertebrates showed no response at any time to the UVR treatments (Table 3.7).

There were no effects of the UVR treatments on invertebrate biomass during the grazer-reduced experiment (Table 3.7), which had on average only 35% of the total invertebrate biomass of the non-canopied site (Fig 3.8). The invertebrate community under the grazer-reduced experiment was extremely depauperate, and was comprised almost entirely of chironomids (Fig 3.9).

Discussion

Effects of riparian canopy on UVR exposure of streams

Canopy density strongly influenced both the intensity and composition of irradiance reaching the stream surface. Interception of irradiance by the full riparian canopy reduced total daily PAR and UVR exposure to only 17% and 12% of above canopy irradiance, respectively. Under dense canopies, a significant proportion of total daily irradiance is transferred in the form of intermittent sunflecks moving across the forest floor

(Reifsnyder et al. 1971, Chazdon 1988). However, openings in the middle of riparian canopies may allow direct sunlight exposure to wider streams for at least some portion of daylight hours, as well as penetration of significant diffuse irradiance over most of the day (DeNicola et al. 1992). The increase in canopy density between the intermediate (33% cover) and full (90% cover) canopies allowed the interception of considerably more diffuse blue light and UVR during periods of shading. The near-noon sunlight exposure of our fully shaded stream reach accounted for more than 95% of the total daily irradiance reaching the stream, and was predominantly composed of longer-wave PAR. Alternatively, our less dense intermediate canopy allowed approximately 51% and 66% of above canopy PAR and UVR irradiance, respectively, over daylight hours. The larger above-stream opening also allowed a higher proportion of diffuse light to reach the stream surface during periods of shade, thereby increasing the relative flux of total daily UVR to the intermediate shaded reach. Therefore, although the intermediate canopy transmitted ≈30% less UVR than the non-canopied site, the increase in UVB relative to longer wavelengths may increase photoinhibitory effects of UVR (Smith et al. 1992).

Riparian canopies minimized fluctuations in UVR flux to the streambed from seasonal changes in water level and DOM. Synergistic decreases in water level and DOM (measured as DOC) resulted in 660 and 186% increases in the amount of UVB and UVA reaching benthic communities over our experiment, resulting in considerable increases in UVB:UVA:PAR. The riparian canopy greatly reduced UVR flux to the streambed during the summer-time decline in flow and DOM. For instance, UVB reaching the streambed under the full riparian canopy increased from only 0.71% to 4.5% of the above canopy irradiance, while under no overhead canopy UVB increased from 3.74% to 28.0%, representing a significant increase in the UVR environment, and a considerable increase in the UVB:UVA:PAR. These changes in solar exposure had profound effects on colonizing benthic communities.

Effects of canopy removal on benthic communities

In the absence of modifications in solar exposure (i.e., PAR+UVA+UVB), reduction in canopy cover caused an increase in algal accrual rates, decreased overall invertebrate biomass, changed the composition of benthic invertebrate communities, and decreased in diversity. The effects of canopy reduction on benthic communities diverged over time, as solar exposure to the streambed increased due to seasonal declines in water level and DOM.

Canopy effects on algal accrual

Complete or partial removal of the riparian canopy increased chl *a* accrual by 30-39% and epilithic C accrual by 181-186% over 91 d. Eplilithic productivity in small streams is often limited by light (Hill and Knight 1988, DeNicola et al. 1992, Hill et al. 1995). In my study, increasing light exposure from 17% to 51% PAR eliminated light limitation. No further increase in accrual rates when solar exposure was further elevated to 100% PAR. The smaller increase in chl *a* than in epilithic C may have resulted from greater chlorophyll content of epilithon at the most shaded site. It is well known that epilithon can compensate for lower solar intensities by increasing the pigment content of cells (Falkowski and LaRoche 1991). Under a full canopy, mean chl *a*:C was approximately double those of the other two sites. There were relatively small differences in chl *a*:C between the reduced canopy sites.

Grazers also indirectly affected algal accrual at the different sites. When grazers were reduced (spawning channel experiment), mean epilithic chl a and C were 117% and 78% higher respectively than treatments with unmodified invertebrate communities and similar solar exposure (i.e., no canopy). Grazers can regulate algal standing crop in streams (Feminella et al. 1989, Steinman 1992). As a result, increases in availability of light or nutrients are not always reflected by increases in algal biomass. It is apparent from my study that grazers strongly influenced algal standing crop, making it difficult to infer direct effects of either our canopy or radiation manipulations on algal accrual. Although I generally observed the lowest accrual rates at our most shaded site, I also observed the greatest invertebrate biomass at this site during parts of the experiment potentially influencing algal accrual. Reduction of the riparian canopy may therefore increase algal accrual by both enhancing algal growth rates and reducing invertebrate density.

Canopy effects on invertebrate colonization

Canopy cover strongly affected the biomass of colonizing invertebrates, community composition, and diversity of communities. Mayflies and stoneflies responded most positively to canopy shading ($p < 0.006$), whereas dipterans ($p = 0.001$), and to a lesser degree caddisflies ($p = 0.437$), increased proportionately with decreasing canopy. Previous research has demonstrated that invertebrate colonization can be inhibited by high intensities of PAR (Bothwell et al. 1993). In the present study, differences in PAR exposure between the different canopied sites did not appear to have a large effect on invertebrate colonization. I found similar densities of most invertebrate groups under all canopy treatments early in the experiment (Day 49) when differences in streambed PAR exposure between were high, whereas differences in streambed UVR were low due to attenuation by river water. The lone exception to this was for dipterans, dominated by chironomids, which consistently colonized more exposed sites at greater densities. Bothwell et al. (1994) observed that chironomids were inhibited high intensity PAR, although I observed just the opposite trend. However, it is difficult to ascertain in the present study if chironomids were actually responding positively to increased algal productivity at more open sites, or were excluded by predators or herbivorous competitors under more shaded canopies. It has been demonstrated that many invertebrates respond to higher availability of food resources (Lamberti et al. 1989).

Temporal trends in invertebrates were also strongly affected by canopy cover. The biomass of most invertebrate groups, particularly mayflies and stoneflies, increased over time under a full canopy, whereas they decreased at partial and open canopied sites under full spectrum sunlight. The decline in mayfly and stonefly biomass under reduced canopies coincided with an period of increased UVR exposure to the streambed from synergistic declines in water level and DOM. It is possible that shaded stream reaches may act as a refuge for UVR sensitive invertebrate taxa that emigrate (drift) from exposed reaches during periods of high streambed-UVR. Indeed, many of the taxa that proliferated at the fully shaded site during this period (e.g., *Paraleptophlebia* spp., *Cymigula* spp.) appeared highly sensitive to UVR at the two reduced canopy sites. It is unlikely that differences in invertebrate biomass between canopy types would have resulted from different growth rates of invertebrates between the shaded and non-shaded sites, because growth rates among insect larvae is controlled mainly by temperature (Sweeney and Vannote 1978, Benke 1993), and temperature did not differ significantly between sites. I selected river reaches of varying canopy removal to minimize this phenomenon, but in areas where canopy removal occurs over longer reaches of the stream this could be an important factor.

Mediation of UVR effects on benthic communities by the riparian canopy

The effects of UVR varied between canopy types, and were most pronounced under intermediate canopy. Effects of the UVR treatments diverged over the experiment, as UVR exposure to the streamed increased from declines in water level and DOM. As expected I observed no significant effects of UVR on benthic communities under full canopy. Under intermediate canopy, UVR decreased the total biomass of invertebrates, mainly by reducing grazing caddisflies, which indirectly affected algal accrual. Unexpectedly I observed no significant effect of UVR on invertebrate communities at the most exposed site, which may have been influenced by overall low abundance of UVR-sensitive taxa. I did observe overall depressions in invertebrate biomass at the non-canopied site at the end of the experiment, when UVR exposure to the streambed was highest. Under no canopy, UVR significantly decreased algal accrual, predominantly due to UVA exposure, but had only minor effects on algal community composition.

UVR effects on algal accrual

Canopy shading changed patterns of algal accrual under the UVR manipulations, predominantly due to its effects on grazers. As expected, I observed no effects of UVR on epilithic chl *a* or C biomass under a full canopy. UVR suppressed algal accrual under a completely open canopy, whereas algal accrual was promoted by UVR under a partial canopy. UVR can reduce algal accrual directly by inhibiting photosynthesis and algal growth rates (Bothwell et al. 1991), or can indirectly promote accrual by suppressing grazers (Bothwell et al. 1994) in a so-called "solar cascade" (Williamson 1995). Direct inhibitory effects of UVR on algal accrual were observed under the open canopy. The removal of UVA+UVB resulting in a 19% increase in chl *a* accrual over 91 d compared to full spectrum treatments. Alternatively, under our partial canopy, indirect effects of UVR on higher trophic levels appeared to be the dominant factor controlling algal accrual. Screening of UVA+UVB suppressed both chl *a* and epilithic C accrual by ≈53% over 91 d in comparison to full spectrum treatments, and promoted the biomass of invertebrates by more than ten-fold.

Reduction of grazers further enhanced the direct effects of UVR on algal accrual, although trends paralleled those of the non-canopied site where the grazers were not modified. Epilithic chl *a* and C were 35% and 75% higher, respectively, after 70 days when selectively shielded from UVR, compared to both PAR+UVA and full spectrum sunlight treatments. Although UVR induced damage to photosynthesis increases with decreasing wavelength (Cullen et al. 1992), our study and the findings of others suggest that UVA is the main contributor to inhibition of algal accrual (Buhlmann et al. 1987, Bothwell et al. 1993, Milot-Roy and Vincent 1994). The predominance of UVA effects on algal accrual could be related to the higher intensity of UVA in the solar spectrum at ground level, or from the selective attenuation of short-wavelength UVR by the water column, which would have removed much more of the incident UVB in the full spectrum treatments. Because UVA wavelengths may also affect invertebrate colonization, discerning the direct effects of UVR on algal productivity may be problematic if indirect effects from invertebrates are not controlled for.

UVR effects on algal community composition

Inhibitory effects of UVR on algal communities have been shown to vary considerably among taxa (Bothwell et al. 1993, Vinebrooke and Leavitt 1999), due to differences in pigmentation (Carreto et al. 1990, Sommaruga et al. 1999), or morphological differences such as cell size or cell wall thickness (Bothwell et al. 1993, Garcia-Pichel 1994). However, under high sunlight exposure (i.e., no canopy) I observed UVR inhibition of all the major taxonomic divisions present. Although UVA accounted for most of the inhibition in algal accrual (primarily inhibition of filamentous greens), suppression of diatoms and cyanobacteria by UVB was also observed, as in other investigations (Vinebrooke and Leavitt 1999). Interestingly, diatoms were least affected by UVR, and by the end of the experiment even had a marginally higher total biovolume under PAR+UVA than under PAR alone, although this was not significant ($p = 0.51$). The dominance of large-celled diatoms, which are generally less sensitive to UV damage, may account for this apparent lack of sensitivity. There was evidence that larger celled diatoms (e.g., *Didymosphenia geminata*) comprised a larger component of those communities exposed to UVR, as previously reported by Karentz et al. (1991) and Bothwell et al. (1993). Similarly, smaller celled taxa, such as *Fragilaria crotonensis* and *Achnanthes minutissima*, comprised a larger proportion of the community under PAR only than UVR exposed treatments. We did not find that UVR-resistant cyanobacteria taxa proliferated under high UVR exposure as others have reported (Leavitt et al. 1997, Vinebrooke and Leavitt 1999, Xenopoulos et al. 2000). In fact, I observed higher cyanobacteria composition (dominated by *Pseudanabaena* spp. and *Anabaena* spp.) under PAR than under either UVR exposed treatments, although they were consistently low in all treatments (<2% of the total biovolume).

UVR effects on invertebrate colonization

Differences in shading by the riparian canopy dramatically changed the effects of UVR on benthic community colonization. Bothwell et al. (1994) demonstrated that chironomid density was significantly inhibited by UVR even when irradiance was reduced to 50% of ambient. At the full canopy site, ambient irradiance at the water surface was 4-11% for UVA, and 1-5% for UVB. This eliminated any negative effects of UVR on invertebrate colonization, even for sensitive taxa. I did not observe any response of invertebrate taxa to the UVR manipulations under a full canopy, or any changes in community diversity.

Partial reduction of the riparian canopy resulted in the most pronounced effects of UVR on invertebrate colonization, predominantly in response to the removal of UVA. I observed a ten-fold increase (or 5.4 g/m^2) in total invertebrate biomass (primarily the caddisfly *Dicosmoecus* spp.) under PAR only compared to UVR exposed treatments. High UVR sensitivity of *Dicosmoecus* spp. was somewhat unexpected, because its case is made of a gravel-matrix that should largely shield it from UVR, with the exception of its head. This supports the observations of others that some insects avoid UVR through visual detection of UVR or PAR (Bothwell et al. 1994, Kiffney et al. 1997b, Donahue and Schindler 1998). Others have suggested that encased or highly pigmented invertebrates are less sensitive to UVR (Ringelberg et al. 1984, Hill et al. 1997). My results suggest caution against these generalizations.

Previous investigators reported that invertebrate taxa were predominantly inhibited by UVB (Bothwell et al. 1994, Kiffney et al. 1997a, 1997b). Inhibition of mayflies (e.g., *Paraleptophlebia* spp.) and stoneflies (e.g., *Amphinemura* spp. and *Sweltsa* spp.) by UVB under intermediate canopy was marginally not significant (e.g., mayflies $p = 0.072$, stoneflies $p = 0.14$), predominantly because they appeared only at the end of the experiment. The high biomass of caddisflies present in UVR-screened treatments may have decreased the differences between our UVR treatments for other invertebrate groups, as territorial aggressive interactions by caddisfly larvae have previously been documented (Hart 1985). Nevertheless, I observed ≈50% lower biomass of *Paraleptophlebia* spp. and *Sweltsa* spp. under PAR+UVA+UVB than under either PAR+UVA and PAR treatments by the end of the experiment. Differential response of invertebrates to UVA or UVB suggests that invertebrate response to UVR may occur in two ways, active avoidance of UVR following visual detection of UVA, and actual physiological damage from UVB. Reasons for different responses are unclear, and may indicate different strategies, differential sensitivity, or other unknown factors.

The complete absence of the riparian canopy unexpectedly resulted in non-significant overall effects of UVR on invertebrates. The apparent lack of response by invertebrates to UVR at our non-canopied site may have occurred because UVR-sensitive colonizers were at very low densities in this highly exposed stream reach. It was evident that several

UVR-sensitive invertebrate taxa were reduced under all treatments from this site. For instance, at the non-canopied site I observed low densities of UVR-sensitive taxa that colonized our partial canopied site (e.g., *Dicosmoecus* spp., *Cymigula* spp., and *Paraleptophlebia* spp.). The community was dominated by dipterans (mainly chironomids), particularly in the latter portion of the experiment. Chironomids can utilize the algal canopy as a protective refuge from UVR (Clare 2000), which could account for the lack of response to UVR in this experiment. It is possible that the small scale manipulations of radiation were ineffective in representing the true response by invertebrate communities, and that the light environment of the whole reach was more influential to the communities that colonized our substrata.

There was evidence that some less UVR-sensitive taxa were inhibited by UVR at our non-canopied site in the latter stages of the experiment when UVB exposure to the streambed was greatest. For example, inhibitory effects of UVR on *Baetis* spp., *Caudaetella* spp., *Isoperla* spp., *Rhyancophila* spp., and Hydracarina were only apparent during this period of high UVB, with no observed effects at lower UVR intensities under either of the more shaded sites. Invertebrate response to UVB is known to be taxon-specific, and may occur in response to a threshold level of UVR (McNamara and Hill 1999, Kelly et al. 2001). The late occurrence of UVB effects on invertebrate colonization at the most exposed site (i.e., between days 70 and 91) coincided with a doubling of stream-bottom UVB (14.8 to 28% UVB), indicating that a threshold intensity of UVR may have been exceeded for several less UVR-sensitive taxa which inhabited this site. Similarly, Kiffney et al. (1997a) only observed UVR inhibition of invertebrate colonization following a decrease in water depth from 40 to 10 cm, and a reduction of UVR absorbance (at 250 nm) by 30%. These findings indicate that effects of UVR on invertebrate communities often occurs in response to seasonal changes in UVR exposure of the streambed resulting from water level fluctuations or DOM decreases.

Community diversity of benthic invertebrates was negatively affected by increases in solar UVR exposure through reduction in the riparian canopy. Although previous investigations have observed reductions in densities of certain taxa under UVR exposure (Bothwell et al. 1994, Kiffney et al. 1997a), no effects of UVR on invertebrate diversity have been reported. Reductions in several invertebrate taxa occurred under reduced canopy sites over the course of the experiment, resulting in significant losses in community diversity over time. These differences became more pronounced at the end of the experiment, coinciding with increases in streambed UVR exposure, and reductions in UVR sensitive taxa. Not surprisingly, Shannon-Wiener diversities remained highest under the full canopy and were unaffected by UVR. The ability of the riparian canopy to limit the magnitude of flux and seasonal fluctuations of UVR to the streambed appears to be important for protecting sensitive taxa and preserving diversity of benthic invertebrate communities.

Effects of UVR on trophic interactions

My findings support the original conclusions of Bothwell et al. (1994) that UVR indirectly mediates algal standing crop through its effects on grazers. The ability of grazers to regulate algal standing crop is well known in streams where light is often limiting (Feminella et al. 1989, Steinman 1992, Hill et al. 1995). Although rates of algal accrual (as estimated with chl *a* and epilithic C) generally increased under decreasing canopy, grazers strongly influenced both overall algal standing crop, and estimates of the direct inhibition of algal accrual by UVR. For example, under intermediate canopy inhibition of invertebrates by UVA+UVB allowed a 152% increase in chl *a* accrual by the end of the experiment, compared to UVA+UVB blocked treatments. This effect was driven mainly by large differences in grazing caddisflies (*Dicosmoecus* spp.), which responded predominantly to UVA exposure. Caddisfly larvae (e.g., *Dicosmoecus gilvipes*) have been shown to control algal biomass in streams under varying amounts of solar irradiance (Feminella et al. 1989, DeNicola et al. 1990). In contrast, indirect effects of UVR on grazers under no canopy cover were less pronounced, and had little effect on algal biomass. The absence of UVR-sensitive grazers such as *Dicosmoecus* spp. at the open canopied site (under all spectral treatments) may have resulted in less pronounced indirect effects of grazers on algal biomass. UVR sensitive grazers may be more likely to colonize partially shaded reaches of streams because they provide some temporal and spatial shading from high UVR exposure, while still maintaining a higher abundance algal of food resources than completely shaded reaches.

UVR can negatively affect invertebrates by altering the nutritional quality of algae (Van Donk and Hessen 1995, Hessen et al. 1997) by impairing nutrient sequestration (Hessen et al. 1995), and reducing cellular fatty acid and protein composition (Wang and Chai 1994, Arts and Rai 1997). Although I have discussed the effects of UVR on invertebrates mainly in the context of direct inhibitory effects, alternatively it is possible that indirect effects of UVR on algal food quality may have affected invertebrate communities. Indeed, the most pronounced inhibition by UVR occurred for scraper and collector taxa that predominantly utilize algal material as a food source. Conversely, it could be argued that these groups may be particularly sensitive to direct inhibition by UVR because they have to spend a large portion of their time feeding on exposed rock surfaces, rather than detrital feeders or predators which can feed in shaded depositional areas or on the under-surfaces of substrata. Two lines of evidence suggest that algal food quality may not have contributed significantly to UVR effects on invertebrates that I observed. Firstly, I observed the highest grazer densities in conjunction with some of the lowest algal standing crops, suggesting that food availability was higher in treatments where grazers were low. Secondly, there were no significant effects of UVR on algal community composition under full solar exposure, indicating that the composition of algal communities had not shifted to larger less-edible taxa under exposure to UVR. Although I did not measure algal nutritional quality directly, I believe that direct inhibition by UVR was more important for the observed trends in invertebrates rather than indirect effects of UVR on algal food-quality.

Conclusions

Increases in solar exposure resulting from the reduction in canopy cover negatively affected benthic communities in our study stream. I observed overall declines in invertebrate biomass and losses of UVR-sensitive taxa at reduced canopy stream reaches. Caddisflies were particularly sensitive to UVR exposure, however declines in mayflies and stoneflies also occurred in response to UVR exposure, mostly at the end of our experiment when UVR flux to the streambed was highest. Although the overall changes in diversity due to UVR were non-significant, it is evident that the riparian canopy provides considerable protection for UVR-sensitive benthic taxa, especially during very low flow conditions.

Small scale radiation manipulations may not be particularly effective at elucidating true responses of invertebrate communities to UVR. Under homogenous canopies (i.e., full and non-canopied), invertebrates appeared to be more highly influenced by the solar exposure of the stream reach than by the radiation treatments. I observed no significant response by invertebrates to UVR at the most exposed site because there were few UVR-sensitive taxa present. Alternatively I observed no response to UVR under full canopies probably due to low overall UVR exposure. The pronounced response by invertebrates to UVR under intermediate canopy likely occurred because UVR exposure to the radiation treatments would been intermittent due to spatial and temporal fluctuations in solar exposure, and higher abundances of UVR sensitive taxa would occur in partially canopied reaches compared to those completely open to sunlight. My results may provide insight into why UVR effects are frequently not reported in similar types of in-stream UVR-manipulation studies (DeNicola and Hoagland 1996, Hill et al. 1997).

Finally our results corroborate the findings of Bothwell et al. (1994) that invertebrate communities are more sensitive to the effects of solar UVR than sympatric algae. Reductions in UVR sensitive grazers through increased solar exposure either by canopy alteration, or reduction in DOM, may increase in the ratio of autotrophic to heterotrophic production in streams, leading to potentially confounding effects at higher trophic levels.

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4. EFFECTS OF SYNERGISTIC INCREASES IN SOLAR ULTRAVIOLET RADIATION AND TEMPERATURE FROM CLEAR-CUT LOGGING ON BENTHIC COMMUNITIES IN A BRITISH COLUMBIA COASTAL STREAM

Introduction

Approximately 65% of the land area in British Columbia (or 60.6 million ha) has been allotted for clear-cut logging, with a current annual allowable harvest of 190 000 ha/yr (Canadian Forest Service 1998). The effects of clear-cut logging on rivers in the Pacific Coastal Ecoregion (PCE) have been the subject of frequent investigations (Brown and Krygier 1970, Newbold et al. 1980, Shortreed and Stockner 1983, Carlson et al. 1990, Ryan and Grant 1991, Hetrick et al. 1998a, b). From these studies it is evident that clear-cutting along stream-sides normally results in large increases in solar exposure to streams either by direct removal of riparian canopy (Shortreed and Stockner 1983, Hetrick et al. 1998a), or indirectly by openings in the canopy from blow-down of riparian strips, landslides, erosion, debris flows, and floods (Ryan and Grant 1991). Although increased solar exposure is commonly cited as a major factor contributing to changes in resident biota following clear-cutting (Newbold et al. 1980, Hawkins et al. 1982, Carlson et al. 1990, Robinson and Rushforth 1987, Hetrick et al. 1998a,b), negative impacts have been mainly attributed to associated increases in stream temperature (Lynch et al. 1984, Holtby 1988). Solar ultraviolet radiation (UVR, 280-400 nm) is increasingly being recognized for its effects on shallow freshwater communities (reviewed by Williamson et al. 1995, Hader et al. 1998), and may interact synergistically with increases in water temperature to affect stream communities. Here I tested the hypothesis that the effects of clear-cutting on benthic communities may be due in part to increases in UVR. I used a series of UV-shielding experiments along a thermal gradient created by clear-cutting the catchment of a mid-sized coastal stream in British Columbia.

Natural intensities of solar UVR can inhibit benthic algae (Bothwell et al. 1993, Vinebrooke and Leavitt 1999, McNamara and Hill 2000, Watkins et al. in press), invertebrates (Bothwell et al. 1994, Kiffney et al. 1997a, Kelly et al. 2001), and their predators (Williamson et al. 1997, Kelly and Bothwell unpublished data). Freshwater taxa can vary considerably in their sensitivity to UVR due to physiological differences (Vincent and Roy 1993, Sommaruga and Garcia Pichel 1999, McNamara and Hill 2000) or avoidance strategies (Siebeck 1994, Kiffney et al. 1997b, Donahue and Schindler 1998). Thus, increases in UVR exposure may result in considerable changes to the composition (Bothwell et al. 1993, Vinebrook and Leavitt 1999, Xenopoulos 2000) and trophic dynamics (Bothwell et al. 1994, Hessen et al. 1997) of resident communities. Shallow riverine communities may be particularly sensitive to increases in UVR (Bothwell et al. 1994, Kelly et al. 2001). Species such as epilithon and grazers which use the exposed surfaces of the substrata may be particularly vulnerable (Vinebrooke and Leavitt 1999). Canopy removal (Meyer and Tate 1983, Hill 2000) and other environmental perturbations such as climate warming and acid deposition (Schindler et al. 1996, Yan et al. 1996, Donahue et al. 1998) can indirectly increase the UVR exposure to streams by altering the export of dissolved organic matter from the terrestrial catchment, the principal UVR attenuator in rivers (Scully and Lean 1994). However, long-term changes to DOM export following timber harvesting have not been examined closely for the PCE.

Studies examining the effects of temperature increases in streams from clear-cutting (Lynch et al. 1984, Holtby et al. 1988, Hetrick et al. 1998a), thermal pollution (Squires et al. 1979), and experimental warming (Hogg and Williams 1996) have documented significant changes to both the productivity and composition of benthic algal and invertebrate communities (reviewed by Ward and Stanford 1982, and DeNicola 1996). Temperature effects are taxon-specific, and highly dependent on the range over which the temperature increase occurs (Ward and Stanford 1982, Raven and Geider 1988). Within optimal temperature ranges, increases in temperature may result in increased net photosynthesis and algal growth rates (Bothwell 1988, Raven and Geider 1988, Denicola 1996), as well as increased invertebrate foraging rates, food assimilation, growth and fecundity (Sweeny 1978, Sweeny and Vannote 1978, Ward and Stanford 1982). Alternatively, temperature increases above optimal ranges can reduce metabolic efficiencies, denature proteins, depress oxygen levels, and cause extirpation of stenothermic species (Sweeny 1976, Lynch et al. 1984, DeNicola 1996). High temperatures have also been shown to interact synergistically with high fluxes of UVB to increase pigment damage in algae by increasing the production of intracellular reactive oxygen species such as superoxide radicals and H_2O_2 (Lesser 1996). The temperature of streams generally increases as it flows through clear-cuts (Brown and Krygier 1970, Holtby 1988, Clare 2000), and may interact with concurrent increases in UVR to differentially affect communities over the length of the cut.

My study examined the effects of UVB (280-320 nm) and UVA (320-400 nm) radiation and temperature (T) on benthic algal and invertebrate communities in the

Salmon River. I predict that the effects of UVR on benthic communities will be absent in uncut upstream stream reaches, increasing with increased solar exposure in clear-cut reaches. I also predicted that UVR effects will interact synergistically with increases in stream temperature to differentially affect stream communities over the length of the clear-cut.

Materials and Methods

Study Site

The Salmon River catchment (1275 km^2) flows ≈47 km northeasterly through the central-eastern portion of Vancouver Island, British Columbia, before entering Johnstone Strait near the town of Sayward (Fig. 4.1). Extensive clear cut logging has occurred in the lower section of the watershed, however the upper 12 km lie within Strathcona Park and remain unlogged. Forests in unlogged sections are old-growth (>250 yr) dominated by Western Hemlock (*Tsuga heterophylla*) and Subalpine Fir (*Abies lasiocarpa*), with some Western Red Cedar (*Thuya plicata*), and Red Alder (*Alnus rubra*), and provide considerable shading to the stream. Flow for this coastal stream is predominantly rain fed, peaking in October through December (measured 23 km downstream, October mean daily flow 24.1 m^3/s, max. 102 m^3/s), with some snowmelt runoff during May and June (May mean daily flow 16.4 m^3/s). Low flows occur from July through September (August mean daily flow 2.0 m^3/s).

My study site (50.1° N, 125.8° W) was located on the northern border of Strathcona Park as the river emerged into a 3.5 km series of connected cut blocks. At the study location the river is a fourth order stream, has an altidue of 85 m, a slope of 0.004, and a mean channel width of 16 m. The canopy height in upstream unlogged section of the stream is approximately 20 m. Cut blocks varied in age, with the oldest cuts (1988) in the lower part of the river and the most recent (spring of the study year, 1997) bordering the park. Small amounts of riparian cover were left along some of the cut blocks, however considerable increases in solar exposure occurred over the 3.5 km section of our study area. The large area of increased solar exposure resulted in up to a 4°C mid-day difference in stream temperature between the upper and lower portion of the clear-cut.

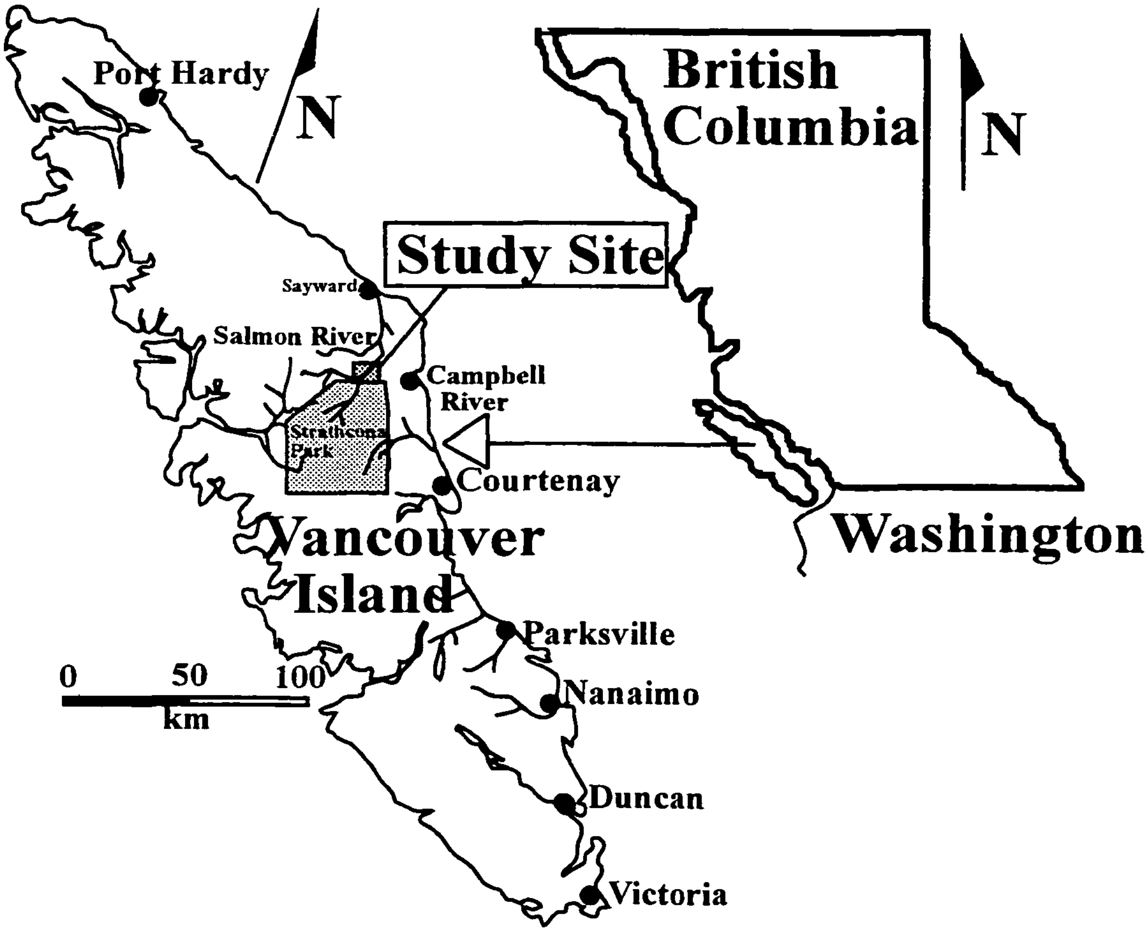

Figure 4.1. Study location on the Salmon River (Vancouver Island, British Columbia), on the northern border of Strathcona Park.

Experimental Design

A 49-d experimental trial was conducted between July 15 and September 7, 1997. Three radiation treatments (photosynthetically active radiation only (PAR), PAR+UVA, and PAR+UVA+UVB [control], Fig. 4.2) were applied at three stream sites. Sites included an old-growth reach 0.8 km upstream of the clear-cut at which both temperature and UVR exposure were low (-UVR / -T), at the top of the clear-cut (≈200 m from the cut margin) where UVR exposure was high and temperature was low (+UVR /-T), and 3.2 km downstream at the bottom of the clear-cut where both UVR and temperature were increased (+UVR /+T). Radiation treatments were replicated in triplicate at each site (3x3 randomized block design) by suspending large area (≈2 m^2) plastic solar filters immediately (≈ 3 cm) above the water surface in shallow riffle zones of approximately equal depth (mean 33 cm; no significant difference between sites, ANOVA, $p = 0.77$) and current speed (mean 23 cm/s; no significant difference between sites, ANOVA, $p = 0.23$). The filters used were, for the PAR+UVA+UVB treatment, OP4 acrylic sheets (CYRO, 4.7 mm thick, 70 - 90% transmittance throughout the UVB and UVA), for PAR, UF4 plexiglass (Rohm and Hass; 6.4 mm thick; 50% transmission at 398 nm), and, for PAR+UVA, Mylar-D (Du Pont; 0.1 mm thick, 50% transmission at 318 nm).

Irradiance

PAR, UVA, UVB, and stream temperature were recorded continuously (at 1 min. intervals) at each site with a Licor (Licor Instruments, Lincoln, NE, USA) LI 1000 data logger equipped with a quantum cosine PAR sensor (Licor LI190SA), and two broadband UVA and UVB sensors (BW20, Vital Technologies, Toronto, ON). Sensors were placed at the mid point of the ≈4 m^2 area in which the radiation treatments were located.

Trends in PAR, UVA and UVB paralleled each other over the experiment, and generally decreased with time from the summer solstice (Fig 4.3). The old-growth canopy site only received direct solar irradiance exposure in the late-afternoon (15:00) as the sun panned accross the channel opening (Fig 4.3). Clear-cutting resulted in a 3.7 fold increase in mean daily PAR at the top of the clear-cut (Student-Newman Kuels [SNK], $p <$ 0.05), and a 4.6 fold increase by the bottom of the clear-cut (SNK, $p < 0.05$) (Fig,4.3a). Some light interception by a thin riparian buffer strip (left behind after clear-cutting) occurred at the top of the clear-cut during mid-afternoon (13:00 - 16:00), resulting in the slightly lower (≈80%) total daily irradiance than at the bottom of the cut (SNK, $p < 0.05$). Increases in mean daily UVR from clear-cutting were less pronounced than for PAR (Fig.

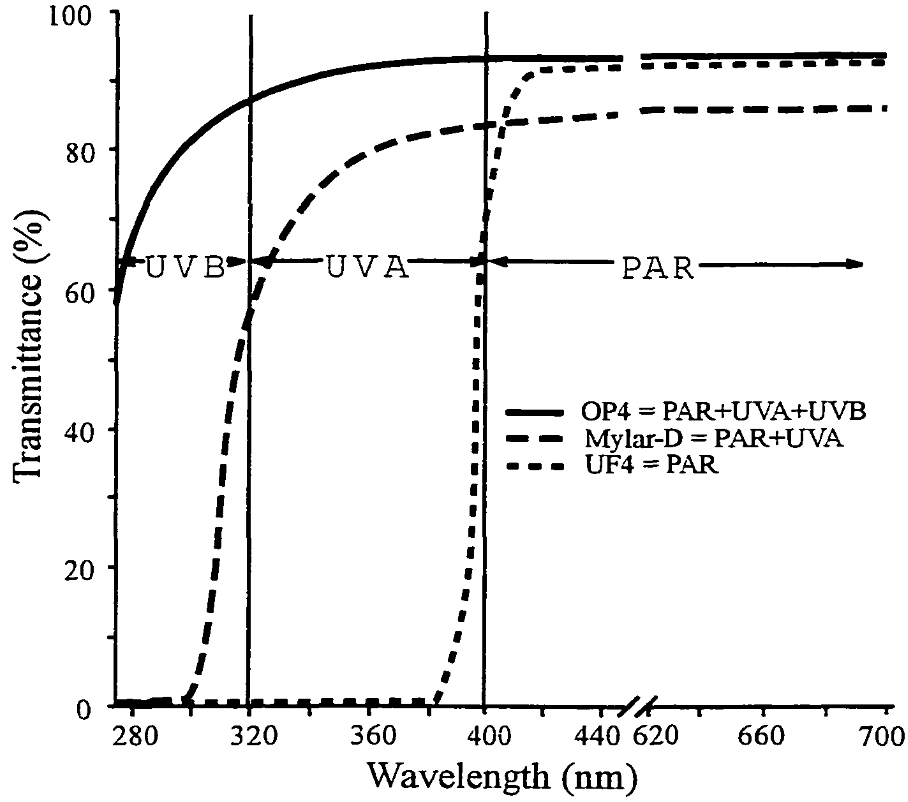

Figure 4.2. Transmittance properties of the four plastic light filters used in the experimental through the mid ultraviolet radiation (UVB, 280 - 320 nm), near ultraviolet radiation (UVA, 320 - 400 nm), and photosynthetically active radiation (PAR, 400 - 700 nm) spectral ranges. The filters used were OP4 acrylic sheets, UF4 acrylic sheets, and Mylar-D.

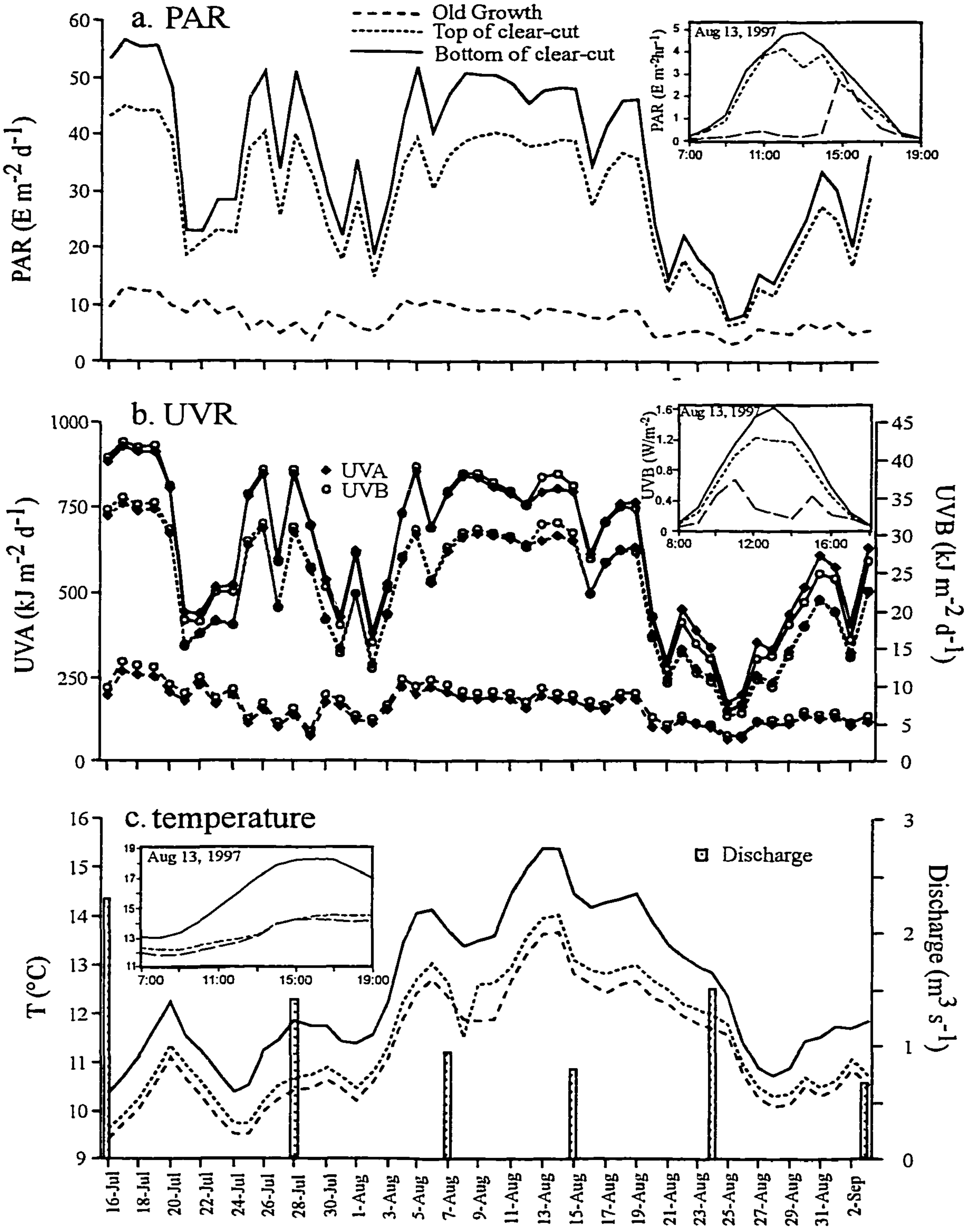

Figure 4.3. (a) total daily photosynthetically active radiation (PAR, 400 - 700 nm), (b) ultraviolet radiation (UVA, 320 - 400 nm, and UVB, 280 – 320 nm), and (c) mean water temperature at sites on the Salmon River in the upstream old-growth, at the top of the clear-cut, and 3.2 km downstream at the bottom of the clear-cut. Figure insets show hourly PAR, UVB, and water temperature at the three sites under cloudless conditions on August 13, 1997.

4.3b), probably resulted from a greater proportion of diffuse UVR reaching the stream surface under the old-growth canopy. Mean daily UVA and UVB increased 3.4 fold and 3.1 fold, respectively, at the top of the clear-cut (SNK, $p < 0.05$), and 3.9 fold and 3.7 fold, respectively, at the bottom of the clear-cut cut (SNK, $p < 0.05$). Mean total daily PAR, UVA, and UVB irradiances at the old-growth site during the experiment were 7.8 E m^{-2} d^{-1}, 160.6 kJ m^{-2} d^{-1}, and 7.9 kJ m^{-2} d^{-1}, respectively. At the top of the clear-cut they were 28.7 E m^{-2} d^{-1}, 502.3 kJ m^{-2} d^{-1}, and 22.6 kJ m^{-2} d^{-1}, respectively. At the bottom of the clear-cut they were 35.6 E m^{-2} d^{-1}, 623.9 kJ m^{-2} d^{-1}, and 27.6 kJ m^{-2} d^{-1}, respectively.

Water Transparency

Light transmittance to the stream bottom (on days 14, 29 and 49) was quantified by measurements of river water absorbance between 280 and 700 nm (at 0.5 nm intervals) using a Cary 50 (Varian Instruments, Walnut Creek, California, USA) scanning spectrophotometer equipped with a 2 cm quartz cuvette. The percentage of total daily above canopy PAR, UVA and UVB reaching the streambed was calculated by multiplying the water column transmittance (over the mean site water depth) by the mean percent of total daily irradiance reaching the stream surface at the site.

Transmittance of UVR to the streambed increased over the experiment due to simultaneous decreases in river depth and DOM (measured as dissolved organic carbon [DOC]) (Table 4.1), which followed trends in stream discharge (Fig. 4.3c). Depth decreased from ≈0.4 m at the initiation of the experiment, to ≈0.26 m on day 49, with no significant differences between sites (SNK, $p < 0.05$).

DOC increased along the clear-cut resulting in considerably less UVR penetrating to the streambed at the bottom of the clear-cut over much of the experiment (at least to day 29). For instance, on Day 14 [DOC] was ≈2.8 times higher at the bottom of the clear-cut (4.98 mg/L) than in the old-growth (1.78 mg/L), which resulted in considerably less UVB penetrating to the streambed at the bottom of the clear-cut (0.1% of above canopy UVB) as upstream in the clear-cut (1.4%) or in the old-growth (2.2%). However, by the end of the experiment (Day 49) all sites had nearly equal DOC (both ≈1 mg/L DOC), and UVB exposure at the downstream clear-cut site was 44% higher than at the top of the clear-cut, and five-fold higher than in the old-growth.

Table 4.1. Dissolved organic carbon, depth,and light exposure to the streambed (expressed as the percent of above canopy irradiance) during a 49-d experimental trial at three sites on the Salmon River along a clear-cut.

Site	Day 14	Day 29	Day 49
Old growth			
Depth (m)	0.40	0.33	0.26
DOC (mg/L)	1.78	1.15	0.93
PAR (%)	22.1	23.4	23.3
UVA (%)	9.3	16.1	16.4
UVB (%)	2.2	7.6	7.9
Top of the Clear-cut			
Depth (m)	0.42	0.35	0.29
DOC (mg/L)	2.44	1.62	1.06
PAR (%)	69.4	73.4	76.6
UVA (%)	18.9	40.0	54.3
UVB (%)	1.4	14.6	27.9
Bottom of the clear-cut			
Depth (m)	0.39	0.31	0.23
DOC (mg/L)	4.98	1.89	1.03
PAR (%)	28.1	87.9	95.5
UVA (%)	2.3	35.4	70.5
UVB (%)	0.1	7.1	40.4

Temperature

Mean hourly stream temperature was recorded (measurements at 1 min intervals) at the streambed inetrface (in the area of the radiation treatments) with a Licor LI 1000 data logger and thermistor. Temperature paralleled trends in irradiance (Fig. 4.3c), and ranged between 7.7 °C at the beginning of the experiment (July 15, 09:00) in the old-growth, to 18.4 °C at the bottom of the clear-cut during low flows (Aug 13, 15:00). Mean daytime temperatures (between 07:00 and 20:00) were on average 1.68°C warmer at the bottom of the clear-cut than at the top of the clear-cut (SNK, $P < 0.05$), and mid-day temperatures were as much as 4°C higher (Aug 13) when river flows were low (0.82 m^3/s). Temperature did not differ significantly (mean 0.07°C) between the old-growth site and the top of the clear-cut (SNK, $P > 0.05$). The greatest variance in daily temperatures also occurred at the bottom of the clear-cut, with maximum daily ranges around 5°C (Aug 13, 13.4 - 18.1 °C) during low-flow periods (inset Fig. 4.3c). Mean daily temperature ranges over the experiment were 2.4°C, 2.6°C and 2.9°C at the old-growth, top, and bottom of the clear-cut, respectively.

Water Chemistry

During the study period, river water (sampled ≈ biweekly, n=4) was circumneutral (pH 7.08), had a conductivity of 40.2 μS/cm, and generally low nutrients (4.9 - 32 mg/L NO_3, 2.3 - 3.0 μg/L total phosphorus [TP]). Phosphorus increased marginally between the top (mean 2.4 μg/L TP, 1.9 μg/L soluble reactive phosphorus [SRP]) and bottom of the clear-cut (mean 2.8 μg/L TP, 2.1 μg/L SRP), whereas nitrogen was unchanged downstream (mean for all sites 16.4 μg/L NO_3, ANOVA, $p > 0.05$).

Response variables

A mixture of air-dried gravel and cobble in 0.092 m^{-2} screened bottomed colonization trays (L=30.3 cm; W=30.3 cm; H=3.0 cm) served as substrata for colonization by the benthic community. The trays were placed into the channel substrata to allow for normal flow over the stream-bottom, and were placed >30 cm from the edge of the UVR filters to ensure the intended light exposure. Individual trays were collected biweekly from underneath all of the UV-filters starting on day 21.

Epilithic Community

Epilithic community response to logging/UVR treatments was quantified by measure-ment of chlorophyll, and both benthic algal community composition. Chlorophyll samples were collected in triplicate by taking 4.92 cm^{-2} scrapings (using a hard bristle brush) from randomly selected rocks and filtered onto Whatman GFC filter papers, frozen and stored in the dark until analysis. Chlorophyll was analyzed fluorometrically following extraction in 10 ml tubes of 90% ethanol at 78°C for five minutes, following the procedure outlined by Nusch (1980). Benthic algal taxonomic samples were collected by pooling four 4.92 cm^{-2} scrapings, and preserving with Lugol's solution until analysis. Algal species composition was determined using standard phytoplankton techniques with a Palmer-Malony chamber. The periphyton was blended breifly (<20 secs) in a Waring blender to fragment the filamentous greens to improve sub-sampling and settling homogeneity (Biggs1987). Samples were allowed to settle in chambers for 24hr prior to counting. Counts were made at 250x magnification and individual cells were enumerated in 20 random Wipple fields from 2 replicate counts. Only cells with visible contents were counted. Taxonomic identifications were done to species level for diatoms, and to genus level for chlorophytes using keys by Patrick and Reimer (1966, 1975), and Prescott (1962). Identification of diatoms was aided by examining sub-samples cleaned in boiling 30% hydrogen peroxide and mounted in hyrax. Diatoms identified in fresh samples were then matched to those identified in mounted samples.

Benthic Invertebrate Community

Benthic invertebrate samples were collected from the remaining substrata washed through a 250 μm mesh sieve. All organisms retained on the sieve were preserved in 70% ethanol until analysis. Insects were identified to genus (except Diptera which were identified to family) using keys by Clifford (1991), and Merritt and Cummins (1996). Other invertebrate groups (e.g., Hydracarina and Oligochaeta) were at very low densities (<1% of total abundance) and not included in the analysis. All invertebrates retained by a 2 mm mesh were enumerated. Those passing through the sieve (250 μm ≤ 2 mm) were diluted to 1 L in an Imhoff cone, and five 50 ml sub-samples collected while air was bubbled through the cone to homogenize the sample (Wrona et al. 1982). Invertebrates were counted in a minimum of three sub-samples, or until at least 100 individuals of the most abundant taxa were counted. Biomass of invertebrate taxa were calculated from mean dry weights measured from at 5 - 20 individuals from both the coarse (> 2mm) and fine (125 μm ≤ 2 mm) fractions at each site for each sampling time. Invertebrates were dried at 60°C overnight and then weighed using a Cahn electrobalance accurate to 1 μg. Mean biomass of invertebrates from both the coarse and fine fractions were then multiplied by invertebrate abundance of the particular fraction to determine the total biomass. The reported invertebrate biomass does not include the fraction that was soluble in alcohol (i.e. lipids) due to their preservation in ethanol. Shannon-Wiener diversity (H') was calculated for insects using the lowest (generic and family) taxonomic resolution.

Statistical analyses

Because we expected differential effects of our UVR treatments on benthic communities between clear-cut and old-growth sites, we examined the effects of clear-cutting and UVR separately. The effect of clear-cutting on the response variables was conducted considering only the full spectrum radiation treatments (i.e., PAR+UVA+UVB). The effect of UVR on the response variables was conducted independently at each site. Repeated measures (RM) tests were used due to multiple sample times for each response variable.

One-way RM-ANOVAs were used to test for the effect of clear-cutting (only PAR+UVA+UVB), and UVR treatments (at each site) on chlorophyll, total epilithic abundance, total invertebrate biomass, and community diversity. One-way RM-MANOVAs were used to test for the effects of clear-cutting and UVR on both benthic algal (groups included chlorophytes, diatoms, cyanophytes, and others) and benthic invertebrate (groups included mayflies, stoneflies, caddisflies, dipterans, and others [Coleoptera, and Collembola]) community composition.

Statistical analysis of the data was completed on Log (n+1) transformed data when necessary to meet homogeneity of variance or normality assumptions. For RM-MANOVAs, both multivariate and univariate test results are reported. Univariate tests represent the equivalent RM-ANOVA of the particular variable (i.e. group or species). Student-Newman-Keuls *post-hoc* tests were performed on univariate RM-ANOVAs. All analyses were conducted using SPSS (v 6.1, 1995, SPSS Inc.) or SuperANOVA (v 1.11, 1991, Abacus Concepts Inc.) statistical packages.

Results

Epilithic community

Clear-cutting effects: Clear-cutting significantly increased chlorophyll (chl) *a* accrual along the clear-cut (RM-ANOVA, $p < 0.001$) (Fig. 4.4a). Under full spectrum sunlight

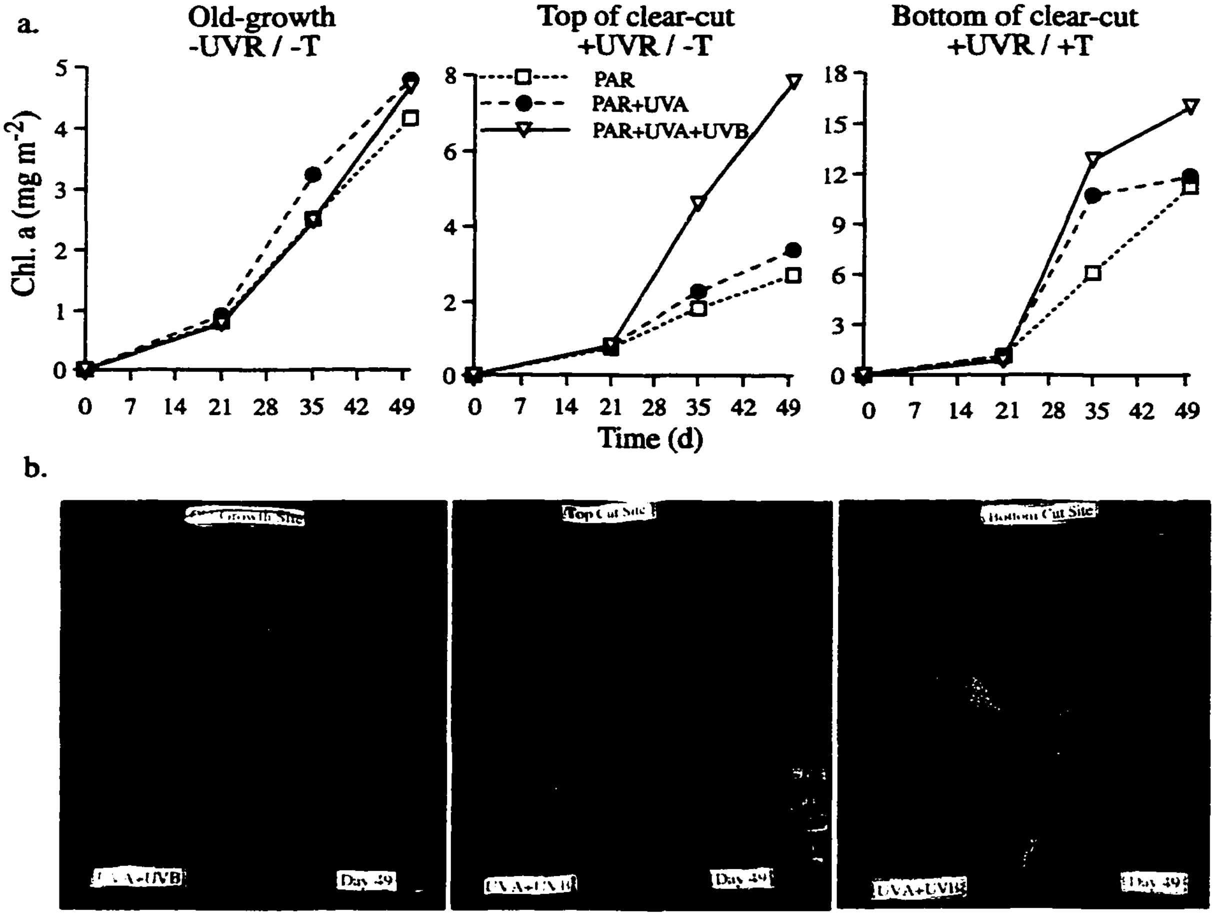

Figure 4.4. (a) Chlorophyll (chl) *a* under PAR, PAR+UVA and PAR+UVA+UVB radiation exposures, and (b) colour photograph of the epilithon community on day 49, at three sites on the Salmon River in the upstream old-growth (-UVR / -T), at the top of the clear-cut (+UV / -T), and 3.2 km downstream at the bottom of the clear-cut (+UV / +T). Chl *a* values are means (n=3) ± SE.

(PAR+UVA+UVB), chl *a* was 66% higher (mean 4.41 mg/m^2) at the top of the clear-cut and 274% higher (mean 9.2 mg/m^2) at the bottom of the clear-cut, than in the upstream old-growth (mean 2.65 mg/m^2) (SNK, $p < 0.05$). Final chl *a* biomass at the bottom of the clear-cut was more than double (16.0 mg/m^2) than at the top of the clear-cut (7.8 mg/m^2).

The composition of algal communities also changed between old-growth and clear-cut sites (Table 4.2), as evidenced by striking visual differences between sites at the end of the experiment (Fig. 4.4b). In the old-growth, the algal community at the end of the experiment (Day 49) was dominated by small celled diatoms such as *Achnanhthes microcephala,* and *Gomphonema* sp. In contrast, algal communities at clear-cut sites on Day 49 were comprised mainly of filamentous green algae (e.g., *Zygnema* sp.) ($p = 0.003$). There were also increases in larger celled diatoms such as *Synedra ulna* ($p = 0.0001$) and *Hannaea arcus* ($p = 0.001$) over the clear-cut. Total algal abundance on Day 49 was at least 2.5-fold higher at the bottom of the clear-cut (mean 2839 cells/mm^2) than both upstream sites (SNK, $p < 0.05$). Total algal abundance (on Day 49) did not differ between the top of the clear-cut (mean 948 cells/mm^2) and the old-growth (mean 1137 cells/mm^2) (SNK, $p > 0.05$).

UVR Effects: The effects of the UVR treatments on chl *a* accrual were weak under the old-growth canopy (RM-ANOVA, $p = 0.099$), however, accrual at both clear-cut sites was significantly lower in UVR shielded treatments (RM-ANOVA, $p < 0.001$) (Fig. 4.4). Chl. *a* increased over time under all radiation exposures at all sites ($p < 0.0001$).

UVR effects on chl *a* accrual were most pronounced at the top of the clear-cut ($p < 0.001$). Mean chl *a* biomass was on average 51% and 60% lower under PAR+UVA and PAR treatments, respectively, than under PAR+UVA+UVB (SNK, $p < 0.05$). There were no differences in chl *a* biomass between PAR and PAR+UVA treatments (SNK, $p > 0.05$). Final Chl *a* biomass under both PAR and PAR+UVA at the top of the clear-cut (mean 2.6 mg/m^2) was ≈45% lower than the mean biomass that occurred under the old-growth canopy (4.7%), despite having ≈370% more daily PAR irradiance.

At the bottom of the clear-cut, chl *a* was on average 20% and 38% lower under PAR+UVA and PAR-only treatments, respectively, than under PAR+UVA+UVB (SNK, $p < 0.05$). Although both types of UVR screening reduced chl *a* biomass, a significantly larger reduction occurred under PAR-alone than PAR+UVA (SNK, $p < 0.05$).

Table 4.2. Mean final (Day 49) abundance of algal taxa exposed to full spectrum sunlight at three sites along the Salmon River, in the old-growth, at top of the clear-cut, and at bottom of the clear-cut. Taxa reported comprise >2% of the total abundance at the site. Values are mean (n=3) abundance (cells/mm^2) and standard deviations (SD). np = not present

	Old-growth		Top Clear-cut		Bottom Clear-cut	
Taxa	Mean	SD	Mean	SD	Mean	SD
Chlorophytes **						
Zygnema sp. ***	1.1	1.9	310.3	132.2	1586	515.6
Mougeotia sp.	np	-	39.1	52.4	9.8	16.9
Ulothrix sp.	np	-	49.0	84.3	np	-
Diatoms						
Achnanthes microcephala	1084	587.5	422.1	311.1	751.9	796.7
Synedra ulna ***	np	-	64.6	56.6	290.9	197.7
Hannaea arcus ***	0.4	0.6	50.1	29.1	151.6	51.9
Synedra sp. **	2.6	2.3	23.0	6.1	40.5	36.4
Gomphonema sp.	48.6	32.6	12.4	9.6	9.3	7.2
Total Abundance **	1137	609.2	947.8	451.2	2839	315.4

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Benthic Invertebrate Community

Clear-cutting effects: Clear-cutting resulted in significant reductions of total invertebrate biomass, changes in community composition, and decreases in diversity (Table 4.3). The total biomass of invertebrates was on average only 6% lower at the top of the clear-cut than in the old-growth (SNK, $p > 0.05$)(Fig. 4.5). However, at the bottom of the clear-cut, total biomass averaged 40% lower than at the old-growth site (SNK, $p < 0.05$) . Significantly lower diversity of communities also occurred at the bottom of the clear-cut (SNK, $p < 0.05$). In contrast upstream clear-cut sites had diversities similar to the old-growth over the entire experiment.

Mayflies and stoneflies were most abundant taxonomic group (by biomass) at all sites, and were most negatively affected by clear-cutting (Fig. 4.6, Table 4.3). Under full spectrum sunlight, mean mayfly biomass was at least 43% lower at the bottom of the clear-cut than at either the top of the clear-cut or old-growth sites (SNK, $p < 0.05$). In contrast, mayflies at the top of the clear-cut averaged only 5% less than at the old growth site (SNK, $p < 0.05$). Although most mayfly taxa such as *Drunella* spp., *Rithrogena* spp., and *Seratella* spp. decreased over the clear-cut (Fig. 4.7), others such as *Baetis* spp. increased by >100%.

In contrast, mean stonefly biomass uniformly decreased by ≈20% at both clear-cut sites under full spectrum sunlight (SNK, $p < 0.05$), driven mainly by a decline in *Plumiperla* spp., which was at least 70% lower in the clear-cut by the end of the experiment. Significant reductions in caddisfly biomass were only apparent at the bottom of the clear-cut (Table 4.3), which was at least 40% lower than the other two sites (SNK, $p < 0.05$). Dipterans, comprised mainly of chironomids and tipulids (*Hexatma* spp.), were the only group to increase in response to clear-cutting (Table 4.3), and were at least 25% higher at both clear-cut sites over the experiment (SNK, $p < 0.05$).

UVR effects: Shielding from UVR had no effects on the invertebrate community under old-growth canopy, whereas in the clear-cut the biomass of several invertebrate groups was significantly lower under full sunlight than when UVR removed (Table 4.3). Effects of UVR on the invertebrate community were most prevalent at the top of the clear-cut (RM-MANOVA, $p = 0.038$), which had significantly higher biomasses of mayflies, stoneflies (Fig. 4.6), and total invertebrates (Fig. 4.5) under PAR and PAR+UVA treatments than under full spectrum sunlight (Table 4.3). Mayflies, the dominant taxa at the top of the clear-cut, had similar biomasses in both PAR and PAR+UVA treatments, and

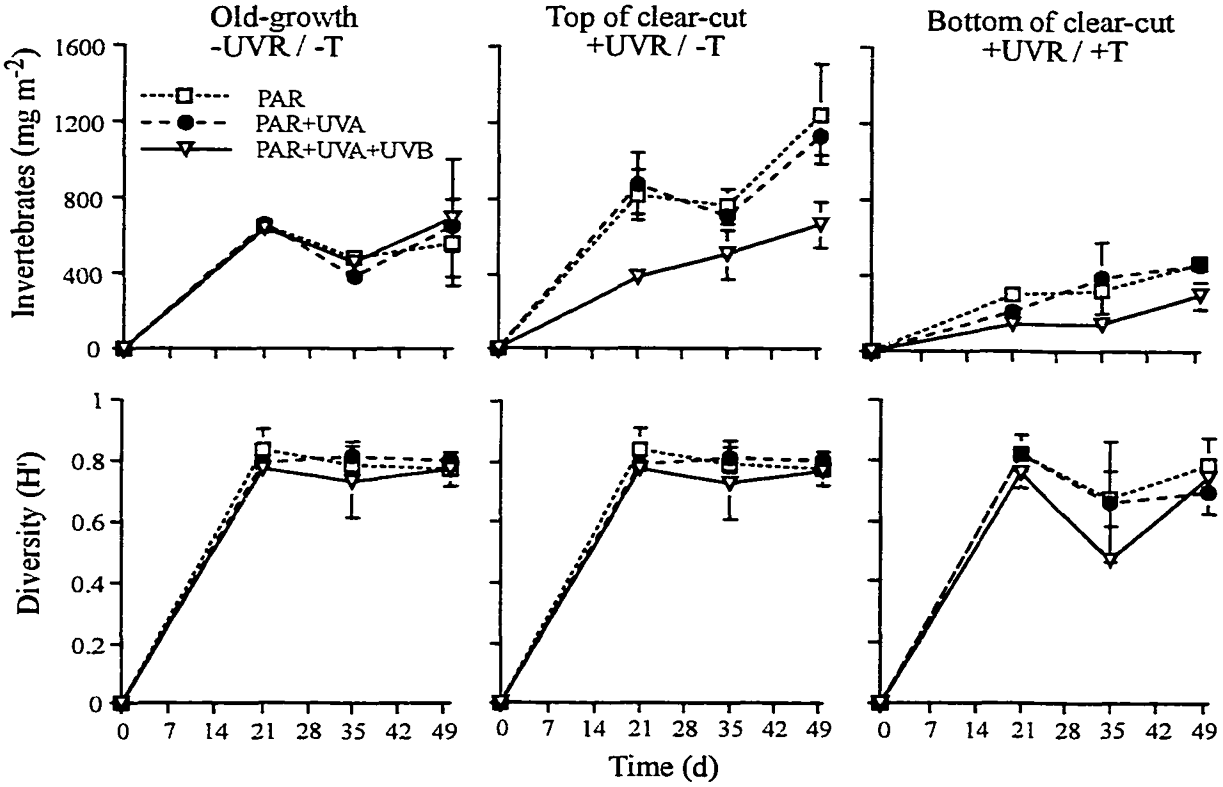

Figure 4.5. Total invertebrate biomass and community diversity (Shannon-Wiener, H') under PAR, PAR+UVA, and PAR+UVA+UVB radiation exposures at sites on the Salmon River in the upstream old-growth (-UVR / -T), at the top of the clear-cut (+UV / -T), and 3.2 km downstream at the bottom of the clear-cut (+UV / +T). Values represent means (n=3) ± SE.

Table 4.3. Results of the RM-MANOVAs of the effects of clear-cutting (Clear-cut) and ultraviolet radiation (UVR) on the biomass of the major invertebrate orders, total invertebrates, and diversity for sites along a clear-cut in the Salmon River. Reported are the results from univariate tests of the four major orders (mayflies, stoneflies, caddisflies,and dipterans), a combined group of all other invertebrate taxa (Other= Coleoptera, Hydracarina, and Oligochaeta), total invertebrate biomass (Total), and Shannon-Wiener community diversity (Diversity). Also resported is the multivariate test incorporating all five sub-groupings of invertebrates (MANOVA). Data given are *F* statistics and *p* values for univariate tests, and Hotelling *F* statistic (H-*F*) for the multivariate test.

		Mayflies		Stoneflies		Caddisflies		Dipterans		Other		Total		MANOVA		Diversity	
Source	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	H-*F*	*p*	*F*	*p*
Clear-cut (PAR+UVA+UVB only)	2	79.11	<0.001	35.84	<0.001	10.52	0.011	11.94	0.008	1.26	0.347	50.90	<0.001	18.15	0.007	19.73	0.002
UVR- Old-growth	2	0.06	0.940	2.07	0.208	3.44	0.101	1.07	0.400	0.16	0.854	0.12	0.888	0.49	0.817	0.24	0.796
UVR - Top clear-cut	2	287.7	<0.001	5.98	0.037	2.42	0.169	4.09	0.076	0.02	0.978	163.9	<0.001	25.12	0.038	1.06	0.402
UVR - Bottom clear-cut	2	23.18	0.002	8.29	0.019	3.73	0.088	0.07	0.930	0.12	0.879	16.51	0.004	2.16	0.185	3.43	0.101
Time - All Factors	3	>9.49	<0.01	>10.7	<0.01	>3.4	<0.10	>1.1	<0.41	>0.1	<0.85	>9.0	<0.01	>5.4	<0.01	>0.2	<0.79
Time x Site	6	7.29	0.003	3.65	0.036	2.43	0.105	1.12	0.393	0.12	0.970	3.94	0.028	3.11	0.021	8.33	0.001
Time x UVR - Old-growth	6	1.00	0.445	0.99	0.446	0.83	0.529	1.17	0.368	1.93	0.170	0.86	0.515	0.90	0.590	0.92	0.483
Time x UVR - Top clear-cut	6	1.94	0.167	1.89	0.177	1.93	0.170	0.54	0.708	0.57	0.689	1.30	0.325	5.28	0.097	0.91	0.486
Time x UVR - Bottom clear-cut	6	3.75	0.033	2.61	0.088	1.50	0.261	1.03	0.432	1.37	0.383	1.99	0.161	1.24	0.296	1.56	0.248

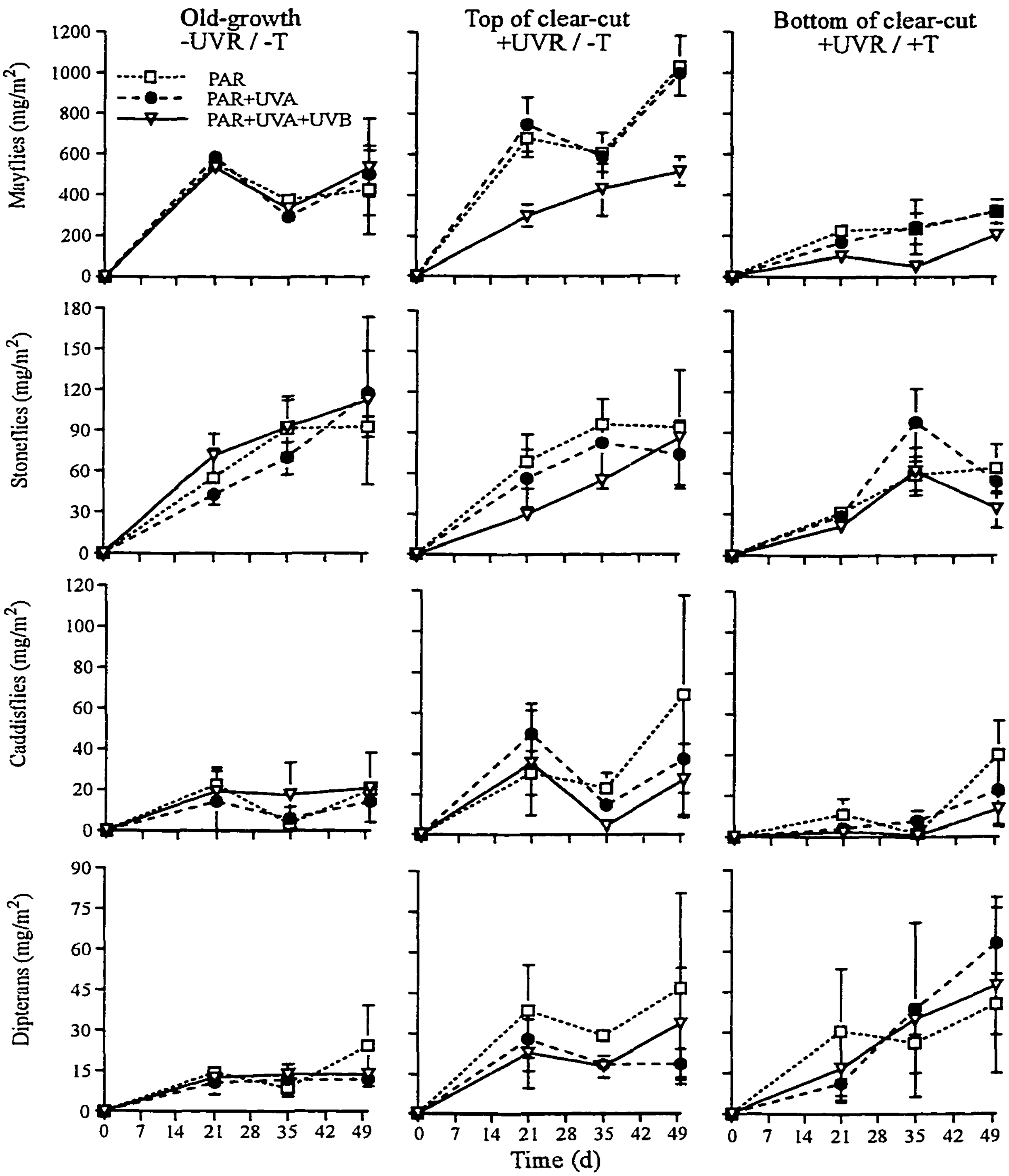

Figure 4.6. Biomass of the dominant invertebrate groups under PAR, PAR+UVA, and PAR+UVA+UVB radiation exposures at sites on the Salmon River in the upstream old-growth (-UVR / -T), at the top of the clear-cut (+UV / -T), and 3.2 km downstream at the bottom of the clear-cut (+UV / +T). Values represent means (n=3) ± SD.

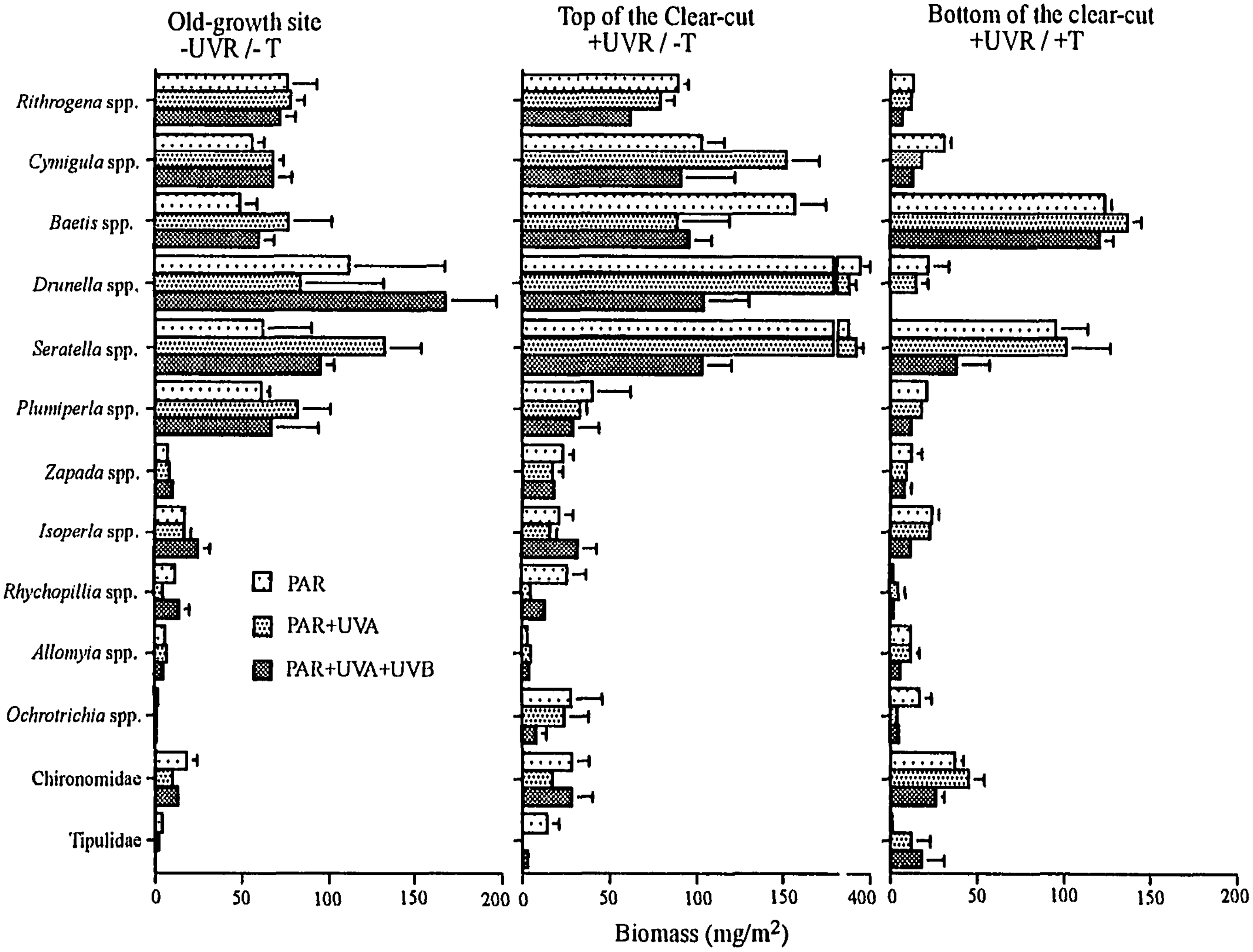

Figure 4.7. Final biomass of the dominant insect taxa under PAR, PAR+UVA, and PAR+UVA+UVB radiation exposures at sites on the Salmon River in the upstream old-growth (-UVR / -T), at the top of the clear-cut (+UV / -T), and 3.2 km downstream at the bottom of the clear-cut (+UV / +T). Values represent means (n=3) + SE.

were on average 86% higher than under full spectrum sunlight (SNK, $p < 0.05$). *Drunella* spp. and *Seratella* spp. were the most responsive mayfly taxa to UVR at this site, and had at least two-fold the biomass under PAR and PAR+UVA treatments than under full spectrum sunlight by the end of the experiment (Fig. 4.7). Other invertebrate groups responded in a stepwise fashion to the screening of UVA+UVB and UVB alone. Stonefly biomass averaged 52% higher under PAR than under PAR+UVA+UVB (SNK, $p < 0.05$), whereas under PAR+UVA biomass was only 24% higher, and not significantly different from PAR+UVA+UVB treatments (SNK, $p > 0.05$). Although caddisflies and dipterans increased under UVR screened treatments at the top of the clear-cut, there were no significant differences between any of the radiation treatments (Table 4.3), and biomass was generally low for all taxa.

Overall effects of UVR on the invertebrate community were less discernible at the bottom of the clear-cut (RM-MANOVA, $p = 0.185$), although the biomasses of total invertebrates (Fig. 4.5), mayflies, and stoneflies (Fig. 4.6) were significantly higher under PAR and PAR+UVA treatments than under full spectrum sunlight (Table 4.3). Differences in biomass of invertebrates between treatments also tended to increase over the experiment, with relatively small differences observed until Day 35. Mayfly biomass averaged 116% higher under PAR and PAR+UVA treatments than under full spectrum sunlight (SNK, $p < 0.05$). Although most mayfly taxa were strongly inhibited by UVR (e.g, *Seratella* spp., *Drunella* spp., and *Cymigula* spp.), the dominant taxon *Baetis* spp. was unaffected by the radiation treatments (Fig. 4.7). Stoneflies under PAR and PAR+UVA were also on average 55% and 34% greater, respectively, than under full spectrum sunlight (SNK, $p < 0.05$). Although caddisflies tended to colonize UVR screened treatments at higher densities, particularly on day 49, both caddisflies and dipterans (mainly chironomids) did not differ significantly between radiation treatments (Table 4.3).

Discussion

Benthic algal community response to clear-cutting

Increased solar exposure from clear-cutting significantly increased algal accrual and changed the species composition of algal communities compared to old-growth sites. Algal accrual, estimated by chl a, increased on average by 148% over 49 d at clear-cut sites. The increase in accrual was not surprising, because light limitation of primary production is commonly reported for forested streams (Shortreed and Stockner 1983, Hill et al. 1995). Although a 3.7 fold increase in PAR exposure between the old-growth site and the top of the clear-cut increased algal accrual by 66%, a considerably larger (≈200%) increase in accrual occurred at the bottom of the clear-cut, where temperatures were significantly higher. Bothwell et al. (1988) observed that temperature accounted for approximately 90% in the annual variability in algal growth rates of non-shaded lotic systems, whereas PAR irradiance accounted for only a small portion. In their experiment, maximum algal growth rates increased approximately 50% in response to a 5°C increase (from 10 to 15°C) of stream temperature under nutrient saturated conditions. In our study stream, chl a biomass increased at least three-fold between the top and bottom of the clear-cut over the first 35 days of the experiment, corresponding to ≈1.7°C increase in mean daytime temperature between sites. Additionally, mid-day temperatures were as much as 4°C higher at the bottom of the clear-cut, which occurred synchronously with peak photosynthetic periods. Our results corroborate the findings of previous field investigations that temperature exerts a large effect on benthic algal accrual in streams (Squires et al. 1979, Lamberti and Resh 1983).

Several other factors may have also contributed to this large increase in algal accrual over the clear-cut. Firstly, we observed an ≈67% decline in total invertebrate biomass between the top and bottom of the clear-cut, indicating that grazing rates would have probably been considerably lower at our downstream site. Grazers have been shown to be important in regulating algal standing crop under varying rates of accrual (Steinman et al 1992). It is also possible that inputs of limiting nutrients from the clear-cut may have contributed to the elevated algal growth rates at the downstream site (Hobbie and Likens 1973, Shortreed and Stockner 1983). Although increases in phosphorus concentrations were generally small (≈0.2 μg/L SRP), the range over which this increase occurred (1.9 – 2.1 μg/L SRP) was within the concentration range that P is considered to limit benthic algal production (3 - 4 μg/L, Bothwell 1985), and thus may have contributed to increased accrual. Although total daily irradiance also increased by ≈25% between our upstream and downstream clear-cut sites, this probably did not contribute significantly to increased algal growth, because light would have already been saturated at the upstream clear-cut site. Our results demonstrate that the combination of increased algal growth rates and reduced grazers occurring along large clear-cuts can lead to extremely high algal standing crops during low-flow summer periods. This could have potentially confounding effects to higher trophic levels such as salmonids, which are sensitive to large diel oxygen fluctuations, although we did not measure this in our experiment.

Clear-cutting significantly changed the composition of algal communities from small-celled diatoms in the old-growth (e.g., *Achnanthes microcephala*), to filamentous green species and large-celled diatoms dominated in the clear-cut (e.g., *Zygnema* sp.). It appears that changes in solar intensity rather than temperature was the dominant contributor to these changes, as no significant shifts in community composition occurred between the top and bottom of the clear-cut, although abundance increased significantly. Filamentous green algae have been commonly reported to dominate communities in open-canopied sections of rivers (Shortreed and Stockner 1983, Lowe et al. 1986), and may be particularly suited to high light environments due to their physiogomy and pigmentation. Filamentous algae may out-compete prostrate or apically attached diatoms by extending their growth further above the substrata, thereby shading low-lying forms. In contrast they are often outcompeted in low light environments because of their lack of accessory light harvesting pigments (Vinebrooke and Leavitt 1999). The increase in the proportion of large:small celled diatoms that occurred in our study has also been reported in previous field studies following canopy removal (Lowe et al. 1986). Larger-celled diatom taxa have been shown to be more tolerant of high UVR exposure than smaller celled species (Karentz et al. 1991, Bothwell et al. 1993), and may be suited to high light environments. In our study, UVR exposure increased by at least 300% between the old-growth and clear-cut sites, resulting in large reductions in the proportion of small-celled diatoms that normally dominate the steam flora in forested reaches. Although increased temperature did not significantly affect algal community composition, it did contribute to large increases in accrual rates by increasing algal growth rates and decreasing grazers.

Benthic invertebrate community response to clear-cutting

Clear-cutting reduced the total biomass, and altered the composition and diversity of invertebrate communities ($p < 0.007$). Effects at the upstream clear-cut site were largely shifts in community composition. Stoneflies (predominantly Plumiperla spp.) were the most severely affected group, and were39% lower in biomass at the top of the clear-cut than in the old-growth (SNK, $p < 0.05$). Stoneflies have previously been reported to be sensitive to clear-cutting (Graynoth 1979). Increased UVR exposure at the top of the clear-cut likely contributed to the decline, as most stonefly taxa increased when either UVB-alone or UVA+UVB were selectively screened (SNK, $p < 0.05$). Although some mayfly species such as *Drunella* spp. were laso lower in biomass at the upstream portion of the clear-cut, the overall effects of clear-cutting on mayfly biomass was not significant. This was partly due to the large abundance of *Baetis* spp. in the clear-cut, which was approximately double in biomass compared with the old-growth site. Previous researchers have also observed large increases in the abundance of Baetis due to logging (Wallace and Gurtz 1986). However, it is difficult to ascertain whether these species proliferated because they were highly tolerant of physical conditions following logging, or due to greater food supply from increased algal production.

Combined increases in UVR and temperature at the bottom of the clear-cut had an even greater effect on invertebrate communities than UVR effects in isolation. Studies on the effects of increased temperature on invertebrate ecology have observed increased growth rates, reduced time to maturity (Sweeney and Vannote 1978), and in some cases increased fecundity (Ward and Stanford 1982). Despite this, field studies have frequently observed overall declines in invertebrates from increases in stream temperatures (Lamberti and Resh 1983, Hogg and Willaims 1996), indicating that species may be optimally adapted to a specific temperature regime (Sweeney and Vannote 1978). We observed 63% less total invertebrate biomass, and a 15% decrease in community diversity between the top and bottom of the clear-cut, corresponding to approximately a 1.7°C increase in mean daytime temperature. Although this increase was relatively small, mid-afternoon temperatures were as much as 4°C higher, potentially exceeding optimal temperature ranges for some cold-water stenothermic species. Mayflies, the dominant species in the old-growth, represented ≈92% of the reduction in total invertebrate biomass at the bottom of the clear-cut. Previous studies have found that mayflies are particularly sensitive to increases in temperature (Sweeney and Vannote 1978), and clear-cutting (Grynoth 1979, Hetrick et al. 1998b). The ability of relatively small temperature changes to have such considerable effects on the invertebrate community warrants concern.

Our results also suggest that increased UVR exposure at the bottom of the clear-cut contributed significantly to negative effects on invertebrates. We observed significant increases in almost all taxa when either UVB-alone, or UVA+UVB were screened at the bottom of the clear-cut. Negative effects of UVR on invertebrate colonization have been shown to depress the abundance of invertebrate communities by up to 66% in shallow clear streams (Kiffney et al. 1997a). In our study, combined increases in temperature and UVR at the bottom of the clear-cut decreased mayflies, stoneflies and caddisflies by 76%, 59%, and 74%, respectively, compared with old-growth sites. Because a given stream reach is colonized by invertebrates drifting from upstream reaches, inhibition of invertebrate communities by UVR and temperature most likely progressively increased downstream along the clear-cut, leading to an amplified decline of invertebrates at the bottom of the clear-cut.

It is likely that several other factors contributed to reductions in invrtebrates observed over the clear-cut. Changes to algal community composition and physiogomy along the clear-cut may have impacted invertebrate communities by changing food quality and habitat structure. The dense growths of filamentous green algae (mainly *Zygnema* spp.) which occurred at the bottom of the clear-cut (Fig 4b) may have acted to physically inhibit some invertebrate taxa (Dudley et al. 1986). Additionally, a reduction in smaller celled diatom species, the preferred food-source of many grazers (Lowe et al. 1986), may have also indirectly impacted invertebrates in the clear-cut. UVR can also negatively affect invertebrates by altering the nutritional quality of algae (i.e., N, P and fatty acid content), or by changing the composition of communities to larger less-edible taxa (Hessen et al. 1997). Although we did not measure algal nutritional quality, we did observe community shifts to larger celled diatoms in under high solar exposure in the clear-cut. Reduced inputs of coarse particulate organic matter (CPOM) from riparian canopies would have also likely occurred downstream along the clear-cut, although I did not specifically quantify this. Decreased CPOM could potentially contribute to reductions of invertebrates which utilize heterotrophic materials, such as shredders and collectors. Although we generally observed low densities of shreeders at all sites, collector taxa such as *Drunella* spp. and *Seratella* spp. did decline at he bottom of the clear-cut. Changes in the quality and availability of food resources from clear-cutting likely contributed to the community shifts in the clear-cut decreased productivity that occurred over the clear-cut.

In summary, our studies show that increasing UVR in clear-cut stream reaches causes shifts in species assemblages of both invertebrates and algae. These effects are amplified downstream, due to the combined effects of increased UVR and temperature and changes in food resources for invertebrate consumers.

Effects of UVR manipulations on benthic communities

To investigate which components of solar irradiance were responsible for the effects on algal and invertebrate communities, we discuss the effects of our different solar radiation manipulations separately.

Increases in UVR exposure by at least three-fold in the clear-cut increased algal accrual by 134% and 48% at the top and bottom of the clear-cut, respectively, over 49 d. UVR can reduce algal accrual directly by inhibiting photosynthesis and algal growth rates (Bothwell et al. 1993), or alternatively, can indirectly promote algal accrual by suppressing grazers (Bothwell et al. 1994, Williamson 1995). It is evident from our study that declines in invertebrates caused by increases of UVR in the clear-cut indirectly increased algal accrual. Coincident with lower rates of algal accrual under UVR screened treatments, we observed significantly higher biomasses of invertebrate consumers ($p < 0.003$). Results from our study corroborate the findings of others that grazers are inhibited predominantly by UVB wavelengths (Bothwell et al. 1994, Kiffney et al. 1997a). The response of a small number of taxa (e.g., Rithrogena spp. Drunella spp., and Plumiperla spp.) occurred in a more stepwise manner with the quantity of UVR removed, however, there were no overall significant differences in any invertebrate groups between PAR and PAR+UVA treatments. Although UVR has been demonstrated to indirectly promote algal accrual in shallow flumes (Bothwell et al. 1994, Kelly et al. 2001), no previous studies have reported this response in field investigations.

The sensitivity of lotic invertebrates to UVR can vary, and may respond to a threshold level in UVR intensity (Kiffney et al. 1997b, McNamara and Hill 1999, Kelly et al. 2001). We observed inhibition of most mayfly and stonefly taxa at streambed UVB exposures of >7% above canopy irradiance, or approximately 2.8 kJ m^{-2} d^{-1} (using mean UVB for the experiment). This was only 25% of the threshold reported by Kelly et al. (2001) for chironomids (>11.8 kj m^{-2} d^{-1}), possibly explaining the lack of response by this group in the present study. Similarly, Kiffney et al. (1997b) and McNamara and Hill (1999) observed significant responses by invertebrates using dose rates from artificial lamps (1.6 - 2.7 W/m^2 UVB) that were at least two-fold higher than the highest mid day streambed intensities present in this experiment ($\approx$ 0.66 W/m^2). It is evident that mayfly and stonefly taxa in our study stream are considerably more sensitive to UVR exposure than reported in other systems (see DeNicola and Hoagland 1996, Hill et al. 1997). Possibly the high amounts of shading that occur in old-growth sections of this coastal stream have favored species less tolerant to solar exposure.

Inhibitory effects of UVR on invertebrates decreased downstream in the clear-cut. Increases in DOC downstream along the clear-cut (mean 35% increase) over the first 29 days of the experiment likely reduced effects of UVB on invertebrates at the bottom of the clear-cut. Indeed, invertebrates at the downstream site were most responsive to UVR later in the experiment (i.e. Day 49) when DOC was low and streambed UVB exposures were high. Increases in DOC export from clear-cut catchments immediately following logging (Hobbie and Likens 1973, Meyer and Tate 1983) may mitigate some of the harmful effects of increased UVR exposure to clear-cut streams. However, these effects may be seasonal, as we observed increases in water clarity during dry periods (August and September) resulting in the lowest DOC, and highest UVR exposures to the streambed at the bottom of the clear-cut. Previous research suggests that increased DOC inputs following clear-cutting may also be short lived (Likens et al. 1973, Meyer and Tate 1983), and decline as young forests regenerate (Tate and Meyer 1983). Long-term studies on the effects of clear-cutting on DOC export in the PCE are needed.

The diminished response of invertebrates to UVR at the bottom of the clear-cut may have additionally been influenced by overall declines in UVR-sensitive species (e.g., Drunella spp., Plumiperla spp.) downstream in the clear-cut. Because our small-area manipulations of radiation exposure were colonized by invertebrates drifting from upstream reaches, communities present under our treatments would be heavily influenced by upstream stream reaches. At the top of the clear-cut, UVR-sensitive colonizers would be far more likely to drift into the our UVR-shielded treatments than at our downstream site. The combination of high UVR exposure and increased temperatures that occurred over the 3.2 km clear-cut severely impacted invertebrate communities by the bottom of the clear-cut.

Conclusions

Results from our study clearly demonstrate that increases in solar exposure to clear coastal stream ecosystems alters the productivity and composition of resident communities by increasing both UVR exposure and stream temperature. Negative effects of temperature increases from large area clear-cutting may be particularly severe for benthic invertebrates, and may act in combination with inhibitory effects of UVR to alter community production, composition, trophic dynamics, and diversity. Although effects of increased solar exposure from clear-cutting in the absence of thermal alterations were less severe for communities in our study stream, inhibition by UVR was more pronounced. Effects of increased UVR exposure and temperature potentially interact with alterations in nutrients and DOC to affect benthic algal and invertebrate communities in a complex manner. Significant alterations in epilithic algal species composition and productivity due to increases in solar exposureand nuntrients from clear-cutting may also indirectly influence higher trophic levels. Increases in solar UVR exposure to coastal streams may have considerable effects on benthic communities, particularly if they are accompanied by thermal alterations.

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5. SOLAR ULTRAVIOLET RADIATION AFFECTS MICROHABITAT SELECTION BY JUVENILE COHO SALMON (*Oncorhynchus kisutch*)

Introduction

Ultraviolet radiation (UVR, 280 – 400 nm) is increasingly being recognized as an important factor affecting organisms in freshwater systems (See review by Häder et al. 1998), Declines in coho salmon (*Oncorhynchus kisutch*) stocks throughout the Pacific Northwest (Simpson et al. 1997) have prompted researchers to speculate on the potential for recent increases in solar ultraviolet-B radiation (UVB, 280 - 320 nm) to impact salmonids during their freshwater rearing stage, leading to reduced ocean survivorship (Walters and Ward 1998). Global change scenarios are attractive explainations for population declines because they have occurred over large geographical areas (Beamish et al. 1997,Coronado and Hilborn 1998). Trends in spring-time stratospheric ozone depletion have been worsening over northern regions (Hansen and Chiperfield 1998), with an estimated 20% increase in DNA damaging UVB per decade at mid-northern latitudes (Kerr and McElroy 1993, Kerr 1995). Additionally, human activities such as deforestation, and the effects of climate warming and acid deposition on dissolved organic matter export (the principal attenuator of UVR in freshwater), synergistically act to increase the exposure of freshwater biota to UVR (Schindler 1998, Kelly et al. in Press). Shallow freshwater systems used by rearing coho may therefore be exposed to considerable amounts of biologically damaging UVR.

UVR can have highly negative physiological effects on freshwater vertebrates, with documented impairment of both fish and amphibian species (reviewed by Siebeck et al. 1994). Findings have included effects of UVB on egg survival (Blaustein et al. 1995, Williamson et al. 1997, Novales-Flamarique and Harrower 1999), larval development (Hunter et al. 1979, Blaustein et al 1997), cataracts (Allison 1965, Steuke et al. 1968), skin lesions (Little and Fabacher 1994, Bullock and Coutts 1985), respiratory control (Freitag et al. 1998), and immune system function (Salo et al. 1998). Early life history stages generally appear to be particularly susceptible to damage by UVR, most notably for species with pelagic non-pigmented larval forms (Hunter et al. 1979). For pigmented fish species damage from UVB often occurs with the formation of epidermal lesions (Bullok and Coutts 1985), but recently has also been linked with sub-lethal impairment of immune system response (Salo et al. 1998). Although salmonid eggs incubate under gravel and fry are pigmented upon emergence, juvenile coho potentially receive high exposure to UVR because of their extended rearing period (up to 2 yrs.) in shallow freshwater environments.

Light is an important abiotic factor influencing habitat selection by salmonids (Fausch 1993). Many investigators have demonstrated that juvenile salmonids preferentially select habitat with overhead canopy cover and reduced ambient light (Lister and Genoe 1970, Platts and Nelson 1989, Heggenes et al. 1991). Counter to these findings, reduction in overhead canopy cover from logging can frequently result in greater production of juvenile salmonids, owing to simultaneous increases in primary and secondary production as a food-source for salmonids (Hawkins et al. 1983, Keith et al. 1998). Microhabitat selection and use of in-stream cover following overhead canopy removal is now recognized as an important factor affecting salmonid production (Dolloff 1987, Shirvell 1990, Bugert et al 1991), and may indicate that salmonids compensate for the adverse effects of large-scale habitat alteration through microhabitat selection. Microhabitat requirements of salmonids are nested within complex trade-offs between energy expenditure, feeding, predator avoidance, and inter- and intraspecific competition (Fausch 1984, Dill and Fraser 1984) with ontogenic shifts in habitat preferences over seasons (Baltz et al. 1991). The influence of light on microhabitat selection is further complicated by the ability of juvenile salmonids to detect long-wave UVR (λ_{max}= 360 - 370 nm), and spatially orient to polarized UVR (Hawryshyn et al. 1990, Novales-Flamarique et al. 1992). Thus juvenile coho select light microhabitat for complex reasons including predator avoidance, feeding enhancement, UVR avoidance, orientation, or some combination of these factors.

While other investigations have examined behavioral responses of juvenile coho to light (Faush 1993), none have addressed the potential for negative phototaxis to UVR. I examined the influence of UVR and visible light on microhabitat selection by juvenile coho using in-stream experimental enclosures. Experimental trials were performed on newly emergent coho (May 13 - 16) and juvenile coho two months post emergence (July 19 - 27), to determine if coho taxis response changed after prolonged exposure to sunlight. My experiments were conducted under different cloud-cover conditions to assess how behavioral response varied with ambient solar intensity.

Methods

Qualicum Channel study site

Experiments were conducted in the Little Qualicum River Spawning Channel (49° 17' N, 124°35' W), located in the Naniamo lowlands on the eastcoast of Vancouver Island, British Columbia. The Little Qualicum Channel serves primarily as a spawning habitat for chum salmon (*Oncorhynchus keta*) but it also provides habitat for other incidental wild populations of spawning salmon including coho salmon, chinook salmon (*O. tshawytscha*), and steelhead trout (*O. mykiss*). Coho which spawn in the channel remain there for up to two years before migrating to the river estuary. The channel has no riparian canopy cover. During the experiments, water in the channel had a slightly basic pH (6.9 - 8.0), a conductivity of 92 µS/cm, an alkalinity of 43 mg $CaCO_3$/L, and low nutrient concentrations (≤ 0.02 mg/L^{-1} NO3, ≤ 0.01 mg/L TP). Water transparency to UVR during base flow periods was high, with a mean DOC concentration of 1.3 mg/L. Mean daily water temperature was a maximum of 18.1 °C (range 15.8 - 21.3 °C) on July 26, and minimum 9.6 °C (range 9.9 - 14.9 °C) on May 20.

Behavioral experiment design

Microhabitat selection by juvenile coho was examined in response to modifications of photosynthetically active radiation (PAR, 400 – 700 nm), near ultraviolet radiation (UVA, 320 – 400 nm), and mid ultraviolet radiation (UVB, 280 – 320 nm). Rectangular enclosures (100 x 50 x 10 cm) constructed from UVR transparent plexiglas were placed in the stream to serve as dichotomous light chambers for behavioral trials with juvenile coho (Fig. 5.1). Enclosures were covered on one half (50 x 50 cm) with transparent plexiglas that allowed transmission of full spectrum sunlight (i.e., PAR+UVA+UVB), and on the other half with one of four light treatments, resulting in exposures of either PAR, PAR+UVA, 50%(PAR+UVA+UVB), or PAR+UVA+UVB (control)(Fig. 5.2). A total of four enclosures (one per paired light treatment) were placed adjacent to each other in the channel (separated by 10 cm) to a depth of ≈8 cm, and a flow of ≈35 cm/s. Flow holes (0.5 cm dia.) along the front and rear margins of the enclosures provided water exchange between the enclosure and the channel water to ameliorate any problems associated with heating or depression of dissolved oxygen.

Irradiance

During behavioral trials, solar irradiance was measured hourly over daylight hours

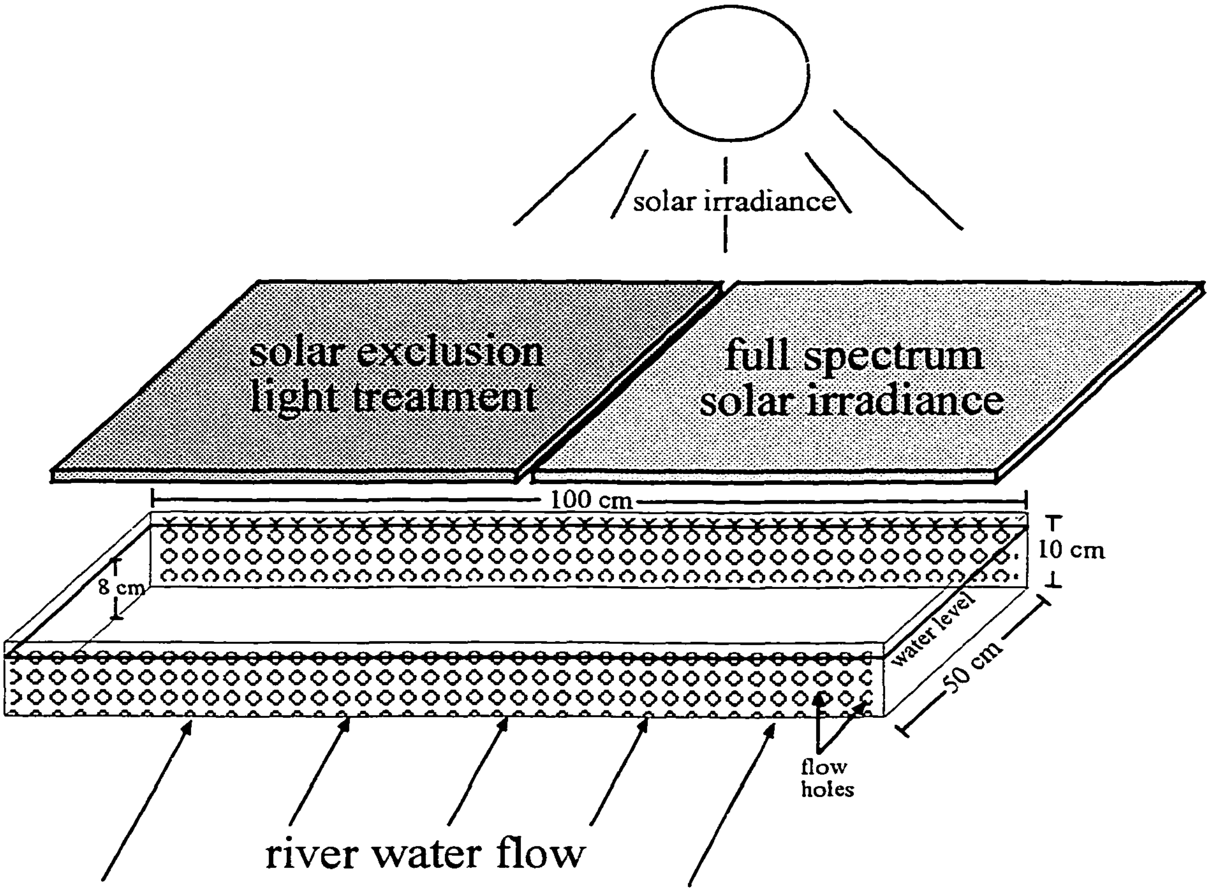

Figure 5.1. Schematic of the in-stream dichotomous experimental enclosures used for the juvenile coho behavioral trials at Qualicum Channels. Enclosures were covered on one side with plexiglas allowing penetration of full spectrum sunlight, and on the other side with one of four solar exclusion treatments. Spectral transmission of solar exclusion treatments are shown in Fig. 5.2.

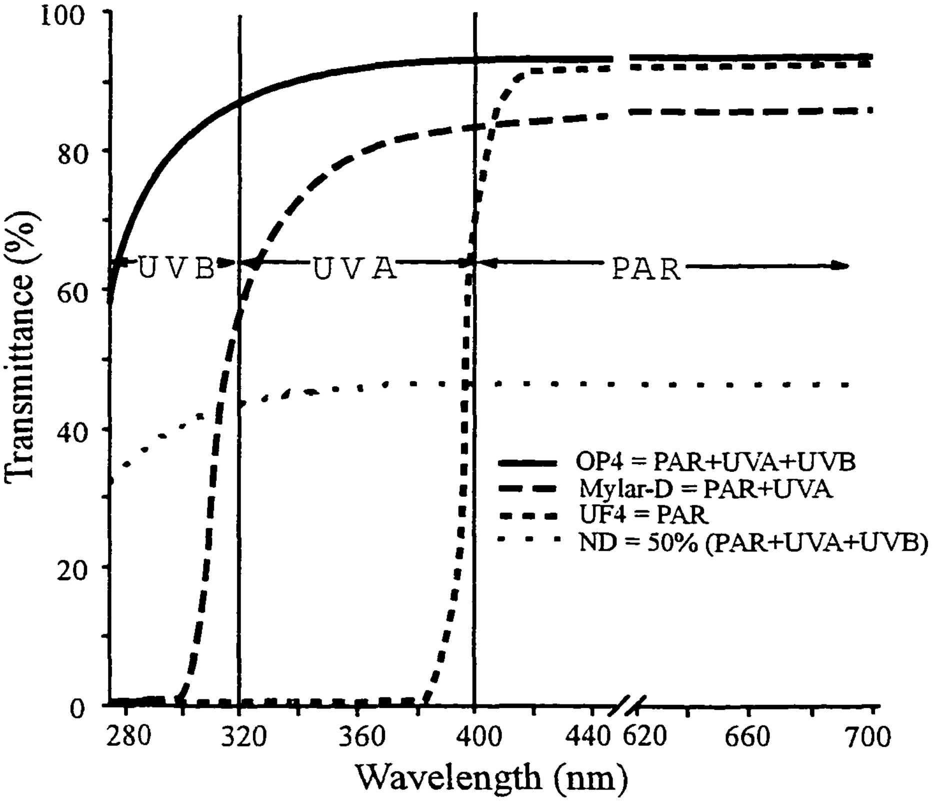

Figure 5.2. Transmittance properties of the four plastic light filters used in the experimental trials at Qualicum Channels through the mid ultraviolet radiation (UVB, 280 - 320 nm), near ultraviolet radiation (UVA, 320 - 400 nm), and photosynthetically active radiation (PAR, 400 - 700 nm) spectral ranges. The filters used were OP4 acrylic sheets (Cyro, 4.7 mm thick, 70 - 90% transmittance throughout the UVB and UVA), UF4 acrylic sheets (Rohm and Hass; 6.4 mm thick; 50% transmission at 398 nm), Mylar-D (Du Pont; 0.1 mm thick, 50% transmission at 318 nm), and neutral density (ND) fine mesh window screening on OP4 acrylic sheets

with an Optronics OL-752 spectroradiometer (Optronic Instruments, Orlando, FL, USA). Scans were made at 2 nm intervals between 280 and 700 nm recorded in W m^{-2} nm^{-1}, and converted to mol m^{-2} hr^{-1} of PAR, UVA and UVB using Planck's equation. Diffuse attenuation coefficient (K_d) and light transmittance (%) to mid (4 cm) and bottom (8 cm) enclosure depths for PAR, UVA and UVB were calculated from absorbance measurements of river-water collected during each trial. Absorbance scans of river-water were made at 0.5 nm intervals between 280 and 700 nm using a Cary 50 scanning spectrophotometer (Varian Instruments, Walnut Creek, CA, USA) equipped with a 2 cm quartz cuvette. Spectral transmittance of solar exclusion filters used in the experiment were also quantified spectrophotometrically over PAR and UVR wavelengths.

Behavioral experiment

Forty juvenile coho were placed in each of the four enclosures and the chambers were covered with one of the four light treatment combinations. Coho were free to move between the two light treatments of each chamber. Coho were allowed to adjust to the treatments overnight, with observations on habitat selection commencing the next morning. The number of coho occupying each treatment was enumerated hourly between 8:00 and 19:00 by photographing the chambers from ≈10 m distance using a Tamron 300-700 mm zoom telephoto lens. Light treatments were initially assigned at random to the four enclosures, and then moved to the adjacent enclosure over the next three days so that each chamber was exposed to the four light treatment combinations for a single day.

Experimental trials were conducted on two age classes of coho, recently emerged fry at age 0 (May 13-16, 1997), and juveniles at age two months (July 19 - 27, 1997). Age 0 coho fry were obtained from the nearby Big Qualicum River hatchery (Department of Fisheries and Oceans, Canada). Coho eggs had been incubated in shallow (2 cm) indoor flowing trays under dimly lit conditions. The fry had nearly finished absorbing their yolk sac, coinciding with the time that coho normally emerge from the gravel to start feeding in the river (Lister and Genoe 1970). Age 2 mo. coho were collected from Qualicum Channels using a beach seine, and transferred into enclosures. Coho were approximately 60 mm or 2.5 g at this time.

Statistical analyses

Goodness of fit analyses were used to test for light microhabitat selection by juvenile coho with the assumption that the distribution of fry would be 1:1 between control

(PAR+UVA+UVB) and treatments (either PAR, PAR+UVA, 50%[PAR+UVR], or PAR+UVA+UVB) if solar radiation had no effect (Zarr 1983). Mean daily counts for each treatment, calculated from the average of all hourly counts, were pooled over the four days in the Chi squared goodness of fit (χ^2) analysis. A heterogeneity Chi squared analysis was used to test if the pooled days were from a homogeneous population.

Results

Irradiance

Mean hourly fluxes of PAR, UVA and UVB during cloudless days were very similar between May and July experimental trials (ANOVA, Student Newman-Keul's test [SNK], $p > 0.05$), likely resulting from their equivalent positioning on either side of the spring equinox (Fig. 5.3). Hourly irradiance ranged between 2 and 7 mol m^2 hr^{-1} PAR, 40 and 350 mmol m^{-2} hr^{-1} UVA and 1.6 and 17 mmol m^{-2} hr^{-1} UVB, with peak solar flux at 13:00. Mean hourly PAR, UVA and UVB fluences on cloud-covered days were 57, 50 and 46% lower (SNK, $p < 0.05$), respectively, than on cloudless days. Water transparency to UVR in enclosures increased marginally between the May and July experimental trials due to small decreases in dissolved organic matter (1.75 to 1.16 mg/L) (Table 5.1). Kd_{UVB} decreased from 10.1 on May 18, to 8.3 by July 26, resulting in a 7.0% increase in UVB penetrating to the bottom of the enclosures (44.6 to 51.6%).

Coho behavioral trials

Coho response to light manipulations during cloudless high light conditions was

Table 5.1. Diffuse attenuation coefficients (K_d), and light transmittance to mid ($T_{4\ cm}$) and bottom ($T_{8\ cm}$) enclosure depths for mid-ultraviolet radiation (UVB), near-ultraviolet radiation (UVA) and photosynthetically active radiation during the two experimental trials at Qualicum Channels.

	May 18, 1997			July 26, 1997		
Variable	UVB	UVA	PAR	UVB	UVA	PAR
Kd (m)	10.1	4.7	0.9	8.3	4.2	0.5
T4 cm (%)	66.7	83.0	96.5	71.8	84.4	98.2
T8 cm (%)	44.6	69.1	93.1	51.6	71.5	96.5

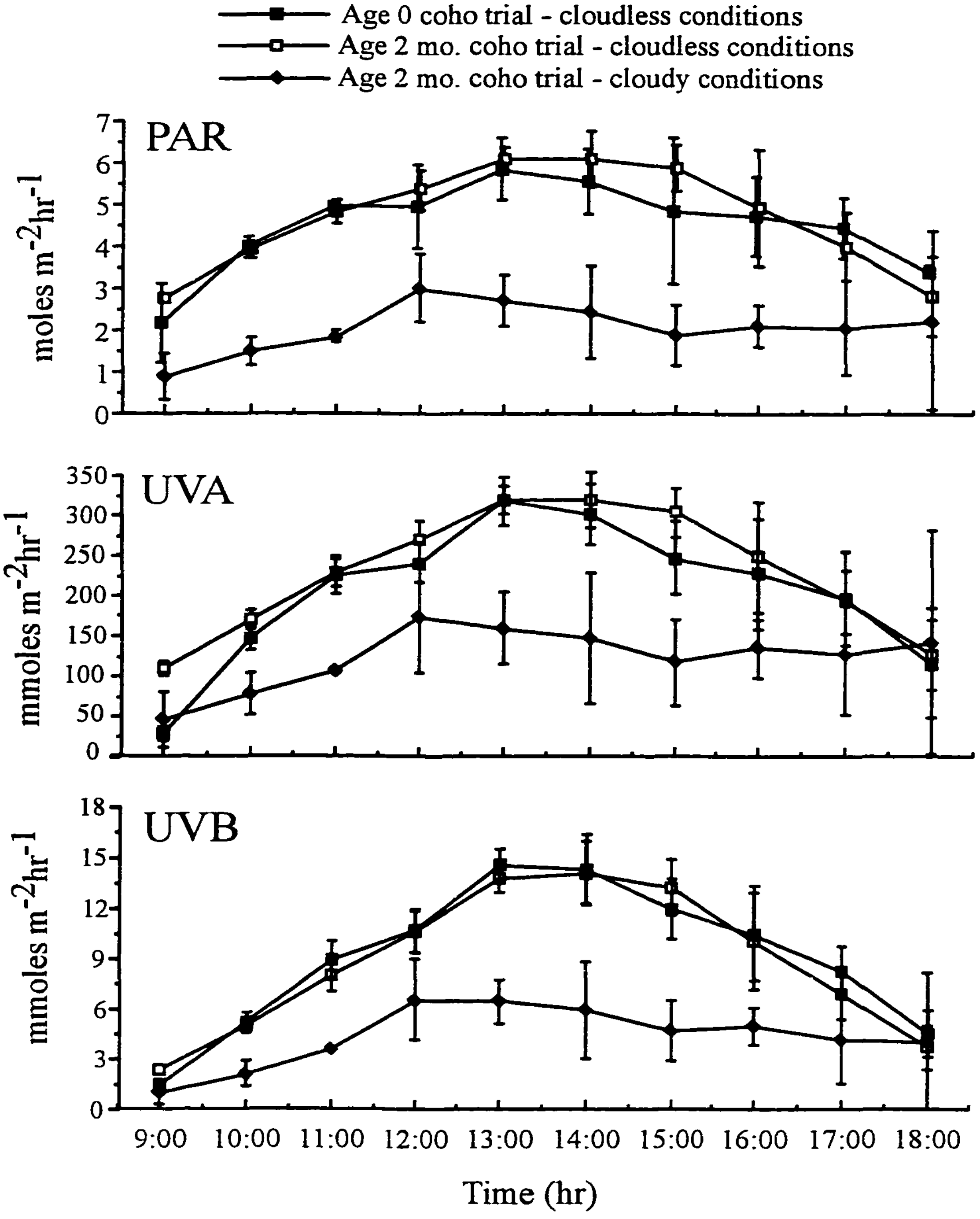

Figure 5.3. Mean hourly flux densities (± 1 SD, n = 4) during daylight hours of photosynthetically active radiation (PAR, 400 - 700 nm), near-ultraviolet radiation (UVA, 320 - 400 nm), and mid-ultraviolet radiation (UVB, 280 - 320 nm) during juvenile coho behavioral trials at Qualicum Channels. Trials run at emergence occurred between May 13 - 16, 1997, and trials run 2 mo. post-emergence occurred between July 19 - 27, 1997.

similar for both age 0 fry and age 2 mo. juveniles (Fig. 5.4). The strongest preference was shown for PAR (χ^2, $p < 0.001$), and 50%(PAR+UVA+UVB) (χ^2, $p < 0.005$) treatments during cloudless trials. For example, age 0 coho frequented PAR treatments an average of 49% more than PAR+UVA+UVB controls. The response was even more pronounced in age 2 mo. coho, most notably for 50%(PAR+UVA+UVB), which was selected by an average of 79.8% of coho (SNK, $p < 0.001$) in the enclosures. Coho also showed a slight preference for PAR+UVA (mean 66%) over PAR+UVA+UVB. While this suggested some negative taxis to UVB, the response was marginally non-significant (χ^2, $p < 0.1$), indicating that the primary negative taxis response of coho to UVR was to UVA. In age 0 fry, negative UVR taxis became more apparent over the day, with relatively small differences between treatment and controls from 9:00 to 10:00 (mean 9:00, 61.8%), quickly developing over the next two hours (mean 11:00, 72.9%). The Age 2 mo. juveniles established their preference for UVA shielded environments earlier in the day (between 9:00 and 10:00). UVR taxis by either age class coho did not diminish towards the evening as solar intensities decreased as they did during morning hours. Under reduced solar intensities from cloud-cover coho showed no taxis response. No significant differences were found for coho frequenting any of the light manipulations (χ^2, $p > 0.25$) during trials conducted on cloudy days.

Discussion

My results demonstrate that UVR, particularly UVA, can significantly influence microhabitat selection by juvenile coho salmon. Under cloudless conditions coho actively avoided exposure to high levels of both UVA and PAR in shallow in-stream enclosures. Coho prefered habitats with no UVR or with full spectrum intensity reduced by 50%. On cloudy days, when sunlight intensity was much lower, juvenile coho showed no preference for any of the spectral modifications presented to them.

The retina of bony fishes possesses four types of light-sensitive cones for detecting color in bright light. One of these cones is most sensitive to ultraviolet wave lengths (Hawryshyn 1992). The sensitivity of the ultraviolet cone varies with fish species, but for rainbow trout (*Oncorhynchus mykiss*) which is closely related to coho, the peak sensitivity is in the middle of the UVA spectral band (λ_{max}= 360-370 nm) (Browman et. al. 1994). Several workers have shown that the ultraviolet photoreceptor mechanism contributes to the detection of prey during visually guided foraging behavior (Bowmaker and Kunz

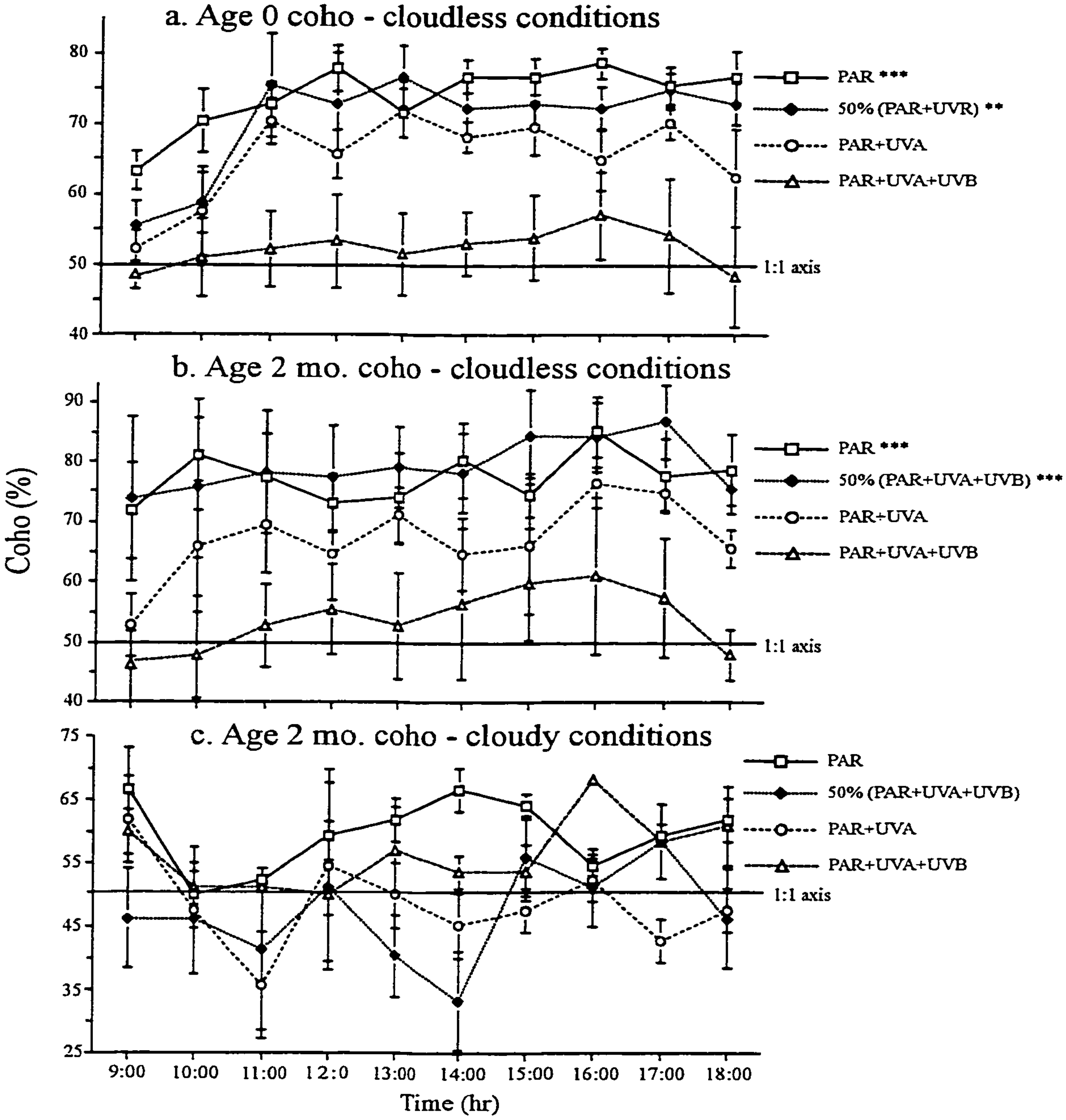

Figure 5.4. Percent divergence from a 1:1 expected ratio of juvenile coho (mean ± SD, n=4) occupying light treatments over daylight hours during three different behavioral trials in Qualicum Channels. All light manipulations were paired against a full spectrum sunlight control (PAR+UVA+UVB). Trials were conducted on, a) age 0 coho (May 13-16, 1997) during cloudless high UVR days, and on age 2 mo. coho (July 19 - 27, 1997) on both b) cloudless high UVR and c) cloudy low UVR days. Light manipulations included photosynthetically active radiation only (PAR, 400 - 700 nm), PAR+UVA, PAR+UVA+UVB, and a neutral density filter which allowed 50% of combined PAR+UVA+UVB. *** = $P<0.001$ ** = $P<0.01$ * = $P<0.05$

1987, Douglas and Hawryshyn 1990, Loew and McFarland 1990, Browman et. al. 1994) and that the ability of the UV-cone to discriminate polarized light is central to prey detection in salmonids (Hawryshyn 1992, Browman et al. 1994). Polarized light in the UV region has also been implicated in the navigation ability of sea-going salmonids (Hawryshyn et al. 1990). My observations suggest that juvenile coho also use the UV-sensitive cone to also to select habitats with low levels of UVA radiation, a new function of UV visual sensitivity in salmonids.

The findings I report here indicate that in addition to serving vital roles in prey detection and navigation, the UV retinal cones might enable the fish to avoid excessive exposure to UVR. When exposed to bright sunlight, coho prefer habitats where UVA and UVB have been excluded but visible light (PAR) remained undiminished. They also show a slight preference for habitats with only UVB excluded. Together these observations clearly implicate the UV-cones, with a demonstrated maximal response in the middle UVA (~365 nm) extending down into the near UVB (310 nm) (Hawryshyn 1992). Since visible light is an important part of the spectrum used by visual predators for detection of movement and locating larger prey (Hawryshyn 1992), it seems unlikely that the response observed was associated exclusively with predator avoidance. Second, I found no UVR avoidance behavior when experiments were conducted on cloudy days when UVB would likely be insufficient to induce photodamaging effects. For instance, Little and Fabacher (1994) only observed formation of epidermal lesions in Lahontan cutthroat trout (*Oncorhychus clarki henshawi*) when irradiances were more than six times higher (357 $\mu W/cm^2$) than my mean mid-day irradiance on cloudy days (61.7 μW/cm2). Although PAR was reduced by cloud cover during these trials, mid-day intensities of visible light would still likely be sufficiently high to allow effective visual detection by predators. Because UVB can penetrate shallow stream environments at biologically significant doses (Kiffney et al. 1997, Kelly et al. 2001), another benefit of UVR avoidance might be to minimize photodamaging effects of UVB. We also observed similar responses to UVR by by age 0 and two month coho, suggesting that fish do not acclimate to high solar intensity following emmergence.

While avoidance of high light environments by stream-dwelling salmonids has long been known, it has been thought to be principally a predator avoidance mechanism with fish taking cover under bank ledges, logs and rootwads (Lister and Genoe 1970, Shirvell 1990). In the absence of overhead cover, coho have been shown to select deeper water habitats (Gibson and Power 1975, Bugert et al. 1991), presumably for the same reason.

Other work has suggested that refuge from high current velocity might be the dominant reason why coho prefer in-stream cover (Fausch 1993). However, our experiments suggest that selection of deeper water may also be to avoid high UVR. Similarly, Williamson et al. (1997) found that yellow perch (*Perca flavescens*) selected deeper egg-laying depths in more transparent lakes, with a demonstrated increase in egg survivorship in response to this behavior. The response of juvenile coho to UVR indicates that it may contribute to the selection of microhabitats in streams, with possible implications for coho survival.

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6. GENERAL CONCLUSIONS

Clear-cut logging, and removal of riparian canopy, can result in considerable increases in solar ultraviolet radiation (UVR, 280 - 400 nm) flux to streams (Holtby et al. 1988, Hetrick et al. 1998, Clare 2000). Logging can also increase UVR exposure to streams by altering the export of dissolved organic matter (DOM) from the terrestrial catchment (Hobbie and Likens 1973, Meyer and Tate 1983), the principle attenuator of UVR in oligotrophic freshwater systems (Scully and Lean 1994). Riparian buffer strips have been adopted to mitigate the effects of canopy removal (Gregory et al. 1991, Osborne and Kovacic 1993), however, the width and composition of prescribed buffer strips can vary considerably, and provide variable protection to the stream from harmful UVR. Although some studies have examined the effects of increased sunlight intensity on stream communities following canopy removal (Shortreed and Stockner 1983, Robinson and Rushforth 1987, DeNicola et al. 1992), my experiments are the first to specifically examine the effects of elevated UVR on streams due to canopy removal.

It is apparent from my research that increases in solar exposure to streams from either direct canopy removal or declines in dissolved organic matter (DOM) impact stream communities. I observed alterations in biomass, species composition, and diversity of benthic communities due to increased UVR. Increased UVR exposure to streams affected riverine food-webs in a complex manner, and clearly altered community interactive processes such as herbivory. Effects of UVR also varied across the spectrum, as previously reported (Bühlmann et al. 1987, Cullen et al. 1992), with near-ultraviolet radiation (UVA, 320-400 nm) predominantly inhibiting benthic algal accrual, and mid-ultraviolet radiation (UVB, 280-320 nm) having the most pronounced effects on invertebrate assemblages. Differential attenuation of photosynthetically active radiation (PAR, 400-700 nm), UVA (320-400 nm), and UVB (280-320 nm) radiation by riparian canopies and DOM also complicated the effects of UVR exposure on stream ecosystems, and led to seasonal trends in the inhibitory effects of UVR.

DOM effects on benthic communities

Deforestation (Meyer and Tate 1983, Hill 2000) and other environmental perturbations such as climate warming and acid deposition (Schindler et al. 1996, Donahue et al. 1998) can indirectly increase UVR exposure to streams by altering the export of dissolved organic matter from the terrestrial catchment. Long-term changes in DOM export following logging in watersheds of British Columbia have yet to be documented for the Pacific Coastal Ecozone (PCE).

Results from my DOM experiment at the Experimental Troughs Research Apparatus (Chapter 2) showed that attenuation of UVR by DOM strongly influenced the colonization dynamics and trophic interactions of algal and invertebrate assemblages in shallow lotic ecosystems. My findings also suggest the existence of a threshold UVR exposure range. Increasing mean daily UVB from 11.8 to 23.8 kJ $m^{-2} d^{-1}$ (27 to 55% ambient) and UVA from 444 to 640 kJ $m^{-2} d^{-1}$ significantly decreased the abundance of colonizing invertebrates and increased algal biomass accrual predominantly through its effects on grazers. No significant impacts were seen leading up to this level, but once this level was exceeded biological effects were consistently apparent. This threshold level occurred in my experiment between 2 and 5 mg/L DOM, or between 0.8 and 2 mg/L DOC, expressed in units of C. I predict that streams with DOM concentrations <2 mg/L DOC could be particularly sensitive to UVR and potentially most negatively affected by future increases in UVR exposure as a result of ozone depletion or DOM decreases.

The effects of canopy removal on benthic communities

Riparian zones surrounding streams are transitional interfaces between aquatic and terrestrial systems that mediate inputs of energy and allochthonous materials to streams (Gregory et al. 1991). Alteration of the riparian canopy can considerably increase light exposure and autotrophic production in streams (Stockner and Shortreed 1976, Hetrick et al. 1998). Clear-cutting frequently results in large increases in solar exposure to streams either by direct removal of riparian canopy (Shortreed and Stockner 1983, Hetrick et al. 1998a), or indirectly by openings in the canopy from blow-down of riparian strips, landslides, erosion, debris flows, and floods (Ryan and Grant 1991). Although increased solar exposure is commonly cited as a major factor contributing to changes in resident biota following clear-cutting (Newbold et al. 1980, Carlson et al. 1990, Robinson and Rushforth 1987, Hetrick et al. 1998), negative impacts have been mainly attributed to associated increases in stream temperature (Lynch et al. 1984, Holtby 1988). Increases in solar ultraviolet radiation may interact synergistically with increases in water temperature to affect stream communities.

Results from two in-stream experiments (Chapter 3 and 4) demonstrate that shading by riparian canopies strongly decreases the effects of UVR on stream communties, and minimizes fluctuations in UVR flux to the streambed from seasonal changes in water level and DOM. In the Little Qualicum River (Chapter 3), canopy shading prevented UVR effects on benthic communities, mainly by reducing impacts on invertebrates which indirectly affect algae. Under reduced canopies, higher UVA radiation inhibited algal accrual, but had little effect on algal community composition. The biomass of several invertebrate taxa (e.g., *Dicosmeocus* spp., Limnephillidae) were inhibited by both UVA and UVB radiation, and community diversity was reduced. Increasing UVR in clear-cut stream reaches caused shifts in species assemblages of both invertebrates and algae in the Salmon River (Chapter 4). These effects were amplified downstream, due to the combined effects of increased UVR and temperature. Mayflies and stoneflies were significantly reduced in clear-cut reaches, and community diversity decreased.

These studies clearly demonstrate that increases in solar exposure to streams alters the productivity and composition of benthic algal and invertebrate communities by increasing both UVR exposure and stream temperature. Reductions in grazers from increases in UVR exposure or thermal alterations due to canopy removal may increase the ratio of autotrophic to heterotrophic production in streams, with potentially confounding effects to higher trophic levels.

UVR effects on higher trophic levels

Declines in coho salmon (*Oncorhychus kisutch*) populations throughout the Pacific Northwest coast have prompted researchers to speculate on the potential for recent increases in solar UVB radiation to impact salmonids during their freshwater rearing stages, leading to reduced survivorship during later ocean rearing stages (Walters and Ward 1998). UVR can have negative physiological effects on freshwater vertebrates, impairing of both fish and amphibian species (Siebeck et al. 1994). Early life history stages particularly susceptible to damage by UVR (Hunter et al 1979). Juvenile coho may be particularly sensitive to UVR exposure because of their extended rearing period (up to 2 yrs.) in shallow freshwater environments.

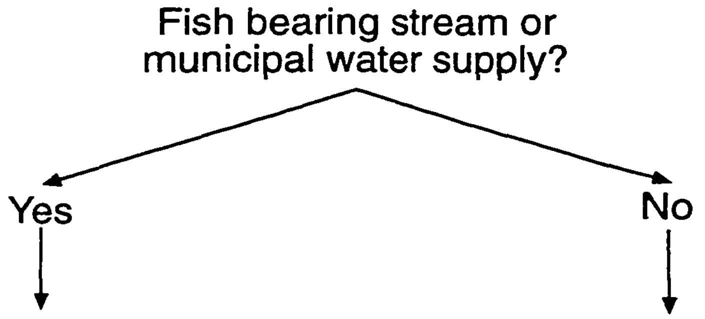
Microhabitat selection by juvenile coho was strongly influenced by high intensities of UVR and PAR in experimental enclosures (Chapter 5). Under high solar intensities (i.e., cloudless conditions) in shallow water, coho avoided wavelengths of both UVA and PAR. They were unresponsive to all light manipulations under low solar intensities (i.e.

cloud-cover). Deeper water conditions (i.e., pools) were not tested by my study, although this would have reduced solar intensity. Coho may use their ability to detect UVA to avoid high intensities of photodamaging UVB. These results suggest that the use of overhead and in-stream cover by coho may also be to avoid UVR, rather than exclusively to avoid predators as previously thought. Increases in UVR exposure to freshwater systems from canopy removal or alterations in DOM could affect habitat use by coho, and has important implications for future management of habitat for coho and other salmonids.

Links to forestry practices in British Columbia

My research clearly demonstrates the importance of preserving riparian corridors for protecting stream benthic communities and salmonids from harmful solar UVR exposure and temperature increases, particularly during the low flow periods of late summer. In British Columbia, the management practices for riparian zones during forest harvesting are designated by the Forestry Practices Code (FPC) (British Columbia Ministry of Forests 1995). Guidelines of the FPC prescribe riparian management areas (RMAs) of varying widths (0-100 m), and allow variable harvesting practices within RMAs (Fig. 6.1), depending upon the width of the stream and whether the stream is a municipal water supply and/or fish bearing. Based on these guidelines RMAs may have an unharvested riparian reserve zone immediately adjacent to the channel (up to 70 m), and an outer riparian management zone in which harvesting of all merchantable timber may occur. Although fairly large reserve zones are left around larger fish bearing rivers, RMAs around smaller streams and non-fish bearing rivers may be subject to little protection from increases in solar exposure. For example, Clare (2000) observed approximately an 8.3 fold increase in light exposure to a British Columbia central-interior stream following timber harvesting with a 30 m riparian management zone. My research suggests that increases in solar exposure of this magnitude can have severe effects for resident stream communities, particularly during low-flow summer months.

Riparian corridors are also important areas for regulating DOM export to waterbodies (Hill 2000). Meyer and Tate (1983) demonstrated that direct contributions of riparian leaf litter to the streams accounted for a large portion of DOM in riverwaters in Coweeta basin. Mature forests also contributed larger amounts of detritus to soil pools compared with younger regenerating forests, resulting in greater export of DOM from the terrestrial



Average Channel Width	Reserve Zone	Total RMA
> 20 m	50 m	70 m
>5-20 m	30 m	50 m
1.5-5 m	20 m	40 m
<1.5 m	0 m	30 m

Average Channel Width	Reserve Zone	Total RMA
> 3 m	0 m	30 m
≤ 3 m	0 m	20 m

Figure 6.1. Specified minimum riparian management area (RMA) widths and reserve zone for the six different stream classifications.

catchment (Tate and Meyer 1987). My research demonstrates that even small changes in DOM from clear-cutting could result in considerable changes to stream communities, particularly if these changes occur over ranges of 1-2 mg/L DOC. Other human-linked environmental perturbations such as acid deposition and climate warming may also decrease DOM export (Schindler et al. 1996, Yan et al. 1996, Donahue et al. 1998). Currently little is known about the long-term changes in DOM export in logged watersheds of the PCE.

Potential areas of future investigation

There is an obvious need for investigation into the long-term effects of clear-cut logging on DOM export dynamics in coastal forests. It is evident from my DOM experimental manipulation study (Chapter 2) that the role of DOM in attenuating solar UVR is of critical importance in protecting benthic communities. In-stream studies on Vancouver Island (Chapters 3 and 4) also demonstrated that even small seasonal declines in DOM resulted in large increases in UVR exposure to the streambed, and pronounced UVR effects on communities in open canopied channels.

Future research is needed to develop models for predicting changes in solar exposure to streams from logging. Models will have to incorporate forest composition, channel width, orientation, river depth, and forest harvesting practices. The models will provide a framework for evaluating RMA guidelines, and design buffer strip policies that adequately protect stream ecosystems from negative effects increased solar exposure.

I have also demonstrated that UVR intensity may affect habitat selection by juvenile salmonids. Research into the physiological effects of UVR on salmonid populations, and comparison of stock success between watersheds differing in DOM, may provide further insight into the potential for UVR to impact salmonid populations.

My research has demonstrated that increases in solar exposure to coastal streams in British Columbia can have pronounced negative effects on aquatic communities. Vancouver Island watersheds are unlike inland regions due to their low storage of snowpack, and thus very low water levels and DOM during summer months. Research in other regions would provide useful insight into the applicability of my findings on a more widespread geographical range. Gradients of increasing DOM generally occur northward and westward in British Columbia. This may decrease the effects of increases in UVR exposure to streams from canopy removal and seasonal variations in stream depth.

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