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EFFECTS OF UVB RADIATION ON ECOSYSTEMS OF SELECTED LAKES IN THE CANADIAN HIGH ARCTIC

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Abstract

Two studies on the effects of enhanced ultraviolet-B radiation (UVB; 280 – 320 nm) on planktonic organisms of Canadian High Arctic lakes are presented. In the first study, the long-term effects of a moderate increase in UVB levels on the planktonic community of a lake were evaluated using *in situ* mesocoms. Four mesocosms (3 m square and 3 m deep) were placed in Two Basin Lake, a small lake (14.2 ha) located on Ellesmere Island (79°55.5'N, 84°40'W; Nunavut, Canada). For 27 days, two mesocosms were exposed to full sunlight (including ambient UVB) while two others were exposed to sunlight plus artificially enhanced UVB. Chlorophyll *a*, zooplankton mean length and carbon allocation into macromolecular constituents were not affected by enhanced UVB. Phytoplankton productivity displayed diverse and inconsistent responses to enhanced UVB. Picocyanobacteria abundance decreased in the enhanced UVB mesocosms, but only at the surface. Enhanced UVB generally increased heterotrophic bacterial abundance and activity. Heterotrophic nanoflagellates and zooplankton abundances increased in the enhanced UVB treatment after 14 days. The cladocerans and rotifers were positively affected by UVB, while the copepods were negatively affected. The high levels ($\geq$ 5 mg L^{-1}) of dissolved organic carbon (DOC) in this lake combined with vertical mixing generally protected the planktonic community from direct damage by enhanced UVB. It is hypothesized that UVB may have indirectly stimulated the microbial food web and the rest of the food chain through increased photodegradation of high molecular weight refractory dissolved organic matter into more bioavailable nutrients.

In the second study, the short-term (2 to 24 h) effects of enhanced UVB on carbon uptake rates, photosynthetic fractionation into three size classes (picoplankton [0.2 - 2 μm], nanoplankton [2 - 20 μm] and netplankton [> 20 μm]) and carbon assimilation into the four main end-products (low molecular weight metabolites [LMW], lipid, polysaccharide and protein) were assessed for nine lakes located near Resolute (74°15'N, 94°50'W) on Cornwallis Island (Nunavut, Canada). These lakes have low DOC levels ($\leq$ 2 mg L^{-1}). For each lake, ^{14}C-inoculated water samples were exposed to 6, 25, 50 and/or 100% surface irradiance levels (E_o) under natural solar radiation (including ambient UVB) or solar radiation plus artificially enhanced UVB. Enhanced UVB inhibited photosynthesis in all nine lakes, except Barren Lake. UVB effects generally depended on the irradiance treatment and duration of incubation, with rapid kinetics of inhibition at $\geq$ 50% E_o and usually no or little effects detected at 6%E_o. The relative contribution of picoplankton to productivity decreased or was unaffected after exposure to enhanced UVB levels while the relative contribution of netplankton increased. The proportion of carbon fixed by nanoplankton showed no consistent trend to UVB. For carbon allocation, the proportion of carbon allocated into protein decreased with exposure to enhanced UVB while that of LMW usually increased. Enhanced UVB decreased the proportion of carbon allocated into polysaccharide in some lakes, but had no effects in others. The relative allocation into lipid was generally unaffected or slightly higher by enhanced UVB. This study suggest that enhanced UVB could be detrimental to phytoplankton in low-DOC lakes by increasing photosynthetic inhibition, causing a shift towards more resistant species/cell sizes and changing their biochemical composition.

Résumé

Deux études sont présentées sur les effets d'une augmentation des rayons ultraviolets-B (UVB; 280 –320 nm) sur les organismes planctoniques des lacs de l'Extrême-Arctique Canadien. Dans la première étude, les effets à long-terme d'une augmentation modérée des rayons UVB ont été évualué sur la communauté planctonique à l'aide d'aménagement d'enceintes dans un lac. Quatres enceintes (3 m^2 et 3 m de profondeur) ont été installé au lac Two Basin, un petit lac (0.14 km^2) situé sur l'île d'Ellesmère (79°55.5'N, 84°40'W; Nunavut, Canada). Durant 27 jours, deux enceintes ont été exposé à la lumière incidente solaire (incluant UVB) pendant que deux autres enceintes ont été exposé à la lumière solaire augmentée avec des rayons UVB de façon artificielle. Chlorophylle *a*, la taille moyenne du zooplankton et la répartition du carbone en macromolécules n'ont pas été affecté par l'augmentation des rayons UVB. La productivité du phytoplancton a démontré des résultats irréguliers et peu cohérents avec l'augmentation des rayons UVB. L'abondance du picoplancton a diminué dans les enceintes exposés à une augmentation des rayons UVB, mais seulement à la surface. UVB a généralement augmenté l'abondance et l'activité des bactéries hétérotrophes. L'abondance des nanoflagellés hétérotrophes et des zooplanctons a augmenté après 14 jours dans les enceintes exposés à une augmentation des rayons UVB. Les cladocères et les rotifères ont été affecté positivement par UVB tandis que les copépodes ont été affecté négativement. Les concentrations élevées ($\geq$ 5 mg L^{-1}) de carbone organique dissous (COD) dans ce lac et le brassage vertical ont généralement protégé les organismes planctoniques des effets directes des rayons UVB. Il est suggéré que l'augmentation des rayons UVB a stimulé indirectement la communauté microbienne et le reste de la chaîne alimentaire avec une augmentation de la photodégradation de la matière réfractive organique dissous de grande masse moléculaire en plus petits éléments nutritifs.

Dans la deuxième étude, les effets à court-terme (de 2 à 24 heures) d'une augmentation des rayons UVB ont été évalué sur les taux d'incorporation du carbone par le phytoplancton, sur la répartition de la productivité du phytoplancton en trois tailles cellulaires (picoplancton [0.2 –2 μm]; nanoplancton [2 –20 μm] et netplancton [> 20 μm]) et sur la répartition du carbone dans les quatres classes principales de biomolécules (métabolites de petite masse moléculaire, lipide, polysaccharide et protéine) pour neuf lacs situé près de Resolute (74°15'N, 94°50'W) sur l'île de Cornwallis (Nunavut, Canada). Ces lacs ont des petites concentrations de COD ($\leq$ 2 mg L^{-1}). Pour chaque lac, des échantillons d'eau inoculés avec du carbone radioactif (C^{14}) ont été exposé à 6, 25, 50 et/ou 100% de la radiation incidente (E_o) solaire (incluant UVB) ou solaire augmentée avec des rayons UVB de façon artificielle. L'augmentation des rayons UVB a diminue la photosynthèse pour tous les lacs, sauf le lac Barren, avec généralement une inhibition rapide à $\geq$ 50%E_o et peu ou pas d'effets à 6%E_o. La contribution relative du picoplancton à la productivité a diminué ou n'a pas été affecté par l'augmentation des rayons UVB tandis que celle du netplancton a augmenté. La proportion de carbone incorporé par les nanoplanctons a été affecté par UVB de façon incohérente entre les lacs. La proportion de carbon incorporé en protéine a diminué avec une augmentation des rayons UVB alors que celle des métabolites de petites tailles a augmenté. L'augmentation des rayons UVB a diminué la proportion de carbone répartie en polysaccharides pour certains lacs mais pas

pour les autres. La répartition relative de carbone en lipide n'a généralement pas été affecté ou a augmenté légèrement avec UVB. Les résultats de cette étude suggèrent que l'exposition à une augmentation des rayons UVB pourraient être néfaste aux populations phytoplanctoniques des lacs ayant des concentrations faibles en COD, en causant une diminition de la photosynthèse, un changement vers des espèces ou tailles cellulaires plus résistantes et un changement dans la composition biochimique.

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General Introduction

This general introduction gives the thesis rationale, an overview of the thesis and a summary of a previous published review (Perin and Lean 2004) of the literature on the influence of stratospheric ozone depletion and climate change on ultraviolet-B radiation (UVB; 280 – 320 nm) and its effects on aquatic systems, especially for Arctic freshwaters. This provided up to date information following earlier reviews by Vincent and Roy (1993), Häder (1994), Häder *et al.* (1998), and Hessen (2002). Reviews on the processes controlling stratospheric ozone depletion and the trends of stratospheric ozone depletion are provided by the World Meteorological Organization (e.g., 2003), Solomon (1999), and Staehelin *et al.* (2001). Reviews on the impact of climate change, including Arctic ecosystems, are provided by Schindler (2001) and ACIA (2004, 2005).

Stratospheric ozone depletion

Ozone, which consists of three oxygen atoms bound together, is a reactive gas naturally present in the Earth's atmosphere. Approximately 90% of all ozone is found in the stratosphere (a region between 10-15 to 35-50 km above the Earth's surface), with a peak concentration at an altitude of about 25 km known as the ozone layer (Staehelin *et al.* 2001; WMO 2003). The other 10% is tropospheric ozone, a serious air pollutant over many cities, which can cause health problems for humans and also affect plants and animals. Ozone concentration in the stratosphere varies greatly with location on time scales that range from daily to seasonal as well as with latitude where the ozone layer is naturally thickest near the poles and thinnest at the equator (WMO 2003).

Under normal conditions (i.e., in an unpolluted atmosphere), global ozone concentration in the stratosphere remains relatively constant and there is generally a balance between the chemical processes that produce and destroy stratospheric ozone (WMO 2003). However, since the mid-1970s, there has been depletion of the stratospheric ozone with the emissions of industrial gases containing chlorine (e.g., chlorofluorocarbons, carbon tetrachloride, methyl chloroform) or bromine into the atmosphere (e.g., halons and methyl bromide; Molina and Rowland 1974; Rowland 1990; Solomon 1999). Although the ozone-depleting gases are present throughout the stratosphere, ozone depletion has been most important over Polar Regions (especially over Antarctica). This is principally due to the presence of polar stratospheric clouds (PSCs), which greatly increase the abundance of the most reactive halogen gases (e.g., chlorine monoxide [ClO]) that can chemically destroy great amount of ozone molecules through a series of catalytic reactions (e.g. Austin *et al.* 1992; Austin and Butchart 1994; Solomon 1999). PSCs require stratospheric temperatures below –78 °C for their formation, which can be reached for weeks to months during the cold season at both poles, mainly in Antarctica (WMO 2003). Meanwhile, ozone depletion has been very small over the tropics and averaged about 10% at middle latitudes (WMO 2003).

The long periods of extremely low stratospheric temperatures (as low as -90°C) during winter as well as the movement of the strong stratospheric winds into a circular pattern are responsible for what is known as the ozone hole formation over Antarctica. These stratospheric winds create a "polar vortex" that allows the formation of PSCs in the ozone layer and result in a sudden and severe loss (but not a complete absence) of ozone molecules over a vast circular region when the sun rises in late August (Solomon 1999;

Staehelin *et al.* 2001). Between 1996 and 1999, the ozone hole reached more than 24 million km^2. The biggest Antarctic ozone hole ever recorded occurred in September 2000 with a size of 28 millions km^2 and the second largest ozone hole ever recorded occurred in late September 2003 with a similar size of ozone hole (WMO 2005).

Because both temperature and wind conditions are much more variable within and between a winter season in the Arctic stratosphere, the area of the vortex, the strength of the warming and the timing of the final breakdown vary tremendously from year to year in the Arctic (Staehelin *et al.* 2001). Altogether, these factors cause the Arctic ozone depletion to be highly variable from year to year, with substantial ozone loss in some years and little or no ozone depletion in other years (e.g., McKenna *et al.* 1990; von der Gathen *et al.* 1995; Rex *et al.* 1997; Manney *et al.* 2003). However, since the 1990s, many Arctic winters have been characterized by record low stratospheric temperatures and stronger polar vortex (e.g. Wirth and Renger 1996; Rex *et al.* 2002, 2004) that have resulted in ozone loss rates comparable to those over the Antarctic (e.g., Müller *et al.* 1997; Guirlert *et al.* 2000; Rex *et al.* 2002). The magnitude of ozone losses seems to have been directly related to the severity of the Arctic stratospheric winter since the persistence of cold temperatures lead to the formation of extensive PSCs. Current investigations are suggesting that climate warming may be responsible for the formation and persistence of the PSCs (and thus greater ozone depletion) observed over the Arctic since the 1990s (e.g., Austin and Butchart 1994; Shindell *et al* .1998; Tabazadeh *et al.* 2000, 2001; Rex *et al.* 2004).

By effectively trapping heat in the troposphere, greenhouse gases (e.g., carbon dioxide CO_2, methane CH_4 and nitrous oxide N_2O) are radiating energy and heat away from the upper stratosphere (Austin *et al.* 1992). Consequently, while the Earth's surface is expected to warm in response to an increase in greenhouse gas levels, the stratosphere is in turn predicted to cool. A cooler stratosphere would cause the stratospheric temperatures to be more commonly low enough for PSCs to become more frequent, form earlier and/or persist longer, thus amplifying ozone loss and delay recovery of the ozone layer (Staehelin *et al.* 2001). The highest chemical ozone destruction ever recorded over the Arctic occurred during the 1999-2000 winter, with ozone concentrations that declined as much as 60% from November 1999 through March 2000 in some parts of the Arctic stratosphere (Sinnhuber *et al.* 2000; Newman *et al.* 2002; Rex *et al.* 2002). Meanwhile, the second highest level of Arctic ozone destruction occurred this past winter 2004-2005, with near 50% depletion in some regions of the stratosphere (NASA 2005).

Because the atmosphere naturally produces the same amount of new ozone each year (although the total amount of ozone being destroyed is higher), the ozone-depleted air from polar regions mixes with the ozone-rich air from outside the poles, leaving the Earth's entire (average) ozone supply slightly more diminished each passing year (ERF 1992). Each spring, the ozone-depleted air from the Arctic drifts south by high-altitude winds towards populated areas of North America, Europe and Russia (WMO 2003). Ozone depletion also occurs directly at latitudes between the equator and Polar Regions, but is smaller compared to depletion in Polar Regions since the amount of reactive halogen gases is much lower (WMO 2003). Although the amount of chlorine and bromine is slowly declining in the atmosphere, the Earth's global ozone layer recovery may not follow their decline and could be delayed by decades because of interactions with factors that could influence its recovery (e.g., climate change, volcanic eruptions, non-ratification and/or non-compliance with the Montreal Protocol and its Amendments and Adjustments; Madronich *et al.* 1998; Tabazadeh *et al.* 2001, 2002; WMO 2003).

Ultraviolet radiation

Stratospheric ozone plays a very important role because it prevents short-wave solar ultraviolet radiation (i.e. wavelengths from 220 to 320 nm) from reaching the Earth's surface (Staehelin *et al.* 2001). Ultraviolet radiation (UVR) is subdivided into three spectral regions. The subdivisions are arbitrary and differ somewhat depending on the discipline involved (Diffey 2002). Environmental and dermatological photobiologists normally define the wavelengths regions as UVC (far UV; 200 – 290 nm), UVB (middle UV; 290 – 320 nm) and UVA (near UV; 320 – 400 nm). The division between UVB and UVC is chosen as 290 nm since UVR at shorter wavelengths is unlikely to be present in terrestrial sunlight, except at high altitudes (Diffey 2002).

Although solar UV accounts for less than 5% of total radiation reaching the surface of the Earth, it contains the most energetic and biologically harmful wavelengths (Diffey 2002). UVA is the least damaging form of UVR. UVA still poses problems to life on Earth (e.g. sunburn and photoinhibition), but is also implicated in DNA reparation. UVA reaches the Earth in greatest quantity since most of it passes through the ozone layer and is not significantly affected by changes in stratospheric ozone concentrations. UVC is the most energetic form and, consequently, the most damaging to biota. Fortunately, UVC is completely absorbed in the atmosphere by oxygen and ozone and thus never reaches the Earth's surface.

Although other factors such as latitude (solar zenith angle), season, time of day, altitude, height and density of cloud cover, rain, air pollution and reflection from surfaces can also affect incident UVB (Madronich *et al.* 1995, 1998; WMO 2003), stratospheric ozone is the major factor affecting the amount of UVB reaching the Earth's surface. As a result, UVB represents only a minor portion of the solar spectrum (less than 1% of total energy). Although solar UVA irradiance is about 20 to 50 times higher than that of UVB under normal conditions, UVB remains a very active and energetic form that easily alters DNA, proteins and other relevant molecules (e.g., Diffey 1991; Mitchell and Karentz 1993; Häder *et al.* 1998; UNEP 1998, 2003) and is believed to be 5,000 times more cancer potent than UVA (UNEP 1998). Biological weighting functions (BWFs) have been applied to describe the effectiveness of radiation of different wavelengths to produce a biological response like the inhibition of photosynthesis (Cullen *et al.* 1992). BWFs have indicated that the biological response is highest in the UVB region relative to UVA (e.g., Boucher and Prézelin 1996; Banaszak and Neale 2001). With the thinning of stratospheric ozone due to anthropogenic emissions of ozone-depleting substances (i.e. chlorine and bromine-containing volatile gases), measurements by ground-based instruments and estimates using satellites data have confirmed that surface UVB has increased on a global scale, more specifically in regions where ozone depletion is occurring (i.e. at high- and mid-latitudes), with no significant change in tropical regions (Madronich *et al.* 1995, 1998; WMO 2003; Staehelin *et al.* 2001).

In the northern latitudes, UVB values have been 20-40% and 10-20% greater than those estimated for the late 1970s during spring and summer months, respectively (IASC 1995). Although natural UVB levels are normally highest in the summer, springtime

UVB levels have exceeded them over some northern polar latitudes in certain years. Significant reductions in ozone levels have also persisted into the summer (IASC 1995; WMO 2003). Recent localized events of severe ozone depletion in the Arctic have also exposed the Earth's surface to sudden and major increases (greater than 40%) in UVB during the spring months (e.g., IASC 1995; WMO 2003). These increases in UVB may have important ecological consequences on Arctic ecosystems.

UVB and aquatic ecosystems

The depth to which UVR penetrates in waters varies widely between aquatic systems because it is highly dependent on the concentration of the chromophore-containing (i.e., colored) constituents of dissolved organic matter (CDOM; e.g., Morris *et al.* 1995; Laurion *et al.* 1997; Lean 1998a,b; Gibson *et al.* 2000). For instance, the depth of water required to remove 90% of the solar radiation at 310 nm can range from about 20 m in the clearest oceanic waters to a few centimetres in brown humic lakes, ponds and rivers (e.g., Smith and Baker 1981; Smith *et al.* 1992; Kirk 1994; Crump *et al.* 1999; Bukaveckas and Robbin-Forbes 2000).

CDOM characterizes the optically active fraction of the bulk dissolved organic matter (DOM) pool (Rochelle-Newall *et al.* 2003). DOM is the organic residue (having a least dimension smaller than 0.45 μm) of decaying organic matter derived principally from terrestrial soils and vegetation and to a lesser extent from microbial activities within the water column. It represents a complex mixture of large organic polymers (from about 1000 to >10 000 Da in molecular weight) composed mainly of humic (dark brown substances) and fulvic acids (yellow to yellow-brown substances). Optically, CDOM affects the color of water and stains the water yellow or brown in high concentrations (Rochelle-Newall *et al.* 2003). The spectral absorbance of the chromophores (aromatic carbon rings with conjugated bonds) increases exponentially with decreasing wavelength over the visible, UVA and UVB ranges (Kirk 1994).

The range of absorption by CDOM is from 300 to 500 nm, which include most of the UVB, all of UVA as well as short wavelengths (blue light) in the visible region (which is a local absorption maximum for chlorophyll; Davis-Colley and Vant 1987; Gibson *et al.* 2000; Magnuson *et al.* 2000). Because DOM is composed of 45 to 50% of carbon, it is often expressed as carbon and referred to as dissolved organic carbon (DOC; Kalff 2002). In oligotrophic and mesotrophic freshwaters, CDOM correlates closely with DOC since it is usually the largest pool of organic carbon and contains most of the chromophores for UV absorbance (Belzile *et al.* 2002). Therefore, UV penetration can generally be predicted by changes in DOC concentrations (or DOC fluorescence or absorbance) in freshwaters (Scully and Lean 1994; Morris *et al.* 1995; Williamson *et al.* 1996; Lean 1998a,b), including those of the Arctic (Laurion *et al.* 1997; Pienitz and Vincent 2000).

Because UVB can penetrate to biologically significant depths in systems with low DOC concentrations, it can be harmful to aquatic life and an increase in underwater UV exposure has the capacity to directly affect organisms from all trophic levels (e.g., Häder *et al.* 1998; Wängberg *et al.* 1999). By increasing solar UVB only, stratospheric ozone depletion also alters the UVB: UVA: PAR (photosynthetically active radiation: 400 - 700 nm) ratios, which may impair the light-dependent responses of aquatic organisms like photosynthesis, photo-orientation, photoinhibition and photoprotection (e.g., Smith *et al.* 1992; Gerber *et al.* 1996; Häder *et al.* 1998).

Since the most severe consequence of the anthropogenic release of ozone-depleting substances has been the formation of an ozone hole over Antarctica, the majority of the investigations on the biological effects of enhanced UVB radiation onto aquatic ecosystems have concentrated on the Southern Ocean, especially on Antarctic marine phytoplankton (e.g., Smith *et al.* 1992; Holm-Hansen 1993; Neale *et al.* 1994; Prézelin *et al.* 1994a,b, 1998). However, with the increased severity of ozone depletion over the Arctic and the potential influence of climate change and other environmental factors (e.g. acid precipitation), studies on the effects of UVB radiation onto aquatic organisms and ecosystems in the northern mid- and high latitudes have significantly increased in the past few years (e.g., Williamson 1995; Chatila *et al.* 1999, 2001; De Lange *et al.* 1999; Van Donk *et al.* 2001; Vincent and Belzile 2001; Wängberg *et al.* 2001). Of the existing UVB studies in the sub-arctic and arctic regions, most are on marine organisms and ecosystems (e.g., Helbling *et al.* 1996b; Wängberg *et al.* 1998, 1999, 2001; van de Poll *et al.* 2002; Aguilera *et al.* 2002; Karsten *et al.* 2003) with very few on freshwaters (e.g., Hessen 1994, 1996; Rae and Vincent 1998; Wickham and Carstens 1998; Hessen *et al.* 1999; Van Donk *et al.* 2001; Rautio and Korhola 2002a,b, 2003).

Phytoplankton are more commonly exposed to harmful levels of solar UVB by being limited to the top layers for photosynthesis. Consequently, deleterious effects of UVB on phytoplankton have been of special interest based on the assumption that declines in primary productivity caused by increases in UVB levels would translate into ecosystem disruption by reducing energy transfer between trophic levels (Karentz and Bosch 2001). Harmful effects of UVBR on phytoplankton are numerous and include DNA damage, deterioration of photosystem II efficiency and inactivation of reaction centers, changes in the biochemical composition, damage to photosynthetic energy-harvesting enzymes and other key enzymes, reduction in synthesis or destruction of cellular pigments, decrease in nutrient (e.g., ammonium, nitrate or phosphorus) uptake, inhibition of motility, and damage to orientation mechanisms (see reviews by Vincent and Roy 1993; Karentz *et al.* 1994; Perin and Lean 2004). However, many studies have shown that phytoplankton differ greatly in their responses to UVB exposure depending on the taxa and/or cell size (e.g., Jokiel and York 1984; Villafañe *et al.* 1995; Davidson *et al.* 1996; Mostajir *et al.* 1999a,b; Mousseau *et al.* 2000; Van Donk *et al.* 2001).

For invertebrates, UVB can directly affect their DNA, fecundity, sex ratio, developmental and growth rates, pigmentation, feeding behavior, swimming behavior, water balance (bloating), and survival (e.g., Karanas *et al.* 1979, 1981; Dey *et al.* 1988; Hessen 1994; Siebeck *et al.* 1994; Williamson *et al.* 1994; Malloy *et al.* 1997; Vinebrook and Leavitt 1999; Browman *et al.* 2000; Leech and Williamson 2000; Rautio and Korhola 2002a,b). Despite its deleterious effects on invertebrates, UV tolerance is highly variable among taxa, species and life-stages (e.g., Karanas *et al.* 1981; Williamson *et al.* 1994; Hurtubise *et al.* 1998; Wickham and Carstens 1998; Leech and Williamson 2000; Cywinska *et al.* 2000). The most severe UVB effects on invertebrates are usually observed during their early developmental stages (e.g., egg, embryos or larval development) as well as in their reproduction capacity (e.g., Karanas *et al.* 1979, 1981; Damkaer and Dey 1983; Bothwell *et al.* 1994; Kuhn *et al.* 2000). The rapid developmental activity and minimal morphological complexity of embryos and larvae seem to make them more vulnerable than adults (Karentz and Bosch 2001).

Studies of the effects of natural UVR on fish are rare but laboratory experiments have shown detrimental effects to UVB for all life stages (eggs, embryos, larvae and adult; e.g., Hunter *et al.* 1979, 1981; Little and Fabacher 1994; Beland *et al.* 1999; Battini *et al.* 2000; Browman *et al.* 2000; Charron *et al.* 2000). UVB effects on fish include skin damage and sunburns (e.g., Hunter *et al.* 1979; Little and Fabacher 1994; Blazer *et al.* 1997), increased infections by opportunistic pathogens including fungi (e.g., Bell and Hoar 1950; Fabacher *et al.* 1994; Little and Fabacher 1994), lesions in the brain and retina (e.g., Hunter *et al.* 1979; Little and Fabacher 1994; Blazer *et al.* 1997), reduced growth rates (e.g., Hunter *et al.* 1979, 1981; Little and Fabacher 1994; Blazer *et al.* 1997), immunosuppression in adults (Salo *et al.* 1998), DNA damage in fish eggs and larvae (Vetter *et al.* 1999) and increased mortality (e.g., Browman *et al.* 2000; Charron *et al.* 2000; Steeger *et al.* 2001). Present UVB levels (neglecting any UVB enhancement from stratospheric ozone depletion) may already challenge their survival (e.g., Williamson *et al.* 1997). However, the imprecisely defined habitat characteristics and the naturally high mortality rates of fish larvae make it difficult to predict the sole effect of small increases in UVB on fish populations (Häder *et al.* 1998). Since fishes have many physiological, morphological and behavioral mechanisms against UVR, there is considerable variability in response to UV exposure between species and developmental life-stages (e.g., Bullock 1988; Little and Fabacher 1994).

Because heterotrophic bacteria are small-sized, lack UV-screening pigments, and have genetic materials that include a significant portion of their cellular volume, direct exposure to UVB is believed to cause more damage to them than other planktonic organisms, even under natural UVB levels (Helbling *et al.* 1995; Jeffrey *et al.* 1996b; Visser *et al.* 1999). Deleterious effects of UVB on bacteria have included damage to DNA (Jeffrey *et al.* 1996a,b), inhibition in protein synthesis (Herndl 1993, depression of ectoenzymes activity (i.e., enzymes responsible for the cleavage/degradation of external organic matter; Garde and Gustavon 1999) and reduction of membrane permeability (Klamen and Tuveson 1982) that can lead to a decrease in nutrient uptake (Kubitschek and Doyle 1981). Each of these effects can then reduce heterotrophic bacterial abundance (e.g., Müller-Niklas *et al.* 1995), metabolic activity (e.g., Herndl *et al.* 1993; Aas *et al.* 1996; Sommaruga *et al.* 1997, 1999; Visser *et al.* 1999), or viability (e.g., Marguet *et al.* 1994; Herndl 1997; Visser *et al.* 1999). Large differences in UVB sensitivity also exist between heterotrophic bacterial isolates (Arrieta *et al.* 2000).

For viruses, solar UVR can affect their infectivity and integrity and thus may play an important role in their dynamics (Sommaruga *et al.* 1999; Sommaruga 2001). DNA damage accumulation caused by UVR has also been detected in viruses (Weinbauer *et al.* 1997, 1999; Wilhelm *et al.* 1998, 2000, 2003; Jeffrey *et al.* 2000). A few studies have shown that exposure to solar UVB impaired the motility and velocity of several heterotrophic protists (e.g. *Astasia longa* and *Stentor coeruleus*), which might ultimately affect their fitness and decrease their overall abundance (Häder 1988, 1994; Häder and Häder 1989, 1991). However, UVB effects on protists appear to be highly species-specific (Häder 1988, 1994; Wickham and Carstens 1998; Sommaruga *et al.* 1999).

In addition to its direct impacts, UVB can also affect aquatic organisms indirectly via two mechanisms: (1) trophic-level interactions i.e., damages caused by direct UVB exposure at a given trophic level can cascade through the food webs and indirectly stimulate or dampen adjacent trophic levels (e.g., Bothwell *et al.* 1994; Cabrera *et al.* 1997; Keller *et al.* 1997; Mostajir *et al.* 1999a); and (2) chemical alteration of the milieu i.e., UVB can interact directly with organic compounds or other photosensitizing agents in humic waters and produce photoproducts that can be beneficial to bacteria and/or phytoplankton through the release of bioavailable nutrients (e.g., Lindell *et al.* 1995, 1996; Wetzel *et al.* 1995; Vähätalo *et al.* 2003) or detrimental to aquatic organisms through the release of high concentrations of trace metals (e.g., copper; Winch *et al.* 2002) and reduced oxygen species (e.g., Zepp *et al.* 1995).

Initially, it was predicted that stratospheric ozone depletion would result in a dramatic collapse of the phytoplankton in the world oceans, especially those living in the southern ocean, and disrupt fish yield and global oxygen and carbon dioxide budgets. This assumption was based on short-term experiments performed under laboratory conditions using artificial irradiance with unrealistic UVB levels (that would seldom be observed in nature) and/or culture organisms with no prior history of UVB exposure (e.g., Döhler 1989, 1995, 1997; Ekelund 1990, 1994; Karentz *et al.* 1991a; Lesser *et al* 1994). The Antarctic phytoplankton has already experienced more than 20 years of stratospheric ozone depletion and yet no abrupt change in the southern aquatic communities have been detected (e.g., McMinn *et al.* 1994). In their environments, UVB effects on natural populations can be modified by other environmental factors like water temperature, nutrient availability, water mixing regime (depth of the mixed layer and mixing rate), water clarity, previous light history and sky conditions (e.g., Jeffrey *et al.* 1996a,b; Häder *et al.* 1998; Neale *et al.* 1998b) as well as by variations between organisms in their susceptibility to UVB due to differences in their physiology, size, morphology, and most importantly in their lines of defense against UVR (e.g., Karentz *et al.* 1991a,b; Siebeck *et al.* 1994; Roy 2000). All of these factors can modify the final expression of UVB damage.

The four main mechanisms of defence that aquatic organisms have to prevent and/or reverse the damaging effects of UVR are: (1) migrations into depths or sediments with reduced UVB levels (e.g., Storz and Paul 1998; Speekmann *et al.* 2000; Leech and Williamson 2001), (2) the production of UV-absorbing compounds like mycosporine-like amino acids (MAAs), melanin and scytonemin (e.g., Karentz *et al.* 1991b; Hessen 1996; Sinha *et al.* 1998), (3) the production of quenching agents that reacts with harmful oxygen species (e.g., carotenoid, ascorbate, detoxifying enzymes; Hessen 1994; Malanga and Puntarulo 1997; Borgeraas and Hessen 2002), and (4) the repair of UV-damaged macromolecules (e.g., DNA; Karentz 1994; Malloy *et al.* 1997; Booth *et al.* 2001). The success of these photoprotective and repair processes to combat UVB damage depends upon the synthetic capabilities of the organism. Short-time exposure to UVB gives only the initial responses of the organisms to elevated UVB and do not take into account the possible acclimatization and/or adaptation of natural populations to UVB after prolonged periods of exposure. Prior light conditions, water temperature, nutrient availability and/or variations between species are all factors that can affect acclimation of natural populations to UVB (Zudaire and Roy 2001).

Arctic freshwaters and UVB

The Arctic region is generally defined as the Arctic Ocean and the surrounding landmasses bounded to the south by the northern tree line and comprises about 10% of the Earth's surface (IASC 1995). Arctic aquatic ecosystems differ significantly from Antarctic environments (Smith 1990a,b). Unlike Antarctica, the Arctic region comprises many freshwater ecosystems including shallow, clear freshwater lakes, enormous areas of wetlands, and unique melt ponds in the pack ice. Arctic freshwaters are home to many species found nowhere else. Huge numbers of migratory species go there to breed each spring. They are also characterized by low nutrient levels, cold temperatures, short growing season, low species diversity, and continuous daylight during the short-ice free period. The largest stratospheric ozone reductions over the Arctic have occurred in late winter and early spring when primary production is just starting and many animal populations are beginning their breeding season or giving birth.

In Arctic freshwaters, DOC levels vary widely and thus display a wide range of sensitivities to UV penetration. For example, DOC levels can range from near 0 to greater than 30 mg L^{-1} in lakes of the Canadian Arctic (Hamilton *et al.* 1994, 2000, 2001; Pienitz and Smol 1994; Pienitz *et al.* 1997). However, many have low DOC concentrations. For example, the median DOC is 1.8 mg L^{-1} for 25 lakes above the treeline in Finnish Lapland (northern Scandinavia; Rautio and Korhola 2002a,b) and mean (± SD) DOC is 3.9 ± 4.6 mg L^{-1} for 221 lakes from the Canadian Arctic Archipelago (Hamilton *et al.* 2001). Many Arctic freshwaters are shallow systems, and therefore lack a depth refuge from UVB exposure. The maximum depth for 98 lakes is 5.1 m (Blom *et al.* 1998) and ponds seldom exceed 1 m in northern Finland (Rautio and Korhola 2002a). In the Canadian Arctic Archipelago, 80% of 204 lakes have maximum depth less than 12 m (Hamilton *et al.* 2001).

Consequently, all functional groups, including some rock-attached benthos, are often exposed to UVR throughout the entire water column. The species that are more benthic or littoral would seldom find shelter since arctic freshwaters contain little aquatic vegetation, especially those in barren catchments. On the other hand, benthic organisms in shallow systems can avoid UVB exposure by seeking refuge in soft sediments (Vinebrooke and Leavitt 1999). Also, the benthic mats and films commonly encountered in the Arctic are usually protected from UVR by a surface layer made of cyanobacterial colonies that strongly absorbs in the UV region (e.g. Quesada *et al.* 1999) and as a result could provide a UV-shield to other benthic algae and invertebrates. Meanwhile, the aquatic biota of large rivers as well as wetlands and peatlands in the Arctic are relatively protected from UV exposure given their high CDOM contents (Gibson *et al.* 2000).

In contrast to polar marine ecosystems, the availability of major inorganic nutrients like nitrogen and phosphorus are much lower in Arctic freshwaters. Low nutrient conditions may reduce the availability of elemental resources (e.g., nitrogen) for building enzyme systems such as those involved in UV repair mechanism or limit the investment in photoprotective mechanisms (e.g., production of UV-absorbing compounds such as MAAs; Neale 2001; Buma *et al.* 2001b). Several studies have shown that the nutrient status plays an important role in relation to the effects of UVB. UVB effects have been observed only during nutrient-limiting conditions (Chatila *et al.* 2001), have been aggravated when a major nutrient is limited (Litchman *et al.* 2002), or have been diminished when nutrients were added (Wulff *et al.* 2000).

Although damage by UVB is not temperature-sensitive, enzymatic processes are temperature-dependent (e.g., Vincent and Roy 1993; Buma *et al.* 2001a). In the Arctic, the cold water temperatures may then increase the susceptibility of aquatic organisms to UV-induced damage by slowing down enzymatic processes such as those involved in UV repair mechanisms (e.g., DNA repair; Neale *et al.* 1998c; Roos and Vincent 1998; Rocco *et al.* 2002) and detoxification of reactive oxygen species (Hessen 1996; Buma *et al.* 2001a). Moreover, low water temperatures may also reduce the affinity for nutrient uptake by membrane transport of cells (Nedwell 1999), further increasing nutrient limitation.

In addition to stratospheric ozone depletion, climate change could also bring important changes in the UVR climate of Arctic freshwaters via two mechanisms: (1) earlier loss of ice and snow cover and/or loss of permanent ice cover through higher mean tropospheric temperatures (e.g., Rouse *et al.* 1997; Elo *et al.* 1998; Magnuson *et al.* 2000) and (2) alter DOC levels through changes in the surrounding vegetation, changes in the inputs of allochthonous DOC, changes in water residence times and/or melting of terrestrial permafrost (e.g., Schindler *et al.* 1996, 1997; Schindler 2001; Freeman *et al.* 2001). Thick ice cover is a common feature in freshwater systems of the Arctic for more than 6 months of the year. Earlier loss of snow and ice cover on Arctic waters would subject aquatic organisms to solar radiation when UV flux and ozone depletion are highest in the spring (i.e., March and April). Paleo-ecological reports, specifically those using fossil pigments or diatoms in lake sediments as quantitative indicators of variations in CDOM, have shown that shifts in vegetation and hydrology caused by warming or cooling trends changed the quantity of CDOM exported from their catchments to the receiving waters, thus affecting underwater UVR climate (e.g. Leavitt *et al.* 1997, 2003; Pienitz and Vincent 2000; Ponader *et al.* 2002; Saulnier-Talbot *et al.* 2003). Hence, with both the influences from stratospheric ozone depletion and climate warming, it becomes important to learn more about the effects of UVR on aquatic organisms and the role of UVR in shaping Arctic freshwater ecosystems.

Thesis rationale and overview

For Arctic freshwaters, the combined effects of stratospheric ozone depletion and climate warming may radically influence UV exposure within the water column and be stressful for the biota, especially with any small changes in snow cover and/or ice in the spring when water temperatures are still cold, but UV flux and ozone depletion are highest. It then becomes increasingly important to understand the impacts of solar UV radiation and its possible role in shaping these ecosystems. Because many lakes in the Arctic region are remote and difficult to access and costs (e.g., transportation, logistics) for conducting research in these regions are very high, our knowledge of these ecosystems is limited. This is especially the case in relation to the possible losses and damages that may be induced by an increase in surface UVB levels.

Most studies related to the effects of UVR or UVB on Arctic freshwater organisms have been done by researchers in Northern European countries (e.g., Hessen 1994, 1996; Hessen *et al.* 1999; Wickham and Carstens 1998; Van Donk *et al.* 2001; Rautio and Korhola 2002a,b. 2003). In Canada, only a few studies have addressed the effects of UVR on sub-arctic lakes (e.g., Milot-Roy and Vincent 1994; Rae and Vincent 1998; Laurion and Vincent 1998) and, to my knowledge, no UVB studies have been conducted further north, except for my M.Sc. thesis (Perin 1996). Perin (1996) assessed the effects of solar UVB on phytoplankton primary production and *in vivo* fluorescence (a measure of photoinhibition) of natural phytoplankton assemblages of two High Arctic lakes located in Mould Bay, Prince Patrick Island, Nunavut (76° N, 119° W). Results from this study showed that present UVB levels inhibited phytoplankton photosynthesis near the surface, especially in the low-DOC lake.

Many of the existing studies on effects of UVB in Arctic freshwaters have been based on treatments that excluded UVB or UVR, which makes results difficult to extrapolate for predicting the impacts of enhanced UVB levels on these ecosystems. This present thesis attempts to evaluate the potential effects of enhanced surface UVB levels on planktonic organisms of Canadian High Arctic lakes. The thesis consists of two chapters. An overview of Chapters 1 and 2 is provided below, including their respective objectives and hypotheses.

Chapter 1 examines the effects of long-term exposure (i.e., 27 days) to enhanced surface UVB levels on the planktonic community of a lake in the Canadian High Arctic using *in situ* mesocosms. This lake is located on the west coast of Ellesmere Island (79°55.5'N, 84°40'W) and contains high DOC levels (average of 11 ± 5 mg L^{-1}), which attenuates UVB rapidly within the water column. The experiment consisted of two UVB treatments: (1) Two mesocosms exposed to solar radiation with ambient UVB levels and (2) two mesocosms exposed to solar radiation plus enhanced UVB using artificial lamps. The main objective of this study was to evaluate the potential direct and indirect (i.e., through trophic-level interactions and/or chemical alteration of the milieu) impacts of enhanced UVB levels on phytoplankton, heterotrophic microbial food web and zooplankton of a humic lake in the High Arctic. Over the course of the study, physical and chemical characteristics were also described between the treatments and the lake to assure consistency between them. This study represents the first one to examine enhanced UVB effects at the ecosystem level for a High Arctic lake.

The main hypotheses for Chapter 1 are: (1) Direct UVB effects on planktonic organisms will be minimized due to the high levels of DOC that will strongly attenuate UVB in the upper layer and due to vertical mixing that will dilute damaging UVB effects (if any) at the surface and allow repair at greater depths; and (2) Indirect effects of enhanced UVB on planktonic organisms will be more important than its direct effects through photochemical reactions of UVB with CDOM in surface waters (e.g., photochemical production of bioavailable nutrients) and through trophic-level interactions.

Chapter 2 examines the effects of enhanced surface UVB levels at four different radiation levels (i.e., 6, 25, 50 and 100% surface irradiance levels) on phytoplankton productivity of nine High Arctic lakes located in the vicinity of Resolute, Cornwallis Island, Nunavut (74°42'N, 94°50'W). More specifically, the effects of enhanced UVB were evaluated on total phytoplankton production, size-fractionation of photosynthesis into three size classes (picoplankton [0.2 –2 um], nanoplankton [2 - 20 um] and netplankton [> 20um]) and partitioning of recently fixed carbon into the four major end-products (low molecular weight metabolites, lipid, polysaccharide and protein). The main objectives were to evaluate the effects of enhanced UVB on total phytoplankton productivity under different irradiance regimes, to determine if sensitivity to UVB differs between cell sizes in relation to photosynthetic inhibition, and to determine if the relative proportions of carbon allocated into the four main end-products are affected by enhanced UVB. Aside from UVB effects, the influence of variations in incident solar radiation on phytoplankton photosynthesis is also illustrated. Photosynthate allocation of these lakes is also discussed in relation to that of other aquatic systems since this is the first time that carbon allocation has been measured for lakes of this region (aside from Two Basin Lake in Chapter 1). Moreover, since many of these lakes have never been described before, their physical and chemical properties are characterized in this chapter.

The main hypotheses for Chapter 2 are: (1) Enhanced UVB will strongly inhibit photosynthesis at 100% surface irradiance levels, with little or no effects at 6% surface levels; (2) In terms of photosynthetic inhibition, enhanced UVB levels will have more damaging effects on picoplankton relative to the bigger cell sizes since picoplankton have greater surface-to-volume ratios; and (3) In relation to carbon allocation into macromolecular constituents, the relative proportion of carbon allocated into protein will be the most negatively affected by enhanced UVB since protein synthesis is closely linked to phytoplankton growth and UVB can impair nitrogen assimilation and amino acid synthesis in phytoplankton.

CHAPTER 1

THE EFFECTS OF INCREASED UVB RADIATION ON THE PLANKTONIC COMMUNITY OF A HIGH ARCTIC LAKE: RESULTS FROM AN *IN SITU* MESOCOSM EXPERIMENT

Abstract

The influence of enhanced ultraviolet-B radiation (UVB) on the planktonic community from a high arctic lake was evaluated for 27 days by comparing replicated mesoscoms exposed to full sunlight (ambient UVB levels) to those exposed with sunlight enhanced with UVB lamps. The mesocosms (3 m square and 3 m deep, 27 000 L) were installed in Two Basin Lake (79°55.5'N, 84°40'W), a small lake (14.2 ha) located in the Fosheim Peninsula on Ellesmere Island (Canada). The mesocosms were open to the sediments, but exchange with outside water was restricted using a heavy chain sown into the base. The enhanced UVB (elevated by 50% unweighted and 300% weighted over ambient UVB levels) was supplied by fluorescent tubes for 3 h each day, leading to a daily dose between 4 to 20% greater (unweighted) depending on the time of day and weather conditions. Chlorophyll *a*, total zooplankton length and carbon allocation into low molecular weight, lipid, polysaccharide, and protein constituents did not differ between the two UVB treatments throughout the experiment. Significant effects of enhanced UVB included: 1) a decrease in total phytoplankton productivity during the first 12 days, but an increase on day 19, with no effects at the end of the experiment; 2) a decrease in the relative proportion of carbon fixed by small phytoplankton (0.2 – 2 μm) but an increase in that of bigger phytoplankton (> 2 μm) during the first 12 days, with little effects thereafter; 3) a slight depression in heterotrophic bacterial abundance during the first 16 days, but an increase thereafter; 4) a general increase in heterotrophic bacterial activity; 5) a decrease in picocyanobacteria abundance, but only near the surface; 6) an increase in the abundances of heterotrophic nanoflagellates (HNFs) and zooplankton after about 14 days and; 7) an increase in the relative abundance of cladocerans and rotifers but a decrease in that of copepods (adults only). The high levels ($\geq$ 5 mg L^{-1}) of dissolved organic carbon (DOC) in this lake reduced UVB penetration and provided more UV protection than expected in low DOC systems commonly found in the Canadian Arctic Archipelago. Vertical mixing also reduced exposure of planktonic organisms to UVB near the surface. The observations are consistent with the hypothesis that exposure to enhanced UVB levels had little direct negative impacts on the planktonic organisms in this high DOC system and indirectly stimulated heterotrophic bacteria, phytoplankton and the rest of the food chain through increased photodegradation of high molecular weight refractory dissolved organic matter into more biologically available nutrients. This study could be representative of more Arctic lakes in the future since lakes with higher DOC levels are expected to become more common in some parts of the Arctic with climate warming.

Introduction

Due to the complexity of intact ecosystems, our ability to predict the consequences of increased ultraviolet-B (UVB; 280 – 320 nm) from stratospheric ozone depletion on living organisms, especially those inhabiting aquatic environments, is poor. Numerous studies have shown detrimental effects on aquatic organisms from all trophic levels with direct exposure to UVB (e.g. reviews by Vincent and Roy 1993; Häder 1994, Häder *et al.* 1998; Perin and Lean 2004). Such effects include damage to DNA, RNA, proteins (including enzymes), and other biomolecules that can ultimately affect a number of physiological and biochemical processes such as pigmentation, photosynthesis, motility, cell division, nitrogen metabolism, feeding behaviour and reproduction (e.g.

Mitchell and Karentz 1993; Hader *et al.* 1998; UNEP 1998, 2003). It remains difficult to predict the changes to be expected on aquatic ecosystems from exposure to increased levels of solar UVB due to the many feedback processes that are interrelated. Most of the research on the effects of enhanced UVB levels has been conducted using short temporal-scales at a single trophic level, mainly on phytoplankton (e.g., Karentz *et al.* 1991a; Helbling *et al.* 1994; Neale *et al.* 1998c). It is then impossible to synthesize the parts to predict whole ecosystem consequences.

In addition to its direct impact on aquatic organisms, indirect effects of UVB via trophic-level interactions and/or chemical alteration of the milieu may also play an important role in ecosystem responses to changes in UVR levels (Perin and Lean 2004). Any direct effects of UVB on a given trophic level can cascade through the food chain and induce important changes to adjacent trophic levels in the long-term (e.g. Bothwell *et al.* 1994). UVB can trigger either a "bottom-up" or "top-down" trophic response. For bottom-up effects, damages on the prey from exposure to UVR can impair the next level of consumer organisms via reduced quantity (e.g. reduction in total biomass or productivity; Keller *et al.* 1997) or quality of food (e.g. reduction in nutritional value and/or shift in less inedible/digestible species; Hessen *et al.* 1997; Scott *et al.* 1999). For example, De Lange and Van Donk (1997) showed a decrease in population growth of *Daphnia pulex* feeding on UVB-irradiated phytoplankton.

For top-down effects, negative effects on the consumers from UVR exposure can decrease grazing pressure or predation on all or selected prey species. This could ultimately change the abundance (e.g. Bothwell *et al.* 1994) and/or species/size composition of prey (e.g. Mostajir *et al.* 1999a). For example, Bothwell *et al.* (1994)

observed an increase, rather than a decrease, in the biomass of benthic stream diatoms with UVB exposure due to lower grazing pressure by invertebrates that were negatively affected by UVB. With the possibility of trophic-level interactions between phytoplankton and zooplankton as well as with bacteria and other components of the microbial food web (e.g., heterotrophic nanoflagellates and ciliates), it becomes even more difficult and complex to assess ecosystem responses to increased UVB levels.

In addition to its biological effects, increases in surface UVB levels can also induce other indirect effects on aquatic organisms resulting from a number of *in situ* photochemical reactions in highly irradiated humic surface waters. These reactions can result in the release of nutrients, e.g., ammonium, amino acids and phosphate (Blough and Zepp 1990; Bushaw *et al.* 1996; Cotner and Heath 1997), labile low molecular weight carbonyl compounds, e.g., fatty acids and keto acids (Wetzel *et al.* 1995; Bertilsson *et al.* 1999; Vähätalo *et al.* 2003), metals previously bound into metal-organic matter complexes, e.g., copper and iron (Zepp *et al.* 1995; Winch *et al.* 2002), and various reactive oxygen species, e.g., superoxide, hydrogen peroxide, hydroxyl radicals and singlet oxygen (Cooper 1989; Scully *et al.* 1997; Lean 1998a,b).

The release of carbon and nutrients through photochemical breakdown of large DOM could lead to an increase in biological activity, stimulating phytoplankton and/or bacterial growth as well as heterotrophic pathways (e.g. Lindell *et al.* 1995; Wängberg *et al.* 1999; Gustavson *et al.* 2000). Through DOC degradation, exposure to increased UVR levels in high humic waters has then the potential to facilitate the transfer of carbon to higher trophic levels via the microbial food web and stimulate ecosystem productivity (De Lange *et al.* 2003). On the other hand, the release of toxic metals (copper and aluminium) and/or production of reactive oxygen species on surface water environments can cause damages to enzymes, lipid membranes as well as to other cellular constituents and processes of the residing organisms (e.g., Xenopoulos and Bird 1997; Borgeraas and Hessen 2000; Aguilera *et al.* 2002b; Rautio and Korhola 2002a).

The above discussion illustrates that the net effects of UVB on a given community might be harmful, beneficial or non-existent depending on the relative strength of direct and indirect consequences. Furthermore, the influence of other environmental factors such as mixing depth, mixing rate, water clarity, and light history (e.g. Fauchot *et al.* 2000; Kunh *et al.* 2000; Xenopoulos and Schindler 2003) as well as the co-occurrence of other stressors such as nutrient limitation and low water temperatures (e.g. Neale *et al.* 1998c; Chatila *et al.* 2001; Xenopoulo *et al.* 2002) can also modify the response of organisms and ecosystems to increased UVB levels.

Long-term experiments that would include more than one trophic level and integrate the negative, positive and adaptive processes are increasingly recognized as a useful approach to a more reliable prediction of UVB effects at the community and ecosystem levels. As a result, the use of experimental enclosures (also called mesocosms) or other forms of manipulated natural systems have become common among researchers for testing the complex effects of UVR on marine and freshwater communities (e.g. Worrest *et al.* 1981; Bothwell *et al.* 1994; Cabrera *et al.* 1997; Demers *et al.* 1998; Wängberg *et al.* 2001). While maintaining all other physical characteristics the same, natural incident solar radiation can be manipulated over mesocosms in order to assess the long temporal effects of UVB on all relevant trophic levels over several generation times as well as detect possible interactions between the different ecosystem components (Oviatt 1993; Demers *et al.* 1998; Forster and Schubert 2001).

Many studies utilizing mesocosms or other manipulated natural systems have used the exclusion of ambient UVB and/or UVA + UVB as their treatments (e.g. Bothwell *et al.* 1993; Cabrera *et al.* 1997; Wickham and Carstens 1998; Wulff *et al.* 1999; Kaczmarska *et al.* 2000; Bergmann *et al.* 2002; Pérez *et al.* 2003) and consequently, have showed the effects of ambient UVB and/or UVR rather than the consequences of increased UVB or UVR caused by stratospheric ozone depletion, climate warming and/or acid precipitation. Meanwhile, other studies have enhanced UVB artificially by using a fixed light intensity that is generally added for a few hours per day in order to mimic an increase of the UVB dose per day following a specific reduction of the stratospheric ozone layer (e.g., Worrest *et al.* 1981; Keller *et al.* 1997; Laurion *et al.* 1998; Odmark *et al.* 1998; Chatila *et al.* 1999; De Lange *et al.* 1999; Mostajir *et al.* 1999a; Wängberg *et al.* 1999; Whitehead *et al.* 2000; Forster and Schubert 2001; Anesio and Granéli 2003). Recently, others studies have enhanced UVB levels modulated by the ambient radiation to give a constant percentage increase in UVB and would take into account natural variations in ambient UVR by factors like cloud cover and time of day (Underwood *et al.* 1999; Wulff *et al.* 2000; Wängberg *et al.* 2001).

Regardless of the UVB treatments used, whole-community or ecosystem responses have been shown to vary greatly between studies. Some have showed strong indirect effects of UVB and/or UVR mediated by food web processes or chemical changes in surface waters (e.g., Bothwell *et al.* 1994; Mostajir *et al.* 1999a; Pérez *et al.* 2003), while some have found no or little effects (e.g., Laurion *et al.* 1998; Vinebrook and Leavitt 1999; Forster and Schubert 2001). Variations in concentrations of dissolved organic carbon (DOC, the principal attenuator of ultraviolet radiation in freshwaters), mixing depth and rates and pre-tolerance of species to UVR are a few of many factors than could explain the discrepancies between studies i.e., between the different ecosystems (De Lange *et al.* 1999; Forster and Schubert 2001).

In this study, the effects over the summer of a moderate increase in UVB levels on the planktonic community, including the microbial food web, of a Canadian High Arctic lake were assessed using *in situ* mesocoms. The following functional and structural variables were measured: chlorophyll a, phytoplankton productivity and carbon allocation into macromolecules, heterotrophic bacterial abundance and activity, photosynthetic picoplankton abundance, heterotrophic flagellate abundance, and zooplankton abundance, species an size composition. The study was carried out at Two Basin Lake, a small lake (14.2 ha) located 20 km from the west coast of Ellesmere Island (Nunavut, Canada) in the Fosheim Peninsula area. This area is characterized by significantly higher temperatures and less rainfall than other regions of the Canadian Arctic Archipelago due to containment and isolation by mountain ranges from the northern ocean currents and northern weather systems (Hamilton *et al.* 1994). As a result, the Fosheim peninsula is one of the most productive regions of the Canadian Arctic Archipelago. During ice-free periods, freshwater systems (i.e., lakes, ponds and wetlands) are biologically important in this region where mammals, insects as well as migratory birds center their activities on these water sources (Hamilton *et al.* 1994).

Because of higher productivity of local vegetation, DOC levels in lakes of the Fosheim peninsula, including Two Basin Lake, are on average as much as 10 times higher than lakes from the southern parts of the Arctic Archipelago (Hamilton *et al.* 2001). Higher DOC levels provide protection from UVR for the living organisms in these lakes. However, aquatic organisms that have evolved in high-DOC lakes may be less adapted to cope with exposure to increased surface UVB levels (e.g. Kaczmarska *et al.* 2000). The release of more toxic chemicals (e.g., oxygen radicals and/or toxic metals) in humic surface waters from exposure to enhanced UVB levels could also be detrimental to some species (e.g., Winch *et al.* 2002). On the other hand, the increased photodegradation of high molecular weight DOC with enhanced UVB levels could stimulate the growth of bacteria and/or phytoplankton (e.g., Wängberg *et al.* 1999; De Lange *et al.* 2003; Pérez *et al.* 2003) and the rest of the food chain. An increase in DOC levels is anticipated in many lakes of the Arctic region (especially those located near the tree line) with climate warming. Therefore, it is important to understand the influence of enhanced UVB levels in these ecosystems.

Materials and methods

Study Site and mesocosms

The experiment was performed for 27 days, from 20 July to 15 August 1994, at Two Basin Lake (TBL; 79°55.5'N, 84°40'W). TBL is a small (14.2 ha), fishless, and colored oligotrophic lake located in the Fosheim peninsula on Ellesmere Island (Nunavut, Canada), at about 30 km from the Eureka Weather Station (Fig. 1-1). TBL has a mean depth of 3.5 m and maximum depth of 9.5 m. It is a typical lake from the Fosheim peninsula area (Hamilton *et al.* 2000), with summer water temperatures ranging from 2 to 9 °C during the ice-free periods, low total phosphorus (TP) and nitrogen (TN) concentrations that averaged 5.4 ± 0.9 and 199 ± 15 μg L^{-1} respectively during the summer, and pH ranging from 8.0 to 8.6 (Appendices A and B).

Four mesocosms were placed in the nearshore part of TBL on 19 July 1994, immediately after ice-free period. The mesocosms were 3 m square and were open to the atmosphere and the littoral sediments. For each mesocosm, the average depth was about 3 m with a total water volume of about 27 000 L. The mesocosms were constructed of a high-density woven black polyethylene (Fabrine-Dupont) resistant to UV degradation. They were left to soak offshore for 10 days prior to installation to remove any dust or surface contamination. They were anchored to the sediments by heavy chains that were sewn into the base of the side skirts. Heavy stones were also attached through a rope at each corner in order to securely maintain the mesocosms in position. Flotation collars of polyurethane foam, extending 10 cm above the water surface, held the sidewalls upright. The mesocosms were arranged in 2 rows with 2 enclosures per row.

The experiment started the day after installation and continued until camp closure by Polar Continental Shelf Project following the first signs of frost. During the experiment, all field measurements and water samples were collected near the central part of the mesocosms from an inflatable boat equipped with a 1 m long wooden extended platform. All water samples were taken using an opaque Van Dorn (2.5 L) sampler and kept in the dark in plastic containers in a cooler until further work in the laboratory.

UVB treatments and measurements

The experiment consisted of 2 UVB treatments with 2 mesocosms per treatment: (1) ambient sunlight with ambient UVB levels (AMB-UVB) and (2) ambient sunlight plus enhanced UVB using artificial lamps (ENH-UVB). The lake was also sampled concurrently to determine whether large discrepancies occurred between the mesocosms and the lake itself.

Enhancement of UVB was obtained using three UVB lamps (National Biological Corporation, model FS20T12/UVB, Tweesmere, Ohio; 0.6 m long; emission peak at 310 nm), which were placed across a metal rod erected 1 m above the ENH-UVB mesocosms. Starting from 20 July until the end of the study period, the UVB lamps were turned on from 11:00 to 14:00 every day to enhance the highest solar UVB flux. The lamps were powered by a generator power source onshore and were not used at other times of the day. The UVB lamps provided essentially a constant UVB intensity throughout their illumination period and were not adjusted for changes in ambient UVB levels, depending on the weather conditions (e.g., cloudy cover). Spectral irradiances were measured at the water surface and underwater at 0.05, 0.10 and 0.50 m for each UVB treatment on August 11 and 12, between 10:00 and 13:00, using an Optronics OL 752 spetroradiometer calibrated with an OL 752-10 E spectral irradiance plug in standard (250-800 nm). The light sensor was a submersible PTFE-coated integrating sphere cosine receptor assembled with a waterproof quartz fibre optic cable 3.5 m long that was fitted to a PMT monochromator (S-20 photomutliplier detector). The instrument was set to take irradiance measurements (Watts cm^{-2} nm^{-1}) every 2 nm from 280 to 800 nm. The system was powered with a 12-volt battery. Although the sky was overcast on both August 11 and 12, the spectral irradiance measurements had to be made on these dates due to logistical constraints.

The lamp installation did not shade the receiving sunlight nor did it affect PAR and UVA levels. From 10 measurements taken on August 11-12, PAR (400 -700 nm) averaged 66 ± 14 and 68 ± 14 W m^{-2} and UVA (320 - 400 nm) averaged 8.6 ± 1.5 and 8.8 ± 1.5 W m^{-2} at the water surface of the AMB-UVB and ENH-UVB mesocosms, respectively. However, the UVB irradiance supplied by the lamps was not fully homogeneous across the surface area of the ENH-UVB mesocosms. Percent UVB enhancement provided by the three lamps varied from almost 0% at the edge of the mesocosm to more than 75% at the water interface directly under the lamps in comparison to UVB levels at the water surface of the AMB-UVB mesocosms. The unweighted ultraviolet radiation spectra (280 – 400 nm) at the water surface of the AMB-UVB and ENH-UVB mesocosms obtained from an average of 10 measurements are presented in Fig. 1-2, top graph. Relative to the AMB-UVB treatment, the enhancement provided by the UVB lamps was highest for the shorter wavelengths (i.e., below 310 nm) and decreased as the wavelength increase, with no significant enhancement in the UVA waveband.

The application of the biological weighting function (BWF) for inhibition of photosynthesis in the marine diatom, *Phaeodactylum* sp. (Cullen *et al.* 1992) to the spectral irradiances is shown in Figure 1-2, bottom graph. This gives some indication of the biological significance of the UVB enhancement provided by the lamps, especially at wavelengths below 310 nm (Fig. 1-2, bottom graph). However, it is acknowledged that the application of the BWF from Cullen *et al.* (1992) may not be appropriate for phytoplankton from TBL since BWFs should be limited to the organisms from which they are derived (Behrenfeld *et al.* 1993; Häder *et al.* 1998). Integrated over the entire UVB waveband (280-320 nm), the unweighted and weighted UVB irradiances were on average 1.53- and 3.72–fold greater respectively for the ENH-UVB treatment relative to AMB-UVB treatment. Assuming the irradiance-dependent model, the biologically effective fluence rates for the inhibition of photosynthesis (dimensioneless E^*_{inh}) by UVB irradiance in *Phaeodactylum* sp. (Cullen *et al.* 1992) would be of 0.04 and 0.14 for the AMB-UVB and ENH-UVB treatments, respectively. This would correspond to an inhibition in the photosynthesis of the diatom *Phaeodactylum* from Cullen *et al.* (1992) of 4% by surface solar UVB irradiance over the AMB-UVB mesocoms and about 3 times higher (i.e., 12%) by surface UVB irradiance provided by the lamps over the ENH-UVB mesocosms.

It is recognized that the enhancement supplied by the lamps was considerably greater than it would be expected from a moderate decrease in stratospheric ozone and also resulted in unnatural UVB:UVA and UVB:PAR ratios, especially on cloudy or foggy days. For example, the ratios of UVB:UVA and UVB:PAR were between 1.5 to 2.0-fold higher at the water surface of the ENH-UVB mesocoms compared to the AMB-UVB mesocosms on cloudy days, with negligible change in the UVA:PAR ratio. While the UVB dosage rate may have been high during the 3-h illumination period, the relative increase in the daily unweighted UVB dose (kJ m^{-2} d^{-1}) received on the ENH-UVB mesocosms was estimated to be only from 4% (on a cloudless day) to 20% (on a cloudy day) higher than ambient UVB levels, estimated from daily UVB data measured at the nearest weather station located in Resolute Bay, Cornwallis Island during the time period of the experiment (WOUDC 2004). These daily UVB increases were well within the range expected from moderate stratospheric ozone depletion for the Canadian Arctic (e.g., WMO 2003).

Physical and chemical variables

Depth profiles of water temperature, conductivity and dissolved oxygen in the mesocosms and surrounding lake (outside the mesocosms) were recorded using a YSI (Yellow Springs Instrument Co Inc) model 33 SCT meter and model 57 oxygen meter, respectively. Measurements were taken weekly starting on 22 July throughout the course of the experiment (Appendix A). Samples were also taken weekly for water chemistry analysis at 0.5 m and near bottom (~2.5 m), in order to determine whether there were large discrepancies between the surface and bottom as well as between the mesocosms and external water (Table B-1). Sample processing for water chemistry followed the procedures outlined in Chapter 2 and the *Analytical Methods Manual* (Environment Canada 1979). All processed bottles and filters were kept cool and in the dark before being shipped to the National Water Research Institute (Burlington, Ontario, Canada) for chemical analyses following the methods given in Environment Canada (1979).

Each sample included the measurements of nitrite (NO_2), nitrate (NO_3), ammonia (NH_3), total nitrogen (TN), soluble reactive phosphate-phosphorus (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total Kjeldahl nitrogen (TKN), unfiltered total phosphorus (TP-UF, including phosphorus in particulate and dissolved phase), total "dissolved" filtered phosphorus (TP-F), particulate organic carbon (POC) and particulate nitrogen (PON), major ions (i.e., calcium [Ca], magnesium [Mg], potassium [K], sodium [Na], chloride [Cl], sulphate [SO_4]), dissolved silica (SiO_2) and trace metals (i.e., silver [Ag], aluminium [Al], barium [Ba], beryllium [Be], cadmium [Cd], cobalt [Co], chromium [Cr], copper [Cu], iron [Fe], potassium [K], lithium [Li], manganese [Mn], molybdenum [Mo], nickel [Ni], lead [Pb], vanadium [V], strontium [Sr], zinc [Zn]; Table B-1).

Chlorophyll a

Water samples were collected weekly at 0.5 and 2.5 m in each mesocosm for a total of 4 sampling dates (day 3, 9, 16 and 23). 1000 mL from each water sample was filtered through a 47 mm diameter Whatman GF/F glass microfibre filter. All filters were then stored frozen in plastic petri dishes wrapped in aluminum foil until analysis. Chlorophyll extractions were done following the SCOR/UNESCO technique (Strickland and Parsons 1972). Each filter was homogenized with a Teflon pestle in a glass mortar filled with 2 mL of 90% acetone and extracted in the dark in 90% acetone for 10 min. The extracts were cleared by centrifugation and assayed at 663, 645, 630 nm with a Beckman model 25 spectrophotometer against a 90% acetone blank. Chlorophyll was calculated following the equation of Strickland and Parsons (1972; Appendix C-1).

Phytoplankton productivity, size distribution and carbon allocation

Phytoplankton productivity was measured every 4 to 7 days during the course of the mesocosm experiment for a total of 5 sampling dates. For each sampling date, triplicate water samples were taken from each mesocosm at about 0.5 m. Three 300 mL sub-samples were transferred into rinsed polyethylene Whirlpak (WP) bags. WP bags are easy to handle, non-toxic for phytoplankton production measurements (Prézelin and Smith 1993; Prézelin *et al.* 1994a,b) and transmit all wavelengths in both PAR and UV regions (Perin 1996). Primary production was measured by the ^{14}C-bicarbonate method

(Lean and Burnison 1979). Each WP bag was inoculated with 50 µL of ^{14}C-sodium bicarbonate ($^{14}NaHCO_3^-$; specific activity of 0.5 mCi mL^{-1}; ICN Biomedicals). The WP bags were incubated between 2 to 3 hours inshore of TBL at about 0.1 m. The incubation for measuring total and size-fractionated productivity as well as carbon allocation were all done under the same irradiance regime (i.e., ambient solar radiation) in order to detect variations between the two UVB treatments that would have originated from long-term changes in the species/size composition, biomass and (or) physiological status of the developing phytoplankton communities in the mesocosms.

After incubation, water subsamples of 150 mL from each bag were pre-filtered through a 20-µm Nitex filters and aliquots of 25 and 75 mL were then filtered through a 0.2-µm and 2-µm Nuclepore filters respectively to determine total phytoplankton productivity and the distribution of phytoplankton productivity in three size classes: *i*) picoplankton (0.2 - 2 µm), *ii*) nanoplankton (2 - 20 µm) and *iii*) netplankton (> 20 µm; Appendix C-2). The size distribution of phytoplankton productivity could not be determined on the last sampling day (Day 26) due to insufficient filter supplies. Duplicate WP bags were also incubated in the dark and filtered the same way. All filters were rinsed with 0.2-µm filtered lake water to remove any residual inorganic ^{14}C.

After filtration, each filter was placed in a scintillation vial and 5 mL of scintillation cocktail (Beckman, Ready Safe) was added. 100 µL of water was also taken from each WP bag and placed in scintillation vials with 100 µl of ethanolamine and 5 mL of scintillation cocktail in order to measure total radioactivity in each bag. All the vials were analysed for radioactivity in disintegrations per minute (DPM) using an internal quench in a Beckman LS counter. DPM uptake rates from the dark samples were subtracted and equivalent to time zeros (T_o) obtained from the light-incubated samples (Appendix C-2).

The composition of the subcellular fractions in the phytoplankton was done by measuring each of the fractions during carbon fixation (Morris *et al.* 1974). 150 mL water subsamples from each WP bags were filtered through 25 mm diameter Whatman GF/F glass microfibre filters, rinsed with 5 mL of filtered lake water to remove any residual inorganic ^{14}C and stored frozen until fractionation. The incorporation of ^{14}C into low molecular weight metabolites, lipids, polysaccharides and proteins were estimated following the sequential method of extraction used by Cuhel *et al.* (1984) and Cuhel and Lean (1987a,b). The low molecular weight metabolites and macromolecules were separated and extracted sequentially based on their solubilization into four operationally defined fractions: *i*) cold 10% trichloroacetic acid (TCA) soluble fraction (low molecular weight material or LMW), *ii*) alcohol-ether soluble fraction (lipid), *iii*) hot TCA soluble material (mainly polysaccharides and also nucleic acids) and *iv)* the insoluble residue (mainly protein). An overview of the types of ^{14}C-labelled molecules and compounds expected in each fraction can be found in Cuhel and Lean (1987a). The amount of radioactivity incorporated into each subcellular fraction was measured with a Beckman LS counter in DPMs. The LMW, lipid, polysaccharide and protein fractions were then expressed as the percentages of the sum of the four fractions (Appendix C-2). Photosynthetic extracellular release of DOC by phytoplankton was not measured.

Heterotrophic bacteria, photosynthetic picoplankton and heterotrophic nanoflagellates

The abundance of photosynthetic picoplankton (PPICO) and heterotrophic nanoflagellates (HNF) was measured twice (day 3 and 16) while that of heterotrophic bacteria (HB) was measured three times (day 3, 16 and 23) during the course of the mesocosm experiment. For each sampling date, water samples were taken from each mesocosm at two depths (0.5 and 2.5 m). Preservation and enumeration of samples was done similarly to the procedures described in Tzaras *et al.* (1999). 90 mL sub-samples were preserved with 10 mL of 10% glutaraldehyde buffered with 0.1M sodium cacodylate (pH 7), except for HB on day 23 where duplicate sub-samples (5 mL) were preserved with 200 µL of 37% formaldehyde in big glass vials (1.4% final concentration of formaldehyde). Samples were then stored cool in the dark for microbial slide preparations, which were made within a few weeks of the collection date.

Direct counts of HB, PPICO and HNF were determined by epifluorescence microscopy. The preserved samples were filtered through 0.2 µm (for HB and PPICO) and 1.0 µm (for HNF) Poretic filters prestained in a 0.2% solution of Irgalan black in 2% acetic acid that were placed on top of 0.45-um cellulose nitrate Sartorius filters. For PPICO, 20 mL from each sample was filtered. Since they lack photosynthetic pigments that fluoresce, HB and HNF were first stained with DAPI (4', 6-diamidino-2-phenyl-indole; Sigma), a fluorochrome used to visualize cells by staining any DNA present (Porter and Feig 1980). The stock solution of DAPI was made by mixing 10 mg of DAPI (SIGMA, lot: 84H4006, D-9542) with 10 mL of dH_2O filtered through a 0.2 µm filter. The DAPI working solution was added in a 3:1 ratio (3 parts sample to 1 part DAPI) to 5 mL (for HB) and 15-20 mL (for HNF), respectively, of sample. Each sample was set to stain for about 7 minutes before filtering. A foil tent was placed over the filtering tower to prevent light from breaking down the DAPI that is sensitive to photolysis. After filtration, all filters were then placed on slides and stored frozen until cell counts.

PPICO counts were performed using red autofluorescence of phycocyanin-containing cells (a pigment found exclusively in cyanobacteria) under green excitation (510 to 570 nm) as described in Pick and Agbeti (1991). HB and HNF counts were conducted under UV excitation, which make the cells appear whitish. Cell enumerations were done using a 100x oil immersion objective on a Zeiss standard epifluorescence microscope fitted with a 100 W HBO mercury lamp for a final magnification of 1250x (Pick and Caron 1987). 20 random whole field views were examined for HB counts. PPICO and HNF were counted along transect since counts were low in each field, for a total of 3 transects per sample. (Appendix C-3).

Heterotophic bacterial incorporation of ^{3}H-thymidine

Heterotrophic bacterial (HB) activity was measured every week for a total of 4 sampling dates. For each sampling date, water samples were taken from each mesocosm at two depths (0.5 and 2.5 m). Three 15 mL sub-samples (one formaldehyde-killed control and two treatment samples) were transferred into sterile vials. Formaldehyde-killed controls were inoculated with 5 mL of 8% sugared formalin (2% final concentration). Heterotrophic bacterial production (i.e. growth rates) was determined by the rate at which exogenously supplied methyl-tritiated thymidine (^{3}H-TdR) is incorporated into bacterial DNA (e.g., Moriarty 1984; tritiated thymidine incorporation bioassay method) since there is a direct correlation between DNA synthesis and bacterial division rate (Moriarty 1986). Each vial (including the killed-formaldehyde controls) was inoculated with 20 µL of ^{3}H-TdR (ICN Biomedicals; specific activity of 1.0 mCi mL^{-1}) to yield a final concentration of 20 nM. The vials were incubated in the dark between 40 to 60 minutes at lake temperature. After incubation, DNA incorporation was terminated with the addition of 5 mL 8% sugared formalin to each vial (2% final concentration; except for killed controls). The entire volume from each vial was then filtered onto a 25 mm diameter Whatman GF/F glass microfibre filter and rinsed with lake water to remove any residual ^{3}H-TdR. The filters were stored in aluminum paper or plastic mini-vials and kept frozen until extraction.

DNA extraction was done following the sequential method of extraction used by Cuhel *et al.* (1984), which separates and extracts low molecular weight materials and macromolecules into four operationally defined fractions (see above in *Phytoplankton productivity, size distribution and carbon allocation*). Following extraction, all fractions (including the formaldehyde-killed controls) were assessed for radioactivity using a scintillation counter (Beckman LS) in DPMs. DPMs from the hot TCA soluble fraction (which contains polysaccharides, DNA and RNA) were used to estimate the tritiated thymidine assimilation rates (pmol ^{3}H-TdR L^{-1} h^{-1}), which had been corrected for abiotic ^{3}H-TdR incorporation by subtracting radioactivity from formaldehyde-killed controls (Appendix C-4).

Zooplankton

Triplicate zooplankton samples were collected weekly (for a total of four sampling dates) in each mesocosm by vertical hauls using a 0.09 m^2 Plexiglass square net equipped with a Rigosha flow meter (Model 5571, Rigosha and Co. Ltd., Tokyo, Japan) and a 40-μm mesh Nitex. The organisms were transferred into 100 mL plastic jars and immediately preserved with 8% sugared formalin to yield a final concentration of 4% formaldehyde for storage. The volume of lake water filtered (V, in m^3) was calculated using the formula in Appendix C-5.

Animal counts and lengths of the preserved samples were made using their video images that were measured with electronic calipers in a semi-automated zooplankton counting system called ZEBRA2 (Allen *et al.* 1994) on a Nikon SMZ-10 dissecting scope (Nikon Canada Instruments, Cooksville, Ontario). Taxonomic identifications were made from several sources, including Pennak (1989), and separated up to the genus/taxa level. Total zooplankton density (total number of zooplankton per unit volume), total zooplankton length and the relative abundance of each genus were then calculated and compared between the two UVB treatments (Appendix C-5).

Statistical Analyses

For chlorophyll *a* and microbial abundances (HB, PPICO, and HNF), the effects of UVB (2 levels; ambient and enhanced) and sampling depths (2 levels; 0.5 and 2.5 m) were assessed using a Model I (fixed effects), two-way factorial analyses of variance with repeated measures (ANOVAR). Total phytoplankton productivity, percent productivity by picoplankton, nanoplankton and netplankton, percent carbon fixed into LMW, lipid, polysaccharide and protein, zooplankton density, total zooplankton length and relative abundance of each zooplankton taxa were assessed using a two-way nested Model III ANOVAR where the "higher" fixed factor is UVB treatment (ambient and enhanced

UVB) and the "lowest" nested factor (random subgroup) is the mesocosm (triplicate samples within each mesocosm for each depth). For heterotrophic bacterial activity, the effects of the two fixed factors (UVB and sampling depths) and the nested factor (mesocosm; duplicate samples within each mesocosm for each depth) were assessed using a Model III nested ANOVAR. ANOVAR allows the use of several dates when comparing treatment effects (UVB and/or sampling depth), but does not assume that sampling dates are independent of each other (Winer 1971). The time (i.e. day) factor consisted of 2 sampling dates for PPICO and HNF abundances, 3 sampling dates for HB abundance, 4 sampling dates for chlorophyll *a*, percent productivity by picoplankton, nanoplankton and netplankton, and heterotrophic bacterial activity and 5 sampling dates for total phytoplankton productivity and percent carbon allocation into LMW, lipid, polysaccharide and protein.

In an ANOVAR, the between-subject effects are those due to the treatment effects (i.e. UVB and (or) sampling depth) and related interaction (if applicable) and the response of the dependent variable to the treatment effect is averaged over the entire sampling period. The within-subject effects reveals how the dependent variable and its responses to the treatments vary with time. Therefore, the tested null hypotheses are the responses of the dependent variable to the different treatments are the same over time. Overall, the ANOVARs evaluated the treatment effect(s), any temporal effects as well as any corresponding interaction effects. The relative contribution of picoplankton, nanoplankton and netplanton to total phytoplankton productivity, the relative proportion of carbon fixed into LMW, lipid, polysaccharide and protein, and the relative abundance of each zooplankton taxa were all first normalized through an arcsine transformation before the ANOVARs were executed (Zar 1984). The normality and homoscedasticity of the residuals were tested by using the Lilliefors' and Levene's tests respectively. If the data did not meet the normality and/or homoscedaticity assumptions for ANOVA, the data were either transformed or ranked. All ANOVARs were run using SYSTAT version 10 (SPSS Science 2000).

Results

Physical and chemical characteristics of mesocosms and lake

TBL has high DOC levels, which averaged (± SD) 11.8 ± 5.3 mg/L in the mesocoms during the study period (Table B-1). DOC concentrations varied between 5 to 18 mg L^{-1} in both the mesocosms and the lake. This may be due to variations throughout the summer of groundwater inputs in the lake of refractory DOC over the permafrost and DOC release from microbial activity. Because DOC levels were high, UVB as well as UVA decreased significantly with depth in the mesocosms (Fig. 1-3). From the underwater spectral irradiance measurements taken in 11-12 August, the attenuations of UVB, UVA and PAR were practically the same between the mesocosms and the integrated attenuation coefficients (K_{dI}) of UVB (280-320 nm), UVA (320-400 nm) and PAR (400-700 nm) were about 6.7, 2.7 and 1.0 m^{-1}, respectively. The depths of the 1% surface UVB, UVA and PAR were then estimated to be 0.7, 1.7 and 4.6 m, respectively. At the bottom of the mesocosms, about 5% of surface PAR was still present (Fig. 1-3).

During the entire period of the experiment, the water temperatures were similar between the mesocosms and surrounding lake water (i.e., outside the mesocoms) and fluctuated between 4.8 to 8.5 °C (Fig. A-1). There was a weak thermal stratification in the mesocosms, mainly at the beginning of the study, with temperature differences of only 0.5-1.3 °C between the surface and the bottom of the mesocosms. However, as the experiment progressed, the water temperatures became the same throughout the water column in all mesocosms. Oxygen levels were also very similar between the lake and mesocosms, except on day 3, where values in the mesocosms were lower than the surrounding water (Fig. A-2). On days 3 and 10, oxygen levels increased from 10 mg L^{-1} at the surface to 11.5 mg L^{-1} at the bottom of the mesocosms. TBL as well as the mesocosms had high water conductivity, with an overall average of 380 ± 12 µS cm^{-1} during the summer of 1994 (Table B-1). In the mesocosms, conductivity levels decreased slightly from top to bottom (differences of $\leq$ 15 µS cm^{-1}) throughout the study period, except at the end where levels were the same throughout the water column (Fig. A-3).

The chemical characteristics of the water inside the mesocoms and outside in the lake over the course of the experiment are summarized in Table B-1. The water was chemically the same between the two UVB treatments as well as between the mesocosms and surrounding lake water during the entire experiment. The chemical characteristics did not change with depth (i.e., between the surface and bottom of the mesocosms and surrounding lake). The concentrations of nitrite, nitrate and ammonium were all below the technical detection limit (except for nitrite on August 15). Total nitrogen averaged 211 ± 22 µg L^{-1} (from all pooled data) and principally occurred as dissolved organic nitrogen (DON) as observed in other lakes of the Canadian Arctic Archipelago (Chapter 2). In addition, most of the DON is refractory and unavailable to plankton. The C/N ratio was about 10, which is indicative of a moderate nitrogen deficiency (D.Lean, personal communication). Total phosphorus (TP) averaged about 6 ± 2 µg L^{-1}, which is similar to other lakes of the Fosheim Peninsula (Hamilton *et al.* 2000), but lower than the average TP (i.e., 12 ±18 μg L^{-1}) for 204 lakes of the Canadian Arctic Archipelago (Hamilton *et al.* 2001). Levels of iron and magnesium, which averaged 58 ± 25 and 17,500 ± 800 μg L^{-1}, were high in this lake, while manganese concentrations were low (average of 6.2 ±3.4 μg L^{-1}).

Chlorophyll a

Chlorophyll *a* levels were low throughout the study period and ranged from 0.4 to 1.4 μg L^{-1}. Chlorophyll *a* concentrations did not differ significantly between the two UVB treatments nor with sampling depths throughout the study period (Table 1-1; ANOVAR, UVB effect: $p = 0.171$; depth effect: $p = 0.756$; Table D-1). However, levels increased slightly after day 9 in all of the mesocosms, regardless of the treatments (Table 1-1; ANOVAR, day effect: $p = 0.020$; average of 0.7 ± 0.2 μg L^{-1} for days 3 and 9 included and of 1.0 ± 0.2 μg L^{-1} for days 16 and 23 included). This increase may be due to a phytoplankton bloom or successional change in phytoplankton species composition.

Phytoplankton productivity, size distribution and carbon allocation

Total productivity rates of phytoplankton populations sampled at about 0.5 m in the mesocoms were low (regardless of the treatment) and ranged from 0.04 to 1.59 μg C L^{-1} h^{-1} (Fig. 1-4), but were within the range found for other High Arctic lakes (Perin 1996; Chapter 2). The rates varied significantly between sampling dates with an average of 0.09 ± 0.03 μg C L^{-1} h^{-1} at the beginning of the study up to 0.72 ± 0.38 μg C L^{-1} h^{-1} on day 19 (Fig. 1-4; nested ANOVAR, day effect: $p < 0.001$; Table D-2). There were significant effects of enhanced UVB on total productivity, but these effects were strongly dependent on the sampling date (nested ANOVAR, UVB effect: $p = 0.02$; UVB * day: $p < 0.001$). Total productivity did not differ significantly between the two UVB treatments at the beginning of the study period (i.e., day 4; 1-way nested ANOVA; $p = 0.127$), but decreased by about 40% in the ENH-UVB mesocosms on day 8 and 12 (1-way nested ANOVA: p's ≤ 0.001). Then, the average total productivity rate raised by about 2-fold on day 19 in the enhanced UVB (0.98 ± 0.36 µg C L^{-1} h^{-1}) compared to the control mesocosms (0.46 ± 0.17 µg C L^{-1} h^{-1}; 1-way nested ANOVA: $p = 0.006$), but became similar between the two treatments at the end of the experiment (i.e., on day 26; Fig. 1-4; 1-way nested ANOVA: $p = 0.307$).

The percent contribution of picoplankton (0.2 – 2 µm) to productivity ranged from 30 to 68% throughout the study period and its mean was lowest on day 8 (Fig. 5, top graph; about 44% on day 8 compared to greater than 50% for the other sampling dates; ANOVAR, time effect: $p < 0.001$). The relative contribution of picoplankton to productivity generally decreased by about 1.2-fold in the enhanced UVB treatment throughout the study period, except for day 19 where means were similar between the two treatments (Fig. 1-5, top graph; overall average of 54.1 ± 8.0% for ambient UVB and 48.3 ± 8.1% for enhanced UVB; ANOVAR, UVB effect: $p = 0.008$, UVB * day: $p = 0.089$). The percent contribution of nanoplankton (2 – 20 µm) to productivity ranged from 22 to 57% during the study and was highest on day 8 (Fig. 1-5, middle graph; about 47% on day 8 compared to less than 40% for the other sampling dates; ANOVAR, time effect: $p = 0.001$). Enhanced UVB levels significantly increased by 1.1- to 1.2-fold the relative productivity of nanoplankton, except on day 19 (Fig. 1-5, middle graph; overall average of 38.6 ± 6.7% for ambient UVB and 42.3 ± 8.2% for enhanced UVB; ANOVAR, UVB effect: $p = 0.021$, UVB * day: $p = 0.023$; Table D-2).

Throughout this study, netplankton (> 20 μm) contributed the least to total productivity compared to picoplankton and nanoplankton, regardless of the UVB treatment. Overall, the relative contribution of netplankton to productivity averaged 8.3 ± 2.3% compared to 51.2 ± 8.5% for picoplankton and 40.5 ± 7.7% for nanoplankton. Percent productivity of netplankton ranged from 5 to 17% during the study period and was highest during the first 8 days, regardless of the treatment (Fig. 1-5, bottom graph, ANOVAR, day effect: $p = 0.005$). The relative contribution of netplankton to photosynthesis increased significantly by 1.3 to 1.6-fold in the enhanced UVB enclosures throughout the study period (Fig. 1-5, bottom graph; overall average of 7.3 ± 1.8% for ambient UVB and 9.4 ± 2.4% for enhanced UVB; ANOVAR, UVB effect: $p = 0.013$; UVB * day: $p = 0.255$; Table D-2).

The percent of carbon fixed in low molecular weight (LMW) ranged from 24 to 43% during the study period and varied significantly between sampling dates (ANOVAR, day effect: $p = 0.002$; Table D-2). Mean percent carbon in LMW was about 30% for days 8, 12 and 19, but increased up to 34% on days 4 and 26 (Fig. 1-6a). The proportion of ^{14}C allocated to the LMW fraction did not change significantly between the two UVB treatments throughout the duration of the experiment (overall average of 31.2 ± 5.3% for ambient UVB and 31.2 ± 4.0% for enhanced UVB; ANOVAR, UVB effect: $p = 0.931$; UVB * day: $p = 0.121$). The percent of carbon fixed in lipid ranged from 17 to 29%. It averaged around 20% for days 4, 12 and 26 but increased up to 25% on days 8 and 19 (Fig. 1-6b; ANOVAR, day effect: $p < 0.001$; Table D-2). There were no significant effects of enhanced UVB levels on the lipid fraction throughout the study period (overall average of 22.3 ± 3.5% for ambient UVB and 21.6 ± 3.0% for enhanced UVB; ANOVAR, UVB effect: $p = 0.249$; UVB * day: $p = 0.119$).

Percent of carbon fixed in the polysaccharide fraction ranged from 11 to 26%. Mean percent carbon into polysaccharides was quite similar between sampling dates (around 20%), except for a slight decrease to 17.8 ± 1.5% on day 19 (Fig. 1-6c; ANOVAR, day effect: $p = 0.026$; Table D-2). The polysaccharide fraction did not differ significantly between the two UVB treatments (overall average of 19.8 ± 2.4% for ambient UVB and 19.6 ± 2.8% for enhanced UVB; ANOVAR, UVB effect: $p = 0.530$; UVB * day: $p = 0.254$). Percent of carbon fixed in protein ranged from 15 to 35%. The mean was similar between sampling dates (around 26%), except for day 12 where it increased to 31.7 ± 2.3% (Fig. 1-6d; ANOVAR, day effect: $p = 0.001$; Table D-2). The protein fraction was similar between the two UVB treatments, except on day 26 where it was 20% higher in the enhanced UVB treatment (overall average of 27.1 ± 3.8% for ambient UVB and 27.4 ± 4.1% for enhanced UVB; ANOVAR, UVB effect: $p = 0.425$; UVB * day: $p = 0.114$). Overall, the LMW, protein, lipid and polysaccharide fractions accounted for 31.2 ± 4.7%, 27.2 ± 3.9%, 21.9 ± 3.3% and 19.4 ± 3.2% of the total ^{14}C fixed respectively in the mesocosms.

Heterotrophic bacteria, photosynthetic picoplankton and heterotrophic nanoflagellates

Although the overall effect of enhanced UVB on heterotrophic bacterial (HB) abundance was not significant (ANOVAR, UVB effect: $p = 0.500$), the effects of enhanced UVB varied significantly between sampling days, regardless of the sampling depths (ANOVAR, UVB * depth: $p = 0.684$; UVB * day: $p < 0.001$; UVB * day * depth: $p = 0.222$; Table D-3). The abundance of HB was 20 to 50% lower in the ENH-UVB mesocosms on day 3 and 16 compared to the AMB-UVB mesocosms (Fig. 7, top graph; overall average of $2.6 \pm 0.7 \times 10^5$ cells mL^{-1} for ambient and $1.4 \pm 0.3 \times 10^5$ cells mL^{-1} for enhanced UVB on days 3 and 16 included; 2-way ANOVA, UVB effect: p's < 0.02; UVB * depth: p's > 0.06). However, on day 23, HB levels became significantly higher (by about 1.5-fold) in the enhanced UVB treatment (average of $3.1 \pm 0.8 \times 10^5$ cells mL^{-1} for ambient and $5.0 \pm 0.7 \times 10^5$ cells mL^{-1} for enhanced UVB on day 23; 2-way ANOVA, UVB effect: $p = 0.003$; UVB * depth: $p = 0.614$).

Hetetrophic bacterial incorporation rates of ^{3}H-thymidine (HB activity) ranged from 0.6 to 2.8 pmol ^{3}H-TdR L^{-1} h^{-1} during the study period. HB activity increased generally by 4 to 75% in the enhanced UVB mesocosms compared to the ambient UVB mesocosms throughout the experiment, except on day 13 where HB activity was about 20% lower in the enhanced UVB treatment (Fig. 1-7, bottom graph; ANOVAR, UVB effect: $p = 0.021$; UVB * day: $p < 0.001$; UVB * day * depth: $p = 0.002$; Table D-4). HB activity averaged 1.1 ± 0.3 pmol ^{3}H-TdR L^{-1} h^{-1} and 1.5 ± 0.4 pmol ^{3}H-TdR L^{-1} h^{-1} in the ambient and enhanced UVB mesocosms respectively when combining day 7, 21 and 25 together, while it averaged 2.3 ± 0.2 pmol ^{3}H-TdR L^{-1} h^{-1} and 1.9 ± 0.3 pmol ^{3}H-TdR L^{-1} h^{-1} in the ambient and enhanced UVB treatments respectively on day 13.

Photosynthetic picoplankton (PPICO) abundance was very low at TBL and in the mesocoms with less than 500 cells mL^{-1}. PPICO levels were significantly lower in the enhanced UVB enclosures at the surface only, especially on day 3 where cell numbers dropped one order of magnitude at 0.5 m (Fig 1-8, top graph; ANOVAR, UVB effect: p =

0.049; UVB * depth: $p = 0.033$; UVB * day: $p = 0.012$; Overall average of 287 ± 70 cells mL^{-1} for ambient and 88 ± 63 cells mL^{-1} for enhanced UVB at 0.5 m). Meanwhile, PPICO abundances were similar between the two UVB treatments near the bottom (Fig 1-8, top graph; Overall average of 171 ± 47 cells mL^{-1} for ambient and 185 ± 75 cells mL^{-1} for enhanced UVB at 2.5 m).

Heterotrophic nanoflagellates (HNF) abundance was low on day 3 and similar between the UVB treatments at both sampling depths, with an average of 89 ± 17 cells mL^{-1} (Fig. 1-8, bottom graph). However, HNF levels increased by 3-fold in the mesocosms exposed to enhanced UVB levels on day 16, regardless of the sampling depths (average of 168 ± 39 cells mL^{-1} for ambient and 507 ± 121 cells mL^{-1} for enhanced UVB on day 16; ANOVAR, UVB effect: $p = 0.010$; UVB * depth: $p = 0.686$; UVB * day: $p = 0.003$; Table D-3).

Zooplankton

Total zooplankton density (i.e., total number of zooplankton greater than 40 μm per unit of volume) ranged from 1889 to 13,559 individuals m^{-3} throughout the study period. Enhanced UVB levels significantly increased total abundance of zooplankton (overall average of 5734 ± 2299 organisms m^{-3} for ambient UVB and 8331 ± 2911 organisms m^{-3} for enhanced UVB), but its effect varied between sampling dates (Fig. 1-9, top graph; ANOVAR, UVB effect: $p = 0.005$; UVB * day: $p = 0.009$; Table D-5). The densities were similar between the two UVB treatments during the first 2 weeks (i.e., on days 6 and 13; 1-way nested ANOVA, UVB effect: p's > 0.25), but increased significantly in the enhanced UVB treatment thereafter (i.e., on days 20 and 27; 1-way nested ANOVA, UVB effect: p's < 0.035). Total zooplankton mean length, which has been corrected for the relative abundance of all taxa, ranged from 0.36 to 0.93 mm during the study. Zooplankton mean length did not differ between the two UVB treatments throughout the experiment and was generally greater than 0.50 mm, except on day 20 where it was slightly lower at 0.48 mm for the ambient UVB treatment only (Fig. 1-9, bottom graph; ANOVAR, UVB effect: $p = 0.113$, day effect: $p = 0.003$, UVB * day: $p = 0.046$; Table D-5). The overall mean length was 0.61 ± 0.12 mm (Appendix H).

The zooplankton (> 40 μm) community at Two Basin Lake consisted of species from the following taxa: *Cyclops* sp. (Phylum Arthropoda, Class Crustacea, Subclass Copepoda, Order Eucopepoda, Suborder Cyclopoida), *Daphnia* sp. and *Diaphanosoma* sp. (Phylum Arthropoda, Class Crustacea, subclass Entomostraca, Order Branchiopoda, Suborder Cladocera), and *Keratella* sp. (Phylum Rotifera, Class Monogononta, Order Ploima). Adult copepod cyclops generally dominated the zooplankton community throughout the duration of the experiment in all the mesocosms and contributed to an average of 46.4 ± 13.6% to total abundance. In the ambient UVB treatment, adult cyclops accounted for more than 60% of the total abundance on the first 13 days and decreased to less than 50% thereafter (Fig. 1-10a; ANOVAR, day effect: $p < 0.001$; UVB * day: $p = 0.008$; Table D-5). The relative abundance of cyclopoid adults decreased significantly (1.4 to 1.7-fold) under enhanced UVB levels, except on day 20 where the relative abundances were similar between the two UVB treatments (overall average of 53.6 ± 14.1% for ambient UVB and 39.2 ± 8.7% for enhanced UVB; ANOVAR, UVB effect: $p < 0.001$). The relative abundance of cyclopoid nauplii was similar between the two UVB treatments during the study period, with an overall average of 28.4 ± 11.4 % and 26.7 ±

8.5% for the ambient and enhanced UVB treatments respectively (Fig. 1-10b; ANOVAR, UVB effect: $p = 0.618$; UVB * day: $p = 0.176$; Table D-5).

Regardless of the UVB treatment, the relative abundance of cladoceran daphnids increased from 4.0 ± 2.5% at the beginning to 19.8 ± 8.6% at the end of the experiment (Fig. 1-10c; ANOVAR, day effect: $p < 0.001$; Table D-5). The relative abundance of *Daphnia* sp. increased significantly in the mesocosms exposed to enhanced UVB levels, except at the end of the study where proportions were similar between the two UVB treatments (overall average of 8.1 ± 8.6% for ambient UVB and 11.9 ± 7.9% for enhanced UVB; ANOVAR, UVB effect: $p = 0.003$; UVB * day: $p = 0.002$). The cladoceran *Diaphanosoma* sp. accounted the least to total zooplankton abundance in both UVB treatments, with an overall average of 1.7 ± 1.6% (Fig. 1-10d). However, like *Daphnia* sp., a greater proportion of *Diaphanosoma* sp. was also observed in the enhanced UVB enclosures throughout the study period (overall average of 1.0 ± 1.3% for ambient UVB and 2.3 ± 1.6% for enhanced UVB; ANOVAR, UVB effect: $p = 0.001$; UVB * Day: $p = 0.821$; Table D-5). As for the rotifers (i.e., *Keratella* sp.), their relative abundance increased between 1.3- to 4-fold in the mesocosms exposed to enhanced UVB levels during the study period and accounted, on overall, for 19.9 ± 7.4% of the total zooplankton abundance compared to 8.9 ± 6.9% in the ambient UVB mesocosms (Fig. 1-10e; ANOVAR, UVB effect: $p = 0.003$; UVB * day: $p = 0.085$; Table D-5).

Discussion

Relevance of mesocosm and enhanced UVB exposure

Research of UVB effects on living organisms in the Arctic region has gained special interest in the scientific community, not only because of stratospheric ozone depletion, but also because of the great importance that climate warming could play in affecting underwater UVR levels in Arctic aquatic systems (e.g. Pienitz and Vincent 2000; Perin and Lean 2004). The present study assessed the long-term response of an Arctic freshwater pelagic ecosystem (that includes multiple trophic levels) to elevated UVB using *in situ* mesocoms.

The advantage of using mesocosms or other forms of manipulated natural systems versus single-trophic level tests is that they also integrate interactions between various species, between trophic levels and between biotic and abiotic components. They also allow the effects of UVB to be assessed under more realistic conditions over a timescale sufficient for the planktonic communities to respond in terms of their physiology, abundance and species composition. Thus, they represent a much more realistic test of the ecological effects of UVB than is typically achieved in either laboratory assays or in short-term *in situ* incubations. On the other hand, large-scale experiments limit our capacity to detect small-scale differences and provide results that are often harder to interpret since they integrate both direct and indirect effects on a given population (De Lange *et al.* 1999). Moreover, in contrast to single-species experiments that can be closely controlled, the exposure level received by organisms in deeper manipulated natural systems is more difficult to determine since UVB radiation is attenuated and water mixing alter the time of exposure (De Lange *et al.* 1999).

In this study, the mesocosms had low surface to volume ratio (9 m^2/27 m^3 = 0.33 m^{-1}), which would have minimized the wall effects. The water column was open to the atmosphere and sediments like in a natural lake environment, thereby reducing containment artefacts. The bio-optical environment in the mesocosms mimicked that of the surrounding lakewater. The planktonic communities were usually similar to that in the lake, giving confidence in the experimental system (Table E-5). Although the daily exposure (i.e., total cumulative unweighted UVB dose per day) was within what would be expected under moderate ozone depletion over the Arctic (IASC 1995; Frederick 1997; WMO 2003), the unweighted UVB dosage rate was quite high (ca 50% increase) in the ENH-UVB treatment relative to the control during the illumination period. The biological weighting calculations from Cullen *et al.* (1992) would also suggest more than 3 times higher inhibition of photosynthesis in *Phaeodactylum* sp. by UVB under the lamps at the water surface. Several studies have found that the recovery of aquatic organisms from UVB-induced damage is more affected by the fluence rate of UVB (i.e., the dose received per given time) than by the total accumulated dose received (e.g., Lesser *et al.* 1994; Siebeck *et al.* 1994; Cywinska *et al.* 2000; Grad *et al.* 2001). These studies suggested that, for equal doses of UVB, a relatively short exposure to high UVB irradiance is more damaging to organisms than a longer exposure to lower UVB irradiance. At high fluence rates, the level of damage by UVB could become too high compared to the DNA repair rates and consequently, could result in irreversible damage to the DNA (Häder 1993; Karentz 1994).

The use of an artificial light source can result in extreme UVB levels relative to PAR and UVA, especially on cloudy days. Significant alteration in the surface ratios of

UVB to UVA and UVB to PAR could then impair damage-repair mechanisms (Banaszak and Trench 2001) and affect light-dependent responses such as photosynthesis, photo-orientation and photoprotection (Gerber *et al.* 1996; Häder *et al.* 1998). For example, Moroz *et al.* (1999) showed that the motility of *Nitzschia linearis* was unaffected on sunny but not on overcast days when exposed to the same UVB intensities. The best approach to increase surface UVB levels would be to modulate the UVB enhancement so that a constant fraction of the incident surface UVB irradiance is achieved (e.g., Underwood *et al.* 1999; Wulff *et al.* 2000; Wängberg *et al.* 2001).

Despite the fact that the lamps provided high UVB fluence rates during the 3 h per day that they were on and greatly altered the surface ratios of UVB to UVA and UVB to PAR, (especially on cloudy days), the planktonic organisms in the ENH-UVB mesocosms were, however, well protected from UVB exposure. Almost all of UVB was attenuated below 1 m due to the high DOC levels in the mesocosms. Furthermore, organisms could easily seek refuge from UVB and/or repair any damages using PAR and/or UVA at lower depths (if they previously experienced any UVB damages in the surface layer). Thus, colored dissolved organic matter (CDOM) is an important factor to consider in natural aquatic systems since it not only reduces irradiance but also has marked effects on UV spectral composition with depth.

In the Arctic, most lakes do not stratify during the summer and water is then mixed continuously from surface to bottom, except for possible diurnal thermoclines. This was also generally observed in the mesocosms. Therefore, the organisms in the enhanced-UVB mesocosms would have been intermittently passively mixed and any UVB damage received at the surface could have been repaired at deeper depths.

However, if mixing rates were slow, organisms could then have sustained greater damage that may not have been reparable (Neale *et al.* 1998b).

While the attenuation of UVR was moderately high in TBL, the integrated attenuation coefficients (K_{dI}) of UVB and UVA calculated from spectral measurements gave much different values than expected using the equations generated from DOC concentrations (e.g. Scully and Lean 1994; Morris *et al.* 1995; Granéli *et al.* 1996). From the equations provided by Scully and Lean (1994), which were derived from temperate lakes with DOC levels less than 8 mg L^{-1}, K_{dI}'s for TBL would have been estimated to be 41 and 13 m^{-1} for UVB and UVA, respectively; 5- to 6-fold higher than the actual K_{dI}'s. In this relationship between the integrated attenuation coefficients and DOC levels, Lean (1998b) observed that the r^2 values dropped from 0.63 and 0.60 (when both clear and humic lake data were used) to 0.15 and 0.11 (when only the high DOC water data was used) for $K_{dI}B$ and $K_{dI}A$, respectively. Crump *et al.* (1999) also demonstrated that DOC was not a useful predictor of the attenuation coefficients for both UVB and UVA in ponds with high DOC levels. Lean (1998b) believed that the factors, which determine attenuation in humic waters, are more complicated than those found in less coloured waters. Crump *et al.* (1999) also suggested that differences in the fraction of DOC capable of absorbing radiation (i.e., chromophores) and the fraction of DOC capable of fluorescing (fluorophores) may explain the lack of a reliable relationship between DOC and attenuation coefficients in high humic waters.

Phytoplankton

During the entire study period, phytoplankton biomass, measured as chlorophyll *a*, did not change significantly when exposed to elevated UVB levels (Table 1-1). Results from other long-term outdoor mesocoms experiments in an alpine lake (Central Alps; Halac *et al.* 1997), in a mesotrophic lake (central Ontario, Canada; Laurion *et al.* 1998), in a fjord (Gullmar fjord, Sweden; Wängberg *et al.* 1999), and in shallow, hypertrophic estuary (Darss-Zingst estuary, Baltic Sea; Fosrter and Schubert 2001) as well as from long-term microcosms experiments (De Lange *et al.* 1999; Wängberg *et al.* 2001) have also shown phytoplankton biomass not to be affected by screening and/or enhancing UVB. No differences in chlorophyll *a* levels were also detected between the surface and bottom of the mesocosms for both UVB treatments. This would also indicate that there were little effects of enhanced UVB at the surface, water in the mesocosms was fairly mixed and/or phytoplankton could repair at deeper depths if they sustained any UVB damages at the surface.

Total productivity of phytoplankton populations sampled at 0.5 m in the ENH-UVB mesocosms was lower than that of AMB-UVB mesocosms in short-term incubations (carbon dioxide fixation) under sub-surface ambient radiation at the beginning of the mesocosm experiment only (Fig.1-4). Then, short-term carbon dioxide fixation of phytoplankton from the ENH-UVB mesocosms increased by almost 2-fold relative to the controls on day 19, and became similar between the two UVB treatments thereafter. Changes in phytoplankton community biomass cannot explain the observed variations in phytoplankton activity between the two UVB treatments given that chlorophyll *a* levels were similar between the two UVB treatments during the length of the experiment (see above). The samples used for measuring phytoplankton productivity were taken at the surface of the mesocosms (~0.5 m) during the time when the UV lamps were on. It is possible that the lower productivity levels observed on the first 12 days may have been caused directly by UVB that damaged or inhibited temporarily some photosynthetic processes or components in the phytoplankton communities at the surface of the ENH-UVB mesocosms, depending on the mixing rate.

Photosynthetic pigments, enzymes involve in photosynthesis (like the carbon dioxide-fixing enzyme RUBISCO) as well as components in the chloroplastic electron transport (especially those of photosystem II) have been shown to be sensitive to UVB (e.g. Renger *et al.* 1998; Aro *et al.* 1993; Vassiliev et al. 1994; Schofield *et al.* 1995; Lesser *et al.* 1996). Laurion *et al.* (1998) found a significant decrease in the light utilization efficiency of the phytoplankton exposed to ambient or enhanced UVB relative to those shielded from UVB during a 20-d mesocosm study in mesotrophic lake, although this effect was not translated into a significant change in phytoplankton community biomass, growth rates or grazing losses. Thus, it is quite possible that phytoplankton near the surface of the enhanced UVB mesocosms experienced some damage to their photosynthetic apparatus. However, these damages may have been only temporary and not representative of the overall effect of UVB on total phytoplankton productivity as a whole, especially since enhanced UVB did show any significant effect on phytoplankton biomass. Alternatively, modifications in the photosynthetic performance of the different size classes and/or in phytoplankton species/size composition could also be a possible explanation for the observed differences in total phytoplankton activity between the two UVB treatments (see below).

For this study, the picoplankton fraction (i.e., cells of size 0.2 – 2 μm) provided the largest contribution (ca 50%) to photosynthesis followed closely by the nanoplankton fraction (i.e., cells of size 2 – 20 μm; ca 40% of total carbon fixed). Meanwhile the netplankton fraction (i.e., cells > 20 μm) accounted the least (less than 10%) to photosynthesis in all of the mesocosms as well as in the surrounding lake water. Photosynthetic picoplankton are well known to be responsible for a large fraction of total phytoplankton productivity in oligotrophic environments (e.g., Perin *et al.* 1996) because of their high surface-to-volume ratio that allows a more efficient transport of nutrients under low substrate levels. Generally, the proportion of carbon fixed by picoplankton was found to be significantly lower in the samples from the ENH-UVB mesocosms compared to those from AMB-UVB mesocosms. Meanwhile, the relative contribution of larger cells (nanoplankton and netplankton) to photosynthesis was generally higher in the ENH-UVB treatment relative to the control (Fig. 1-5).

Since phytoplankton species identification and abundance was not done for this study (except for picocyanobacteria abundance), it is hard to determine whether changes in the size fractionation of phytoplankton productivity were as a result of a direct increase or decrease in the abundance/growth of certain individual species or size classes under the enhanced UVB treatment or simply as a result of differences in the photosynthetic performance (i.e., in the physiological state) between the three size classes. While picoplankton abundance was similar at deeper depths between the two UVB treatments, the decline in the proportion of carbon fixed by picoplankton could have resulted from the lower number of picoplankton found in the surface portion of the ENH-UVB mesocosms, the depth at which water had been collected for measuring carbon dioxide fixation (Fig.8, top graph). Bergeron and Vincent (1997) have observed a decline in picocyanobacteria by solar UVR under P enrichment in a subarctic lake.

Furthermore, since small cells generally have higher photosynthetic activity than large cells (e.g., Desortova 1976; Malone 1980), it is possible that the decrease in total phytoplankton productivity observed on the first 12 days of the study for the ENH-UVB treatment may have resulted from the declines in picoplankton abundance and/or the relative photosynthesis of the picoplankton. Cell migration to greater depths in order to avoid the damaging effects of enhanced UVB levels near the surface when the lamps were on or a decrease in viable cells at the surface are possible factors responsible for the lower number of picoplankton at the surface of the UVB-ENH mesocosms. However, since integrated water samples through the entire water column were not taken, it is not known whether picoplankton abundance had declined overall in the ENH-UVB mesocosms.

Small cells are usually believed to be more sensitive to UVR because they have high illuminated surface to volume ratios and little self-shading (Karentz *et al.* 1991a; Bothwell *et al.* 1993). Also, the UV-screening pigments in small cells would not be as effective given their short pathlength (Garcia-Pichel 1994). Long-term UVB studies (days to weeks) have shown conflicting results in relation to algal cell size (e.g., Bothwell *et al.* 1993; Mostajir *et al.* 1999a, b; Van Donk *et al.* 2001; Wängberg *et al.* 1996, 2001). For instance, a 9-d incubation experiment on phytoplankton species from two oligotrophic Arctic lakes near Spitsbergen (Norway) indicated a significant decrease in the growth rates of small chlorophytes, diatoms and picocyanobacteria while the growth of the larger colony-forming species (e.g. cyanobacteria, *Planktothrix* sp.) was mainly

(Van Donk *et al.* 2001). On the other hand, a 20-d mesocosm experiment conducted in a temperate mesotrophic lake showed no significant change in picocyanobacteria biomass and no clear differences in the total abundance of nanoplankton (Laurion *et al* 1998). Meanwhile, other long-term studies (≥ 7 days) have found that larger phytoplankton cells were usually more UVB-sensitive than smaller cells (e.g., Mostajir *et al.* 1999a; Wängberg *et al.* 1996; Wängberg *et al.* 2001). Retardation of cell division and inhibition of photosynthetic rate by UVB may also cause cell size enlargement as observed by Mostajir *et al.* (1999b) in Prymnesiophyceae during their 7-d mesocosm study.

Earlier work has shown that the phytoplankton community at Two Basin Lake included species from all algal divisions (e.g, chrysophyte *Dinobryon,* cyanobacteria, chlorophytes) but was dominated by diatoms (e.g. *Cyclotella bodanica* var. *lemanica* O. Müller and *Fragilaria pinnata*; Hamilton *et al.* 2000). Many studies have found that diatoms were usually more sensitive to UVB than other taxa (e.g. Danilov and Ekelund 2000; Mousseau *et al.* 2000). From an outdoor mesocosm experiment, lasting 48 days in a high-altitude Andean Lake (33 °S; 2700 m a.s.l.), Cabrera *et al.* (1997) found that the chlorophyte *Ankyra judayi* was more abundant in the UVB-inlcuded treatment, while the diatoms *Fragilaria construens* and *F. crotonensis* were more abundant in the UVB-excluded treatment. Due to differences in UVB-sensitivity between species, it is possible that some species were affected while others were not in the mesocosms exposed to enhanced UVB levels that ultimately could have changed the phytoplankton community size/species structure, although this can only be speculative.

It is assumed that the positive responses in total productivity from phytoplankton communities developing in the enhanced UVB mesocosms on day 19 originated from indirect rather than direct effects of UVB. This could have been through increased photolytic activities by enhanced UVB. UVB is able to induce photochemical degradation of allochthonous high-molecular dissolved organic matter (DOM) into simpler and more biodegradable compounds (e.g., Mopper *et al.* 1991; Wetzel *et al.* 1995; Moran and Zepp 1997). These compounds have been shown to increase organic substrates for bacteria (e.g., Lindell *et al.* 1995; see below) as well as increase the turnover of inorganic nutrients originally bound to DOM (e.g. Bushaw *et al.* 1997; Cotner and Heath 1997), which could then stimulate phytoplankton.

During an 8-d mesocosm experiment in the Gullmar fjord on the Swedish west coast, Wängberg *et al.* (1999) found an increase in phytoplankton productivity (but no change in algal biomass) under enhanced UVB exposure during spring when levels of photodegradable DOM were high. Meanwhile, they found no effects of enhanced UVB on photosynthetic carbon fixation rates during a similar mesocosm experiment performed later in June/July when levels of photodegradable DOM were believed to be lower (Wängberg *et al.* 1999). Laurion *et al.* (1998) also suggested that the observed stimulation of the mixotrophic species *Ochromonas* sp. under UVB (up to 3.6 times higher cell number) might have resulted from an increase in the photochemical liberation of organic nutrients for osmotrophy or phagotrophy via bacterial production (Lindell *et al.* 1995; Wetzel *et al.* 1995).

Any or some of the UVB effects observed on total and size-fractionated productivity of phytoplankton during the study period could also have originated indirectly from changes at the consumer level (protozoans and zooplankton). Variations in the abundance and species composition of consumers by enhanced UVB (see below) could have affected their grazing pressure on phytoplankton and modified the species/size structure as well as total and size-fractionated productivity of phytoplankton. The positive effect of enhanced UVB through photochemical degradation in phytoplankton productivity could also have been overriden through the increase grazing pressure of protozoans (e.g. HNFs) and zooplankton taxa (cladocerans and rotifers) on phytoplankton (especially on small cells) as seen by similar phytoplankton productivity rates between the two UVB treatments at the end of the study period. It is also important to consider that acclimation of phytoplankton to enhanced UVB levels through photoadaptive processes (i.e., vertical migration, photoprotective compounds and/or photorepair) may also explain the lack of negative effects of UVB on total phytoplankton production as the experiment progressed.

Any UVB effects at the physiological and/or species/size levels of phytoplankton could affect the relative allocation of carbon to the main macromolecular end products of photosynthesis. Furthermore, the synthesis of photoprotective compounds such as mycosporine-like amino acids (MAAs; Karentz *et al.* 1991b; Xiong *et al.* 1997; Jeffrey *et al.* 1999), carotenoids (Paerl *et al.* 1985; Karentz *et al.* 1994; Quesada and Vincent 1997) or scytonemin (Garcia-Pichel and Castenholz 1991; Proteau *et al.* 1993; Sinha *et al.* 1998) could also influence carbon allocation during photosynthesis by temporarily diverting carbon from lipid and polysaccharide production (Arts and Rai 1997). However, in this study, any differences observed in total and size-fractionated phytoplankton productivity as well as in picoplankton abundance between the two UVB treatments did not alter the nutritional quality of the phytoplankton overall. The proportion of carbon allocated into low molecular weight metabolites (LMW), lipids, polysaccharides and protein did not vary between the two UVB treatments throughout the study period (Fig. 1-6).

Previous long-term studies (≥ 4 days) have showed differential effects of enhanced UVB levels on carbon allocation. For instance, studies on marine microphytobenthic communities have showed that exposure to enhanced UVB levels increased the fractions allocated to proteins and lipids and decreased the fractions allocated to polysaccharides and LMW compounds (Sundbäck *et al.* 1997), decreased the proportion of carbon allocated to polar lipids (Odmark *et al.* 1998), or increased the proportion of carbon allocated to proteins (Wulff *et al.* 2000). A long-term study on marine phytoplankton by Wängberg *et al.* (1998) found an increase in the fraction allocated to polysaccharides balanced by a decrease in the LMW fraction with UVB exposure only at the beginning of their experiment as well as lower ratios between carbon allocated to polar and neutral lipids in the UVB-exposed communities. The differences in UVB-mediated changes in carbon metabolism between studies may be explained by the fact that, aside from UVB exposure, the distribution patterns of photosynthetically incorporated carbon into LMW compounds and macromolecules are also controlled by a combination of both abiotic and biotic environmental factors (e.g., Shifrin and Chilsom 1981; Wainman and Lean 1996; Madariaga 1992). The interactive effects between all of these factors will ultimately influence the direction of carbon flow in phytoplankton populations (Perin *et al.* 2002).

In this study, the LMW fraction accounted for the largest fraction (>30%; Fig. 1-6a). The extremely low nutrient levels (especially nitrogen) in Two Basin Lake probably explain the higher proportion of carbon allocated in the LMW pool observed generally throughout the study period (see Chapter 2, *Photosynthetic carbon allocation in High Arctic lakes*). The percent ^{14}C incorporated into lipids was on average 21 ± 3% during the experiment, which is similar to values observed from short-term assays in phytoplankton communities from other Arctic lakes (Chapter 2) as well as from temperate lakes (Perin *et al.* 2002). When combining all of the data, the LMW fraction was found to negatively correlate with the lipid fraction, but especially with the protein fraction (Table 1-2). This inverse trend between the protein and LMW fractions has also been observed in temperate lakes (Madariaga 1992; Wainman and Lean 1996; Perin *et al.* 2002) and other Arctic lakes (Chapter 2). The polysaccharide fraction also negatively correlated with the lipid fraction (Table 1-2) as observed in temperate regions (e.g., Madariaga 1992; Perin *et al.* 2002) and other Arctic locations (Chapter 2). Here, the inverse trend between lipid and polysaccharide syntheses may be linked to differentiation in species composition between the two UVB treatments and/or during the study period (regardless of the UVB treatment) since some phytoplankton species preferentially accumulate carbon into lipids while others mainly store carbon into polysaccharides under similar environmental conditions (Madariaga 1992).

Heterotrophic bacteria

In order to circumvent the controversy surrounding conversions factors (thymidine conversion factor and carbon conversion factor), heterotrophic bacterial activity, in this study, has been reported as ^{3}H-thymidine assimilation rates as opposed to growth (productivity) rates. However, if, for example, a thymidine conversion factor of 2.2×10^{18} cells mol^{-1} (Moriarty 1986) and a carbon conversion factor of 1×10^{8} μg C cell^{-1}

(Bell 1993) would have been used, bacterial growth rates in the enclosures would have ranged from 10 to 60 ng C L^{-1} h^{-1} and accounted to about 8% of total phytoplankton productivity measured at 0.5 m. However, it is important to note that this ratio between heterotrophic bacterial production and phytoplankton production integrated over the entire water column may have been much higher, especially as water depth increases where heterotrophic production would have exceeded phytoplankton production. Heterotrophic bacterial abundance (average of $2.9 \pm 1.5 \times 10^5$ cells mL^{-1}) and productivity (average of 30 ± 12 ng C L^{-1} h^{-1}) measured at Two Basin Lake and the mesocosms were within values measured for other lakes from the Canadian High Arctic (Granéli *et al.* 2004).

Long-term studies ($\geq$ 6 days) have mostly shown from undetectable to small effects of UVB on natural bacterial communities (e.g., Bergeron and Vincent 1997; Odmark *et al.* 1998; Rae and Vincent 1998; Vinebrook and Leavitt 1998; Wickham and Carstens 1998; Chatila *et al.* 2001; Forster and Schubert 2001). For instance, no significant effects of ambient or enhanced UVB (10 and 20% higher) levels were found on heterotrophic bacterial biomass and productivity (H^3-leucine incorporation) after a 10-d experiment using aquaria filled with surface seawater from the Gullmard Fjord (Swedish west coast; Wängberg *et al.* 2001). On the other hand, Sommaruga *et al.* (1999) observed a reduction in the abundance and productivity (^{3}H-thymidine uptake) of non-filamentous bacteria (< 10 μm long) by ambient UVB levels, but filamentous bacteria (> 10 μm) were not affected during a 16-d *in situ* mesocosm experiment in an alpine lake.

In this study, heterotrophic bacterial abundance was unaffected or negatively affected by enhanced UVB levels during the first three weeks only, but was stimulated thereafter (Fig. 1-7, top graph). Meanwhile heterotrophic bacterial activity (^{3}H-thymidine uptake) was generally higher in the enhanced UVB mesocoms throughout the study period (except on day 13; Fig. 1-7, bottom graph). This stimulation of heterotrophic bacteria may have been the result of an increase in bioavailable organic compounds after long-term exposure to enhanced UVB levels. It has been established that, aside from negatively affecting heterotrophic bacteria through direct exposure, UVB can concurrently affect heterotrophic bacteria through indirect effects mediated by photolysis of large, refractive dissolved organic matter (DOM) to low molecular weight, bioavailable compounds (e.g., Mopper *et al.* 1991; Lindell *et al.* 1995; Wetzel *et al.* 1995; Bushaw *et al.* 1997; Moran and Zepp 1997; Vähätalo *et al.* 2003) and/or modification of readily consumable DOM (e.g., phytoplankton-exudate DOM and peptonic DOM) to less bioavailable DOM (Naganuma *et al.* 1996). Bacteria are believed to readily assimilate the products formed when high molecular weight DOM is exposed to UVR (Wetzel *et al.* 1995; Bertilsson and Tranvik 1998; Obernosterer *et al.* 1999), which could then stimulate their growth as well as heterotrophic pathways (e.g., Lindell *et al.* 1995, 1996, Gustavson *et al.* 2000; De Lange *et al.* 2003; Vähätalo *et al.* 2003).

Although the average molecular size of DOM and metabolic mineralization of organic carbon by bacteria were not measured in this study, it is possible that long-term exposure to enhanced UVB given by the lamps may have increased photochemical breakdown of DOC in the mesocosms, which in turn could have masked any negative effects of UVB and stimulate heterotrophic bacterial growth as well as protozoans and zooplankton (see below). A long-term mesocosm study (i.e., during two consecutive summers) by Pérez *et al.* (2003) showed a decrease in colored dissolved organic matter

(CDOM) levels (i.e., absorbance) and average molecular size (i.e., a_{250nm}:a_{365nm} ratio) in the UV-exposed mesocosms, which coincided with higher bacterial biomass and productivity than the UV-shielded mesocosms.

The effect of photochemical degradation by solar UVR have been demonstrated to vary among lakes, depending on the source and composition of DOC, the *in situ* DOC processes, and previous photochemical degradation (Morris and Hargreaves 1997). From a study on 38 Swedish lakes, Bertilsson and Tranvik (2000) have demonstrated that DOC from oligotrophic humic lakes was more easily photomineralized than DOC from eutrophic lakes. Thus, although vertical water motion may affect photochemical processes (Zagarese *et al.* 2001), this photochemical loss of carbon by UVR could especially be important in high-DOC lakes of the Arctic, including Two Basin Lake.

Aside from photochemical breakdown of allochthonous DOC, other studies have also suggested that bacterial growth could be stimulated through the increased release of photosynthetic carbon from UVR-stressed phytoplankton (e.g, Ridal and Moore 1993; Maurin *et al.* 1997). Forster and Schubert (2001) observed an increase in bacterial production with time in all of their mesocosms (regardless of their UVB treatments) and suggested that this increase could have been a response to an increased supply of organic substrates from phytoplankton exudates rather than photodegradation of DOC since photochemical "bleaching" of DOC was not detected in both the ambient and enhanced UVB treatments. In my study, a steady increase in bacterial abundance was not observed in the mesocosms. However, a close coupling seemed to have existed between phytoplankton and bacteria during the length of this study, both phytoplankton and bacteria generally had lower growth rates at the beginning but both increased after 3 weeks in the enhanced UVB mesocosms. Thus, both indirect effects on phytoplankton productivity and photochemical breakdown of allochthonous DOM could have been responsible for the observed effects on bacteria in the enhanced UVB mesocosms rather than direct negative effects of enhanced UVB levels on bacteria.

Heterotrophic nanoflagellates and zooplankton

Because of factors like water mixing regimes, water clarity, vertical distribution and displacement through the water column (e.g., Hessen 1994; Zagarese *et al.* 1998a; Kuhn *et al.* 2000; Leech and Williamson 2001), indirect effects of UVR (e.g. through changes in food quantity and quality) on zooplankton and HNFs may play a more important role than its direct effects in their natural environments. The occurrence of photoprotective pigments such carotenoids and melanin would also protect some zooplankton from the damaging effects of UVB in their natural habitats (Zellmer 1995; Hessen *et al.* 1999; Rautio and Korhola 2002b), although this would be more important for species that inhabit clear waters where refuge from UVB is not possible (Zellmer 1995, 1998; Rautio and Korhola 2002a). Thus, since DOC levels were high in the mesocosms, the effects of enhanced UVB levels on zooplankton and HNFs were most likely mediated through indirect rather than direct impacts of enhanced UVB. Although the total abundances of HNFs and zooplankton (> 40 um) were unaffected by enhanced UVB at the beginning of my experiment, they increased significantly under enhanced UVB thereafter (Fig. 1-8, bottom graph and 1-9, top graph). Zooplankton from the enhanced UVB-exposed communities experienced significant change in their species structure. In general, the cladocerans and rotifers were stimulated while the copepods were negatively affected in the enhanced UVB treatment (Fig. 1-10).

Since unicellular protozoa, especially the HNF, have been recognized as the principal consumers of free-living bacteria (e.g., Rassoulzadegan and Sheldon 1986; Berninger *et al.* 1991), it is likely that the increase in heterotrophic bacterial abundance and productivity in the enhanced UVB treatment probably stimulated the growth of HNFs. More HNFs could then have be grazed by bigger HNFs and ciliates, which in turn could have preyed upon by microzooplankton such as rotifers and small crustaceans, or by macrozooplankton such as the larger filter-feeding cladocerans. Many planktonic rotifers have been shown to be relatively unselective, feeding on particles in the size range of 0.5 to 20 μm, which includes heterotrophic bacteria, HNFs and picoplankton (Rothhaupt 1990). Zooplankton (especially *Daphnia* sp.) and ciliates are both potential consumers of HNFs (Sanders and Porter 1990; Weisse *et al.* 1990; Pace and Funke 1991; Jürgens 1994; Sanders *et al.* 1994). Some of the larger herbivorous cladocerans (e.g. *Daphnia* sp.) can also directly graze on large bacteria (e.g., Riemann 1985). This could explain the increased proportions of rotifers and cladocerans in the enhanced UVB treatment relative to the control. Since picoplankton are an important food source for HNFs (e.g., Šimek *et al.* 1997), higher abundance of HNFs may have been responsible for the decrease in picoplankton abundance and productivity.

Grazing experiments by Bertilsson *et al.* (2003) on the size-selective feeding behaviour of different zooplankton groups on pelagic microoorganisms from Canadian High Arctic tundra freshwater systems showed that the cladoceran *Daphnia* were effective predators on all sizes of prey, including bacteria, while copepods had lower feeding rates on bacteria and preyed most efficiently on larger prey (e.g., *Fragilaria* sp.; 75 µm). They also found that *Daphnia* had a negative impact on bacterial abundance implying that Arctic *Daphnia* can also disrupt the microbial loop by feeding directly on bacteria. Bertilsson *et al.* (2003) also suggested that copepods would likely be out-competed first since *Daphnia* were more efficient in ingesting all food particles sizes, especially bacteria and medium-sized (~15 µm) organisms.

For the mesocosm experiment, the lower grazing efficiency of copepods on bacteria and HNFs and the increased competition with cladocerans for food might then explain the decrease in the relative abundance of adult copepods, despite the increase in bacteria and HNFs observed in the enhanced UVB treatment. This would not exclude the possibility that potential changes in the species/size composition of phytoplankton from enhanced UVB levels could also have affected the relative abundance of copepods, although this could not be verified. There is also the possibility that, while increased photodegradation of DOM was occurring in the enhanced UVB mesocosms, heterotrophic bacterial and picoplankton abundances were lower during the first 20 day of the experiment because of high grazing pressures by protozoans and macrozooplankton. However, as HNFs increased in abundance, grazing by zooplankton on HNFs may have increased concurrently, thereby releasing heterotrophic bacteria and picoplankton from protozoan predation thereafter.

Long-term studies on zooplankton and HNFs have shown various responses to UVB exposure (Sommaruga *et al.* 1999; Vinebrook and Leavitt 1999; Forster and Schubert 2001). For instance, during 30 to 48 days mesocosm studies in a low-DOC alpine lake, Cabrera *et al.* (1997) found that ambient solar UVB reduced the abundance of the cladoceran *Chydorus sphaericus* and the rotifer *Lepadella ovalis* while the calanoid copepod, *Boeckella gracilis*, was not affected. An 8-week indoor microcosm study with DOC levels of 5 mg L^{-1} by De Lange *et al.* (1999) showed no significant effects of UVB on the zooplankton community, except on certain weeks for certain taxa (e.g., cladoceran abundance decreased in week 2 only under UVB). They suggested that the high DOC levels in the microcosms (i.e., 5 mg L^{-1}) conferred sufficient protection against the detrimental effects of increased UVB radiation. As in my study, Wängberg *et al.* (1998) indicated that the biomass of bacteria and other heterotrophs (e.g., chrysophytes and choanoflagellates) became greater in the UVB exposed communities (relative to those exposed to PAR only) from a 6-d microcosm study and suggested that photolysis of recalcitrant DOM into labile forms by UVB may have been responsible for this stimulation of heterotrophs.

Forster and Schubert (2001) have also observed greater microzooplankton biomass in their mesocosms exposed to UVB (8 to 14 d) and suggested that an improvement in food "quality" might have increased zooplankton biomass. However, an increase in the food quality of phytoplankton in the enhanced UVB treatment was unlikely in this study, since the biochemical composition of phytoplankton populations did not differ between the two UVB treatments (see above *Phytoplankton*). A 30-d mesocosm study by Keller *et al.* (1997) on highly colored coastal water showed a significant decrease in copepod nauplii abundance in the enhanced UVB treatment during the third and fourth weeks of their study, but this did not translate into a decrease in the abundance of copepodites or adult copepods. Here, the relative abundance copepod nauplii generally did not change significantly between the two UVB treatments. On the other hand, the relative abundance of adult copepods decreased in the enhanced UVB treatment. Perhaps the cyclopoid copepods changed their diet with age, with grazing of smaller plankton like bacteria, picoplankton or small HNFs during the nauplius stage.

Conclusion

One of the present challenges of UVB research is the extrapolation of results from laboratory and short-term field experiments to natural populations. The use of mesocosms has provided a useful tool that allows testing of long-term exposure to UVB of communities in their natural environments. However, it is acknowledged that the use of fixed lamps can result in high mean UVB at the surface as well as in extreme changes in ratios of UVB to PAR and UVA, which can profoundly influence the outcome (Karentz 1994; Prézelin *et al.* 1994a; Franklin and Forster 1997; Laurion *et al.* 1998). Furthermore, these experiments are much harder to interpret owing to the multitude of possible direct and indirect effects that may override and/or cancelled each other, unlike short-term single species experiments. Long-term effects of UVB in studies using mesocosms or other manipulated systems have generally showed no major collapse of populations to ambient or increased UVB exposure (e.g. Wängberg *et al.* 1999, 2001; Sundbäck *et al.* 1997; Halac *et al.* 1997; Bergeron and Vincent 1997; Laurion *et al.* 1998), with responses that have usually been smaller relative to those typically reported from laboratory or short-term studies.

A summary of the overall effects of enhanced UVB on all the variables measured during this study is presented in Table 1-3. Negative effects of enhanced UVB were found on total phytoplankton productivity, heterotrophic bacterial abundance and activity and picocyanobacteria abundance, especially at the beginning of the experiment. However, most of these effects were weak or transitory. The high levels of DOC in the lake strongly attenuated UVB in the upper layer (e.g., Scully and Lean 1994; Morris *et al.* 1995; Laurion *et al.* 1997; Lean 1998a,b; Pienitz and Vincent 2000), which reduced the negative impacts of enhanced surface UVB levels for these communities. Lack of overall harmful effects of UVB on planktonic communities has also been demonstrated elsewhere for high-DOC systems (e.g. Laurion *et al.* 1998; De Lange *et al.* 1999; Danilov and Ekelund 2001; Forster and Schubert 2001). Vertical mixing in the mesocosms could also have either diluted any UVB effects that occurred in the upper centimeters of the water column or allowed repair of UVB damage at depths where UVB was attenuated.

The size distribution of phytoplankton productivity was also shown to be slightly affected by enhanced UVB. The relative contribution of picoplankton to productivity decreased while that of nanoplankton and especially netplankton increased. This may have been directly related to decrease in picoplankton abundance observed at the surface. However, direct UVB damage to the photosynthetic apparatus may also have occurred, mainly on the smaller cells. Any UVB effects on total and/or size-fractionated productivity throughout the study period did not, however, affect the allocation of carbon to the different biomolecules on phytoplankton. Thus, the nutritional value of phytoplankton for consumers did not change between the two UVB treatments. However, since phytoplankton species composition was not verified, the possibility that certain phytoplankton species were negatively affected by UVB directly through UVB-induced damage or indirectly through increased grazing by HNFs and zooplankton cannot be ruled out.

Indirect impacts of UVB were more important on the planktonic community during this study rather than its direct effects. Increased photolysis of allochthonous DOM by long-term exposure to enhanced UVB levels may have been responsible for the increased in heterotrophic bacterial abundance and activity and possibly in phytoplankton productivity on day 19. In turn, higher bacterial and/or phytoplankton growths might have been responsible for stimulating protozoans, i.e., HNFs, as well as zooplankton communities in the enhanced UVB mesocosms.

The zooplankton community structure also changed significantly in response to enhanced UVB levels. The relative abundance of rotifers and cladocerans increased while that of adult copepods decreased. Rotifers were most likely stimulated as a result of an increase in food available to them (i.e., bacteria and protozoans) in the enhanced UVB mesocosms. Meanwhile, although the copepods still dominated the zooplankton community in the enhanced UVB mesocosms, the relative abundance of cladocerans was favored possibly because they are better grazers, especially of bacteria, than copepods (Bertilsson *et al.* 2003). There is also the possibility that shift in the species/size composition of bacteria, phytoplankton, and/or protozoans could also have affected the community structure of the zooplankton community.

Furthermore, strong grazing pressures by HNFs on bacteria and picocyanobacteria may have been responsible in decreasing their abundances at the beginning of the study, hiding the positive effect of enhanced UVB levels on photochemical degradation of DOM into bioavailable forms. While high DOC levels conferred protection to the planktonic organisms from UVB damage in the mesocosms, the organisms may also have been fairly resistant or became adapted to UVB through the presence or induction of defense mechanisms against UVB (i.e., vertical migration, production of UV-absorbing pigments, production of quenching agents, and/or reparation of UV-damaged macromolecules).

From this study, it can be concluded that even a substantial 27-d increase in UVB exposure did not induce major inhibitory effects on the plankton community of this high-DOC lake of the High Arctic. Vertical mixing (which reduce residence time of planktonic organisms in the surface layers) and high concentrations of DOC (which greatly reduce the penetration of UVB), both combined to protect the planktonic community from UVB damage. Ecosystem effects are likely less severe than those predicted solely from laboratory-based assays. Instead, the planktonic community was generally stimulated by enhanced UVB possibly due to an indirect effect from UVB-induced degradation of DOM, which increased microbial activities and zooplankton, increased the turnover of inorganic nutrients and/or modified the standing crop by grazing pressure (i.e., affected predator-prey interactions).

The DOC levels at Two Basin Lake are higher than many other Arctic lakes, where concentrations of DOC are typically below 4 mg L^{-1} and thus much greater UVB penetration would occur (Hamilton *et al.* 1994; 2000; 2001). Therefore, results from this study should not be extrapolated to lakes with lower DOC values. Nevertheless, my conclusions could become more representative of many Arctic lakes in the future since DOC levels are predicted to increase, especially in regions near or above the tree line, as a result of permafrost melting, increase soil erosion and increase growth of vegetation expected with the raise in global average temperatures in the troposphere.

Table 1-1. Mean chlorophyll *a* levels (μg L^{-1}) in the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels at 0.5 and 2.5 m and when both UVB treatments are combined together for each of the 4 sampling dates (day 3, 9, 16 and 23). Values are based on one sample taken at each depth from duplicate mesocosms respectively (except for the last row). n = 2, except for the last row (n = 8). ± SD.

	Day 3		Day 9		Day 16		Day 23	
	0.5 m	2.5 m	0.5 m	2.5 m	0.5 m	2.5 m	0.5 m	2.5 m
AMB-UVB	0.5 ±0.1	0.9 ±0.1	0.6 ±0.1	0.8 ±0.2	1.1 ±0.2	1.0 ±0.1	1.2 ±0.3	0.9 ±0.1
ENH-UVB	0.5 ±0.1	0.7 ±0.4	0.9 ±0.0	0.7 ±0.4	0.9 ±0.1	1.0 ±0.2	1.0 ±0.1	0.7 ±0.1.
Overall	0.6 ±0.2		0.7 ±0.2		1.0 ±0.1		0.9 ±0.3	

Table 1-2. Pearson correlation coefficients between percent ^{14}C-sodium bicarbonate assimilated into low molecular weight (LMW), lipid, polysaccharide (POLY) and protein when all data have been pooled together, including data from the surrounding lake. Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and NS = not significant. Sample size = 75.

	LMW	LIPID	POLY
LMW	- - -	- - -	- - -
LIPID	-0.346*	- - -	- - -
POLY	-0.296^{NS}	-0.402**	- - -
PROTEIN	-0.692***	-0.152^{NS}	-0.037^{NS}

Table 1-3. Summary of the overall effect of enhanced UVB (i.e., between-subject effect of UVB from ANOVAR) on all variables measured during the mesocosm experiment. Abb: NS = not significant, - = weak negative effect ($p < 0.05$), -- = intermediate negative effect ($p < 0.01$), --- = strong negative effect ($p < 0.001$), + = weak positive effect ($p < 0.05$), ++ = intermediate positive effect ($p < 0.01$), +++ = strong positive effect ($p < 0.001$).

	UVB effect
Chlorophyll *a*	NS
Total phytoplankton productivity	+
Size-fractionation of photosynthesis:	
% Picoplankton (0.2 – 2 μm)	--
% Nanoplankton (2 – 20 μm)	+
% Netplankton (> 20 μm)	+
% Carbon allocation into:	
Low molecular weight (LMW)	NS
Lipid	NS
Polysaccharide	NS
Protein	NS
Heterotrophic bacterial abundance	NS
Heterotrophic bacterial activity	+
Picocyanobacteria abundance	-
Heterotrohic nanoflagellates abundance	+
Total zooplankton abundance	++
Total zooplankton mean length	NS
Relative abundance (%) of:	
Cyclops (adults)	---
Cyclops (nauplii)	NS
Daphnia	++
Diaphanosoma	++
Keratella	++

Figure headings

Figure 1-1. Location of Two Basin Lake (indicated by a black square) on Ellesmere Island, Nunavut, Canada.

Figure 1-2. Unweighted spectral irradiances (top graph) at the water surface of the AMB-UVB and ENH-UVB mesocosms from an average of 10 measurements taken on cloudy days (11-12 August 1994) between 10:00-13:00 at Two Basin Lake (79°N), with a mean total column ozone of 290 Dobson Units (measured at Resolute Bay, Cornwallis Island, Canada, 74°N; WOUDC 2004); Weighted spectral irradiances (bottom graph) determined by the product of the biological weighting function for inhibition of photosynthesis by UVR in *Phaeodactylum* sp. of Cullen et al. (1992) with the spectral irradiances from top graph.

Figure 1-3. Depth profiles of UVB, UVA and PAR in the mesocosms estimated from the integrated attenuation coefficients (K_{dl}) that were calculated from irradiance measurements taken at different depths on 11 and 12 August 1994. K_{dl} values used for PAR, UVA and UVB were 1.0, 2.7 and 6.7 m^{-1}, respectively. Percent surface irradiance (%E_o) was calculated following the equation: $\%Eo = e^{KdlZ} * 100$, with Z = water depth.

Figure 1-4. Phytoplankton productivity (incorporation of ^{14}C-bicarbonate after 2-3 h exposure to ambient solar radiation at 0.1 m in TBL) for the ambient UVB (AMB-UVB; white bars) and enhanced UVB (ENH-UVB; hatched bars) treatments during the study period. Error bars represent the standard deviation (SD) between the duplicate mesocosms (n = 2).

Figure 1-5. Percent of total fixed carbon by picoplankton (0.2 – 2 μm; top graph), nanoplankton (2 – 20 μm; middle graph), and netplankton (> 20 μm; bottom graph) for the ambient UVB (AMB-UVB; white bars) and enhanced UVB (ENH-UVB; hatched bars) treatments during the study period. With SD bars (n = 2).

Figure 1-6. Percent of total photosynthate in (a) low molecular weight material (LMW), (b) lipid, (c) in polysaccharide, and (d) in protein for phytoplankton from the ambient-UVB (AMB-UVB; white bars) and enhanced-UVB (ENH-UVB; hatched bars) treatments during the study period. With SD bars (n = 2).

Figure 1-7. Heterotrophic bacterial abundance (top graph; cells mL^{-1}) and incorporation rates of tritiated thymidine (bottom graph; HB activity; pmol ^{3}H-TdR L^{-1} h^{-1}) at 0.5 and 2.5 m in the mesocosms exposed to ambient UVB (AMB-UVB; white bars) and enhanced UVB (ENH-UVB; hatched bars) levels during the study period. With SD bars (n = 2).

Figure 1-8. Abundances of picocyanobacteria (top graph) and heterotrophic nanoflagellates (bottom graph) at 0.5 and 2.5 m in the ambient UVB (AMB-UVB; white bars) and enhanced UVB (ENH-UVB; hatched bars) mesocosms on day 3 and 16 of the study period. With SD bars (n = 2).

Figure 1-9. Total zooplankton density (number of organisms m^{-3}; top graph) and total zooplankton mean length (mm; bottom graph) in the ambient UVB (AMB-UVB; white bars) and enhanced UVB (ENH-UVB; hatched bars) mesocosms during the study period. Mean lengths have been corrected for the relative abundance of all taxa. With SD bars (n = 2).

Figure 1-10. Percent relative abundance of (a) copepod *Cyclop* sp. (adults); (b) cyclopoid nauplii; (c) cladoceran *Daphnia* sp.; (d) cladoceran *Diaphanosoma* sp., and (e) rotifer *Keratella* sp. in the ambient UVB (AMB-UVB; white bars) and enhanced-UVB (ENH-UVB; hatched bars) mesocosms during the study period. With SD bars (n = 2).

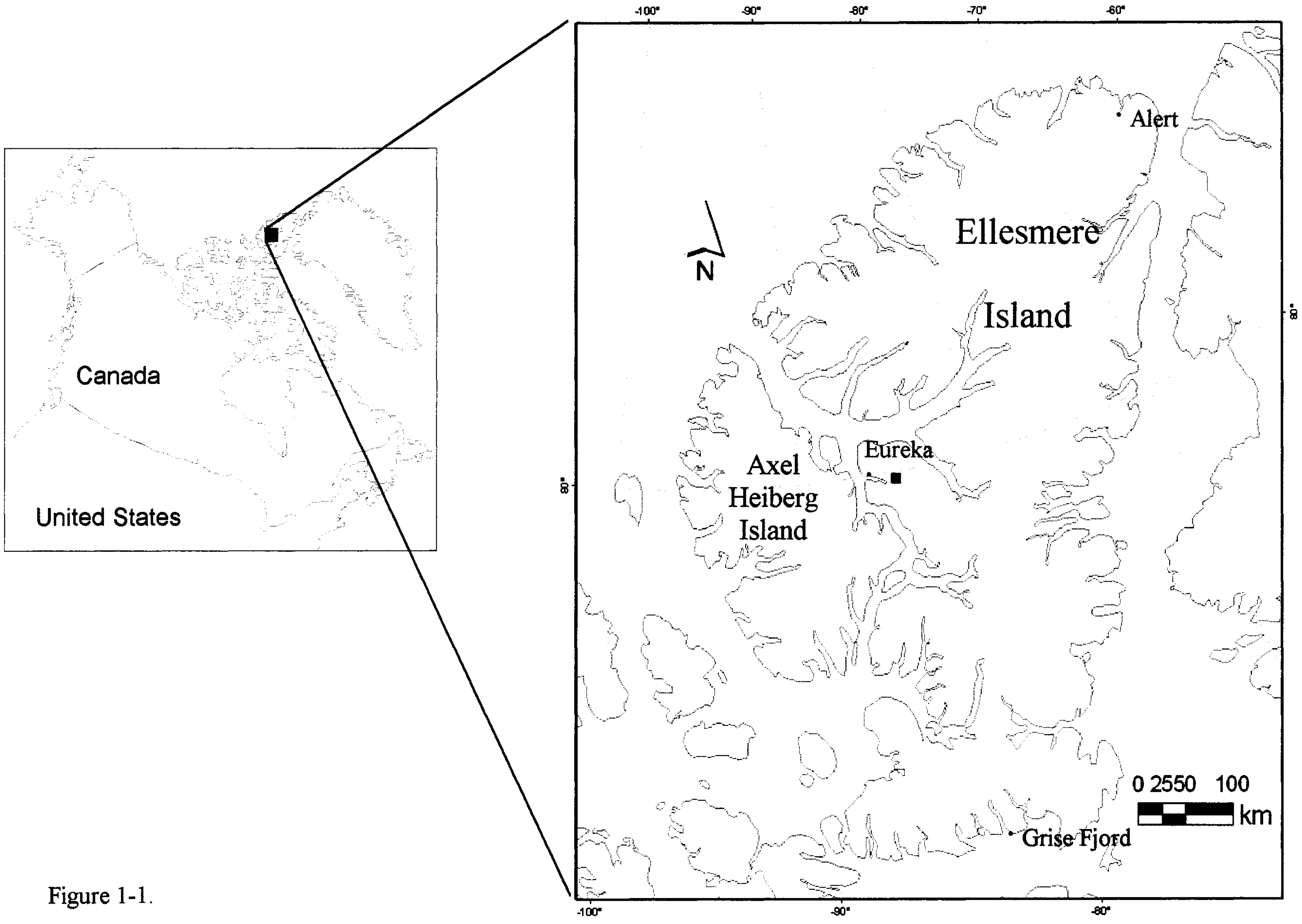

Canada
United States
-100°
-90°
-80°
-70°
-60°
80°
N
Alert
Ellesmere
Island
Eureka
Axel
Heiberg
Island
Grise Fjord
0 2550 100
km

Figure 1-1.

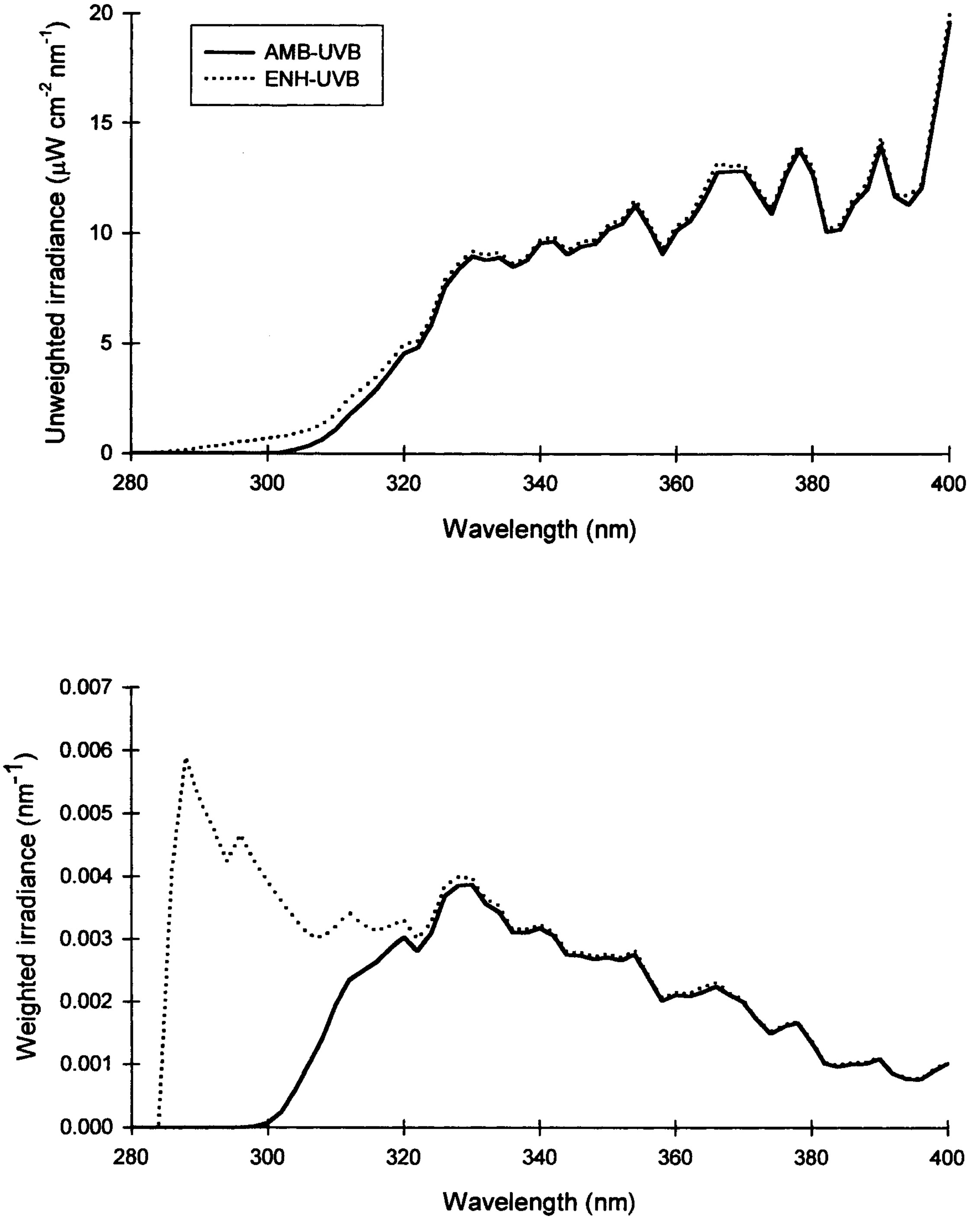

Unweighted irradiance (μW cm^{-2} nm^{-1})
20
15
10
5
0
AMB-UVB
ENH-UVB
280
300
320
340
360
380
400
Wavelength (nm)
Weighted irradiance (nm^{-1})
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
280
300
320
340
360
380
400
Wavelength (nm)

Figure 1-2.

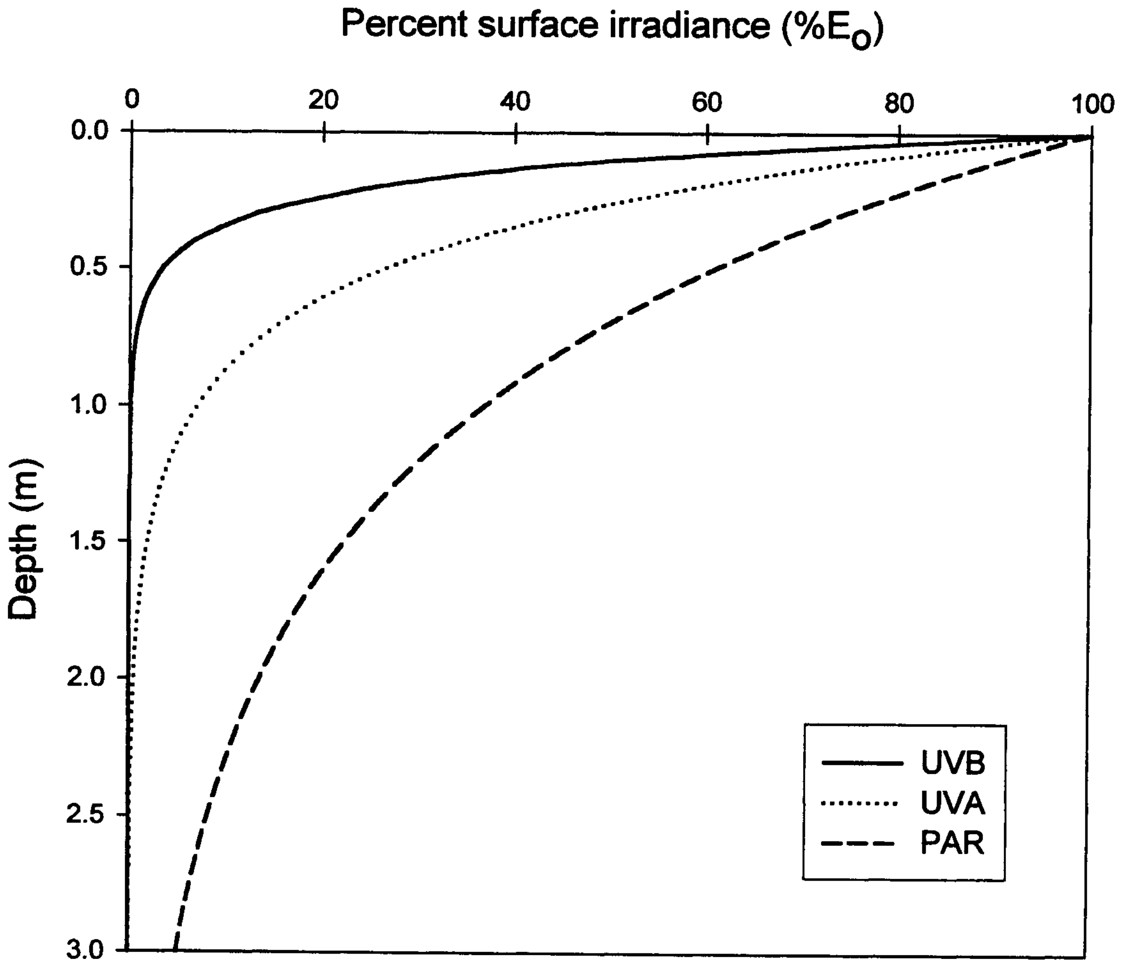

Percent surface irradiance (%E$_0$)
0
20
40
60
80
100
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Depth (m)
UVB
UVA
PAR

Figure 1-3.

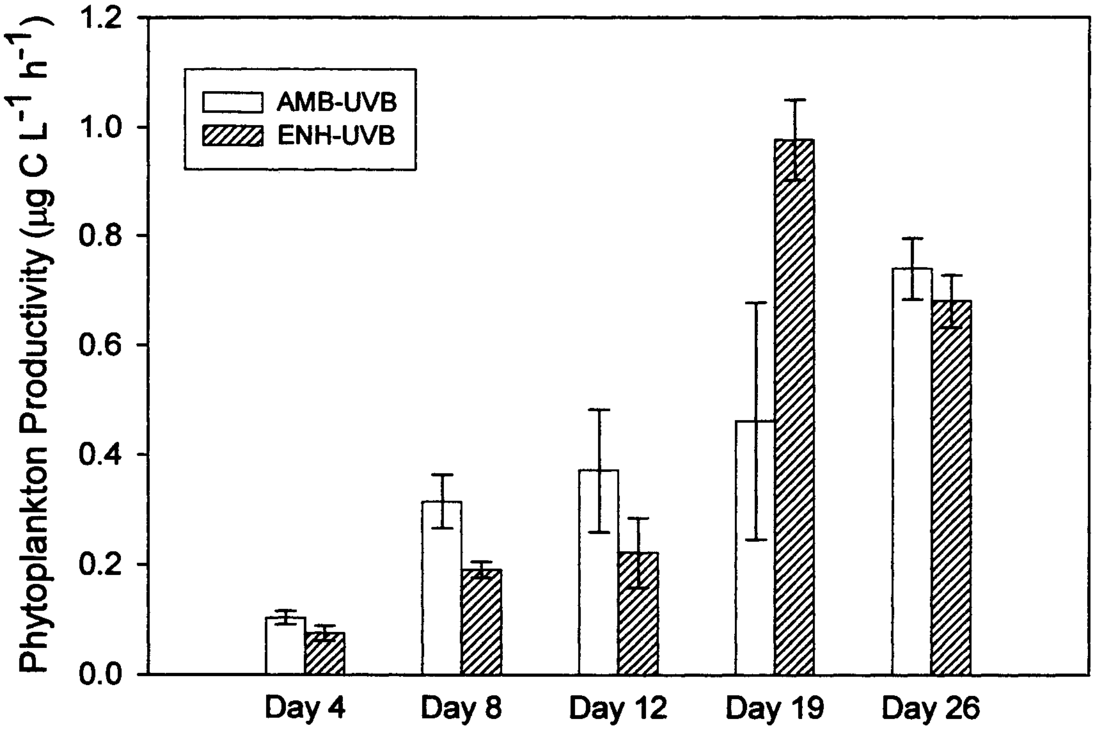

Phytoplankton Productivity (µg C L-1 h-1)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
AMB-UVB
ENH-UVB
Day 4
Day 8
Day 12
Day 19
Day 26

Figure 1-4.

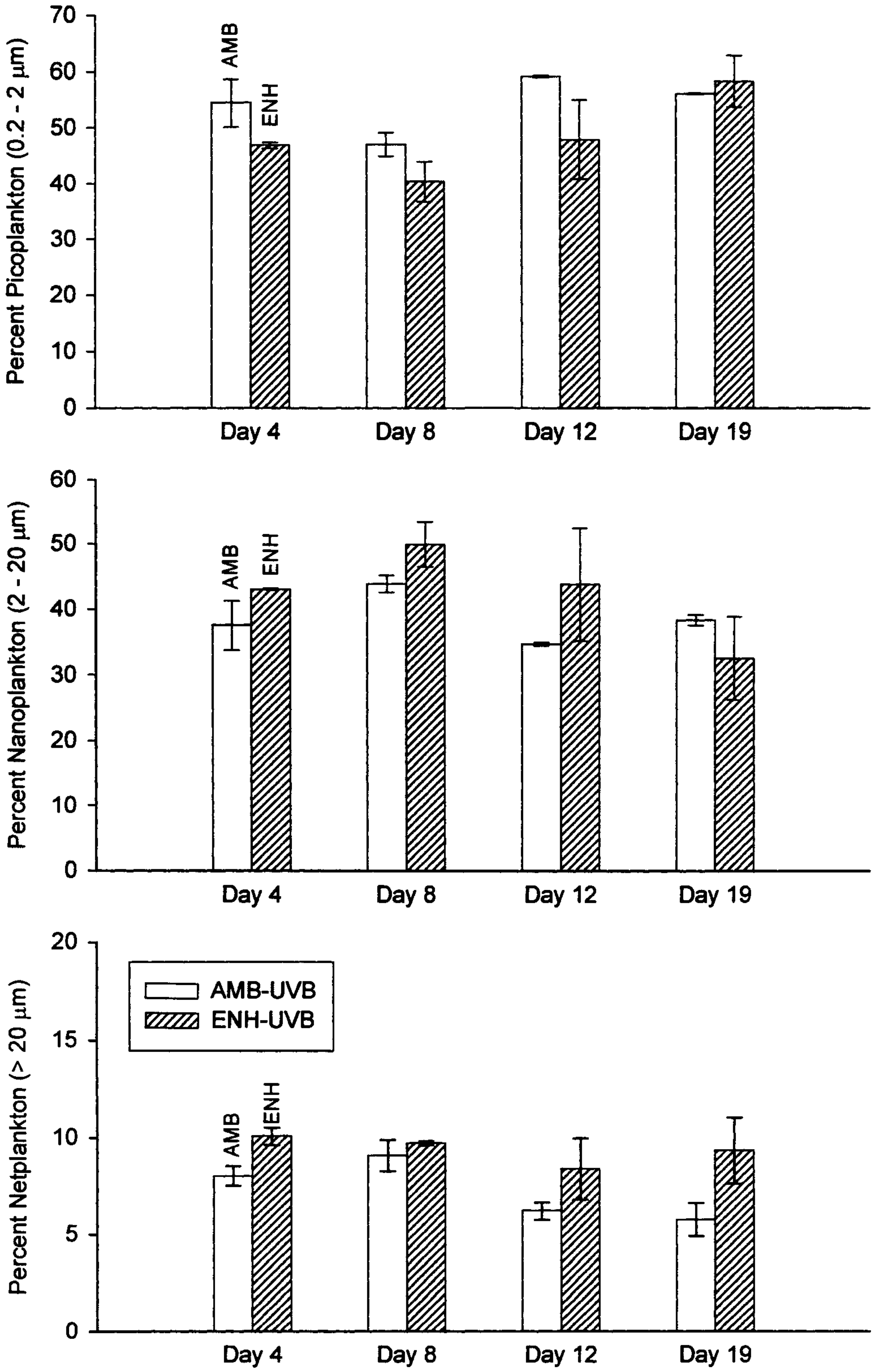

70
60
50
40
30
20
10
0
Percent Picoplankton (0.2 - 2 µm)
AMB
ENH
Day 4
Day 8
Day 12
Day 19
60
50
40
30
20
10
0
Percent Nanoplankton (2 - 20 µm)
AMB
ENH
Day 4
Day 8
Day 12
Day 19
20
15
10
5
0
Percent Netplankton (> 20 µm)
AMB-UVB
ENH-UVB
AMB
ENH
Day 4
Day 8
Day 12
Day 19

Figure 1-5.

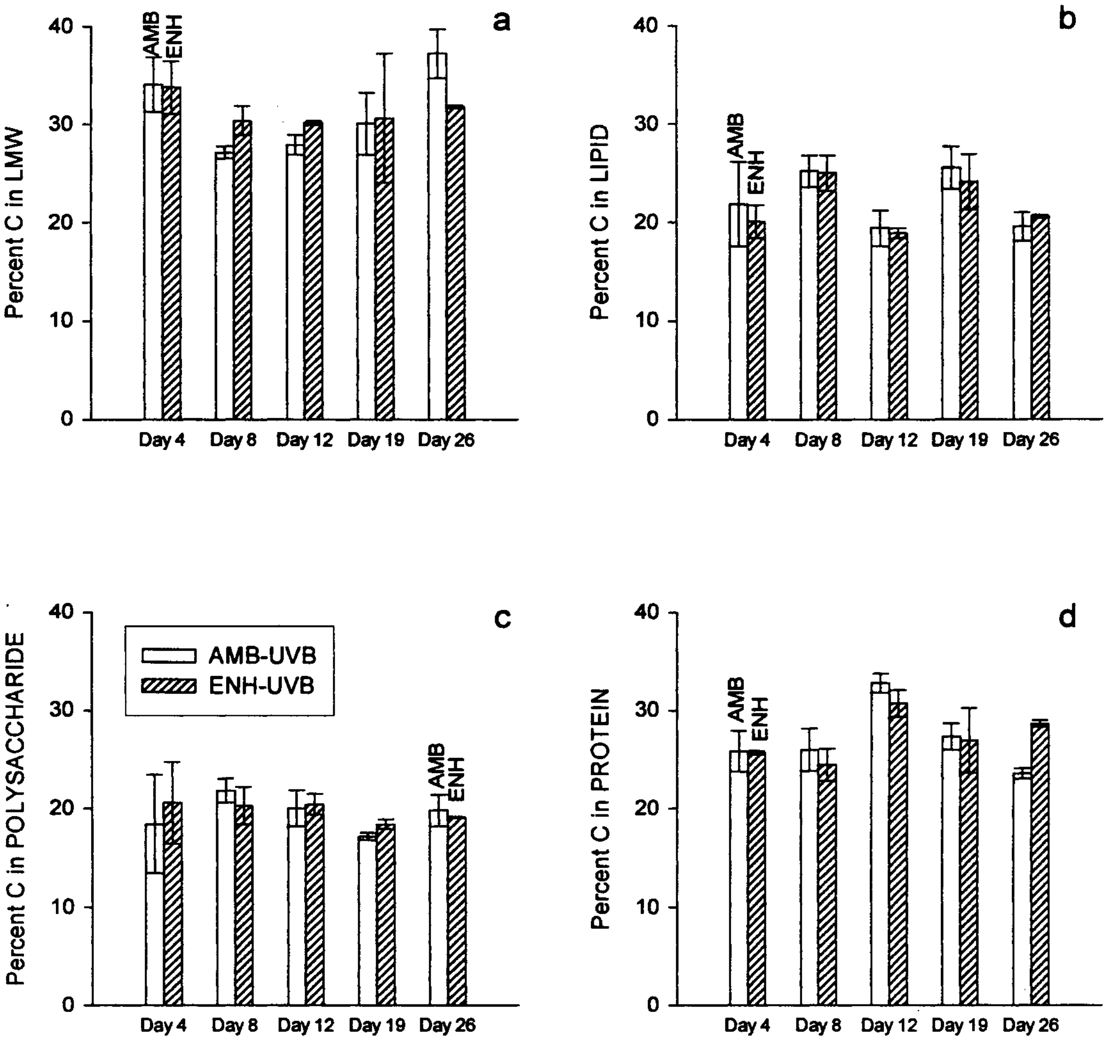

a
Percent C in LMW
0
10
20
30
40
AMB
ENH
Day 4
Day 8
Day 12
Day 19
Day 26
b
Percent C in LIPID
0
10
20
30
40
AMB
ENH
Day 4
Day 8
Day 12
Day 19
Day 26
c
Percent C in POLYSACCHARIDE
0
10
20
30
40
AMB-UVB
ENH-UVB
AMB
ENH
Day 4
Day 8
Day 12
Day 19
Day 26
d
Percent C in PROTEIN
0
10
20
30
40
AMB
ENH
Day 4
Day 8
Day 12
Day 19
Day 26

Figure 1-6.

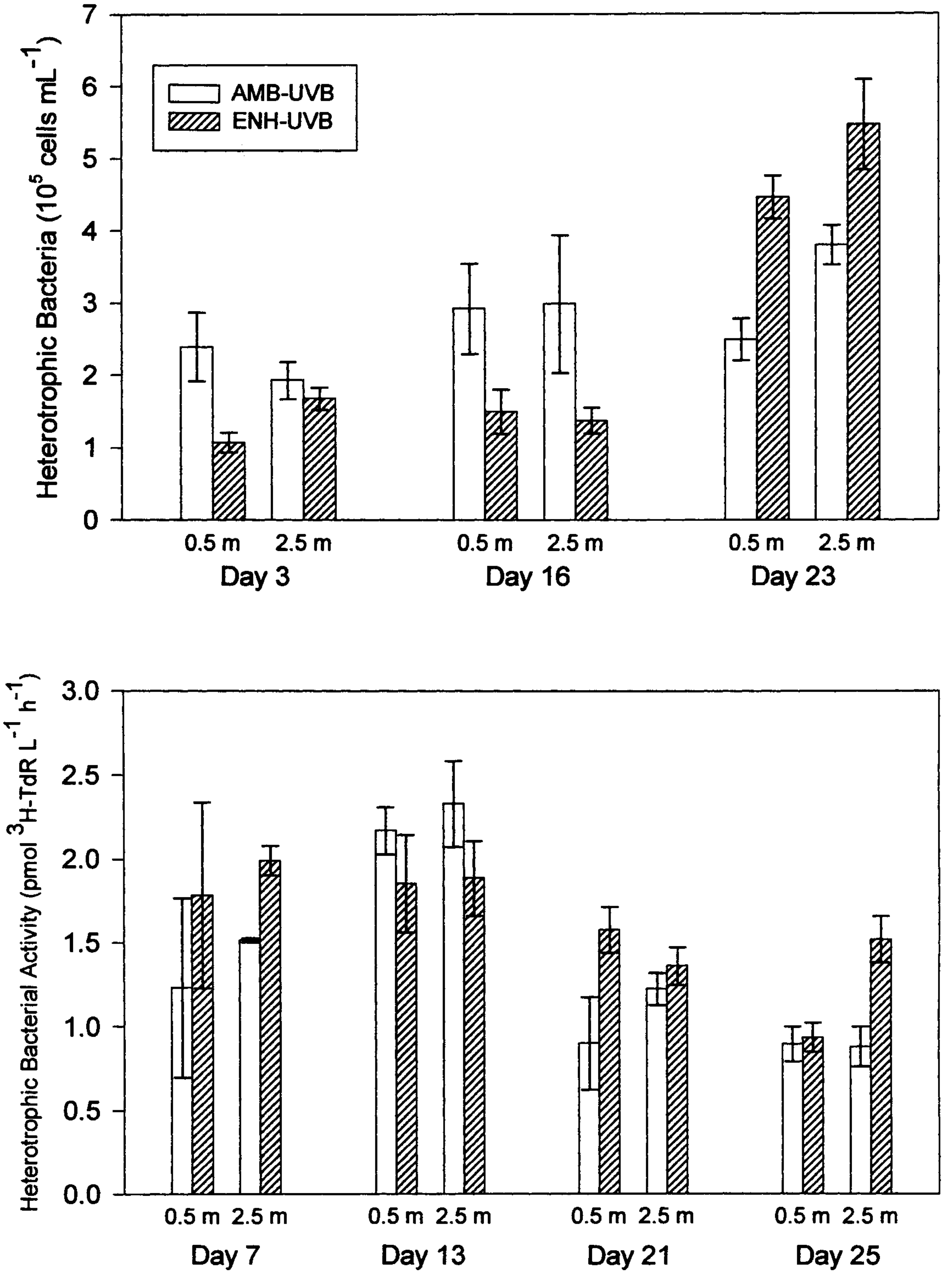

Heterotrophic Bacteria (10^5 cells mL^{-1})
0
1
2
3
4
5
6
7
AMB-UVB
ENH-UVB
0.5 m
2.5 m
Day 3
Day 16
Day 23
Heterotrophic Bacterial Activity (pmol ^{3}H-TdR L^{-1} h^{-1})
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Day 7
Day 13
Day 21
Day 25

Figure 1-7.

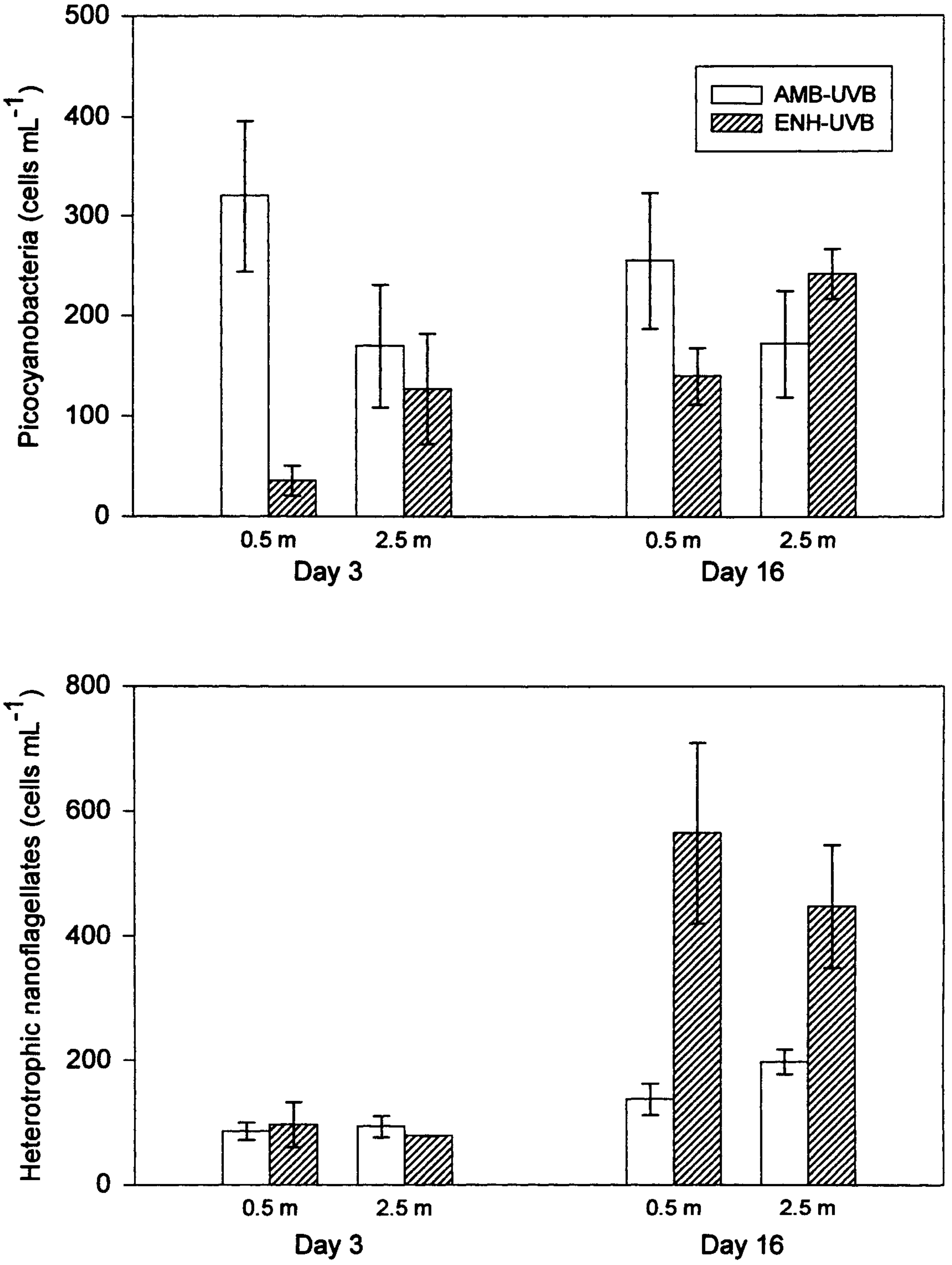
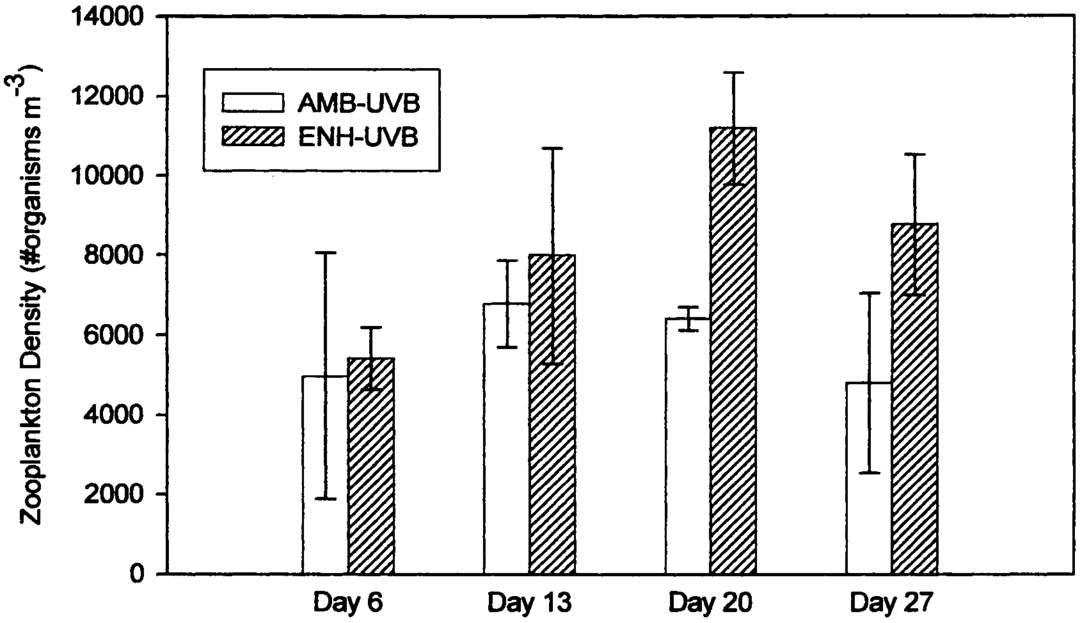

500
400
300
200
100
0
Picocyanobacteria (cells mL^{-1})
AMB-UVB
ENH-UVB
0.5 m
2.5 m
Day 3
0.5 m
2.5 m
Day 16
800
600
400
200
0
Heterotrophic nanoflagellates (cells mL^{-1})
0.5 m
2.5 m
Day 3
0.5 m
2.5 m
Day 16

Figure 1-8.


Zooplankton Density (#organisms m^{-3})
14000
12000
10000
8000
6000
4000
2000
0
AMB-UVB
ENH-UVB
Day 6
Day 13
Day 20
Day 27

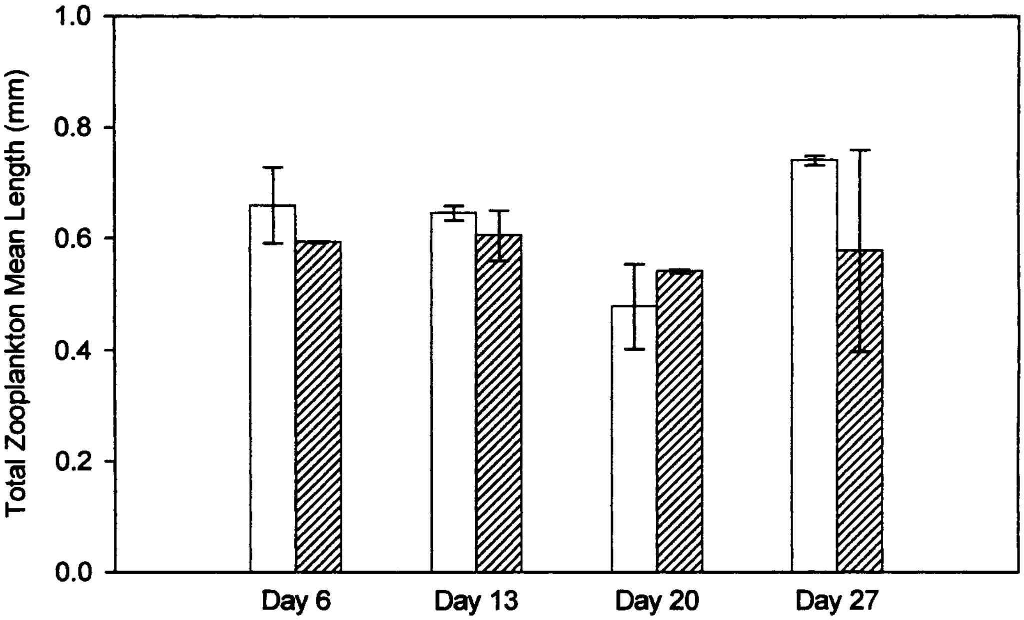

Total Zooplankton Mean Length (mm)
1.0
0.8
0.6
0.4
0.2
0.0
Day 6
Day 13
Day 20
Day 27

Figure 1-9.

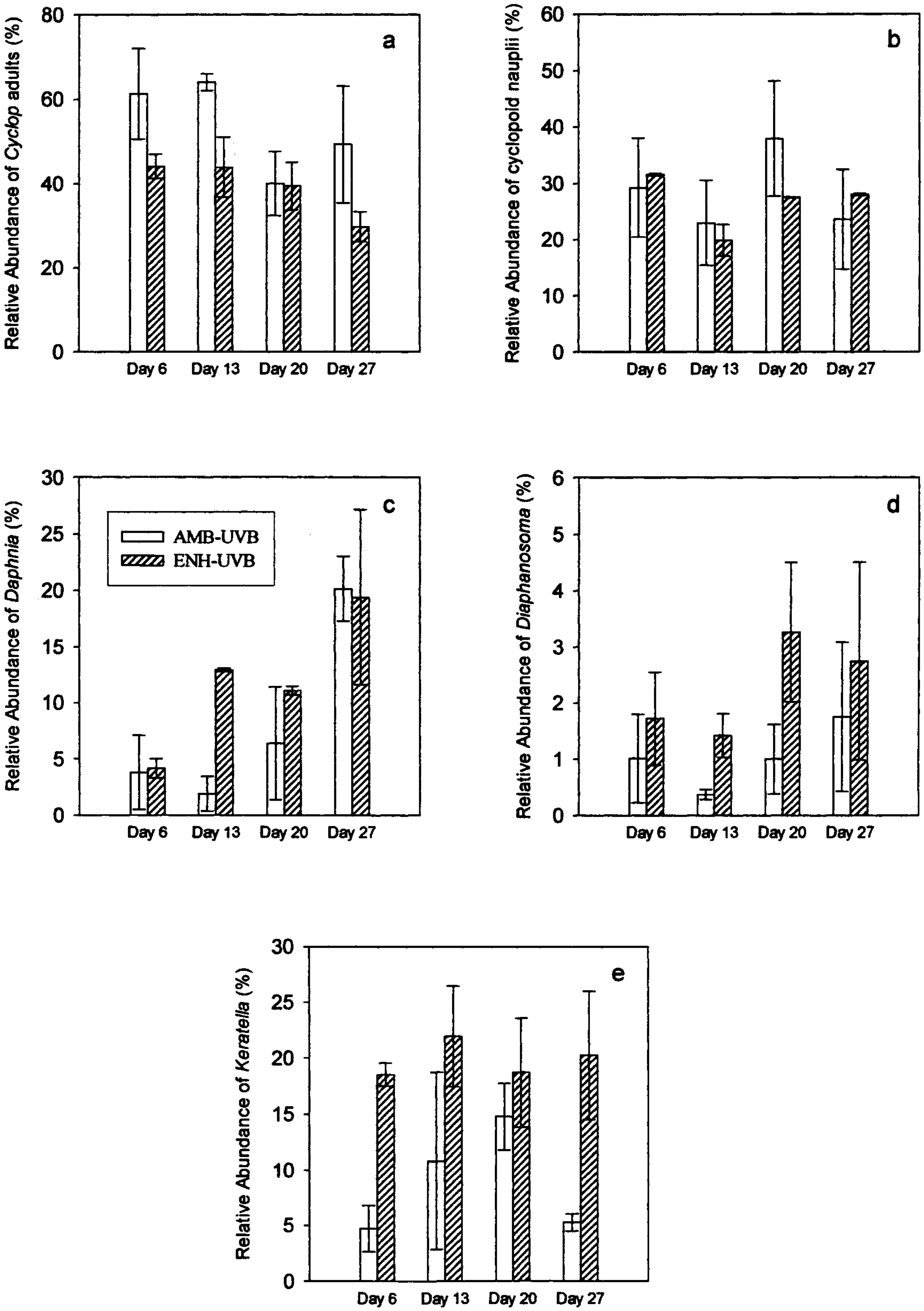

a
Relative Abundance of Cyclop adults (%)
0
20
40
60
80
Day 6
Day 13
Day 20
Day 27
b
Relative Abundance of cyclopoid nauplii (%)
0
10
20
30
40
50
60
Day 6
Day 13
Day 20
Day 27
c
Relative Abundance of Daphnia (%)
0
5
10
15
20
25
30
AMB-UVB
ENH-UVB
Day 6
Day 13
Day 20
Day 27
d
Relative Abundance of Diaphanosoma (%)
0
1
2
3
4
5
6
Day 6
Day 13
Day 20
Day 27
e
Relative Abundance of Keratella (%)
0
5
10
15
20
25
30
Day 6
Day 13
Day 20
Day 27

Figure 1-10.

CHAPTER 2

SHORT-TERM EFFECTS OF ENHANCED UVB RADIATION ON PHYTOPLANKTON PRODUCTIVITY OF HIGH ARCTIC LAKES

Abstract

Experiments were carried out during the summer of 1996 on natural phytoplankton assemblages from nine High Arctic lakes to determine the effects of ultraviolet-B (UVB; 280-320 nm) enhancement on total photosynthetic rates, fractionation of photosynthesis into three size classes (picoplankton [0.2 – 2 um], nanoplankton [2 – 20 um] and netplankton [> 20 um]), and partitioning of photosynthetically fixed carbon into major end-products (low molecular weight metabolites [LMW], lipid, polysaccharide and protein). The lakes were Barren, Black Char, Clear, Char, Meretta, North, Resolute, Small and Tern lakes, which are located in the vicinity of Resolute (Cornwallis Island, Nunavut, Canada; 74°42'N, 94°50'W;). These lakes have low dissolved organic carbon (DOC) levels ($\leq$ 2 mg L^{-1}), with estimated UVB integrated attenuation coefficients that ranged from 0.4 m^{-1} (North Lake) to 2.1 m^{-1} (Clear Lake). Samples were inoculated with labelled carbon ($NaH^{14}CO_3$) and placed in an incubator at 6, 25, 50 and/or 100% surface irradiance levels (E_o) under natural solar levels (ambient UVB) or sunlight plus artificial UVB (enhanced UVB) supplied by fluorescent tubes that elevated UVB by about twice its natural levels. The effects of UVB generally depended on the irradiance treatment and/or duration of incubation, with usually low or insignificant effect at 6%E_o to 83% inhibition at 100%E_o after 8 h. Kinetics of inhibition by enhanced UVB was rapid at 50%E_o and 100%E_o, with $\geq$40% of total inhibition in the first two hours of incubation. The proportion of carbon fixed by netplankton increased in the enhanced UVB treatment in all of the lakes (except Resolute Lake). The proportion of carbon fixed by nanoplankton also increased with exposure to enhanced UVB in two lakes, but did not change or decreased in the other lakes. Enhanced

UVB decreased the relative contribution of picoplankton to productivity in four lakes, but not in the other lakes. Although the total carbon fixed declined with exposure to enhanced UVB, the proportion of ^{14}C allocated into protein decreased in all lakes, the proportion of carbon allocated into polysaccharides decreased or did not change, while relative incorporation into lipids was insensitive or increased when exposed to UVB. The relative allocation into LMW usually increased with exposure to enhanced UVB, most likely as a result of a concomitant decrease in the synthesis of macromolecules.

Introduction

Phytoplankton represent one of the first levels of aquatic trophic structures because most contain chlorophyll pigments that enable them to use solar energy for photosynthesis, converting carbon into energy that is transferable to other trophic levels of the aquatic food web (Wetzel 1975). Because these microscopic organisms require visible light (i.e., photosynthetic active radiation or PAR; 400-700 nm) for photosynthesis and growth, they populate the euphotic zone (operationally defined as the zone in which PAR is $\geq 1\%$ of that entering the water). They live in the upper strata of lakes and oceans in order to receive sufficient PAR. This implies that phytoplankton are also simultaneously exposed to the other potentially harmful component of the solar spectrum i.e., ultraviolet radiation (UVR; 280 – 400 nm). UVR at the Earth's surface includes both ultraviolet-B radiation (UVB; 280 – 320 nm; however, there is no significant surface irradiance at wavelengths below 290 nm) and ultraviolet-A radiation (UVA; 320-400 nm; Diffey 2002).

Since the discovery of the stratospheric ozone depletion and the resultant increase in surface UVB levels, there have been many studies carried out on the possible effects of increased UVB on aquatic organisms, especially on phytoplankton (see Perin and Lean 2004 for review). Both PAR and UVA remain essentially unaffected by stratospheric ozone depletion. UVA has both beneficial and deleterious effects on phytoplankton (Karentz *et al.* 1991a, c; Vincent and Roy 1993). The inhibition of photosynthetic rates by UVR has been established in wide range of freshwater and marine environments. Antarctic marine phytoplankton have received special attention because of the annually occurring springtime ozone hole (e.g., Helbling *et al.* 1992; 1994, 1996; Holm-Hansen *et al.* 1993; Boucher et al. 1996; Lesser *et al.* 1996; Neale *et al.* 1998b; Bracher and Wiencke 2000), but studies also exist for phytoplankton in temperate regions (e.g., Gala and Giesy 1991; Behrenfeld *et al.* 1993; Helbling *et al.* 1993, 2001a; Moeller 1994; Ferreyra *et al.* 1997; Villafañe *et al.* 1999, 2004; Marwood *et al.* 2000; Banaszak and Neale 2001; Barbieri *et al.* 2002; Hiriart *et al.* 2002; Palffy and Voros 2003; Xenopoulos and Schindler 2003), sub-Arctic regions (e.g., Milot-Roy and Vincent 1994; Nielsen and Ekelund 1995; Laurion and Vincent 1998), alpine regions (e.g., Montesino *et al.* 1997; Villafañe *et al.* 1999; Helbling *et al.* 2001b, c) and tropical regions (e.g., Helbling *et al.* 1992).

It has been suggested that the kinetics of photosynthetic inhibiton by UVB are similar to those caused by excess PAR or UVA (e.g., Cullen and Lesser 1991). UVB is believed to affect phytoplankton photosynthesis by: (1) reducing the performance of the photosystem II through inactivation or destruction of its reaction centers (Renger *et al.* 1989; Kroon *et al.* 1994; Schofield *et al.* 1995; Perin 1996), inhibiting photosynthetic enzyme activities (e.g., carbon-fixing enzyme, ribulose-1,5-biphosphate carboxylase-oxygenase or RUBISCO; Neale *et al.* 1993; Vassiliev *et al.* 1994; Lesser *et al.* 1996) and/or inhibiting the synthesis or destroying certain photosynthetic pigments (e.g., chlorophyll *a*; Döhler 1995, Döhler and Hagmeier 1997; Lohmann *et al.* 1998), which in turn may decrease the ability of a cell to photosynthesize and hinder the carboxylation process; and/or (2) by inducing DNA damage (Karentz *et al.* 1991c; Karentz 1994; Buma *et al.* 2001a,b) like the dimerization of certain DNA bases leading to the formation of cyclobutane pyrimidine dimers (CPDs; e.g. Prézelin *et al.* 1998; Visser *et al.* 1999; Boelen *et al.* 2000). CPDs or other types of DNA damage may then arrest the cell cycle in the DNA synthesis phase (unless the damage is quickly repaired) and inhibit *de novo* synthesis of proteins, including the enzyme RUBISCO, required for adequate functioning of the photosynthetic process (Buma *et al.* 2001b).

Although numerous studies have shown that UVB, even at unaffected levels, inhibit photosynthesis in phytoplankton (e.g., Helbling *et al.*1992, 1993; Cullen *et al.* 1992; Behrenfeld *et al.* 1993; Neale *et al.* 1994; Furgal and Smith 1997; Banaszak and Neale 2001), the level of photoinhibition in natural phytoplankton populations is modified by the differential sensitivity among phytoplankton as well as by the many factors in their natural environments that influence the amount and extent of UVB exposure (e.g., attenuation of UVB, water mixing regimes, near-surface thermoclines; e.g., Milot-Roy and Vincent 1994; Neale *et al.* 1998b; Marwood *et al.* 2000; Xenopolous *et al.* 2000; Xenopoulos and Schindler 2003) and/or alter the sensitivity of phytoplankton to UVR (e.g., water temperature, nutrient availability, previous light history; e.g., Cullen and Lesser 1991; Helbling *et al.* 1992; Neale *et al.* 1998c; Chatila *et al.* 2001; Hiriart *et* *al.* 2002; Xenopolous *et al.* 2002). Sensitivity to UVB has been shown to vary greatly among phytoplankton species and/or size assemblages because of differences in their phenotypic (e.g., external morphology and cellular organelle arrangement) and genotypic (e.g., DNA base content and sequence as well as repair and photoprotective capabilities) characteristics (Karentz *et al.* 1991a, 1994; Neale *et al.* 1998c; Roy 2000).

More specifically, a variety of evidence from theoretical analyses of light absorption and experimental results using cultures or natural assemblages exposed to different spectral UVR regimes have suggested that the sensitivity of planktonic cells to UVR may be of function of cell size, with small cells being more vulnerable to UVR than large cells (e.g., Karentz *et al.* 1991a; Garcia-Pichel 1994). Because small cells have higher illuminated surface area to volume ratios than larger cells and specific absorption by macromolecules (e.g., DNA, proteins and photosynthetic pigments) generally increases with decreasing cell size and decreasing internal molecular self-shading (phenomenon referred to as package effect; Morel and Bricaud 1981), small cells are expected to have higher exposure to UVB per cell volume and sustain greater absorption of damaging UVB photons per unit DNA and/or other cellular components than larger cells (Karentz *et al.* 1991a). Furthermore, since the protective efficiency of UV-absorbing compounds is a function of the cellular concentration but also cell size (through its effect on molecular self-shading), model calculations by Garcia-Pichel (1994) have indicated that, while bigger cells (nano- and netplankton; > 2 μm) may contain sufficient UVR-screening pigments to confer protection against UVR, these photoprotective compounds would not be as effective in the small cell volume of picoplankton (0.2 – 2 μm).

Although studies have found that small cells were generally more vulnerable to

UVB-induced DNA damage than larger cells (e.g., Karentz *et al.* 1991a; Buma *et al.* 2001a,b), the relationship between UVR exposure and phytoplankton cell size has been highly variable in the literature when addressing photosynthetic inhibition. Some studies have actually shown that the small cells were more resistant to photosynthetic inhibition by UVR than larger cells (e.g., Helbling *et al.* 1992; Laurion and Vincent 1998), while others have shown opposite findings (e.g., Perin 1994; Hiriart *et al.* 2002) or equal photosynthetic sensitivity among the size classes (Perin 1996). Despite this variability, it is evident that any shifts in the size structure of phytoplankton communities from exposure to UVR can be potentially as important as effects of UVR on total phytoplankton productivity since it can have wide-range implications for pelagic food web processes by affecting phytoplankton's suitability as food for grazers and for interactions with the benthos via sedimentation (Kiørboe 1993; Karentz *et al.* 1994; Williamson 1995; Wängberg *et al.* 1996; Van Donk *et al.* 2001).

Through photosynthesis, phytoplankton fix inorganic carbon into simple carbon precursors (i.e., raw materials) for the biosynthesis of the main macromolecular end products (lipid, polysaccharide and protein). The partitioning of these photosynthates into major end products is well known to be affected by the taxonomic composition of the community (e.g., Madariaga and Fernandez 1990; Madariaga 1992; Maurin *et al.* 1995), by the physiological state of the phytoplankton (e.g., Morris 1981; Smith and Geider 1985) and by environmental factors such as light intensity (e.g., Morris *et al.* 1974; Cuhel and Lean 1987b; Rai 1995), nutrient availability (e.g., Konopka and Schnur 1981; Morris *et al.* 1985; Groeger and Kimmel 1988), water temperature (e.g., Morris and Farrell 1971; Thompson *et al.* 1992; Wainman and Lean 1996) and pH (e.g., Guckert and Cooksey

1990). In addition to its pronounced effects on phytoplankton photosynthesis, UVB exposure has been shown to inhibit the uptake of inorganic nitrogen in both cultured species and natural phytoplankton assemblages (Döhler 1992, 1995, 1997; Behrenfeld *et al.* 1995; Döhler and Hagmeier 1997; Lohmann *et al.* 1998; Fauchot *et al.* 2000). Other studies have demonstrated significant negative effects of UVB on specific molecular groups including lipids, fatty acids (FA), proteins and pigments (Agrawal 1992; Döhler and Biermann 1994; Goes *et al.* 1994, 1995; Döhler 1996).

Therefore, it is possible that any harmful effects on algal physiology with exposure to UVB radiation could have general metabolic consequences, including changes in the total metabolism and in the biosynthesis of the principal end products in phytoplankton. Furthermore, the synthesis of photoprotective compounds such as mycosporine-like amino acids or MAAs (e.g., Karentz *et al.* 1991b; Xiong *et al.* 1997; Neale *et al.* 1998c) and/or the synthesis of compounds involved in UV-repair activities (e.g., Mitchell and Karentz 1990; Vincent and Roy 1993; Karentz 1994) could also influence the partitioning of photosynthetically fixed carbon into the main end products. Unfortunately, the effects of UVR on the quality, as opposed to the quantity, of phytoplankton photosynthetic products have received comparatively little attention (e.g, Arts and Rai 1997; Smith *et al.* 1998; Furgal *et al.* 1998).

Because of the nutritional importance of proteins, carbohydrates, and lipids to higher trophic levels (Scott 1980; Ahlgren *et al.* 1990; Rothhaupt 1990; Muller-Navarra 1995; Vanderploeg *et al.* 1996), changes in the distribution of these main macromolecular end-products in phytoplankton as a result of exposure to UVB could have important consequences for invertebrate and vertebrate community structure and energy flow in aquatic food webs. Changes in the allocation of carbon to cellular lipid pools by UVB may especially have profound effect on higher trophic levels, which capitalize on periods when lipid production by algae is maximal (Arts *et al.* 1992, 1993, 1997).

In this study, phytoplankton communities from nine High Arctic lakes located in the vicinity of Resolute (Cornwallis Island, Nunavut, Canada) were exposed to levels of 6, 25, 50 and/or 100% incident solar radiation (Eo) with and without enhanced UVB. The main objective was to evaluate the effects of enhanced UVB on total productivity rates, on size-distribution of productivity (picoplankton, 0.2 - 2 µm; nanoplankton, 2 - 20 µm; netplankton, > 20 µm), and on carbon allocation into low molecular weight metabolites (LMW; e.g., amino acids, organic acids and monosaccharides) and three main macromolecular classes (lipid, polysaccharides and protein) when exposed to variable radiation regimes. More specifically, the following questions were asked: (1) Does enhanced UVB inhibit total photosynthetic rates? (2) Does cell size control the degree of UVB inhibition of photosynthesis? (3) Does UVB influence the partitioning of photosynthetic carbon into LMW and macromolecular pools? and (4) If there are any effects of enhanced UVB on total productivity, size-fractionation or carbon allocation, how long does it take for them to be observed, are they the same at all irradiance regimes and are they consistent for all studied lakes?

Limnological characteristics of these lakes were also described since they have never been documented before for most of these lakes. To my knowledge, this is the first study, aside from Chapter 1, to report on the effects of enhanced UVB on phytoplankton photosynthesis of high arctic lakes in North America and on photosynthetic carbon allocation into major end products. These lakes contain low DOC levels (≤ 2 mg L^{-1}), which are within a concentration range where small variations in DOC could give rise to large changes in underwater spectral UVR (Laurion *et al.* 1997; Lean 1998a; Perin and Lean 2004).

Materials and methods

Sampling sites

Experiments were conducted from 4 July to 17 August of 1996 using nine lakes situated in the vicinity of Resolute Bay, Cornwallis Island (74°42'N, 94°50'W; Nunavut, Canada; Figure 2-1). This region has a cold, desert climate with a mean annual temperature of -16°C and a mean total annual precipitation of 150 mm (Environment Canada 2004). The lakes in this area are only ice-free for 1 to 10 weeks between July and September, depending on the local climate around the lake and the summer temperature (Schindler *et al.* 1974a). The ice cover is about 2 m thick in early spring and does not always completely melt every year (Schindler *et al.* 1974a; Welch 1974). In most years, lakes around Resolute are typical cold, monomictic polar lakes, with a brief period of mixing during the ice-free period in the summer (Shindler *et al.* 1974a, b). Water temperatures in large lakes (i.e., those with mean depths > 4 m) do not exceed 4°C, but small lakes with mean depths < 4 m may rise slightly above 4°C (Welch 1974).

The investigated lakes were Barren Lake, Black Char Lake, Char Lake, Clear Lake, Meretta Lake, North Lake, Resolute Lake, Small Lake, and Tern Lake (Figure 2-1). The lakes range from about 0.15 to 1.19 km^2 in surface area and have mean depths ≤ 10.5 m (Table 2-1). During the sampling year, incomplete melting of the ice was observed for many of these lakes. Little limnological information exists on these lakes, except for Char and Meretta Lakes. The latter lakes were major study sites for the International Biological

Program (IBP) between 1968 and 1972 (Kalff and Welch 1974; Schindler *et al.* 1974a,b; Welch and Kalff 1974; Rigler 1978). Meretta Lake received sewage effluent between 1949 and early 1970s via a series of watercourses from the so-called "North Base" of the Canadian Department of Transport at Resolute (Schindler *et al.* 1974b) and, as a result, represented the first detailed study of high arctic lake eutrophication. However, the use of the North Base has declined markedly since the time of IBP and recent data from Douglas and Smol (2000) have indicated less eutrophic conditions in Meretta Lake than during the IBP study period. Plants are virtually absent in some lakes like Char and Barren or sparsely distributed around the lakes as patches of lichens, filamentous algal mats, mosses, and/or low herbs. Only Meretta Lake has a relatively dense vegetation in part of the watershed around a creek that received sewage effluent. Both Char and Meretta lakes drain into Resolute Lake and thus have an influence on its limnological characteristics, especially the small addition of nutrients from Meretta Lake.

Resolute area was chosen over other locations in the Canadian high Arctic for logistical reasons (e.g., availability of laboratory space, workshops and tools, ATVs), which all contributed for this project to be feasible. For this study, all field measurements and water samples were collected from an inflatable boat over the central or deepest part accessible of the lakes if ice was present. All water samples were taken using an opaque Van Dorn (2.5 L) sampler and transferred into plastic containers that were kept in the dark in coolers until further work in the laboratory.

Physical and chemical variables

Profiles of water temperature, conductivity and dissolved oxygen (DO) were measured for all nine high Arctic lakes using a YSI (Yellow Springs Instrument Co Inc) model 33 SCT meter and model 57 oxygen meter, respectively. The profiles were taken twice during the summer for North Lake: on 28 June when the ice still covered the lake and on 31 July when the lake was nearly all ice free. Profiles were also done for all the eight lakes under ice-free conditions, except for Small Lake where measurements were recorded under the ice.

For all nine high Arctic lakes, water samples were taken at 0.5 m intervals down the water column that were all subsequently integrated together into 30 L plastic bottles for "whole lake" chemical analyses. Water samples were also taken at different depths on 28 June and 31 July in North Lake for comparison in chemical profiles between ice-covered and ice-free conditions. Water samples were brought back to the lab usually < 1 hour and treated following the *Analytical Methods Manual* (Environment Canada 1979).

A total of thirty-six chemical variables were measured for each water sample. Water for nutrient and carbon analyses, which include nitrite (NO_2), nitrate (NO_3), ammonia (NH_3), soluble reactive phosphate-phosphorus (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and total Kjeldahl nitrogen (TKN), was filtered though a 47 mm diameter Sartorius (11106) cellulose acetate filters (pore size = 0.45 μm) and placed in rinsed 100-mL glass bottles. The same filtration was used to obtain water for analyses of total "dissolved" phosphorus (TP-F). 1 mL of 30% H_2SO_4 was added to both the filtered (TP-F) and the unfiltered total phosphorus (TP-UF, including phosphorus in particulate and dissolved phase) and placed in 100 mL glass bottles. Between 200 to 250 mL of water was filtered through ashed 47 mm diameter Whatman GF/F glass microfibre filters that were then stored in plastic petri dishes, wrapped in aluminum foil, for analyses of particulate organic carbon (POC) and particulate nitrogen (PON). Major ions (i.e., calcium [Ca], magnesium [Mg], potassium [K], sodium [Na], chloride [Cl], sulphate [SO_4]), dissolved silica (SiO_2) and trace metals (i.e., silver [Ag], aluminium [Al], barium [Ba], beryllium [Be], cadmium [Cd], cobalt [Co], chromium [Cr], copper [Cu], iron [Fe], potassium [K], lithium [Li], manganese [Mn], molybdenum [Mo], nickel [Ni], lead [Pb], vanadium [V], strontium [Sr], zinc [Zn]) were determined from samples stored in 100-mL plastic bottles. All bottles and filters were kept cool and in the dark before being shipped to the National Water Research Institute (Burlington, Ontario) for chemical analyses following the methods given in Environment Canada (1979).

DOC fluorescence (DOCFL) was also measured according to the method of Scully and Lean (1994) using a Turner Designs fluorometer. Water samples were placed in a 2 cm diameter optically clear quartz cuvette and DOCFL was measured at an excitation wavelength of 365 nm and emission wavelength of 437 nm. Fluorescence values were then standardized and expressed as quinine sulphate units (QSU) where 1 QSU = 1 $\mu g\ L^{-1}$ quinine sulphate in 0.1N H_2SO_4 (Scully and Lean 1994).

Chlorophyll a

Of the "depth-integrated" water samples taken for chemistry analyses (see above), triplicate subamples (500 to 2000 mL) were also filtered onto 47 mm diameter Whatman GF/F glass microfibre filters for measuring phytoplankton chlorophyll *a* (Chl *a*). Profiles of Chl *a* were also done for North Lake (under ice-covered and ice-free conditions) and for Char, Meretta, and Resolute lakes (under ice-free conditions only) from water samples collected at different depths within the water column and filtered following the same procedure above. After filtration, all filters were kept frozen in the dark in plastic petri dishes, wrapped in aluminum foil, until they were extracted with boiling 95% (vol/vol) ethanol. The fluorescence of the extracts was then measured with a Turner Designs model 10 fluorometer equipped with a blue lamp (F4T5), blue (Corning CS5-60) excitation filter, a reference (Corning CS3-66) filter, and a red (Corning CS2-64) emission filter. Fluoresence values were standardized and expressed in $\mu g\ L^{-1}$ using calibration curves with Chl *a* from *Anacystis nidulans* (Sigma Biochemical Co) and the final Chl *a* concentration was calculated following the equation from Appendix C-1.

Photosynthetic picoplankton

90 mL water subsamples were preserved with 10 mL fixative solution of glutaraldehyde/ paraformaldehyde (final concentration of 1%/0.1%). The preserved samples were filtered through a 25 mm diameter 0.2-μm black Nuclepore filter placed on top of a 0.45-μm cellulose nitrate Sartorius filter. The black Nuclepore filters were then placed on slides and stored frozen in the dark until cell counts i.e., within 1-2 months later. Picoplankton counts were performed on a 100x oil immersion objective of a Zeiss standard epifluorescence microscope equipped with a 100-W HBO mercury lamp at a magnification of 1250x (Pick and Caron 1987) by using the red autofluorescence of phycocyanin-containing cells (a pigment found in cyanobacteria) under green excitation (510 to 570 nm) as described in Pick and Agbeti (1991). Picocyanobacteria were counted

either from 20 random whole field views or along 3 transects if counts were low within a field (Appendix C-3).

Phytoplankton productivity, size distribution and carbon allocation

Phytoplankton photosynthetic rates were measured by the ^{14}C-bicarbonate technique (Steeman-Nielsen 1952) in an incubator (see below) for all nine high Arctic lakes on the dates outlined in Table 2-2. Depth integrated water samples were used for all ^{14}C experiments, except for North Lake on 10 July where samples were taken only at depths between 0.5 to 1 m below the ice (Table 2-2). Water subsamples of 250 mL were transferred into rinsed polyethylene Whirlpak (WP) bags. The WP bags were kept in the dark at *in situ* temperatures until the initiation of the photosynthesis incubations, usually less than 2 h after sampling. Each WP was inoculated with 25-30 µL of ^{14}C-sodium bicarbonate (^{14}NaHCO$_3^-$; stock concentration of 1 mCi mL^{-1}; ICN Biomedicals). The WP bags were incubated for 2 and 8 hours for all nine lakes, except for Clear Lake (5 hours only) and Small Lake (2, 6 and 12 hours; Table 2-2). Two additional 24-h experiments were also performed using North Lake on 10 July and 9 August, with triplicate samples taken from each treatment at different time intervals during the incubation period (Table 2-2).

Most of the ^{14}C experiments consisted of exposing the phytoplankton to the following eight treatments, using triplicate WP bags per treatment:

Natural sunlight i.e., ambient UVB	Natural sunlight + enhanced UVB
(1) Full surface irradiance i.e., 100%E_o	(2) 100%E_o
(3) 50%E_o	(4) 50%E_o

(5) 25%E_o (6) 25%E_o

(7) 6%E_o (8) 6%E_o

However, ^{14}C inoculated samples were exposed to only 50%E_o and 100%E_o under both ambient and enhanced UVB levels for North Lake on 9 August and WP bags were exposed to 6%E_o after 12 h incubation only (not after 2 and 6 h) for Small Lake (Table 2-2).

100 or 150 mL from each bag was prefiltered onto 25 mm diameter 20 μm Nitex filter after incubation. Then, 15-20 and 30-45 mL aliquots of the filtrate were filtered onto 25 mm diameter 0.2- and 2-μm Nuclepore filters, respectively. However, for the two 24-h experiments on North Lake, filtration was done only on 0.2 μm Nuclepore filters. All filters were rinsed with 0.2-μm filtered lake water to remove any residual inorganic ^{14}C. For each ^{14}C experiment, triplicate WP bags were also incubated in the dark and filtered the same way as the "light-incubated" samples. The filters were then placed into scintillation vials where 5 mL of scintillation cocktail (Beckman, Ready Safe) was added after 24 h. The vials were later counted for radioactivity in a Beckman LS counter in disintegrations per minute (DPM) using an internal quench curve. "Dark" uptake rates were subtracted from the "light" uptake rates to obtain the photosynthetic carbon uptake (Appendix C-2). The distribution of phytoplankton productivity was also separated into three size classes: (1) picoplankton (0.2 - 2 μm); (2) nanoplankton (2 - 20 μm); 3) netplankton (> 20 μm) and expressed as percentage of total photosynthetic rates (obtained from 0.2 μm filter; Appendix C-2).

The incorporation of ^{14}C into low molecular weight (LMW) metabolites, lipids, polysaccharides and protein were measured for five of the nine lakes: Clear, North, Small, Tern, and Meretta lakes (Table 2-2). After ^{14}C incubation (see above), triplicate water subsamples of 150 mL were filtered through 25 mm diameter Whatman GF/F glass microfibre filters, rinsed with filtered lake water to remove any residual inorganic ^{14}C and stored frozen until analyses. The composition of the subcellular fractions in phytoplankton was then estimated by measuring each of the fractions during carbon fixation (Morris *et al.* 1974). This method avoids the need for separating phytoplankton from other detritus of similar sizes and offers the advantages of speed, large sample throughput, and relatively ease of execution (Cuhel and Lean 1987a; Arts and Rai 1997). Because almost all of the inorganic carbon is fixed by photosynthetic cells, the amount of carbon entering each fraction reflects the amount of each fraction in phytoplankton.

The macromolecules and LMW compounds were separated and extracted sequentially based on their solubilization into four operationally defined fractions as described in Cuhel *et al.* (1984) and Cuhel and Lean (1987a): cold 10% trichloroacetic acid (TCA) soluble fraction (LMW material); alcohol-ether soluble fraction (lipid); hot TCA soluble material (mainly polysaccharides, but also nucleic acids) and the insoluble residue (mainly protein). An overview of the types of ^{14}C-labelled molecules and compounds found in each fraction is shown in Cuhel and Lean (1987a). The amount of radioactivity incorporated into each subcellular fraction was counted in a Beckman LS counter in DPM using an internal quench curve.

The LMW, lipid, polysaccharide and protein fractions were then expressed as the percentage of the sum of the four fractions (Appendix C-2). It is important to note that the sum of the derived fractions from the sequential extraction method equals to the total cell's carbon uptake (Cuhel and Lean 1987a; Perin *et al.* 2002). This was also confirmed in this study where the mean carbon uptake rate derived from the sum of all fractions was similar to the mean total carbon uptake measured from unprocessed 0.2-μm Nuclepore filters (Two-sample t test: $t = -0.397$, DF = 478, $p = 0.692$). Accordingly, the DPMs obtained from the sum of the derived fractions and the ones from unprocessed 0.2 μm Nuclepore filters were found to be highly correlated (Fig. F-1, Pearson correlation coefficient = 0.989, $p < 0.001$).

Incubator and treatments

All ^{14}C experiments took place in a waterproof incubator constructed of wood. The dimensions of the incubator were 101 cm long, 71 cm wide and 28 cm deep. The incubator was placed on the flat roof of a Polar Continental Shelf building in Resolute to avoid any disturbances and shading. The incubator was divided into 8 compartments in order to achieve the desired exposure treatments (see section above). Variations in irradiance levels were achieved by covering the divided sections of the incubator with one, two or four thickness of screens, which transmitted about 50%, 25%, and 6% respectively of the incoming surface solar irradiance (E_o). Enhanced UVB levels were achieved using two UVB lamps (National Biological Corporation, model FS20T12/UVB, Tweesmere, Ohio, 1.2 m long; emission peak at 310 nm), which were placed on a wooden frame erected 0.6 m above the incubator. Shade provided by the wooden frame was negligible (less than 10%).

Total incident radiation, UVA and UVB levels were measured for each treatment at the start and at the end of each incubation period during all ^{14}C experiments (Table G-1). Total solar incident light was measured using a Licor radiometer and total incident

UVA and UVB were measured using Goldilux (Oriel Instruments) UVA (model 70211; 315-400 nm) and UVB (model 70213; 280-315 nm) meters respectively, with built-in detector and display. For the enhanced UVB treatment, the UVB lamps supplied essentially a constant intensity during the incubation period and increased integrated UVB by 20% to 700% depending on the weather conditions (i.e., presence of clouds or fog) and time of day (Table G-1), but the increased was generally about 2 times the integrated natural UVB levels. All experiments were conducted in the incubator in order to expose the phytoplankton communities from all nine lakes to somewhat similar environmental conditions and UVB enhancement, although surface irradiance levels could differ greatly during the incubation period and between ^{14}C experiments due to variations in weather conditions and time of day (Table G-1). Therefore, it is acknowledged that the total received amount of solar radiation, UVA and UVB levels as well as ratios of UVB-to-longer wavelengths may have differed between the experiments.

Statistical Analyses

The effects of irradiance, UVB and time of incubation on total phytoplankton productivity, size distribution (i.e., on the relative proportion of carbon fixed by picoplankton, nanoplankton, or netplankton) or carbon allocation (i.e., on the relative proportion of carbon fixed in LMW compounds, lipids, polysaccharides, or proteins) were assessed using a model I, three-way analysis of variance (3-way ANOVA) for all ^{14}C experiments, except for the one on Clear Lake that was assessed using a 2-way ANOVA since there was no time effect (i.e., samples were incubated only once after 5 h). It tests for differences among means through three factors (i.e., UVB, irradiance and time of incubation) or two factors for Clear Lake only (i.e., UVB and irradiance) and also tests for possible interactions among the factors. Irradiance had four levels (6%E_o, 25%E_o, 50%E_o, and 100%E_o), except for North Lake on 9 August that had 2 levels (50%E_o and 100%E_o) and Small Lake that had three levels (25%E_o, 50%E_o and 100%E_o for the first 6 hours). UVB had two levels (ambient and enhanced levels). Time of incubation usually had two levels (2 h and 8 h), except for Small Lake that had three levels (2, 6 and 12 h), North Lake on 10 July that had 4 levels (3, 6, 12, and 24 h) and North Lake on 9 August that had 5 levels (2, 4, 8, 12, and 24 h). If significant effects of irradiance or time of incubation were detected by the ANOVA, the Bonferroni multiple comparison test was then used to determine which means were significantly different at the 5% significant level.

Correlation analyses were also used to measure the degree of linear association between the sums of the derived subcellular fractions and unprocessed filters, between the relative proportion of carbon fixed by the three phytoplankton size classes, and between the relative proportion of carbon fixed into the four subcellular fractions. When the data did not meet the assumptions for ANOVA or correlation, they were either transformed or ranked. All statistical analyses were run using SYSTAT version 10 (SPSS Science 2000).

Results

Physical and chemical characteristics of the lakes

Early in the summer, when ice was still covering most of the lake, there was an inverse stratification with cooler temperatures at the top (near the ice; ~ 0 °C) and warmer temperatures (~ 4 °C) at the bottom, as shown for North Lake (Fig. H-1, top graph) and for Small Lake (Fig. H-2). Dissolved oxygen levels were generally about 15 mg L^{-1} for water right under the ice and decreased steadily down the water column to 7 mg L^{-1} at the bottom for North Lake (Fig. H-1, middle graph). For Small Lake, oxygen levels were also near 15 mg L within the water column and decreased to values below 10 mg L^{-1} near the bottom (Fig. H-3). Percent saturation of dissolved oxygen was estimated to vary between 57% (at the bottom) and 105% (just beneath the ice) for North Lake and between 76% (at the bottom) and 145% (within the water column) for Small Lake. High oxygen levels near the surface beneath the ice is believed to be caused by the exclusion of oxygen from the ice as well as higher oxygen solubility in colder water, while oxygen depression at the bottom might be caused by microbial respiration (Rigler 1978). Water conductivity levels were much lower ($\leq$ 10 µS cm^{-1}) just beneath the ice due to dilution of solutes from the melting ice, but increased with depth with the increased concentrations of salts (mainly Ca; see below, Fig. I-1) and reached values greater than 100 µS cm^{-1} for North Lake (Fig. H-1, bottom graph) and 300 µS cm^{-1} for Small Lake at the bottom (Fig. H-4).

The 24-h sunshine during the summer rapidly thawed the ice and snow. The melting snow on land created streams that ran into the lakes and, combined with thawing of near snow-free shoreline, led to the formation of a moat in each lake. As the summer progressed, the moat gradually widened in all of the nine lakes and the ice was either free-floating or completely gone. Under these conditions, water mixing occurred and temperatures were fairly uniformed down the water column in all nine lakes and ranged from 0.5 to 2.2 °C in July and August of 1996 (Fig. H-1 and H-2). Oxygen levels were generally around 15 mg L^{-1} throughout the water column in all nine lakes, except for Tern

Lake where levels decreased from 15 mg L^{-1} at the top to 5 mg L^{-1} at the bottom (Fig. H-1 and H-3). Conductivity levels were also quite uniform throughout the water column for all nine lakes during ice-free conditions and ranged from 105 µhoms cm^{-1} in Clear Lake to 240 µhoms cm^{-1} in North Lake (Fig. H-1 and H-4).

A comparison between the chemical characteristics of North Lake during ice-covered (28 June) and ice-free (31 July) conditions is shown in Fig. I-1. Nitrite (NO_2), nitrate (NO_3) and ammonia (NH_3) levels were generally low (i.e., below their detection limits) throughout the water column when the ice was still present, but increased after ice melting. Total nitrogen (TN) and total Kjeldahl nitrogen (TKN) levels were fairly similar between the two ice conditions; except for low levels at the surface of the ice hole (Fig. I-1). Particulate nitrogen (PN), particulate organic carbon (POC) and total phosphorus (TP; unfiltered and filtered) concentrations were generally slightly higher through the water column under the ice, except at the surface. Soluble reactive phosphorus (SRP) levels were low (i.e., 0.001 mg L^{-1}) when the lake was ice-covered, but increased up to about 0.004 mg L^{-1} near the surface during ice-free conditions. Dissolved inorganic carbon (DIC) gradually increased from near 10 mg L^{-1} just beneath the ice to above 20 mg L^{-1} at the bottom, while levels were uniform at 14 mg L^{-1} throughout the water column when the ice was gone. Major ions (i.e., Ca, Mg, Na, Cl, SO_4), dissolved silica (SiO_2) and some trace metals (i.e., Ba and Sr) also showed a general increase in their levels from the top (near the ice) down to the bottom, while their levels were fairly uniform through the water column in the absence of ice thereafter (Fig. I-1). As for K and Zn, their levels were usually about 0.2 and > 0.002 mg L^{-1} respectively during the ice-covered period, but were below the detection limit (> 0.2 mg L^{-1}) during ice-free conditions. Al, Fe and Mn levels were usually below their detection limits when the ice was present (except within the ice hole) and were about 0.03, 0.03 and 0.0015 mg L^{-1} respectively when there was no ice (except for non-detectable levels at the water surface; Fig. I-1).

The depth-integrated chemical characteristics of all nine lakes are summarized in Table I-1. TN varied from 95 µg L^{-1} in Barren Lake to 245 µg L^{-1} in Clear Lake. For all nine lakes, TKN accounted for more than 60% of TN, followed by PN (10-20% of TN). NO_2 and NO_3 levels were low for all lakes i.e., $\leq$ 4 µg L^{-1} and 21 µg L^{-1} respectively. Total phosphorus (TPUF) concentrations were between 1.2 µg L^{-1} in Barren Lake to 9.6 µg L^{-1} in Black Char Lake. Ratios of TN:TPUF were very high i.e., $\geq$25, which would indicate that P is limiting to algal biomass in these lakes, as suggested by Schindler *et al.* (1974a,b). The nutrient levels in Meretta Lake were within the range found for the other lakes and much lower than those recorded in the early 1970s when the lake received significant sewage effluent (Schindler *et al.* 1974b). This would indicate that Meretta Lake is recovering from eutrophication, which has been demonstrated in more details by Douglas and Smol (2000). SRP ranged from 0.4 µg L^{-1} in Barren and Black Char to 3.0 µg L^{-1} in Small Lake. The POC:PN ratios were between 8 (Meretta and North lakes) and 22 (Barren Lake), which would indicate extreme nitrogen limitation or high carbon content especially for Barren Lake. Na, Cl, and SO_4 levels were much higher in lakes near human developments (i.e., Resolute, Char, Small and Meretta lakes) than the other lakes, probably due to salt deposition on nearby roads. Heavy metals such as Cd, Cu, Cr, and Pb were below detection levels in all of the lakes (Table I-1).

DOC, DOC fluorescence and attenuation coefficients of UVA and UVB

A particular feature of polar desert catchments is their sparse vegetation cover and resultant low concentrations of dissolved organic carbon (DOC). For all nine lakes, DOC levels were less than 2.5 mg L^{-1} (Table 2-3). For North Lake, DOC levels were slightly lower ($\leq$ 1 mg L^{-1}) during the ice-free season compared to values $\geqslant$ 1 mg L^{-1} under ice-covered conditions (Fig. I-1). However, DOC levels were quite uniform throughout the water column with or without ice cover, except at the water-ice interface where levels were more than 3 mg L^{-1} (Fig. I-1). DOC levels varied little with depth also for Char and Meretta lakes, but slightly decreased with depth for Resolute Lake (Fig. I-2).

The integrated attenuations of both UVA and UVB can be accurately estimated from DOC concentrations ($r^2 \geq 0.95$) following the equations of Scully and Lean (1994) for lakes with DOC levels lower than 8 mg L^{-1}. The diffuse UVB attenuation coefficients for radiation integrated between 300 and 320 nm ($K_{dI}B$) and UVA attenuation coefficients for radiation integrated between 320 and 400 nm ($K_{dI}A$) were then calculated for all nine lakes as a power function of DOC concentrations. $K_{dI}B$'s and $K_{dI}A$'s were low in all nine lakes, with values $\leq$ 2.1 and 1.1 m^{-1}, respectively (Table 2-3). Estimated depths of 1% integrated UVB varied from 2.2 m in Clear Lake to 11.1 m in North Lake, with an average of 5.8 ± 3.2 m. Meanwhile, estimated depths of 1% integrated UVA varied from 4.0 to 15.4 m, with an average of 8.1 ± 4.0 m. Calculated integrated attenuation coefficients of total incident radiation (mainly PAR; $K_{dI}PAR$) in Char, Meretta, North and Resolute lakes were also very low ($\leq$ 0.3 m^{-1}; Table 2-3) and, although they were not calculated, similar K_{dI}'s would have probably been found for the other lakes. Scully and Lean (1994) have also found that $K_{dI}B$ and $K_{dI}A$ could also be estimated from DOC fluorescence (DOCFL) as a linear function. In this study, DOCFL levels varied from 2.7 quinine sulphate units (QSU) for Char Lake to 8.8 QSU for Barren Lake (Table 2-3). The attenuation coefficients estimated from DOCFL were generally higher those generated from DOC levels (Table 2-3). $K_{dI}B$'s and $K_{dI}A$'s ranged from 1.4 to 4.3 m^{-1} and from 0.7 to 1.8 m^{-1}, respectively.

Because of their low DOC levels and their mean depth is much lower than 10 m, a substantial amount of surface UVR levels can then be reached down the water column in these lakes. Patterns of underwater UVB, UVA and PAR (as a percentage of surface irradiance) generated from the calculated or estimated K_{dI}'s (from DOC and DOCFL) in Table 2-3 are shown for North Lake in Figure J-1. 6, 25 and 50% of total surface incident light (i.e., the irradiance treatments used for all ^{14}C experiments) were reached at about 12, 6 and 3 m, respectively in North Lake. For UVA, the depths of 6, 25 and 50% were estimated to be about 9, 5 and 2 m respectively based on DOC or 3, 1.5 and 0.8 m respectively based on DOCFL. For UVB, the depths of 6, 25 and 50% were estimated to be about 7, 3.5 and 2 m respectively based on DOC or only 1.3, 0.7 and 0.3 m respectively based on DOCFL. Meanwhile, there were still 30%, 22% (estimated from DOC) and 14% (estimated from DOC) of surface PAR, UVA and UVB respectively at 5 m (i.e., the mean depth) in North Lake (Fig. J-1).

Chlorophyll a and photosynthetic picoplankton

Chlorophyll *a* (Chl *a*) concentrations ranged from 0.18 μg L^{-1} in Barren Lake to 2.91 μg L^{-1} in Tern Lake (Table I-1). Because of the nutrient loading from sewage effluents in the past, Meretta Lake still has higher Chl *a* levels than most of the other lakes. Resolute Lake also has high levels likely due to the small addition of nutrients from Meretta Lake that drained into Resolute Lake. Surprisingly, Tern Lake has the highest mean Chl *a* concentrations, but also the largest variations. Therefore, it is possible that some samples from Tern Lake had been contaminated with benthic algae or included large planktonic colonies. Depth profiles in North Lake show that, during the ice-covering period, Chl *a* levels were much lower (close to zero) beneath the ice and increased with depth (Fig. K-1a). However, Chl *a* was relatively consistent throughout the water column during ice-free conditions (Fig. K-1a). Profiles in Char, Merreta and Resolute lakes also showed uniform Chl *a* concentrations with depth during ice-free conditions, except for slightly higher levels at the bottom in Resolute Lake (Fig. K-1b). This may have been caused by contamination with benthic algae during sampling for the bottom samples.

Photosynthetic picoplankton (PPICO) varied from as little as 50 cells mL^{-1} to greater than $5x10^4$ cells mL^{-1} between the nine lakes during ice-free conditions. Barren, Black Char, Clear, Meretta and Tern lakes only had ≤ 500 picoplankton mL^{-1} while Char, Small, and Resolute lakes had more than $2x10^4$ picoplankton mL^{-1} (Table I-1). For North Lake, PPICO abundance was greater than $5x10^4$ cells mL throughout the water column beneath the ice on 28 June, but counts were lower within the ice hole (Fig. K-2a). The abundance of PPICO decreased by more than 10-fold thereafter during the ice-free period and counts diminished a little with depth, except at the bottom (Fig. K-2a). Profiles from Char and Resolute lakes are showing, however, that the abundance of PPICO was generally quite uniform throughout the water column (Fig.K-2b).

Total phytoplankton productivity:

i) 24-h incubation experiments - North Lake

Two 24-h experiments were conducted using North Lake: one on 10 July when the lake was still more than 80% ice-covered and later on 9 August when the lake was completely ice-free. Photosynthetic rates for the total phytoplankton community exposed to natural solar radiation (i.e., ambient UVB levels) averaged (± SD) 0.04 ± 0.02 μg C L^{-1} h^{-1} on 10 July and 0.13 ± 0.03 μg C L^{-1} h^{-1} on 9 August. This represents more than a 3-fold increase in rates from 10 July to 9 August. This increased photosynthesis per unit volume was probably a direct result of an increase in phytoplankton biomass (mean Chl *a* of 0.14 ± 0.00 μg L^{-1} on 10 July and 0.50 ± 0.03 μg L^{-1} on 9 August) as the summer progressed since mean chlorophyll-specific productivity rates remained the same between the two dates (average chlorophyll-specific value of 0.28 ± 0.11 μg C μg Chl a^{-1} h^{-1} on 10 July and 0.26 ± 0.07 μg C μg Chl a^{-1} h^{-1} for 9 August).

Productivity levels were generally similar when exposed to 6, 25 and 50% surface irradiance (E_o) under natural UVB on 10 July, but high PAR and/or ambient UVR levels inhibited photosynthesis by an average of 30% under full solar radiation (i.e., 100%E_o) throughout the duration of the experiment (3-way ANOVA, irradiance effect: $p < 0.001$; T * E: $p = 0.122$; Table L-1; Fig. 2-2, top graph). Although rates were not measured at 6 and 25%E_o on 9 August, photosynthetic rates were also inhibited by an average of 40% at 100%E_o compared to those measured at 50%E_o under ambient UVB conditions (3-way ANOVA, irradiance effect: $p < 0.001$; T * E: $p = 0.05$; Fig. 2-2, bottom graph). Under natural solar radiation, productivity rates declined with the duration of incubation for the 10 July experiment, except between 12 h and 24 h of incubation where rates were similar between the two incubation periods (3-way ANOVA, time effect: $p < 0.001$). On 9 August, rates were highest after 2 h of incubation at 0.15 ± 0.04 µg C L^{-1} h^{-1}, were similar between 4, 8 and 12 h of incubation (average of 0.13 ± 0.03 µg C L^{-1} h^{-1}) and were lowest after 24 h (0.10 ± 0.02 µg C L^{-1} h^{-1}; 3-way ANOVA, time effect: $p < 0.001$). These declines with the duration of incubation were most likely a direct result of change in irradiance levels due to the weather conditions (e.g., presence of clouds, rain, or fog) during the experiment and time of day, especially in the evening and at night where irradiance levels were much lower despite the 24-h daylight at these latitudes during the summer (Table G-1).

On 10 July, exposure to enhanced UVB decreased phytoplankton productivity rates by 15 to 85%, depending on the time of incubation and irradiance treatment (3-way ANOVA, UVB effect: $p < 0.001$; UVB * T: $p= 0.001$; UVB * E: $p = 0.011$; UVB * T * E: $p = 0.001$; Table L-1; Fig. 2-2, top graph). The greatest decreased by UVB occurred at 50 and 100%E_o (especially after 6 hours of incubation), with lower inhibition at 6%E_o (15 to 40% UVB inhibition; Fig. 2-2, top graph). On 9 August, enhanced UVB also inhibited photosynthesis by 24 to 95%, depending on the irradiance level and time of incubation (3-way ANOVA, UVB effect: $p < 0.001$). The greatest decrease occurred under full sunlight (i.e., 100%E_o), especially after 24 hours of exposure to enhanced UVB where productivity levels were near 0 (Fig. 2-2, bottom graph).

ii) All nine lakes

The average productivity and chlorophyll-specific photosynthetic rates of all nine lakes after exposure to solar radiation (i.e., ambient UVB) and natural sunlight plus enhanced UVB are shown in Table 2-4. Across all irradiances levels under ambient UVB, the productivity rates ranged from 0.02 μg C L^{-1} h^{-1} for Barren Lake to 0.72 μg C L^{-1} h^{-1} for Merreta Lake, with an overall average of 0.24 ± 0.16 μg C L^{-1} h^{-1} and median of 0.22 μg C L^{-1} h^{-1}. Barren and North lakes had the lowest productivity rates with values less than 0.20 μg C L^{-1} h^{-1}, followed by Char, Tern, Black Char, Resolute, and Small lakes that had productivity rates less than 0.50 μg C L^{-1} h^{-1} (Table 2-4). Clear and Merreta lakes had the highest average productivity, with rates that reached values near 0.80 μg C L^{-1} h^{-1}. On the other hand, the average P^B rates was lowest for Tern Lake with chlorophyll-specific values less than 0.20 μg C μg Chl a^{-1} h^{-1} and highest for Clear with chlorophyll-specific values close to 1.00 μg C μg Chl a^{-1} h^{-1}. P^B averaged between 0.30 to 0.50 μg C μg Chl a^{-1} h^{-1} for Barren, Black Char, Char, Meretta, North, Resolute, and Small lakes (Table 2-4). Differences in total radiation levels during incubation, phytoplankton taxonomic and size composition, previous light history, nutrient levels, water temperature, and ice conditions are among factors that could explain the differences in total phytoplankton productivity rates between the lakes.

The lakes displayed diverse photosynthetic responses with exposure to four different irradiance treatments (i.e., 6, 25, 50 and 100%E_o) under natural ambient UVB conditions. For Char, Meretta, North and Resolute lakes, rates were generally higher at 6 and/or 25%E_o, but were inhibited by 15 to 50% at ≥ 50%E_o when irradiance levels were generally greater than about 300 μmol photons m^{-2} s^{-1} (Table L-1; Fig. 2-3a and Fig. 2-4c, e, f). On the other hand, for Black Char and Clear lakes, productivity rates were similar at ≥ 25%E_o when irradiance levels ranged from 55 μmol photons m^{-2} s^{-1} at 25%E_o up to 1100 μmol photons m^{-2} s^{-1} at 100%E_o. However, they were significantly lower (by 15 to 50%) at 6%E_0 when levels were less than 50 μmol photons m^{-2} s^{-1} (Table G-1; Fig. 2-4b, d). Meanwhile, for Barren and Tern lakes, photosynthetic rates were not significantly different between all four irradiance treatments (ANOVA, irradiance effect: p's > 0.05; Table L-1; Fig. 2-4 a, h), although total incident radiation levels varied from less than 65 μmol photons m^{-2} s^{-1} at 6%E_0 to greater than 200 μmol photons m^{-2} s^{-1} under full sunlight (100%E_0) during the incubation period (Table G-1). For Small Lake, differences in productivity between the irradiance treatments depended on the duration of incubation (ANOVA, irradiance effect: $p < 0.001$; E * T: $p < 0.001$; Fig. 2-4g). There was photoinhibiton at 100%E_0 after 2 h of incubation when irradiance levels were higher than 300 μmol photons m^{-2} s^{-1}, then no significant differences were observed between 25, 50 and 100%E_0 after 6 hours of incubation when irradiance levels ranged from only 30 to 120 μmol photons m^{-2} s^{-1}. Meanwhile, productivity rates became greater at 50 and 100%E_0 after 12 h incubation when surface solar irradiance levels were lower in the evening (Fig. 2-4g).

Eight out of the nine lakes showed a significant negative effect of enhanced UVB on total phytoplankton productivity (Table L-1). Although exposure to enhanced UVB decreased productivity rates by an overall of 18% for Barren Lake, its effect was not significant due to high variability within each UVB treatment, especially after 2 h of incubation (3-way ANOVA, UVB effect: $p = 0.331$; Fig. 2-4a). For North Lake, enhanced UVB inhibited photosynthesis by more than 25%, regardless of the time of incubation or level of irradiance, especially under full sunlight (100%E_0) where rates were lower by 65 to 70% (3-way ANOVA, UVB effect: $p < 0.001$; UVB * T: $p = 0.549$; UVB * E: $p = 0.810$; Fig. 2-3a). Exposure to enhanced UVB also significantly decreased productivity rates in Black Char Lake by 40 to 78%, except at 25%E_0 after 2 h and 6%E_0 at all times (3-way ANOVA, UVB effect: $p < 0.001$, UVB * T: $p = 0.041$, UVB * E: $p < 0.001$, UVB * T * E: $p = 0.010$; Fig. 2-4b). After 5 hours of exposure to enhanced UVB, productivity rates of Clear Lake decreased significantly (by an average of 60%) for samples incubated under full sunlight (i.e., at 100%E_0) and, although not significant, also decreased by an average of 20% at 50%E_0 (2-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p = 0.001$; Fig. 2-4d).

For Char, Resolute and Tern lakes, there was no or little decrease in photosynthesis by enhanced UVB after 2 h of incubation, but significantly decreased after 8 h of incubation (3-way ANOVA: UVB effect: p's < 0.001; UVB * T: p's < 0.010), especially at ≥ 50%E_0 where photosynthesis declined by 40 to 80% (Fig. 2-4c, f, h). Enhanced UVB caused some photoinhibition (15 to 26%) for samples exposed to 25%E_0 and 50%E_0 after 2 h of incubation for Meretta Lake, but decreased photosynthesis by 55 to 75% after 8 h of incubation at all irradiance levels, except 6%E_0 (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p < 0.001$; UVB * T: $p < 0.001$; UVB * E * T: $p = 0.001$; Fig. 2-4e). For Small Lake, exposure to enhanced UVB slightly decreased photosynthesis by an overall of 17% after 2 h, then by 48 to 76% at ≥ 50%E_0 after 6 h, and finally by 40 to 80% at ≥ 25%E_0 (but not at 6%E_0) after 12 h incubation (UVB effect: $p < 0.001$; UVB * T: $p < 0.001$; UVB * E: $p < 0.001$; UVB * T * E: $p = 0.022$; Fig. 2-4g).

Size fractionation of productivity:

i) Picoplankton (0.2 – 2 μm)

The contribution of picoplankton to total phytoplankton productivity ranged from 24.7% to 63.7% under natural sunlight (i.e., ambient UVB) among all nine lakes, with an overall average of 45.2 ± 8.1% and median of 45.6%. Clear and Tern lakes had the lowest average at around 35% (Table 2-5). Percent productivity of picoplankton averaged between 40 and 50% for Resolute, Char, Meretta, Small and Barren lakes and just over 50% for North and Black Char lakes (Table 2-5). Under ambient levels, the relative proportion of carbon fixed by picoplankton generally did not change significantly with variations in irradiance levels for most lakes (Fig. 2-3b and 2-5). The proportions were slightly higher (by 1.08 to 1.10-fold) at 100%E_0 than the other irradiance treatments for Black Char Lake, while they were significantly lower at 6%E_0 for Meretta Lake and at 25%E_0 for Clear Lake (3-way ANOVA: Irradiance effect: p's < 0.04; Fig. 2-5 b, d, e). On the other hand, for North Lake, percent productivity of picoplankton was slightly lower (by 1.07 to 1.15-fold) under full sunlight (i.e., 100%E_0) compared to the other irradiances levels (3-way ANOVA: Irradiance effect: $p < 0.001$; Fig. 2-3b).

Exposure to enhanced UVB did not significantly change the relative productivity of picoplankton for Barren, Black Char, Clear, Resolute and Small lakes (3-way ANOVA's, UVB effect: p's > 0.244; Table L-1; Fig. 2-5a, b, d, f, g) On the other hand, enhanced UVB significantly decreased percent productivity of picoplankton by 1.4-fold at 100%E_0 after 2 h incubation and by an average of 1.2-fold in all irradiance treatments after 8 h for Char Lake (UVB: $p = 0.003$; UVB * T: $p = 0.046$; Fig. 2-5c). For Tern Lake, there were no significant effects of enhanced UVB after 2 h incubation, but percent productivity of picoplankton decreased by an average of 1.4-fold after 8 h incubation, especially at 25 and 50%E_0 (UVB effect: $p < 0.001$; UVB * T: $p = 0.003$; Fig. 2-5h). For Meretta Lake, the proportion of carbon incorporated by picoplankton decreased by an average of 1.14-fold during the duration of the experiment when exposed to enhanced UVB levels, especially at 100%E_0 with 1.3-fold lower proportions (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p = 0.052$; Fig. 2-5e). The proportion of carbon fixed by picoplankton also significantly decreased by 1.1- to 1.4-fold with exposure to enhanced UVB for North Lake, except at 6%E_0 (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p = 0.042$; Fig. 2-3b).

ii) Nanoplankton (2 – 20 μm)

Similar to picoplankton, the contribution of nanoplankton to total phytoplankton productivity ranged from 26.6% to 62.8% under natural solar conditions among all nine lakes, with an overall average of 42.0 ± 7.0% and median of 41.7%. Black Char, Meretta and Resolute lakes had the lowest average between 35 and 40% (Table 2-5). Percent productivity of nanoplankton averaged between 40 and 50% for Barren, Char, North, Small, and Tern lakes and over 50% for Clear Lake (Table 2-5). Under ambient levels, the relative proportion of carbon fixed by nanoplankton generally did not change significantly between the four irradiance treatments for all lakes (Table L-1; Fig 2-3c and 2-6), except for Black Char Lake where proportions were on average 1.2-fold lower at 100%E_0 (3-way ANOVA; Irradiance effect: $p = 0.005$; Fig. 2-6b) and for Clear Lake where the relative productivity of nanoplankton was 1.1 to 1.2-fold higher at 25%E_0 than the other irradiance levels (3-way ANOVA, Irradiance effect: $p = 0.491$; E * UVB: $p = 0.022$; Fig. 2-6d).

Exposure to enhanced UVB did not have a significant effect on the proportion of carbon fixed by nanoplankton for Barren, Clear, Resolute, Small, and Tern lakes (3-way ANOVA's: UVB effect: p's > 0.132; Fig. 2-6a, d, f, g, h). However, for North Lake, percent productivity of nanoplankton significantly increased by about 1.2 to 1.3-fold in irradiance treatments during the experiment with exposure to enhanced UVB, except at 6%E_o after 8 h incubation (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p = 0.022$; UVB * T * E: $p = 0.019$; Fig. 2-3c). Enhanced UVB also increased the relative productivity of nanoplankton for Char Lake by 1.36-fold at 100%E_o after 2 h incubation and by an average of 1.13-fold at all irradiance levels after 8 h incubation (3-way ANOVA, UVB effect: $p = 0.013$; Fig. 2-6c). On the other hand, for Black Char Lake, exposure to enhanced UVB decreased the proportion of carbon incorporated by nanoplankton by 1.18 to 1.24-fold at all irradiance levels after 8 h incubation only, except at 6%E_o (3-way ANOVA, UVB effect: $p = 0.042$; UVB * T: $p = 0.044$; Fig. 2-6b). In the enhanced UVB treatment, percent productivity of nanoplankton increased significantly by 1.27-fold at 100%E_o after 2 h incubation, but then decreased by 1.1 to 1.2-fold at $\geq$ 50%E_o after 8 h incubation for Meretta Lake (3-way ANOVA, UVB effect: $p = 0.799$; UVB * T: $p < 0.001$; UVB * T * E: $p = 0.058$; Fig. 2-6e).

iii) Netplankton (> 20 µm)

The contribution of netplankton to total phytoplankton productivity was generally more than 2-fold lower than those contributed by picoplankton and nanoplankton. It ranged from as low as 3.6% to as high as 31.4.8% under natural sunlight (i.e., ambient UVB levels) among all nine lakes, with an overall average of only 12.8 ± 7.4% and median of 9.7% (Table 2-5). North and Small lakes had the lowest average, which was below 10%. The percent productivity of netplankton averaged between 10 and 15% for Barren, Black Char, Char, and Clear lakes and was over 20% for Meretta, Resolute and Tern lakes (Table 2-5).

The relative proportion of carbon fixed by netplankton did not change significantly between the irradiance treatments under ambient UVB conditions for Barren, Clear, Small and Tern lakes (Fig. 2-7a, d, g, h). Under natural UVB levels, the relative productivity of netplankton was generally slightly higher at both the lowest irradiance level (i.e., 6%E_o) and highest irradiance level (i.e., 100%E_o) relative to the intermediate levels (25%E_o and 50%E_o) for Char Lake (3-way ANOVA, Irradiance effect: $p = 0.031$; Fig. 2-7c) and after 8 h only for Black Char Lake (3-way ANOVA, Irradiance effect: $p = 0.001$; E * T * UVB: $p = 0.001$; Fig. 2-7b). Meanwhile, for Meretta Lake, the proportion of carbon incorporated by netplankton was significantly higher by about 1.2- to 1.5-fold at the lowest irradiance level (i.e., 6%E_o) than the other levels throughout the experiment under ambient UVB (3-way ANOVA, Irradiance effect: $p < 0.001$; Fig. 2-7e). Percent productivity of netplankton was also generally higher at low irradiance levels (6 and 25%E_o) for Resolute Lake (3-way ANOVA, Irradiance effect: $p < 0.001$; Fig. 2-7f). On the other hand, for North Lake, the relative productivity of netplankton was highest at the highest irradiance treatments (i.e., 50 and 100%Eo) throughout the duration of the experiment (3-way ANOVA, Irradiance effect: $p = 0.005$; Fig. 2-3d).

The proportion of carbon incorporated by netplankton significantly increased with exposure to enhanced UVB for all lakes, except for Resolute Lake where proportions did not change after 2 h of incubation but were 1.2-fold lower with UVB exposure after 8 h of incubation (average of 27.8 ± 2.1% for AMB-UVB and 22.4 ± 5.0% for ENH-UVB after 8 h; 3-way ANOVA, UVB effect: $p < 0.001$; UVB * T: $p < 0.001$; Fig. 2-7f). For Char and North lakes, enhanced UVB significantly increased the relative productivity of netplankton at all irradiance levels throughout the duration of the experiment by an average of 1.1- to 1.2-fold (3-way ANOVA's , UVB effect: p's ≤ 0.005; UVB * T: p's ≥ 0.201; UVB * E: p's ≥ 0.524; UVB * E * T: p's ≥ 0.295; Fig. 2-3d and 2-7c). For Barren, Meretta and Tern Lakes, percent productivity of netplankton was not significantly affected by enhanced UVB after 2 h of incubation, but increased significantly from 1.1- to 1.8-fold after 8 h incubation at all irradiance levels, except at 6%E_o for Tern Lake (3-way ANOVA's, UVB effect: p's ≤ 0.006; UVB * T: p's ≤ 0.05; Fig. 7a, e, h). For Clear and Small lakes, percent productivity of netplankton significantly increased at 50%E_o and 100%E_o (within 1.2 to 2.0-fold) with enhanced UVB, but not at 6%E_o and 25%E_o (3-way ANOVA's, UVB effect: p's < 0.001; UVB * E: p's ≤ 0.001; Fig. 2-7d, g). For Black Char Lake, exposure to enhanced UVB significantly increased percent productivity of netplankton at 25%E_o and 100%E_o only after 2 h of incubation and then increased it by 1.5 to 1.8-fold at all irradiances, except 6%E_o, after 8 h of incubation (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E: $p < 0.001$; UVB * T * E: $p = 0.001$; Fig. 2-7b).

Carbon Allocation into:

i) LMW

The proportion of carbon allocated into the low molecular weight (LMW) fraction by phytoplankton was generally higher than those allocated into the other fractions (i.e., lipid, polysaccharide and protein) for the five lakes. It ranged from 23.9% to 64.2% among the lakes under natural solar radiation (i.e., ambient UVB treatment), with an overall average of 46.1 ± 8.3% and median of 48.3% (Table 2-6). Clear Lake had the lowest average, which was below 40%. Meanwhile, percent ^{14}C into LMW averaged between 40 and 50% for Meretta and North lakes and a little over 50% for Small and Tern (Table 2-6). For North Lake, percent carbon in LMW was generally higher by 1.2-fold at 50%E_0 compared to surface irradiance levels in the ambient UVB treatment (3-way ANOVA, Irradiance effect: $p < 0.001$; Fig. 2-8a). Meanwhile, the relative proportion of carbon allocated into LMW did not change significantly between the four irradiance treatments under natural UVB levels for Clear, Meretta, Small and Tern lakes (Fig. 2-9). The only exceptions were at 6%E_0 after 12 h for Small Lake where proportions were on average 44.4 ± 2.4% at 6%E_0 and just over 50% for the other irradiance levels (3-way ANOVA, Irradiance effect: $p = 0.360$; E * UVB * T: $p = 0.009$; Fig. 2-9c) and also at 25%E_0 after 2 h for Tern Lake where proportions were 60.0 ± 5.2% at 25%E_0 and near 50% for the other irradiance levels (3-way ANOVA, Irradiance effect: $p = 0.007$; I * UVB * T: $p = 0.059$; Fig. 2-9d).

The proportion of ^{14}C into LMW generally increased with exposure to enhanced UVB for all five lakes, but the UVB effect was usually dependent on the irradiance treatment and/or the time of incubation. For North Lake, percent carbon into LMW was not significantly affected by enhanced UVB after 2, 8 and 12 h of incubation under both 50%E_o and 100%E_o (Fig. 2-8a). However, it increased significantly by 1.3-fold at both irradiance levels after 4 h incubation and decreased to 0% at 100%E_o only after 24 h incubation with exposure to enhanced UVB (3-way ANOVA, UVB effect: $p = 0.008$; UVB * T: $p < 0.001$; UVB * E: $p = 0.006$; Fig. 2-8a). For Clear Lake, the relative allocation of carbon into LMW was significantly higher under enhanced UVB levels after 5 h incubation in all irradiance treatments (3-way ANOVA, UVB effect: $p < 0.001$; Fig. 2-9a). Enhanced UVB also increased percent ^{14}C into LMW at all irradiance levels for Meretta Lake, especially after 8 h incubation where percentages were about 1.5-fold higher under enhanced UVB at ≥ 25%E_o, but only 1.1-fold higher at 6%E_o (3-way ANOVA, UVB effect: $p < 0.001$; UVB * E * T: $p = 0.011$; Fig. 2-9b). For Small Lake, the proportion of carbon allocated to LMW also increased with exposure to enhanced UVB by an overall of 1.1-fold after 2 h and 6 h incubations and increased by about 1.2-fold at ≤ 50%E_o (but not at 100%E_o) after 12 h incubation (3-way ANOVA, UVB effect: $p < 0.001$; UVB * T * E: $p = 0.009$; Fig. 2-9c). For Tern Lake, enhanced UVB significantly increased the relative amount of carbon allocated to LMW by 1.2-fold at 100%E_o only after 2 h incubation and by 1.1-fold overall after 8 h incubation (UVB effect: $p < 0.001$; UVB * T * E: $p = 0.059$; Fig. 2-9d).

ii) Lipid

Percent carbon allocated into lipid ranged from 16.0% to 33.8% among the five lakes under natural UVB levels, with an overall average of 21.4 ± 3.5% and median of 20.9% (Table 2-6). Clear lake had the lowest average, which was below 20%.

Meanwhile, percent ^{14}C fixed into lipid averaged around 20% for Meretta, Small and Tern lakes and 25% for North Lake (Table 2-6). Variations in irradiance levels in the ambient UVB treatment did not have a significant impact on the relative proportion of carbon allocated into lipid for all five lakes (Table L-1; Fig. 2-8b and 2-10).

The proportion of carbon fixed into lipid was not affected with exposure to enhanced UVB in all irradiance treatments for Clear and Meretta lakes (Fig. 2-10a, b). There were also no effects of enhanced UVB on percent lipid at all irradiance levels for Small Lake, except for a slight decrease by UVB of 1.1-fold average after 6 h incubation (3-way ANOVA: UVB: $p = 0.216$; UVB * T: $p = 0.021$; Fig. 2-10c). For North Lake, enhanced UVB did not have an impact on the lipid fraction on the first 4 hours of incubation but significantly increased percent lipid between 1.4- to 2.5-fold thereafter (3-way ANOVA, UVB: $p <0.001$; UVB * T: $p < 0.001$; Fig. 2-8b). Percent lipid also increased significantly by an overall of 1.1-fold from 20.7 ± 1.2% to 23.2 ±2.7% for Tern Lake, regardless of the incubation time and irradiance levels (UVB: $p < 0.001$; Fig. 2-10d).

iii) Polysaccharide

Percent carbon allocated into polysaccharide ranged from less than 1.0% to 29.7% among the five lakes under natural solar radiation, with an overall average of 14.3 ± 5.7% and median of 13.4% (Table 2-6). Percent ^{14}C fixed into polysaccharide averaged between 10 and 15% for Meretta, North, Small and Tern lakes, while it was over 25% for Clear Lake (Table 2-6). Under ambient UVB, percent carbon into polysaccharide was similar between the two irradiance levels (i.e., $50\%E_o$ and $100\%E_o$) for North Lake (3-

way ANOVA: Irradiance effect: $p < 0.001$; E * UVB: $p < 0.001$; Fig. 2-8c) and between all irradiance levels for Small Lake at all times (3-way ANOVA, Irradiance effect: $p = 0.011$; E * T * UVB: $p = 0.001$; Fig. 2-11c). Meanwhile, the proportion of carbon allocated into polysaccharide increased linearly from 6%E_o to 50%E_o, but decreased again under full ambient sunlight (i.e., 100%E_o) for Clear Lake (2-way ANOVA: Irradiance effect: $p < 0.001$; Fig. 2-11a). Percent carbon into polysaccharide was usually slightly higher at 25%E_o relative to the other irradiance levels during the experiment for Meretta Lake in the ambient UVB treatment (Irradiance effect: $p < 0.001$; Fig. 2-11b). For Tern Lake, percent carbon into polysaccharide was generally higher in the highest irradiance treatments (i.e., ≥ 50 %E_o) compared to the lowest irradiance treatments (i.e., 6 and 25%E_o) for both incubation times under ambient UVB levels (Irradiance effect: $p = 0.073$; E * UVB: $p = 0.022$; Fig. 2-11d).

Percent ^{14}C into polysaccharide usually decreased with exposure to enhanced UVB, depending on the length of exposure and/or irradiance treatments. For Meretta Lake, percent carbon allocated into polysaccharide decreased significantly at 6%E_o and 100%E_o (down to about 0%) only after 2 h incubation and decreased between 1.5- to 2.5-fold at ≥ 25%E_o (but not 6%E_o) after 8 h incubation (3-way ANOVA. UVB: $p < 0.001$; UVB * T * E: $p = 0.010$; Fig. 2-11b). For North Lake, there were no significant UVB effects after 2 and 4 h incubations, but enhanced UVB levels significantly decreased percent ^{14}C into polysaccharide to 0% under full sunlight (i.e., 100%E_o) and by 1.5- to 2.0-fold at 50%E_o after 8, 12 and 24 h incubations (UVB effect: $p < 0.001$; UVB * T: $p < 0.001$; Fig. 2-8c). Enhanced UVB decreased the proportion of carbon allocated into polysaccharide by 1.4-fold at 100%E_o only after 2 h for Small Lake, but no significant effects of UVB were observed thereafter at all irradiance levels (UVB effect: $p = 0.760$; UVB * E * T: $p = 0.001$; Fig. 2-11c). For Tern Lake, percent C into poly decreased by an overall of 1.6-fold in the highest irradiance treatments (i.e., 50% and 100%E_o) from 13.8 ± 2.1% under ambient UVB to 8.9 ± 3.3% under enhanced UVB, but not at 6% and 25%E_o throughout the experiment (UVB effect: $p< 0.001$; UVB * E: $p = 0.022$; Fig. 2-11d). Meanwhile, For Clear Lake, percent ^{14}C into polysaccharide increased by 1.1-fold under full sunlight (i.e., 100%E_o) only from exposure to enhanced UVB for Clear Lake (UVB effect: $p = 0.094$; UVB * E: $p = 0.007$; Fig. 2-11a).

iv) Protein

Percent carbon allocated into protein ranged from 7.5% to 41.7% among the five lakes under natural irradiance levels, with an overall average of 18.2 ± 5.3% and median of 17.7% (Table 2-6). Percent ^{14}C fixed into protein averaged between 15 and 20% for Meretta, Small and Tern lakes while it was a little over 20% for Clear and North lakes (Table 2-6). Between the four irradiance treatments under natural UVB levels, percent carbon into protein decreased from 6%E_o to 50%E_o, but then increased again at 100%E_o (Irradiance: $p < 0.001$) for Clear Lake (Fig. 2-12a). Meanwhile, percent carbon into protein was highest at 100%E_o compared to the other irradiance levels for Meretta Lake (Irradiance effect: $p = 0.010$; Fig. 2-12b) and compared to 50%E_o for North Lake (Irradiance effect $p < 0.001$; Fig. 2-8d) at all times under ambient UVB. Generally, there was no difference between the irradiance treatments on percent ^{14}C into protein at all times for Small Lake, except for higher proportions at 6%E_o after 12 h (Irradiance effect: $p = 0.405$; Fig. 2-12c). For Tern Lake, the proportion of carbon incorporated into protein was slightly lower at 25%E_o and 50%E_o compared to 6%E_o and 100%E_o at all times (Irradiance effect: $p = 0.017$; Fig. 2-12d).

The relative allocation of carbon to protein generally decreased with exposure to enhanced UVB in all five lakes. For Small Lake, percent carbon into protein decreased by an overall of 1.4-fold under enhanced UVB conditions at all irradiance levels throughout the experiment (UVB: $p < 0.001$; Fig. 2-12c). For Clear Lake, percent ^{14}C into protein decreased with UVB at all irradiance levels, but only a little (by 1.1-fold) at 6%E_o (UVB: $p < 0.001$; UVB * E: $p = 0.056$; Fig. 2-12a). Enhanced UVB also decreased percent carbon allocated into protein for Meretta Lake by about 2-fold at $\geq$ 25%E_o (from an average of 17.3 ± 4.3% under ambient UVB to 8.2 ±1.0% under enhanced UVB) and by 1.3-fold at 6%E_o (from 14.5 ± 1.5% to 11.1 ± 2.3%; UVB effect: $p < 0.001$; UVB * E: $p < 0.001$; Fig. 2-12b). For North Lake, no UVB effects were observed after 2 h incubation, but percent ^{14}C into protein decreased significantly with UVB between 1.4 to 2.0-fold during the rest of the experiment at both irradiance levels (UVB effect: $p <0.001$; UVB * T: $p < 0.001$; Fig. 2-8d). There were also no UVB effects detected after 2 h of incubation for Tern Lake, but percent carbon into protein decreased at all irradiance levels from an average of 17.1% under ambient UVB down to 11.1% under enhanced UVB after 8 h incubation (UVB: $p < 0.001$; UVB * T: $p = 0.003$; Fig. 2-12d).

Discussion

Arctic lakes and UVB

Aquatic ecosystems, particularly at high latitudes, have been experiencing changes in their underwater UVR associated with stratospheric ozone depletion (e.g., Smith *et al.* 1992; Kerr and McElroy 1993; Madronich *et al.* 1998) and climate-related changes in spectral UVR attenuation in the water column (Schindler *et al.* 1996; Vincent and Pienitz 1996; Pienitz and Vincent 2000). The penetration of UVR into freshwater lakes is controlled primarily by the concentration of colored dissolved organic matter (CDOM) in the water (e.g., Scully and Lean 1994; Morris *et al.* 1995; Laurion *et al.* 1997; Lean 1998a,b). Most lakes in the High Arctic have low DOC levels and thus great penetration of UVR. Mean DOC (± SD) for the nine high Arctic lakes in this study was 1.6 ± 0.5 mg L^{-1} (Table 2-3), which is similar to values found in other parts of the Arctic. For instance, the median DOC was found to be 1.8 mg L^{-1} for 25 lakes above the treeline in Finnish Lapland (northern Scandinavia; Rautio and Korhola 2002a,b) and 2.4 mg L^{-1} for 13 Arctic tundra lakes near Contwoyto Lake (Northwest Territories, Canada; Pienitz *et al.* 1997).

Since the lakes in this study and many other Arctic lakes have DOC values near or below 2 mg L, they would be the most susceptible to changes in UVR penetration with minor variations in DOC levels caused by climate warming (Vincent *et al.* 1998; Pienitz and Vincent 2000; Perin and Lean 2004), which would have large implications on the planktonic organisms of these lakes. Relationships between the depths of 1% integrated UVB as a function of DOC have shown that the depth of 1% UVB increase exponentially with decreasing DOC when levels are below 4 mg L^{-1}, with very high UVB penetration below the inflection curve at DOC levels near 2 mg L^{-1} (Schindler *et al.* 1996; Lean 1998a; Perin and Lean 2004). Therefore, for lakes that have DOC concentrations near or below 2 mg L^{-1}, both UVB and UVA can penetrate to several meters in depth within the water column (Schindler *et al.* 1996; Laurion *et al.* 1997; Fig. J-1). From paleo-ecological reports, shifts in vegetation and hydrology caused by warming or cooling trends have been shown to affect the quantity of DOC exported from catchments to the receiving waters, thus affecting underwater UVR penetration (e.g., Leavitt *et al.* 1997, 2003; Pienitz and Vincent 2000; Ponader *et al.* 2002; Saulnier-Talbot *et al.* 2003). For Arctic freshwaters, climate change may decrease or increase DOC levels, depending on the local change in tropospheric temperatures and the landscape surrounding the bodies of water (Perin and Lean 2004).

In this study, the depths of 1% integrated UVB estimated from DOC concentrations for all nine lakes were close to their respective mean or maximum depth (Table 2-1 and 2-3). This would indicate that UVB radiation is essentially present throughout the entire water column or within great portions of the water column. This would also be true for many Artic lakes since most are shallow systems. For instance, the mean maximum depth is 5.1 m for 98 lakes in Northern Finland (Blom *et al.* 1998) and the maximum depth is less than 12 m for over 160 lakes in Canadian Arctic Archipelago (Hamilton *et al.* 2001).

Lakes in the High Arctic are usually covered with thick ice for more than 8 months of the year, with ice melting starting around May or June (Schindler *et al.* 1974a; Welch 1974). Accordingly, it would be assumed that planktonic organisms are well protected from UVR exposure prior to ice break-up in the spring when stratospheric ozone depletion is highest. However, because the overlying ice in lakes and rivers generally contain less colored, less complex and lower molecular weight organic molecules, ultraviolet diffuse attenuation coefficients have been shown to be 8 times lower in the ice relative to the underlying waters (Belzile *et al.* 2002). This could cause organism trapped near the surface to experience high exposure to UVR prior to ice break-up, depending on the type of ice (clear or white) and the degree of snow (Belzile *et al.* 2001, Vincent and Belzile 2003). Moreover, earlier melting of snow and/or ice expected from climate warming could radically influence the below-ice UV penetration in arctic waters and be especially stressful for the biota by occurring during their critical growth phase in the spring when water temperatures are still cold and UV flux and ozone depletion are highest (Perin and Lean 2004).

In this study, UVB levels were usually increased by more than twice the natural solar value in the enhanced UVB treatment for all experiments. This would represent an extreme treatment and far in excess of current losses to the ozone column for this location and time of year (Frederick 1997). Such enhancement has also been used in previous studies (e.g., Arts and Rai 1997; Chatila *et al.* 2001; Forster and Schubert 2001) and was chosen deliberately here in order to identify, in term of photosynthesis, which phytoplankton populations, size classes and photosynthetic main macromolecular end-products fractions were most sensitive from exposure to enhanced UVB under different irradiance regimes (i.e., at 6, 25, 50 and 100% of surface irradiance or E_o). It is interesting to note that most of the UVB levels measured in the enhanced UVB treatments (especially for those measured in the $\leq$ 50%E_o radiation treatments) were within the range found for ambient solar UVB levels treatments (Appendix K). However, the constant intensity provided by the UVB lamps greatly altered the ratios of UVB to UVA and UVB to PAR, especially on cloudy/foggy days and in the evening or at night when natural UVB levels were lower. This can lead to increased damage to organisms by disrupting the repair mechanisms. More specifically, short wavelengths in PAR- (i.e., blue light) and/or UVA-stimulated repair processes (called photoreactivation or photoenzymatic repair, which is the light-dependent repair mechanism) may not be induced at sufficiently rapid rates to counteract damages by UVB (Karentz 1994). This would especially be important for aquatic organisms that rely mainly on this type of repair mechanism compared to the dark (light-independent) repair mechanisms (e.g., nucleotide excision repair and SOS repair).

Phytoplankton Productivity

Phytoplankton in High Arctic lakes are subjected to abrupt changes in light and UVB levels due to rapid break up and removal of the ice in late spring or early summer. Under these conditions, they must adapt not only to high irradiance levels but also to high UVR levels that can fluctuate greatly (from near 0 to maximum UVB doses) within a period of weeks. During the ice-free period, Arctic lakes are also exposed to extreme weather conditions ranging from warm cloudless sunny days to windy cold snowy days, with periods of fog and/or rain in between. With the added stress of cold-water temperatures and low nutrients in High Arctic lakes, phytoplankton in high Arctic lakes are then living under extreme adverse conditions.

Phytoplankton productivity rates are extremely low in Arctic and sub-Arctic lakes. In this study, volumetric photosynthetic rates and chlorophyll-specific photosynthetic rates (P^B) were ≤ 0.7 µg C L^{-1} h^{-1} and ≤ 1.1 µg C µg Chl a^{-1} h^{-1}, respectively, for all nine lakes under natural solar radiation (i.e., with no artificial UVB enhancement). These values are similar to those found in other Arctic (e.g., Kalff and Welch 1974; Perin 1996; Markager *et al.* 1999; Chapter 1) and sub-Arctic (e.g., Milot-

Roy and Vincent 1994; Laurion and Vincent 1998) lakes, but lower than typical values for temperate oligotrophic lakes, which can range from 2 to 12 μg C L^{-1} h^{-1} over the summer; Perin *et al.* 1996; Ferguson 1998). Markager *et al.* (1999) showed that light-saturated photosynthetic rate and other photosynthetic parameters were 3- to 6-fold lower in Arctic lake phytoplankton in comparison with other low temperature communities (e.g., marine algae from polar oceans, sea ice algae and algal cultures over the same low-temperature range) possibly because of severe nutrient stress and the persistence of non-active pigments in cold water.

Phytoplankton Chl *a* concentrations were also low in this study and averaged 0.50 ± 0.39 μg L^{-1} when combining data from all nine lakes (Table I-1; Fig. K-1). This value is similar to the mean Chl *a* of 0.55 ± 0.70 μg L^{-1} found by Hamilton *et al.* (2001) from a survey of 204 lakes from the Canadian Arctic Archipelago. Schindler *et al.* (1974b) suggested that the low nutrients levels, mainly phosphorus, in high arctic lakes is responsible for low phytoplankton biomass since Meretta Lake had higher Chl *a* levels than Char Lake during the period when Meretta Lake was receiving significant inputs of nutrients from sewage effluents and also when phytoplankton biomass increased with enrichment in phosphorus or phosphorus + nitrogen (but not with nitrogen only) during a 4-week experiment in Char Lake.

In this study, the lakes showed different responses to changes in irradiance levels under natural conditions (i.e., with no artificial UVB enhancement). Photosynthesis was inhibited by 15 to 50% at $\geq$50% surface levels in phytoplankton populations from deeper lakes (i.e., Char, Meretta, North, Small and Resolute lakes) when radiation levels were generally higher than 300-500 μmol photons m^{-2} s^{-1} (Fig. 2-3a and 2-4c,e,f;g; Table

G-1). Kalff and Welch (1974) also showed inhibition of photosynthesis for both Meretta and Char lakes when exposed to solar radiation >300 μmol photons m^{-2} s^{-1} and found that the depths of maximum photosynthetic rate were generally between 7 and 20 m for Char Lake. Their results would suggest that maximum photosynthetic rates occurred between 6 to 37% of surface irradiance for Char Lake, consistent with findings from this study where rates were highest at 6%E_o and 25%E_o for Char Lake (Fig. 2-4c).

On the other hand, for the shallower lakes (i.e., Barren, Black Char, Clear and Tern lakes), no significant inhibition of photosynthesis was found with exposure to surface solar radiation levels. For instance, the photosynthetic rates of phytoplankton populations from Tern Lake were similar among the four solar irradiance treatments, although the levels ranged from about 60 μmol photons m^{-2} s^{-1} at 6%E_o to over 800 μmol photons m^{-2} s^{-1} at 100%E_o (Fig. 2-4h; Table G-1). Neale *et al.* (1998c) also found that Antarctic marine phytoplankton assemblages from shallower mixed layers were generally more tolerant to UVR. Since UVR and high PAR are present throughout most of the water column, phytoplankton populations in these clear shallow lakes are not able to seek refuge and may have developed other survival strategies (e.g., production of photoprotective compounds) to cope with these conditions in comparison to phytoplankton populations from deeper lakes than can avoid high PAR and/or UVR and repair photodamages at greater depths.

Although phytoplankton populations from these shallow clear lakes showed more tolerance to high PAR and/or natural UVR levels than the deeper lakes, they did not have, however, an increased tolerance to enhanced UVB levels. Photosynthetic rates of phytoplankton populations from all nine lakes, except Barren Lake, were significantly inhibited (by 15 to 95%) with exposure to artificial UVB enhancement (Fig. 2-3a and 2-4). For Barren Lake, total productivity decreased by an average of 4% and 37% with exposure to enhanced UVB levels after 2 and 8 h of incubation, respectively. However, the UVB effect was not significant due to the high variability within each treatment, especially during the first 2 h of incubation. Barren Lake probably represents one the least productive lakes in this region as shown by its extremely low metabolic rate (Welch 1974) and by having one of the lowest phytoplankton productivity rates and lowest nutrient and Chl *a* levels relative to the other studied lakes in this study (Table I-1; Fig. 2-4a), with very little zooplankton present within the water column (pers. obs.).

The inhibitory effects of UVB usually depended on the time of incubation and irradiance treatments. The kinetics of photoinhibition by UVB generally decreased with decreasing radiation levels. When compiling data from all nine lakes, enhanced UVB significantly diminished photosynthesis after 2 h of exposure from an average of almost 40% at surface irradiance levels down to an average of 1.6% inhibition (not significant) at 6%E_o (Table 2-7). Meanwhile, after 8 h of incubation, exposure to enhanced UVB levels resulted to near 65% inhibition of photosynthesis at ≥ 50% of surface irradiance down to about 16% inhibition at 6%E_o (Table 2-7).

Although there was strong variability between the nine lakes, UVB significantly inhibited phytoplankton photosynthesis in the enhanced UVB treatment at 25%E_o levels by an average of 10% and 40% after 2 h and 8 h of incubation, respectively (Table 2-7). Throughout this study, UVB levels at 25%I_o in the enhanced UVB treatments average 0.3 ± 0.1 W m^{-2}, which were generally similar to UVB levels at 50%I_o in the ambient UVB treatment (i.e., mean of 0.3 ± 0.2 W m^{-2}; Table K-1), although the UVB-to-longer-wavelengths ratios were different. These values are similar to that found by Helbling *et al.* (2001b) where the threshold for inhibition of photosynthesis was about at 0.3 W m^{-2} for UVB, below which no inhibiton was detected for phytoplankton populations of Lake Titicaca (Bolivia). Using DOC-derived equations from Scully and Lean (1994), the depths of 50% and 25% surface UVB levels were estimated to be on average 0.6 and 1.3 m respectively for the studied lakes. This would represent a significant portion of the water column, especially in the shallow lakes. However, phytoplankton populations from these shallow lakes may be better adapted to withstand UVB levels at these depths, especially under natural UVB levels, since no significant inhibition were detected at solar UVB levels at 50%E_o (i.e., around 0.3 W m^{-2}; Fig. 2-4).

Significant inhibition of photosynthesis by UVB near the surface (under natural or enhanced UVB levels) has been demonstrated in many studies (e.g., Moeller 1994; Boucher and Prézelin1996; Furgal and Smith 1997), with diminishing UVB effects as levels decrease with depth (e.g., Behrenfeld *et al.* 1993; Nielsen and Ekelund 1995; Helbling *et al.* 1993, 2001a, b; Villafañe *et al.* 1999). For example, a short-term (< 4 h) *in situ* experiment by Perin (1996) showed more than 57% inhibition in productivity rates of phytoplankton populations incubated at surface solar radiation levels in a high Arctic lake on Prince Patrick Island, with no significant inhibition at 2 m (Nunavut, Canada; Perin 1996). In this study, generally more than half of the photosynthetic inhibition by enhanced UVB was realized within the first 2 hours at 100% exposure levels, while little or no significant inhibiton was attained at 6% of surface irradiance during the same duration of incubation (Fig. 2-4; Table 2-7). Rapid kinetics of photosynthetic inhibition by UVB have also been observed by Marwood *et al.* (2000) and Hiriart *et al.* (2002) for phytoplankton populations of Lake Erie exposed to natural surface UVB levels.

Several studies have indicated that, for equal doses of UVB, a relatively short exposure to high UVB levels is more damaging to photosynthesis than a longer exposure to lower UVB levels (Cullen and Lesser 1991; Cullen *et al.* 1992; Lesser *et al.* 1994; Neale 2000) since the damage incurred can exceed the capacity of photoprotective and repair processes at high UVB fluence rate (i.e., UVB dose received per given time; Neale 1987). Given that enhanced UVB levels were generally more than twice those of natural solar levels in my study, the rate of damage was most likely occurring too fast in relation to the rates of repair, especially by the light-dependent repair mechanisms, considering that UVB-to-longer wavelengths were greatly altered. More photosynthetic inhibition was generally observed as the time of incubation progressed, further implying that UVB-induced damage accumulated and exceeded repair mechanisms. This is further demonstrated with the observations that, after 24-h exposure to enhanced UVB levels, photosynthetic rates of phytoplankton populations from North Lake were near 0 suggesting that most cells were probably no longer viable (Fig. 2-2).

Since most UVB studies on phytoplankton productivity (including this one) have been derived from static incubations, the interpretation of the results from these studies may involve some degree of uncertainty and may not be representative of what would actually happen in a system where natural mixing regimes change the amount and duration of exposure to UVR and where UV levels would greatly vary in time and space within the water column. Depending on the mixing rates and depth of the mixed surface layer, the inhibitory effects of UVB on phytoplankton photosynthesis could be diminished or aggravated relative to those calculated under static incubations conditions.

In shallow Arctic systems with mixing conditions within the photic zone (like Barren, Black Char, Clear, Tern lakes) and where refuge from UVR is not possible, there could be an increase in inhibition of photosynthesis and in the total number of cells damaged from exposure to moderate increases in UVB levels as compared with static incubations (Neale *et al.* 1998b). On the other hand, the opposite could also be true if these populations have already been selected to adapt or adjust to such levels (but not necessarily to extreme UVB enhancement like those used in this study). For deeper lakes like Char, North and Resolute lake that have greater mixing depths, vertical mixing could lessen inhibition of photosynthesis since phytoplankton populations have the possibility to avoid harmful UVB levels and/or repair damages at lower depths and the deep phytoplankton can contribute a large portion of the water column-integrated photosynthesis, as shown for Char Lake (Kalff and Welch 1974).

However, the predicted increased in tropospheric temperatures from climate change could lead to the formation or increase the frequency of near-surface thermoclines during periods of high solar surface radiation and calm winds in arctic lakes. These thermoclines can then retain phytoplankton under high irradiance levels for periods of time and, consequently, increase the severity of UVR effects (Milot-Roy and Vincent 1994; Xenopoulos *et al.* 2000). In nature, inhibiton of water-column productivity of phytoplankton by UVB would then be more likely influenced by water mixing regime, water clarity, wind speed, and sky conditions than stratospheric ozone depletion alone since these factors would all affect the dosage rate (the irradiance received by phytoplankton) and the duration of exposure to harmful levels within the water.

Furthermore, recovery of phytoplankton populations from exposure to UVB would also depend on the efficiency of the photoprotective and/or repair processes available, the depth of the mixed layer, the rate of mixing and the kinetics of damage.

Cell size and photosynthetic inhibition by UVB

For this study, the picoplankton (i.e., cells of size 0.2 – 2 μm) and nanoplankton (i.e., cells of size 2 – 20 μm) contributed the most to total photosynthetic rates in all nine lakes, with each fraction that accounted for an average ≥ 35% of the total carbon fixed under natural solar radiation levels (Table 2-5). Meanwhile, the netplankton fraction (i.e., cells of size > 20 μm) contributed the least (≤ 31%) to total phytoplankton productivity rates in all nine lakes. These results are similar to findings from other Arctic lakes (Perin 1994; Chapter 1) and sub-Arctic lakes (Laurion and Vincent 1998). This would confirm that small phytoplankton are generally common in oligotrophic systems (including those encountered in the Arctic) since their high surface-to-volume ratio allows a more efficient transport of nutrients under low nutrient levels. Depending on the lake, duration of exposure and irradiance treatment, the effects of artificial UVB enhancement on the relative photosynthesis of each cell size fraction were highly variable in this study. Even under natural solar radiation, no consistent trends were found between the relative contributions of each cell size fraction and percent variation in surface irradiance levels (Fig. 2-3, 2-5, 2-6 and 2-7).

The proportion of carbon fixed by picoplankton did not change with exposure to enhanced UVB levels for five of the nine lakes. Meanwhile, for the other four lakes, exposure to enhanced UVB levels decreased the relative contribution of picoplankton to productivity, depending on the exposure time and/or irradiance treatments. For nanoplankton, its relative contribution to photosynthesis did not change between the two UVB treatments for five of the lakes. Meanwhile, for the other lakes, it generally increased in two lakes but decreased after 8-h of exposure in Black Char Lake and Meretta Lake under enhanced UVB conditions. On the other hand, more consistent findings were found in relation to the netplankton fraction. Exposure to enhanced UVB levels generally increased the proportion of carbon incorporated by netplankton for all studied lakes, except for Resolute Lake. Changes in the relative productivity of netplankton generally negatively correlated with the relative productivity of picoplankton and a little with the relative productivity of nanoplankton (Table L-2).

It is quite possible that larger phytoplankton, especially those greater than 20 μm, generally showed more photosynthetic tolerance to enhance UVB in this study since they may have sustained less damage to their cellular components (e.g. DNA and photosynthetic pigments) given their size and surface-volume ratios that may have afforded a better degree of protection to sensitive targets, notably the nucleus (Karentz *et al.* 1991a). Furthermore, the presence of photoprotective compounds such as MAAs may have been able to confer more protection in the big cells compared to the small cells, although this was not verified. Inhibition by UVB on photosynthesis is believed to occur primarily through inactivation of photosystem II reactions centers, deterioration of associated proteins (e.g., D1 protein; Renger *et al.* 1989) and enzymes (e.g., RUBISCO; Herrmann *et al.* 1996; Lesser *et al.* 1996) and/or reduction in synthesis or destruction of photosynthetic pigments (e.g., Häder *et al* 1988; Döhler 1995, 1996, 1998; Lohmann *et al.* 1998). Although this was not studied, the phytoplankton populations from the studied lakes most likely sustained other cellular damage (e.g., DNA) in addition to damages to their photosynthetic apparatus from exposure to enhanced UVB levels, especially in the 100%E_0 treatment, given that they were generally exposed to more than a two-fold increase in UVB-to-PAR and UVB-to-UVA ratios. DNA damages may inhibit *de novo* synthesis of proteins (e.g., enzymes like RUBISCO) required for adequate functioning of the photosynthetic process (Buma *et al.* 2001b), which would further increase photosynthetic inhibition.

Earlier studies on a variety of marine phytoplankton have shown that cell size may determine the vulnerability of phytoplankton species for DNA damage accumulation, with smaller cells that usually sustain more UVR-induced DNA damage than larger cells (e.g., Karentz *et al.* 1991a; Jeffrey *et al.* 1996a; Boelen *et al.* 2000; Buma *et al.* 2001a, b). These authors suggested that small cells would be more sensitive to UVR due to their unfavourable surface area to volume ratios, little self-shading and the small effectiveness of screening pigments considering their low cell volume (e.g., Karentz *et al.* 1991a; Garcia-Pichel 1994). On the other hand, other studies have shown conflicting results when addressing photosynthetic inhibition. A number of these studies have found that small cells were generally more resistant than large cells (e.g., Helbling *et al.* 1992, 2001a,c; Milot-Roy and Vincent 1994; Laurion and Vincent 1998; Villafañe *et al.* 2004). However, these studies were based on treatments that excluded UVB or UVR, not on UVB levels that were enhanced.

In my study, picophytoplankton populations of all nine lakes consisted also mainly of cyanobacteria as indicated from epifluorescence microscopy. Although their relative photosynthesis was not inhibited in five lakes, it was more inhibited than that of the nano- and/or netplankton fractions in the four other lakes. Although cyanobacteria have been shown to display a wide range of protective strategies against UVR (e.g., Vincent 1999) and seemed to be more resistant to current solar UVB levels (e.g., Laurion and Vincent 1998; Kaczmarska *et al.* 2000), they may not necessarily be able to withstand enhanced UVB levels like those used in this current study.

Other short-term studies have also shown that small phytoplankton were equally or less tolerant to photosynthetic inhibition by UVB (Perin 1994; Perin 1996; Bracher and Wiencke 2000; Hiriart *et al.* 2002). For instance, *in situ* short-term assays on phytoplankton photosynthesis in two lakes of the Canadian High Arctic (Prince Patrick Island, Nunavut) showed that photosynthetic inhibition by natural solar UVB was generally not accompanied by any changes in the relative contribution of pico-, nano- and netplankton to total productivity, suggesting that all cell sizes were equally affected by ambient UVB levels (Perin 1996). Meanwhile, short-term incubation experiments on natural phytoplankton populations of Lake Erie by Hiriart *et al.* (2002) showed that the share of picoplankton to total production decreased with exposure to UVR, especially by UVB, while larger phytoplankton were generally less affected. Long-term studies (i.e., days to weeks) have also demonstrated a wide range of findings in relation to cell size and sensitivity to UVB (e.g., Bothwell *et al.* 1993; Mostajir *et al.* 1999a, b; Van Donk *et al.* 2001; Wängberg *et al.* 1996, 2001; Chapter 1).

Considering the inconsistent results among the nine lakes in this study (especially in relation to pico- and nanoplankton) and the strong variability between findings among the existing studies, it is evident that cell size alone is not the only factor determining the sensitivity of phytoplankton populations to UVB exposure. Other factors such cell characteristics (e.g., presence of setae, formation of colonies or chains, placement of organelles; DNA base and sequence, molecular composition of RNA, proteins and pigments), species-specific capability of photoprotective and repair mechanisms, previous light history, succession patterns, physiological state of the community, trophic-level interactions can also influence the final expression of UVB-induced damage on natural phytoplankton communities.

Photosynthetic carbon allocation in High Arctic lakes

Although the partitioning of photosynthetically fixed ^{14}C-labelled bicarbonate into low molecular weight (LMW) metabolites and macromolecules (lipids, polysaccharides and proteins) has been measured quite extensively for Arctic sea ice-algae (e.g, Smith *et al.* 1987, 1989, 1990, 1997; Smith and Herman 1992), patterns of intracellular photosynthate allocation by Arctic freshwater phytoplankton remained largely unknown. To my knowledge, no previous data exist on LMW and macromolecular labeling patterns by phytoplankton communities of Canadian High Arctic lakes, except for Two Basin Lake in Chapter 1.

Like for Two Basin Lake (Chapter 1), the LMW metabolites generally accounted for the largest pool of newly fixed carbon, with an average higher than 30% of carbon allocated into this fraction by phytoplankton assemblages of all five lakes under natural sunlight conditions (Table 2-6). The LMW fraction includes a mixture of biosynthetic intermediates including small sugars, amino acids and polypeptides. Although these metabolites are precursors for the synthesis of macromolecules, the LMW fraction still remain a constant fraction of total carbon fixed (Cuhel and Lean 1987b; Wainman and

Lean 1996; Perin *et al.* 2002). Several studies have found that the assimilation of carbon into the LMW fraction by phytoplankton was greater under low nutrient conditions (e.g., Konopka and Schnur 1981; Barlow 1982), which may be caused by the slow utilization rate of the intermediate precursors for the synthesis of macromolecules rather than a fast production rate of LMW metabolites (Madariaga 1992). For High Arctic lakes, the slow rate of macromolecular synthesis may be affected by the lack of appropriate nutrients (especially nitrogen) to synthesize the larger compounds and/or by the cold-water temperatures that slows down all metabolic and enzymatic activities, including those involved in the synthesis of macromolecules.

Many studies on cultured algae, Arctic sea ice-algae, and natural phytoplankton populations from temperate regions have observed that more carbon accumulated into storage products (polysaccharides and/or lipids) at the expense of protein synthesis under nutrient deficient conditions (e.g., Morris 1981; Harrison *et al.* 1990; Feuillade *et al.* 1992; Mock and Gradinger 2000). However, such relationship has generally failed to apply in freshwaters systems (e.g., Wainman and Lean 1992; Furgal *et al.* 1998; Perin *et al.* 2002). Here, despite the low nutrient levels in the lakes, the proportion of carbon allocated into protein was generally higher than that allocated into polysaccharides and similar or slightly lower than that allocated into lipids in this study. The mesocosm study at Two Basin Lake in Ellesmere Island (Nunavut, Canada) also showed that the proportion of carbon allocated into protein by phytoplankton populations was higher than those incorporated into lipid or polyssacharide (Chapter 1).

Other studies on temperate lakes have suggested that the fraction of carbon entering the polysaccharide pool would increase when daylength is shorter in order to fuel the necessary energy for metabolism and protein synthesis during the longer night period (Wainman and Lean 1996; Cuhel and Lean 1987b; Lean *et al.* 1989; Smith *et al.* 1990). Here, such relationship would not be applicable in the High Arctic since there is 24 h daylight during the summer. The relative amount of carbon allocated into polysaccharide was generally lower than those allocated in the other fractions for Meretta, North, Small and Tern lakes ($< 15\%$; Table 2-6; Bonferoni test, p's < 0.001) and also for Two Basin Lake (Ellesmere Island; Chapter 1). However, for Clear Lake, percent carbon allocation to polysaccharide was significantly higher (average of 27%) than those allocated into the lipid and protein fractions. These variations between lakes (1-way ANOVA: $p < 0.001$; Bonferoni test, p's < 0.001) show that there is no consistent trend with daylight period

Several studies on cultured algae and natural phytoplankton populations of temperate lakes have demonstrated that the proportion of carbon allocated into protein positively correlated with water temperature (Morris and Farrell 1971; Cuhel and Lean 1987b; Wainman and Lean 1996; Perin *et al.* 2002). Water temperature is believed to be an important factor regulating protein content and synthesis in phytoplankton since water temperature limits the maximum growth of phytoplankton (Eppley 1972) and protein synthesis may be closely related to phytoplankton growth (Morris 1981; Madariaga and Fernández 1990; Fernàndez 1992). In High Arctic lakes, the water temperatures generally do not exceed 4 °C in large lakes, but may rise > 4 °C in smaller lakes during the summer months (Welch 1974). Here, during the study period, the recorded water temperatures were lower than 4°C in all of the lakes. Accordingly, these cold temperatures would suggest very low protein synthesis by phytoplankton in these lakes.

Interestingly, percent carbon incorporated into protein averaged 18.2 ± 5.3% in this study when incubated under natural sunlight conditions. This value is similar to those found for temperate lakes during the summer months (e.g., Cuhel and Lean 1987b; Ferguson 1998; Furgal *et al.* 1998; Smith *et al.* 1998). For example, percent carbon incorporated into protein by phytoplankton populations from a lake in the Laurentides (Québec, Canada) averaged 20.2 ± 4.7% when water temperatures were about 22 °C (Perin *et al.* 2002) Other studies have also demonstrated that the positive relationship between protein synthesis and water temperatures does not always apply and found that the proportions of carbon incorporated into protein increased or showed no consistent trend with a decline in water temperatures (e.g., Morris *et al.* 1974; Priscu *et al.* 1987; Hawes 1990; Henderson *et al.* 1991; Thompson *et al.* 1992).

Many studies, including those on cultured algae (Morris *et al.* 1974), freshwater phytoplankton (Groeger 1986; Cuhel and Lean 1987b; Feuillade *et al.* 1992; Rai 1995; Maurin *et al.* 1995; Furgal *et al.* 1998; Perin *et al.* 2002), Arctic marine ice algae (Smith *et al.* 1987, 1989), Antarctic freshwater phytoplankton (Priscu *et a*l. 1987; Hawes 1990) and marine phytoplankton (Morris *et al.* 1974; Li *et al.* 1980; Smith and D'Souza 1993), have demonstrated that the protein synthesis or the proportion of carbon incorporated into protein was inversely proportional to light intensity (being highest at low irradiance levels). It is believed that this increase proportion of carbon fixed into protein at low irradiance levels may reflect the lower saturation level of radiation for protein synthesis than for total photosynthesis and the other metabolites (Morris *et al.* 1974; Cuhel and Lean 1987b; Hawes 1990; Rai 1995).

Here, the proportion of carbon that entered the protein pool did not show consistent trends with light variations under natural UVB levels. Percent carbon allocation into protein did not change between the 4 irradiance treatments for Small Lake, it was highest under full sunlight for North and Meretta lakes, and it was generally lowest at 25 and 50%E_o for Tern Lake (Fig. 2-8d and 2-12). Only Clear Lake generally showed a decrease in percent carbon into protein with increasing light levels, but increased again under full sunlight (Fig. 2-12a). Since the experiments were performed outside under natural sunlight conditions, surface radiation levels could have varied greatly depending on the weather conditions during the incubation period and, as a result, the radiation levels were not necessarily constant in each irradiance treatment as well as between lake experiments. However, the overall mean total irradiance levels during the study ranged from 45 ± 28 μmol photons m^{-2} s^{-1} at 6%E_o to 706 ± 455 μmol photons m^{-2} s^{-1} at 100%E_o (Table G-1), which is similar to the irradiance levels used in the literature (e.g., Cuhel and Lean 1987b). Considering the low photosynthetic performance of phytoplankton populations from lakes around Resolute as a result of low nutrients and water temperatures (Markager *et al.* 1999), findings from this study would suggest that the radiation level for saturation of protein synthesis may, in general, be similar to that of total photosynthesis and/or other macromolecules and may also be dependent on the phytoplankton community structure of a given lake.

In turn, several studies have showed that the decrease in the proportion of carbon incorporated into protein with increasing light intensity appeared to be offset by an increase in the proportion of carbon allocated into lipid and/or polysaccharide (e.g., Morris *et al.* 1974; Priscu *et al.* 1987; Feuillade *et al.* 1992; Perin *et al.* 2002). It is believed that an increase in storage products occurs after protein saturation, when excess fixed carbon and energy (derived from photosynthesis) are available (Konopka and Schnur 1980). In this study, the proportion of carbon incorporated into lipids did not change significantly between the 4 irradiance treatments for all five lakes (Fig. 2-8b and 2-10). Of all four fractions, the lipid fraction of carbon fixation was generally the one that varied the least throughout the study period, even with exposure to enhanced UVB levels (see below). A mesocosm study by Perin *et al.* (2002) has also showed that the lipid fraction remained the most conservative fraction compared to the other fractions, despite changes in nutrient levels, water temperatures, and phytoplankton biomass, production and species/size composition. The percent ^{14}C incorporated into lipids averaged between 18 to 26% in all five lakes (Table 2-6) under natural solar radiation, which are similar to values found for phytoplankton communities of Two Basin Lake (Chapter 1) and temperate lakes (Ferguson 1998; Perin *et al.* 2002).

Similar to the protein fraction, the proportions of carbon allocated into polysaccharide and LMW also showed no consistent trends with variations in solar radiation levels (Fig. 2-9 and 2-11), except for a slight increase in percent carbon allocated into polysaccharide with increasing radiation levels for Clear and Tern lakes only (Fig. 2-11a and d). Cuhel and Lean (1987b) also found no significant effects of light intensity on LMW and polyssacharide fractions for phytoplankton community of Lake Ontario. In turn, Konopka and Schnur (1981) showed an increase in relative polysaccharides incorporation and a decrease in the LMW and protein fractions with increasing irradiance when cultures of cyanobacteria were not nutrient limited, while all of these effects were abolished when the cultures were nutrient limited. Although environmental variables such as light, nutrients, and water temperature can control the metabolic pathways of phytoplankton, variations in the patterns of macromolecular synthesis in phytoplankton populations can also be dependent on the species and/or size composition (e.g., Amblard and Bourdier 1990; Madariaga and Fernández 1990; Madariaga 1992; Feuillade *et al.* 1992; Rai 1995), which in turn, could explain some of the discrepancies in results between the five lakes and also between the existing studies.

There is evidence that variations of the LMW fraction might be linked to some extent with changes and demands from the macromolecular classes (Perin *et al.* 2002). More specifically, it has been found that the proportion of carbon allocated to lipid, polysaccharide and/or protein negatively correlated with the allocation of carbon into LMW (Madariaga 1992; Wainman and Lean 1996; Ferguson 1998; Perin *et al.* 2002; Chapter 1). Here, under natural solar conditions, the proportion of carbon allocated into the LMW fraction was found to strongly negatively correlate with the proportion of carbon incorporated into protein for all five lakes, but its correlation with polysaccharide and lipid fractions varied between the lakes (Table L-3). However, when combining data from all lakes together, the LMW fraction strongly negatively correlated with all three fractions (Table L-3). This would confirm that the production of lipids, protein and/or polysaccharide was done at the expense of the LMW metabolites and/or intermediate precursors found in the LMW pool.

No significant correlation was found between percent carbon allocated into lipid and polysaccharide for each of the five lakes, but a strong inverse correlation was found between the two fractions when data from all five lakes were pooled together (Table L-3). Such correlation has also been found in marine phytoplankton (Madariaga 1992), Two Basin Lake (Chapter 1) and temperate lake (Perin *et al.* 2002). Here, the inverse trend between lipid and polysaccharide syntheses may be linked to differentiation in species composition between the lakes. According to Madariaga (1992), some phytoplankton species preferentially accumulate carbon into lipids while others mainly stored carbon into polysaccharides under similar environmental conditions.

Correlations between the protein fraction and the lipid or polysaccharide fractions varied greatly between the five lakes under natural UVB levels (Table L-3). Like LMW, it has been shown that lipids and/or polysaccharides can serve as the primary short-term storage products for protein synthesis (Cuhel and Lean 1987b; Priscu *et al.* 1987; Perin *et al.* 2002). However, storage products might also act as long-term product or consecutive component of the organisms (Priscu *et al.* 1987). Priscu *et al.* (1987) argued that the size and turnover rate of the metabolite pools need to be measured and other potential pathways of carbon assimilation need to be evaluated in order to truly understand the interaction between protein and specific storage products.

Photosynthetic carbon allocation and UVB effects

The effects of UVB on photosynthate allocation has received very little attention compared to its effects on photosynthetic rates in natural phytoplankton populations. Although UVB, even at current levels, has been shown to significantly inhibit photosynthesis (especially near the surface) in wide range of aquatic systems, very little is known in regards to the impacts of UVB on the relative allocation of carbon to the main macromolecular end-products of photosynthesis. UVB is well known to have numerous detrimental effects on the physiology of phytoplankton, such as decreasing energy income and growth, decreasing nutrient uptake, arresting cell division, and disrupting membrane integrity (e.g., Mitchell and Karentz 1993; Vincent and Roy 1993; Van Donk and Hessen 1995; Häder *et al.* 1998; Perin and Lean 2004). Therefore, any effects of UVB on the physiological state of phytoplankton could potentially influence *in situ* patterns of intracellular photosynthate allocation. UVB could also alter the relative proportion of carbon allocated to the main macromolecular end-products through its effects on photosynthetic extracellular release of organic carbon i.e., increase the proportion of dissolved organic carbon relative to the total carbon fixed, similar to the effects by high irradiance levels (e.g., Maurin *et al.* 1997). Thus, because UVB can have so many possible effects on phytoplankton at the molecular, cellular and physiological levels, it becomes difficult to predict the outcomes that UVB stress will have in relation to LMW and macromolecular labelling patterns.

If the growth and viability of the phytoplankton is threatened by UVB, then the effect of UVB on the major end-products may be seen more clearly in the protein fraction since protein synthesis is believed to be closely related to phytoplankton growth (Morris 1981; DiTullio and Laws 1983; Laws 1991; Madariaga 1992). Furthermore, UVB has been shown to inhibit the assimilation of inorganic nitrogen (NH_4^+ and NO_3^-), the activity of associated enzymes (e.g., nitrogenase), and the synthesis of specific amino acids (Döhler 1992, 1994, 1995; 1996; Behrenfeld *et al.* 1994, 1995; Goes *et al.* 1995a,b; Lohmann *et al.* 1998), which may specifically inhibit protein synthesis. In this study, the proportion of carbon allocated into protein decrease with exposure to enhanced UVB levels in all five lakes, with the most significant effects generally observed under high irradiance levels or longer exposure time (Fig. 2-8d and 2-12).

Many other studies have also shown that protein synthesis was inhibited by UVB or UVR (e.g., Jeffrey *et al.* 1996a; Arts and Rai 1997; Smith *et al.* 1998). For example, Visser *et al.* (1999) also observed that both protein and DNA synthesis was inhibited by about 30% when exposed to surface solar UVR in natural bacterioplankton populations of the Coastal Caribbean Sea. On the other hand, a study of UVR effects on photosynthate allocation by phytoplankton from Georgian Bay (Lake Huron) revealed no significant effect of natural or artificial UVB levels on the proportion of carbon allocated into protein from spring through fall (Furgal *et al.* 1998). Meanwhile, Buma *et al.* (1996) showed that the protein content actually increased with UVR exposure in diatom cultures, but decreased with further increases of UVR levels.

The synthesis and/or increased production of UV-protective compounds, such as mycosporine-like amino acids (MAAs; e.g., Karentz *et al.* 1991b; Xiong *et al.* 1997), have also been suggested to affect the relative allocation of carbon to main macromolecular end products by, for instance, temporarily diverting carbon from lipid and polysaccharide synthesis to the LMW pool, which includes amino acids. In this study, percent of total uptake into the LMW fraction increased when exposed to enhanced UVB levels in all five lakes, except for North Lake where UVB effects were not consistent (Fig. 2-8a and 2-9). This accumulation of carbon in the LMW fraction by phytoplankton in the studied lakes is more likely a consequence of lower or slower synthesis of polysaccharide and/or protein with exposure to enhanced UVB levels rather than UV-induced stimulation of MAAs synthesis, although this cannot be confirmed since MAAs were not measured. In the enhanced UVB treatment, the proportion of carbon allocated into LMW inversely correlated with the proportion of carbon allocated into protein and/or polysaccharide for all lakes, except for North Lake where it negatively correlated with lipid fraction (Table L-3). Döhler (1996) also found that, in addition to reduce the protein content, UVB exposure increased the amino acid contents (part of the LMW fraction) in cultures of marine diatoms.

The potential disruption of nitrogen assimilation by UVB might also have important implications on carbon allocation into storage products. More specifically, an accumulation of lipids and/or polysaccharides may be expected in UV-stressed phytoplankton (Hessen *et al.* 1997) since carbon allocation into storage products (lipids and polysaccharides) has been commonly shown to increase at the expense of protein synthesis under conditions of nitrogen limitation (Morris *et al.* 1985; Harrison *et al.* 1990; Madariaga and Joint 1992). In this study, the labelling pattern into lipids was generally insensitive to enhanced UVB for Clear, Meretta and Small Lake, but increased significantly for Tern and North lakes (Fig. 2-8b and 2-10). As for the polysaccharide synthesis, the proportion of carbon allocated into this fraction generally decreased in the enhanced UVB treatment for Meretta, North and Tern Lake, depending on duration of exposure and/or irradiance treatment, while enhanced UVB had little effect on allocation into polysaccharide for Clear and Small lakes (Fig. 2-8c and 2-11). Although they contribute little to the total pool, the polysaccharide class also include nucleic acids. Thus, it is possible that UVB-induced damages to DNA and/or inefficient capabilities of DNA repair processes may have been reflected in the polysaccharide fraction. Short-term incubation experiments by Smith *et al.* (1998) on Lake Ontario phytoplankton assemblages during the spring and summer also showed that carbon allocation to total lipids and among the major lipid classes (i.e., neutral lipids, glycolipids and phospholipids) was relatively insensitive to natural UVR levels while carbon allocation into polysaccharide was the most sensitive class to UVR stress. The intracellular carbohydrate content of the phytoplankton populations from the Coastal Caribbean Sea was also lower with exposure to natural UVB levels (Visser *et al.* 1999). Goes *et al.* (1996) found that the decline in the rates of production and pool sizes of neutral monosaccharides within the storage carbohydrate fraction were largely responsible for the decrease in the overall carbohydrate content in the cells of natural assemblages of marine phytoplankton.

Meanwhile, Furgal *et al.* (1998) generally found no significant effects of natural or artificial UVB levels on the proportion of carbon allocated into total lipids and polysaccharides by phytoplankton assemblages from Georgian Bay (Lake Huron), even during periods when total photosynthesis was inhibited by 80%. However, they observed some effects of UVB on allocation among the lipid classes i.e., mostly a stimulation in the allocation to phospholipids that may reflect repair of damaged membranes (specifically their unsaturated fatty acids). Several studies have shown that exposure to UVB reduced the levels of essential fatty acids in algae (e.g., Döhler and Biermann 1994; Wang and Chai 1994; De Lange and Van Donk 1997; Goes *et al.* 1994), which may have significant implications for nutrition and energy flow in both freshwater and marine ecosystems (Arts 1997). Here, because of their different chemical structure and function, there is the possibility that the various classes of lipid may have responded differently to enhanced UVB. However, their overall effects may not haven been detected on allocation to total lipids if they responded in complementary fashion.

Although variations in the UVB dose rate, length of exposure to UVB and/or extracting methods of the biochemical constituents may account for some of the discrepancy in the responses of the LMW and macromolecular pools to UVB exposure between studies, other factors such as species may also have contributed to the different findings among the existing studies and between the five lakes in this study. Short-term assays on three phytoplankton species by Arts and Rai (1997) showed that the effects of UVB on the allocation of carbon to the main macromolecular end-products were dependent on the UVB dosage rate, macromolecular classes and the time of exposure, but were also species-specific. Other studies on cultured phytoplankton have also shown differential responses to UVB between species in relation to the biosynthesis of macromolecular classes (e.g., Agrawal 1992; Wang and Chai 1994) and nitrogen uptake (e.g., Döhler 1996). It is also important to consider that photoinhibition by high PAR and/or ambient UVR levels may also have affected labelling patterns of LMW and macromolecules in my study, especially in the treatment exposed to full sunlight, making it harder to detect significant effects of UVB between the two treatments.

Conclusion

Photosynthetic rates of natural phytoplankton assemblages from the lakes in the vicinity of Resolute were quite low (below 1 μg C L^{-1} h^{-1}), probably as a result of their low water temperatures and nutrient levels (Markager *et al.* 1999). It is well known that exposure to UVB, even at ambient levels, can cause inhibition of photosynthesis in phytoplankton from all parts of the world. A summary of the overall effects of enhanced UVB on all the variables measured during this study is presented in Table 2-8. It was found that enhanced UVB levels, which were about twice above its natural levels (unweighted), caused inhibition of photosynthesis in all of the lakes, except for Barren

Lake. Barren Lake had high variability within each UVB treatment and extremely low productivity rates, which made it difficult to significantly detect any UVB effects. Photosynthetic sensitivity to enhanced UVB was usually depended on the irradiance treatment and the duration of exposure, with greatest photoinhibition during prolonged periods of exposure at surface levels (i.e., 100%E_o). However, the kinetics of inhibition by UVB was usually rapid, with more than 50% of the total photosynthetic inhibition attained within the first 2 hours of exposure at 100%E_o.

As a percent of total photosynthetic rate, the larger phytoplankton, especially those greater than 20 μm, were generally more tolerant to enhanced UVB levels than picoplankton in all of the lakes, except for Resolute Lake. These findings are not consistent with those found by several studies on photosynthetic inhibition, where small cells have been shown to be more resistant to solar UVR than large cells (e.g., Helbling *et al.* 1992; Laurion and Vincent 1998; Villafañe *et al.* 2004). However, results from this study are similar to those from most DNA studies, which have indicated more vulnerability to UVB by smaller cells compared to larger cells (e.g., Karentz *et al.* 1991a; Buma et al. 2001 a,b). Consequently, results from this study would suggest that the larger cells performed better photosynthetically under enhanced UVB conditions than smaller cells since they were probably more protected from these elevated UVB levels i.e., they might have sustained less damage to their photosynthetic apparatus, energy-harvesting enzymes, photosynthetic pigments and/or DNA, given their longer pathlength.

Results on the patterns of intracellular photosynthate allocation into the major end-products (i.e., LMW, lipid, polysaccharide and protein) from five of the lakes in this study have shown no consistent trends with changes in irradiance levels. These findings differ from most existing studies conducted elsewhere (i.e., marine phytoplankton, sea-ice algae, freshwater phytoplankton from temperate and Antarctic regions; e.g., Li *et al.* 1980; Cuhel and Lean 1987b, Priscu *et al.* 1987; Smith *et al.* 1989). Results from this study are also suggesting that the other observed relationships found in the literature between macromolecular labelling patterns and abiotic factors such as nutrients, water temperature or daylength (e.g., Morris *et al.* 1985; Cuhel and Lean 1987b; Harrison et al. 1990; Wainman and Lean 1996) may not be applicable for High Arctic freshwater phytoplankton populations considering their adaptation to adverse living conditions under cold water temperatures, low nutrient levels, and 24 h daylight during the summer months.

Exposure to enhanced UVB levels changed the labelling patterns of biosynthesis into LMW and macromolecular classes by phytoplankton assemblages in this study, although these changes were usually not consistent between the five lakes. The strongest effect of UVB was on protein synthesis, where the proportion of carbon allocated into protein decreased in samples exposed to enhanced UVB for all five lakes. This may be linked to a decrease in the growth and viability of phytoplankton (Morris 1981), inhibition of inorganic nutrient uptake and associated enzymes, and/or inhibition in the synthesis of specific amino acids (e.g., Döhler 1994, 1996; Behrenfeld *et al.* 1995) by UVB exposure. The proportion of carbon allocated into polysaccharides did not change or decreased with UVB exposure. Meanwhile, allocation into lipids usually did not change for three lakes when exposed to UVB, but increased for the other two lakes. As for labelling patterns of LMW, it usually demonstrated an increase with exposure to enhanced UVB, possibly as a result of a decrease in polysaccharide and/or protein synthesis by UVB. Variations in the effects of UVB on patterns of intracellular photosynthate allocation between the lakes may have been related to differences in phytoplankton community structure (size and/or species composition) and/or phytoplankton physiological status (i.e., previous light history, photoprotective and repair capabilities). Perin *et al.* (2002) have suggested that, although many biotic and abiotic factors can influence LMW and macromolecular labelling patterns, it is the interactions between all of these factors that will ultimately influence the direction of carbon flow and food quality of phytoplankton.

Overall, this study has shown that enhanced UVB can have strong effects on total phytoplankton productivity, size-fractionation of photosynthetic and carbon allocation into major end-products on phytoplankton communities from High Arctic lakes. However, it is acknowledged that results from these short-incubation experiments may not be applicable in nature, where the predicted increase in UVB levels from stratospheric ozone are lower and where many other factors such as UVB attenuation within the water column, water mixing regimes, trophic-level interactions, acclimation to UVB over time through UV defense mechanisms may influence the kinetics of damage by UVB. Because of their low DOC concentrations at around 2 mg L^{-1}, it is also important to consider that these lakes may undergo large changes in underwater spectral UVR with small variations in their DOC levels caused by climate change (Perin 2004), which could have great implications on their biota.

Table 2-1. Morphometric characteristics of the nine lakes. Lake area was estimated from topographical maps, unless stated otherwise.

	Area (km^2)	Depth (m)	
		Mean	Max.
Barren L.	0.38	n/a	7.5[b]
Black Char L.	0.15	n/a	4.2‡
Char L.	0.53[a]	10.2[a]	27.5[a]
Clear L.	0.18	n/a	2.0‡
Meretta L.*	0.20[c]	3.25[c]	9.0[c]
North L.	0.70[d]	5†	12.0[b]
Resolute L.	1.19[b]	8.3[b]	22.0[b]
Small L.	0.17	n/a	9.5[b]
Tern L.	0.60	n/a	3.6‡

* Applies for the upper basin only where samples were taken.

[a] Data from Schindler *et al.* 1974a.

[b] Data from Welch 1974.

[c] Data from Schindler *et al.* 1974b.

[d] Data from Markager *et al.* 1999.

† Estimates from 10 depth measurements and Markager *et al.* 1999.

‡ Deepest value observed

Table 2-2. Summary of all the ^{14}C experiments conducted during the study period. Shown are the dates at which the experiments were performed for all nine high Arctic lakes, the water depths used for each experiment, the UVB (ambient and enhanced) and irradiance (shown as percent surface irradiance [%E_o]) treatments used during each experiment, and whether or not size fractionation and carbon allocation of phytoplankton productivity were measured for each experiment.

	Date	Depth (m)	Incubation time (h)	UVB Treatment	Irradiance Treatment (%E_o)	Size Fract.	Carbon Alloc.
24-h exp.							
North L.	10 July	0.5 – 1.0*	3, 6, 12, and 24,	AMB, ENH	6, 25, 50 and 100%	no	no
North L.	9 August	0.5 - 12.0	2, 4, 8, 12, and 24	AMB, ENH	50 and 100%	no	yes
Barren L.	5 August	0.5 - 3.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	no
Black Char L.	7 August	0.5 - 4.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	no
Char L.	14 August	0.5 - 10.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	no
Clear L.	21 July	0.5 - 2.0	5 only	AMB, ENH	6, 25, 50 and 100%	yes	yes
Meretta L.	12 August	0.5 - 6.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	yes
North L.	1 August	0.5 – 9.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	no
Resolute L.	17 August	0.5 – 11.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	no
Small L.	28 July	0.5 – 5.0	2, 6, and 12	AMB, ENH	25, 50 and 100% for 2, 6 h; 6, 25, 50 and 100% for 12 h	yes	yes
Tern L.	3 August	0.5 – 3.0	2 and 8	AMB, ENH	6, 25, 50 and 100%	yes	yes

* Water samples were taken under the ice.

Table 2-3. Depth of 1% total incident light (mainly PAR), UVA and UVB of all nine high Arctic lakes generated from the downwelling diffuse attenuation coefficients of total irradiance (referred to as K_dPAR) and for radiation integrated between 320 and 400 nm ($K_{dI}A$) and between 300 and 320 nm ($K_{dI}B$) respectively. $K_{dI}A$ and $K_{dI}B$ were estimated from dissolved organic carbon (DOC) in mg · L^{-1} and DOC fluorescence (DOCFL) in quinine sulphate units (QSU) following the equations[1] generated by Scully and Lean (1994) for the nine high Arctic lakes.

				From DOC (m^{-1})					From DOCFL (m^{-1})			
Lake	K_dPAR (m^{-1})	1%PAR (m)	DOC (mg L^{-1})	$K_{dI}A$ (m^{-1})	1%UVA (m)	$K_{dI}B$ (m^{-1})	1%UVB (m)	DOCFL (QSU)	$K_{dI}A$ (m^{-1})	1%UVA (m)	$K_{dI}B$ (m^{-1})	1%UVB (m)
Barren L.	n/a	N/a	1.4	0.5	9.2	0.8	5.9	8.8	1.8	2.6	4.3	1.1
Black Char L.	n/a	N/a	2.0	0.9	5.3	1.5	3.1	7.4	1.5	3.0	3.6	1.3
Char L.	0.14[a]	32.9	1.1	0.3	13.3	0.5	9.3	2.7	0.7	6.6	1.4	3.3
Clear L.	n/a	N/a	2.4	1.1	4.0	2.1	2.2	5.6	1.2	3.8	2.8	1.7
Meretta L.**	0.26[a]	17.7	2.0	0.9	5.3	1.5	3.1	4.9	1.1	4.3	2.4	1.9
North L.	0.24§	19.2	1.0	0.3	15.4	0.4	11.1	4.1	0.9	4.9	2.1	2.2
Resolute L.	0.16[a]	28.8	1.4	0.5	9.2	0.8	5.9	3.7	0.9	5.3	1.8	2.5
Small L.	n/a	N/a	1.9	0.8	5.8	1.4	3.4	4.8	1.1	4.3	2.4	1.9
Tern L.	n/a	N/a	1.5	0.6	5.2	0.9	8.3	3.5	0.8	5.5	1.7	2.6
Average	0.2	25	1.6	0.7	8.1	1.1	5.8	5.1	1.1	4.5	2.5	2.1
± SD	± 0.1	± 7	± 0.5	± 0.3	± 4.0	± 0.6	± 3.2	± 2.0	± 0.4	± 1.3	± 0.9	± 0.7
Median	0.20	24.0	1.5	0.6	5.8	0.9	5.9	4.8	1.1	4.3	2.4	1.9

[a] Data from Markager *et al.* 1999.

§ Calculated with an underwater Licor Radiometer

[1] Equations from Scully and Lean (1994): $K_{dI}B = 0.415DOC^{1.86}$; $K_{dI}A = 0.299DOC^{1.53}$; $K_{dI}B = 0.0778 + 0.477DOCFL$; $K_{dI}A = 0.226 + 0.17$

Table 2-4. Average total phytoplankton productivity rates (µg C L^{-1} h^{-1}) and chlorophyll-specific photosynthetic rates (P^B; µg C µg Chl a^{-1} h^{-1}) of all nine lakes in the vicinity of Resolute after combining all irradiance levels (6, 25, 50 and 100%E_o) under ambient (AMB-UVB) and enhanced UVB (ENH-UVB) conditions. ± SD.

	Total Productivity (µg C L^{-1} h^{-1})		P^B (µg C µg Chl a^{-1} h^{-1})	
	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Barren L.	0.06 ± 0.03	0.05 ± 0.03	0.32 ± 0.14	0.26 ± 0.17
Black Char L.	0.26 ± 0.06	0.13 ± 0.06	0.39 ± 0.09	0.19 ± 0.09
Char L.	0.15 ± 0.06	0.14 ± 0.07	0.31 ± 0.11	0.27 ± 0.13
Clear L.	0.48 ± 0.13	0.38 ± 0.17	0.84 ± 0.22	0.66 ± 0.29
Meretta L.	0.50 ± 0.12	0.33 ± 0.16	0.45 ± 0.11	0.30 ± 0.15
North L.	0.07 ± 0.02	0.04 ± 0.02	0.32 ± 0.10	0.19 ± 0.10
Resolute L.	0.28 ± 0.09	0.24 ± 0.14	0.27 ± 0.09	0.24 ± 0.14
Small L.	0.28 ± 0.05	0.16 ± 0.08	0.51 ± 0.09	0.29 ± 0.15
Tern L.	0.21 ± 0.03	0.12 ± 0.06	0.13 ± 0.02	0.08 ± 0.04
Average (± SD)	0.24 ± 0.16	0.16 ± 0.14	0.36 ± 0.19	0.25 ± 0.18
Median	0.22	0.12	0.34	0.21

Table 2-5. Average percent of total fixed carbon by picoplankton (0.2 – 2 µm), nanoplankton (2 – 20 µm) and netplankton (> 20 µm) of all nine lakes in the vicinity of Resolute combining all irradiance levels (6, 25, 50 and 100%E_o) under ambient (AMB-UVB) and enhanced UVB (ENH-UVB) conditions. ± SD.

	Picoplankton (0.2 – 2 µm)		Nanoplankton (2 – 20 µm)		Netplankton (> 20 µm)	
	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Barren L.	49.13 ± 4.60	47.75 ± 6.00	40.76 ± 3.87	40.76 ± 5.29	10.11 ± 1.70	11.50 ± 1.64
Black Char L.	54.05 ± 4.55	54.08 ± 4.55	38.19 ± 4.40	35.70 ± 5.08	7.76 ± 1.42	10.21 ± 1.32
Char L.	43.08 ± 6.17	38.00 ± 5.73	47.71 ± 5.86	51.67 ± 5.65	9.34 ± 1.23	10.33 ± 1.18
Clear L.	35.48 ± 4.12	34.98 ± 7.13	54.80 ± 4.06	52.52 ± 4.34	9.72 ± 0.89	12.50 ± 5.48
Meretta L.	44.33 ± 4.69	38.65 ± 4.91	34.70 ± 3.80	34.92 ± 6.50	20.98 ± 3.61	26.43 ± 5.25
North L.	53.20 ± 5.91	44.78 ± 6.97	40.12 ± 4.23	46.94 ± 5.59	6.69 ± 2.29	8.28 ± 2.17
Resolute L.	40.59 ± 6.51	42.27 ± 3.75	35.45 ± 4.81	36.83 ± 3.55	23.92 ± 4.50	20.90 ± 4.04
Small L.	47.04 ± 4.30	45.81 ± 3.91	47.40 ± 4.06	46.43 ± 3.70	5.56 ± 1.19	7.77 ± 2.60
Tern L.	34.65 ± 4.58	29.14 ± 5.64	43.60 ± 3.37	44.33 ± 3.94	21.75 ± 3.27	26.54 ± 7.11
Average (± SD)	45.17 ± 8.07	42.23 ± 8.73	42.00 ± 7.03	42.91 ± 7.72	12.84 ± 7.41	14.86 ± 8.25
Median	45.63	42.46	41.67	42.97	9.70	11.46

Table 2-6. Average percent of total fixed carbon allocated into low molecular weight metabolites (LMW), lipid, polysaccharide (POLY) and protein of the five lakes after combining all irradiance levels (6, 25, 50 and 100%E_o) under ambient (AMB-UVB) and enhanced UVB (ENH-UVB) conditions. ± SD.

	% C in LMW		% C in LIPID		% C in POLY		% C in PROTEIN	
	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Clear L.	33.4 ± 2.3	38.1 ± 2.9	17.6 ± 1.2	17.1 ± 1.1	27.5 ± 1.3	28.3 ± 2.3	21.4 ± 3.0	16.4 ± 3.9
Meretta L.	48.3 ± 6.1	60.6 ± 5.2	21.4 ± 1.7	21.7 ± 1.1	13.7 ± 4.2	8.8 ± 4.9	16.6 ± 3.9	8.9 ± 1.9
North L.	40.2 ± 7.7	35.1 ± 19.8	25.5 ± 3.8	43.4 ± 19.7	11.7 ± 4.8	4.1 ± 5.1	22.7 ± 6.3	17.4 ± 10.5
Small L.	51.8 ± 2.7	57.1 ± 3.8	19.1 ± 1.4	18.6 ± 1.6	13.6 ± 1.8	13.5 ± 2.3	15.5 ± 3.0	10.8 ± 1.8
Tern L.	51.4 ± 4.9	55.7 ± 4.9	20.7 ± 1.2	23.2 ± 2.7	12.4 ± 2.4	9.3 ± 2.9	15.5 ± 3.2	11.8 ± 2.8
Average (± SD)	46.1 ± 8.2	50.0 ± 15.0	21.3 ± 3.6	26.2 ± 14.2	14.3 ± 5.6	10.8 ± 7.7	18.3 ± 5.4	13.0 ± 6.5
Median	47.9	55.0	20.8	21.4	13.4	10.8	17.8	11.5

Table 2.7. Average percent inhibition of phytoplankton photosynthetic rates (P) by enhanced UVB levels after 2 and 8 h of exposure to four irradiance treatments (6, 25, 50 and 100% of surface irradiance [E_o]) when combining all lake experiments together. ± SD.

	% UVB inhibition	
%E_o	2 h	8 h
6	1.6 ± 26.2_7	**16.5 ± 13.4_7**
25	**10.6 ± 10.8_8**	**40.2 ± 14.4_7**
50	**24.6 ± 16.9_9**	**64.0 ± 14.1_8**
100	**38.9 ± 25.3_9**	**64.8 ± 14.7_8**
Overall	**20.3 ± 24.2_{33}**	**47.6 ± 24.2_{30}**

Note: % UVB inhibition was calculated as $[(P_{AMB\text{-}UVB} - P_{ENH\text{-}UVB})/P_{AMB\text{-}UVB}] * 100$. Subscripts are the number of experiments used in the average computation. Bold values are significantly different from zero from the one-sample t-test at $\alpha = 0.05$.

Table 2-8. Summary of the overall effect of enhanced UVB (i.e., UVB effect from ANOVA) on all variables measured for all nine lakes. Abb: B = Barren Lake, BC = Black Char Lake, Ch = Char Lake, Cl = Clear Lake, M = Meretta Lake, N = North Lake, R = Resolute Lake, S = Small Lake, T = Tern Lake, N/A = not available, NS = not significant, - = weak negative effect ($p < 0.05$), -- = intermediate negative effect ($p < 0.01$), --- = strong negative effect ($p < 0.001$), + = weak positive effect ($p < 0.05$), ++ = intermediate positive effect ($p < 0.01$), +++ = strong positive effect ($p < 0.001$).

	B	BC	Ch	Cl	M	N	R	S	T
Phytoplankton productivity	NS	---	---	---	---	---	--	---	---
Size-fractionation of photosynthesis:									
% Picoplankton (0.2 – 2 µm)	NS	NS	--	NS	---	---	NS	NS	---
% Nanoplankton (2 – 20 µm)	NS	-	+	NS	NS	+++	NS	NS	NS
% Netplankton (> 20 µm)	++	+++	++	+++	+++	+++	---	+++	+++
% Carbon allocation into:									
Low molecular weight	N/A	N/A	N/A	+++	+++	--	N/A	+++	+++
Lipid	N/A	N/A	N/A	NS	NS	+++	N/A	NS	+++
Polysaccharide	N/A	N/A	N/A	NS	---	---	N/A	NS	---
Protein	N/A	N/A	N/A	---	---	---	N/A	---	---

Figure headings

Figure 2-1. Location of the nine studied lakes near Resolute on Cornwallis Island, Nunavut. Map of Nunavut (top left) was obtained online from http://engsoc.queensu.ca/qpid/images/countries/nunavut_map.gif

Figure 2-2. Total phytoplankton productivity (in μg C L^{-1} h^{-1}) of North Lake on 10 July (top graph) and 9 August (bottom graph) during 24 h of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-3. (a) Total phytoplankton productivity (in μg C · L^{-1} · h^{-1}; a) and percent of total fixed carbon by (b) picoplankton (0.2 – 2 μm), (c) nanoplankton (2 – 20 μm), and (d) netplankton (> 20 μm) for North Lake on 1 August after 2 and 8 h of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-4. Total phytoplankton productivity (in μg C · L^{-1} · h^{-1}) of (a) Barren Lake, (b) Black Char Lake, (c) Char Lake, (d) Clear Lake, (e) Meretta Lake, (f) Resolute Lake, (g) small Lake and (h) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-5. Percent of total fixed carbon by picoplankton (0.2 - 2 μm) for (a) Barren Lake, (b) Black Char Lake, (c) Char Lake, (d) Clear Lake, (e) Meretta Lake, (f) Resolute Lake, (g) small Lake and (h) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-6. Percent of total fixed carbon by nanoplankton (2 – 20 μm) for (a) Barren Lake, (b) Black Char Lake, (c) Char Lake, (d) Clear Lake, (e) Meretta Lake, (f) Resolute Lake, (g) small Lake and (h) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-7. Percent of total fixed carbon by netplankton (> 20 μm) for (a) Barren Lake, (b) Black Char Lake, (c) Char Lake, (d) Clear Lake, (e) Meretta Lake, (f) Resolute Lake, (g) small Lake and (h) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-8. Percent of total photosynthate in (a) low molecular weight (LMW), (b) lipid, (c) polysaccharide, and (d) protein fractions for North Lake on 9 August during 24 h of exposure to two irradiance treatments (50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-9. Percent of total photosynthate in the low molecular weight (LMW) fraction for (a) Clear Lake, (b) Meretta Lake, (c) Small Lake and (d) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-10. Percent of total photosynthate in the lipid fraction for (a) Clear Lake, (b) Meretta Lake, (c) Small Lake and (d) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-11. Percent of total photosynthate in the polysaccharide fraction for (a) Clear Lake, (b) Meretta Lake, (c) Small Lake and (d) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

Figure 2-12. Percent of total photosynthate in the protein fraction for (a) Clear Lake, (b) Meretta Lake, (c) Small Lake and (d) Tern Lake after the indicated hours of exposure to four irradiance treatments (6, 25, 50 and 100% surface irradiance [E_o]) under ambient (AMB; white bars) and enhanced (ENH; hatched bars) UVB conditions. With SD bars (n = 3).

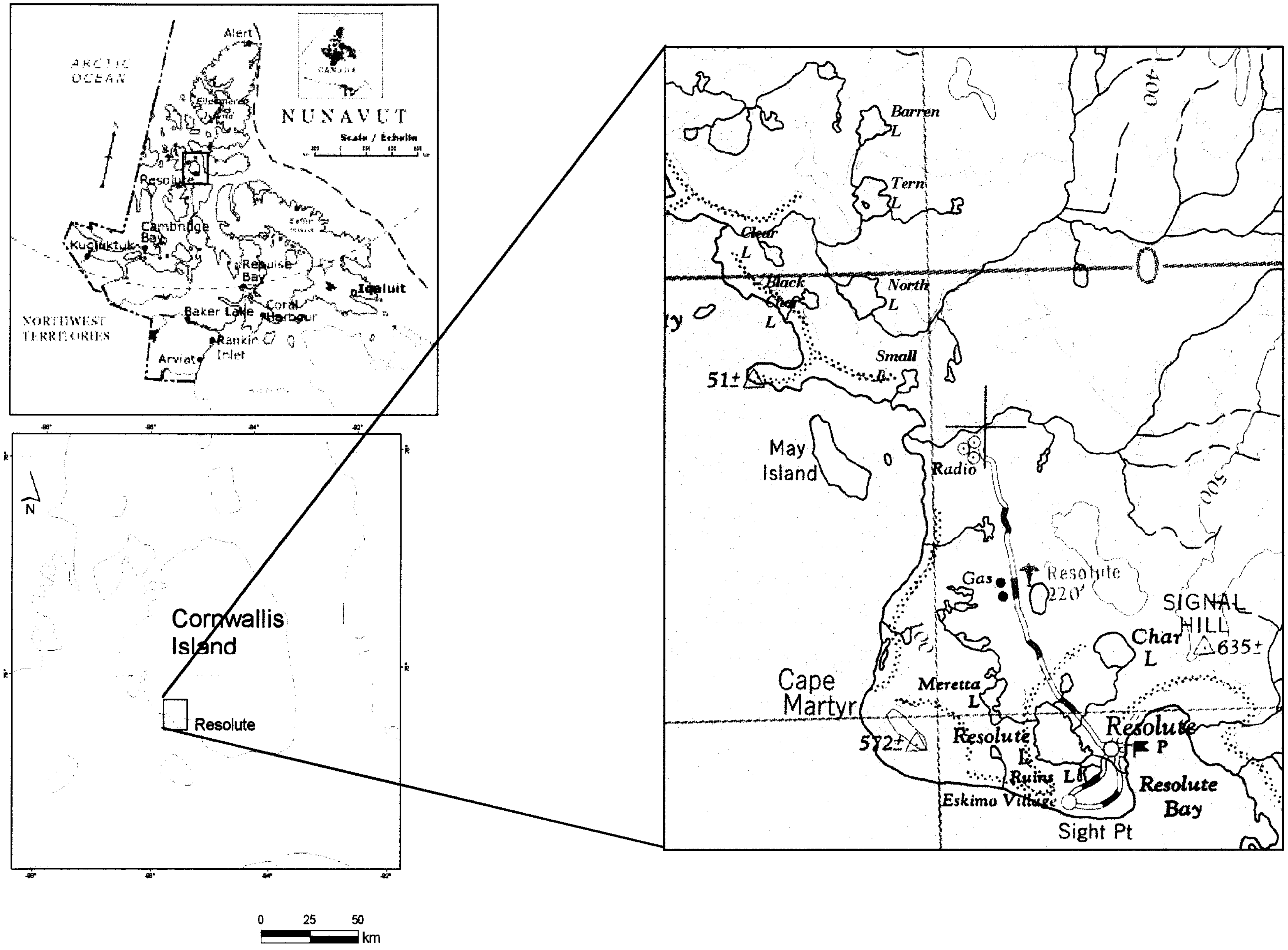

ARCTIC OCEAN
NUNAVUT
Scale / Echelle
Alert
Ellesmere Island
Resolute
Cambridge Bay
Kugluktuk
Repulse Bay
Iqaluit
Baker Lake
Coral Harbour
Rankin Inlet
Arviat
NORTHWEST TERRITORIES
CANADA
N
Cornwallis Island
Resolute
0
25
50
km
400
Barren L
Tern L
Clear L
Black
Char L
North L
Small L
51±
May Island
Radio
500
Gas
Resolute 220'
SIGNAL HILL
Char L
635±
Cape Martyr
Meretta L
572±
Resolute L
Resolute
P
Ruins L
Eskimo Village
Resolute Bay
Sight Pt

Figure 2-1.

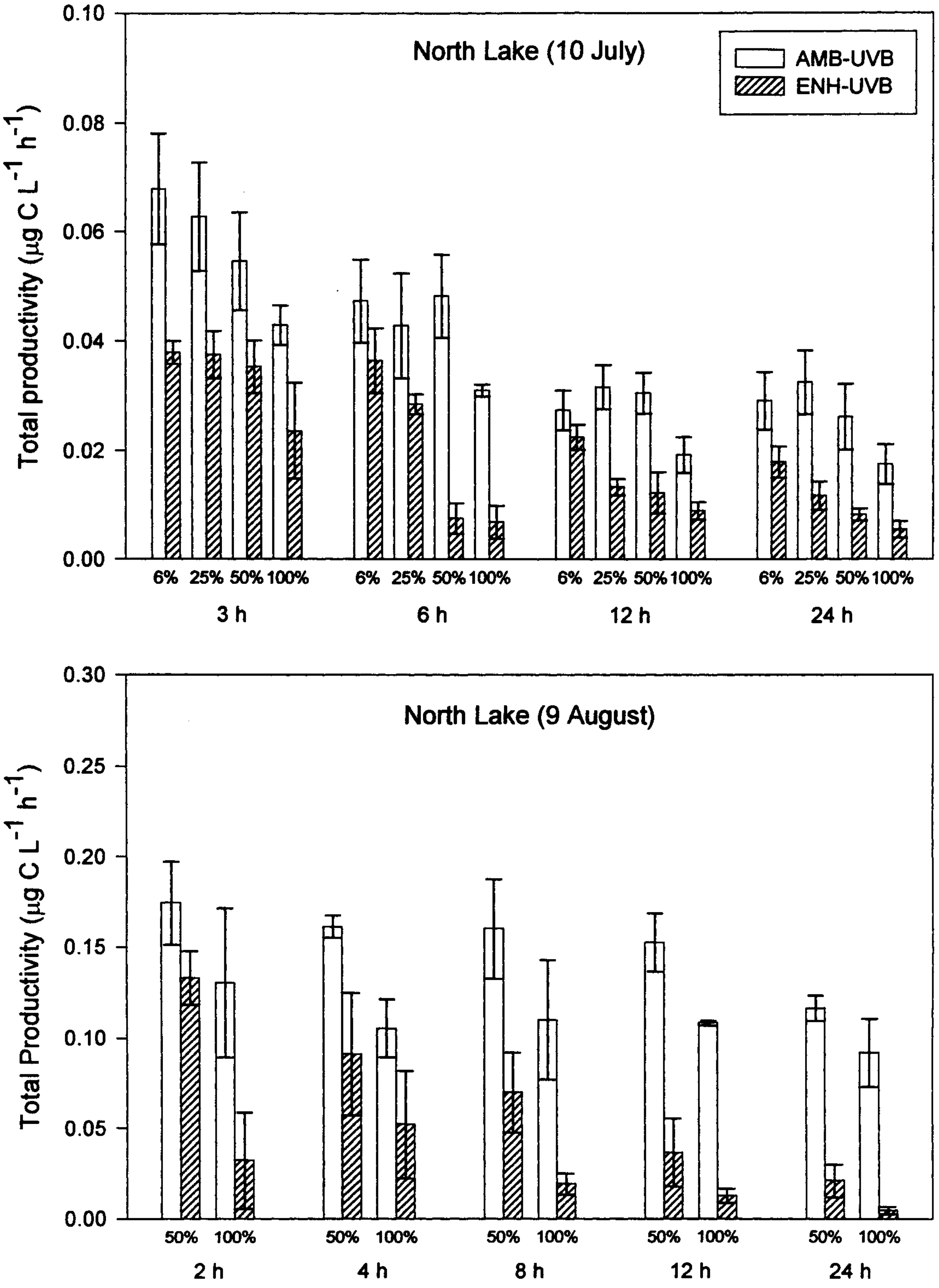

North Lake (10 July)
AMB-UVB
ENH-UVB
Total productivity (μg C L^{-1} h^{-1})
0.10
0.08
0.06
0.04
0.02
0.00
6% 25% 50% 100%
3 h
6 h
12 h
24 h
North Lake (9 August)
Total Productivity (μg C L^{-1} h^{-1})
0.30
0.25
0.20
0.15
0.10
0.05
0.00
50% 100%
2 h
4 h
8 h
12 h
24 h

Figure 2-2.

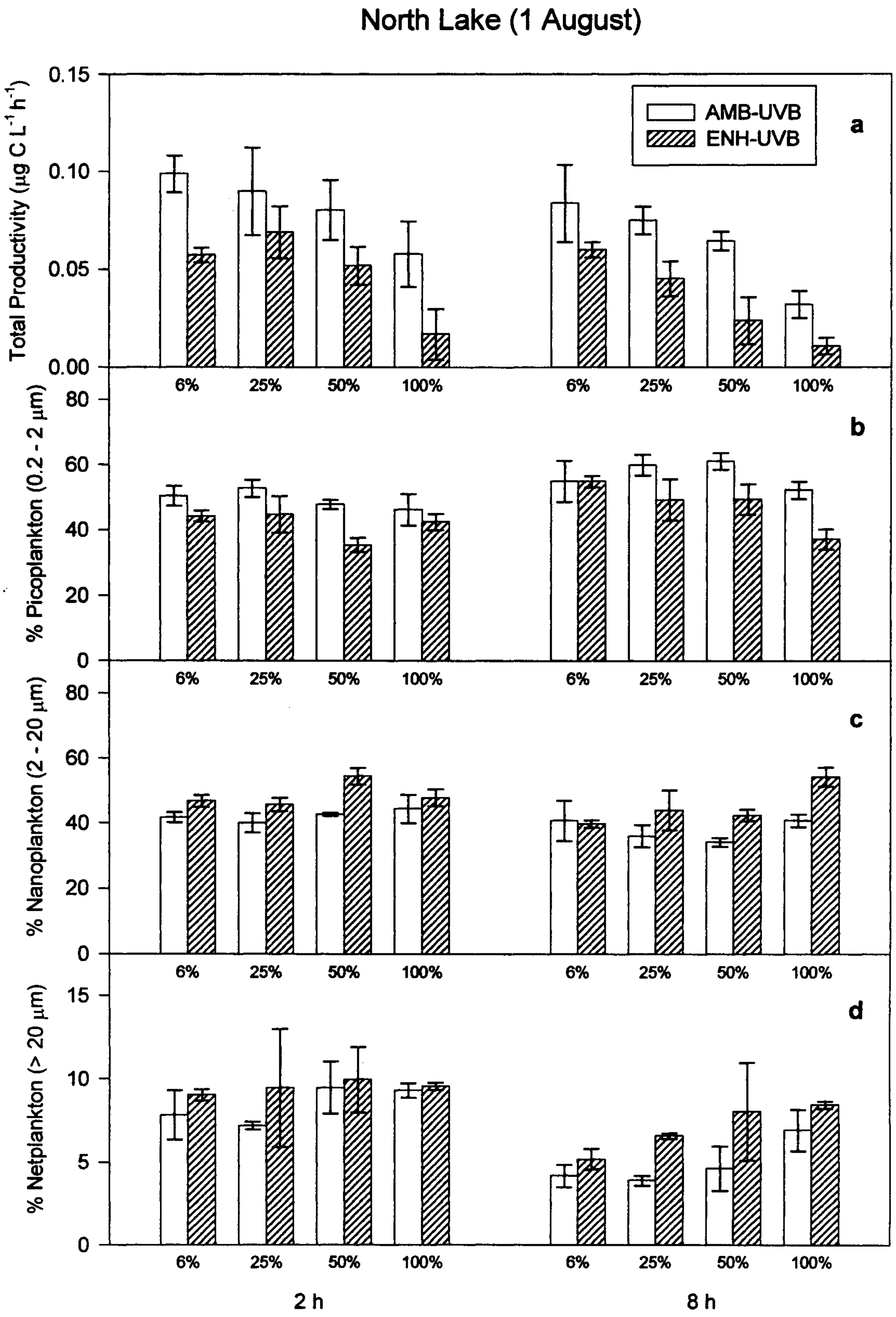

North Lake (1 August)
Total Productivity (μg C L-1 h-1)
0.15
0.10
0.05
0.00
AMB-UVB
ENH-UVB
a
% Picoplankton (0.2 - 2 μm)
80
60
40
20
0
b
% Nanoplankton (2 - 20 μm)
80
60
40
20
0
c
% Netplankton (> 20 μm)
15
10
5
0
d
6%
25%
50%
100%
6%
25%
50%
100%
2 h
8 h

Figure 2-3.

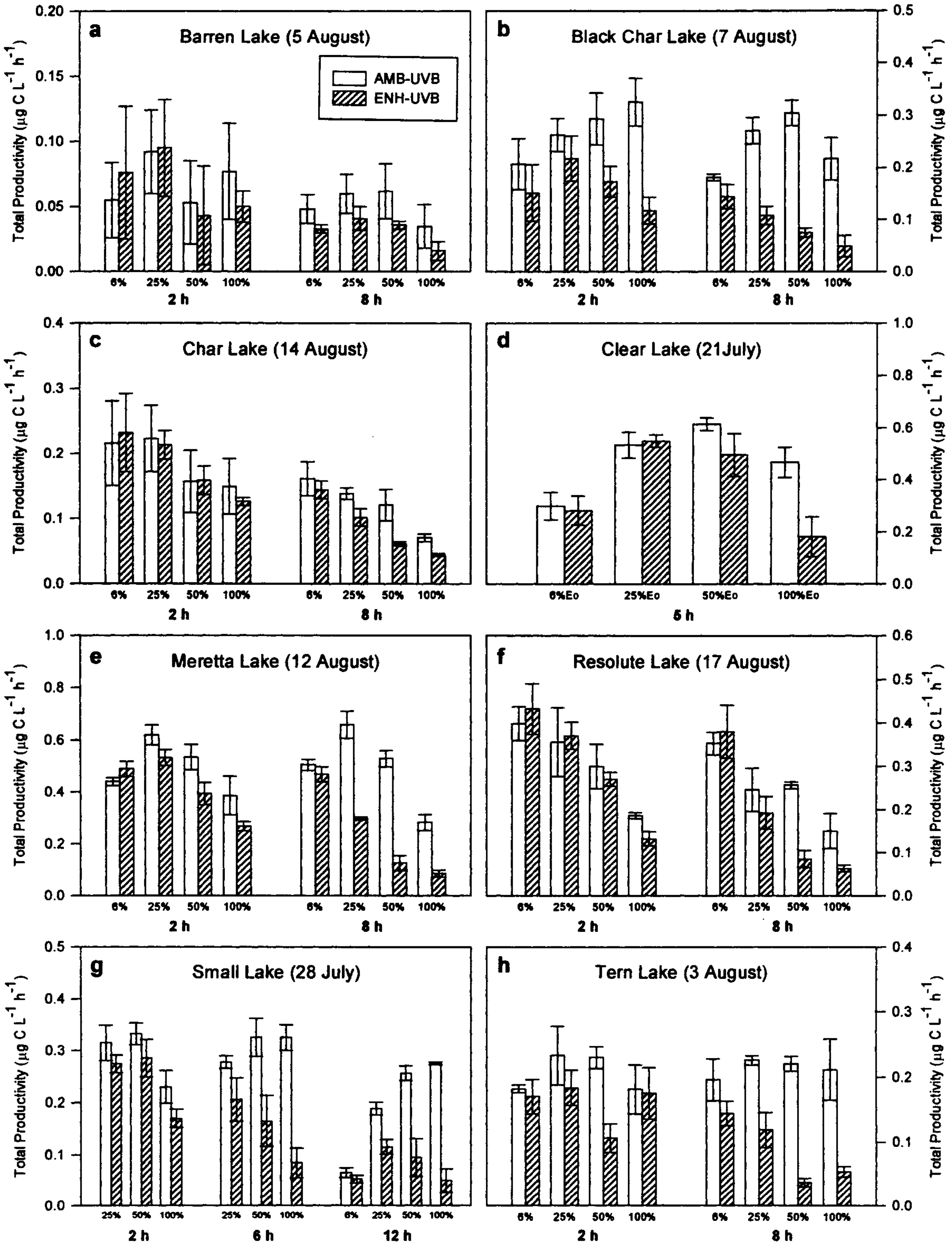

a
Barren Lake (5 August)
AMB-UVB
ENH-UVB
b
Black Char Lake (7 August)
c
Char Lake (14 August)
d
Clear Lake (21July)
e
Meretta Lake (12 August)
f
Resolute Lake (17 August)
g
Small Lake (28 July)
h
Tern Lake (3 August)
Total Productivity (µg C L^{-1} h^{-1})
0.00
0.05
0.10
0.15
0.20
0.0
0.1
0.2
0.3
0.4
0.5
0.8
0.6
1.0
6%
25%
50%
100%
6%Eo
25%Eo
50%Eo
100%Eo
2 h
5 h
6 h
8 h
12 h

Figure 2-4.

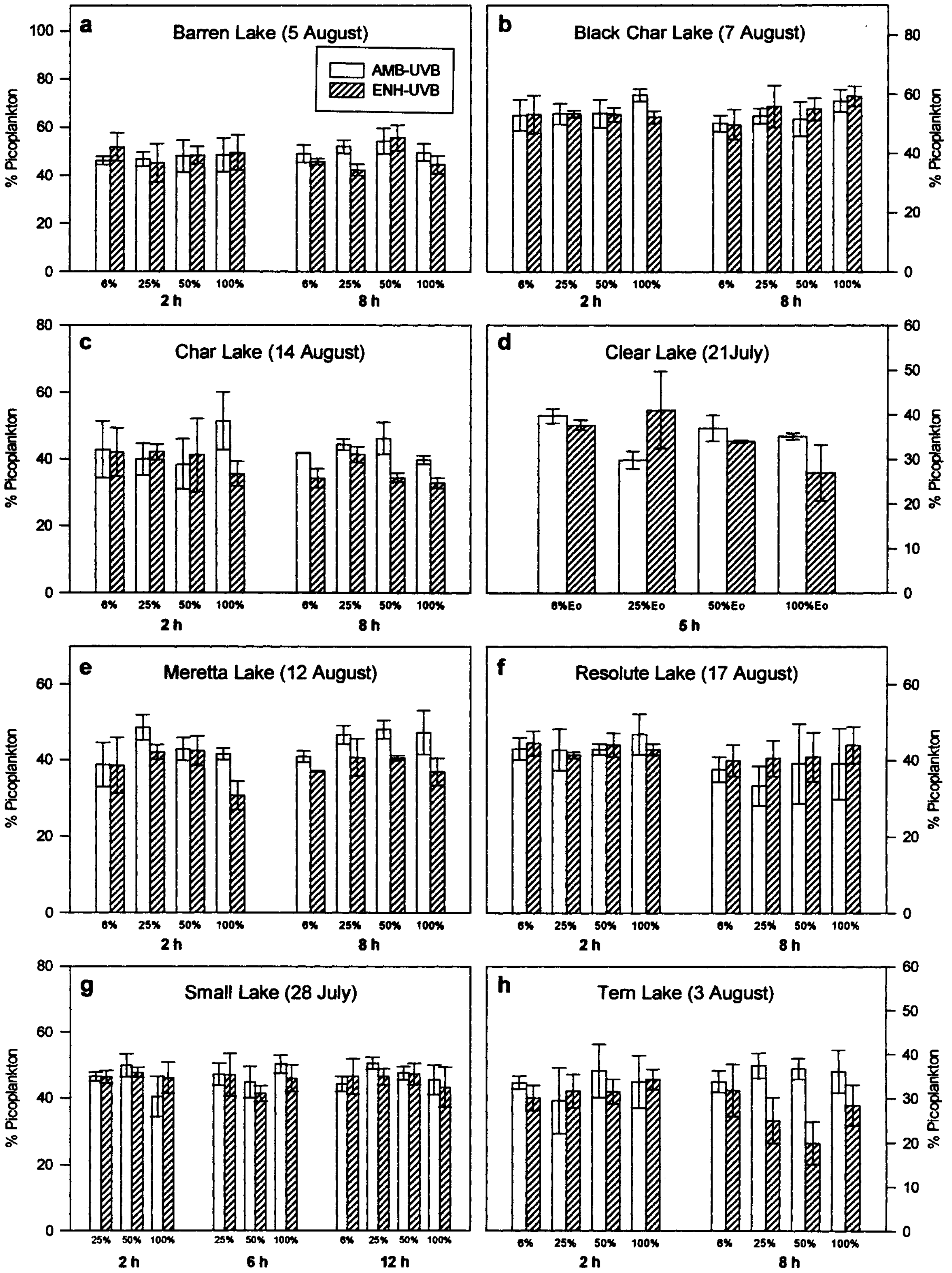

a
Barren Lake (5 August)
AMB-UVB
ENH-UVB
b
Black Char Lake (7 August)
c
Char Lake (14 August)
d
Clear Lake (21July)
e
Meretta Lake (12 August)
f
Resolute Lake (17 August)
g
Small Lake (28 July)
h
Tern Lake (3 August)
% Picoplankton
6%
25%
50%
100%
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6 h
8 h
12 h
0
10
20
30
40
50
60
80
100

Figure 2-5.

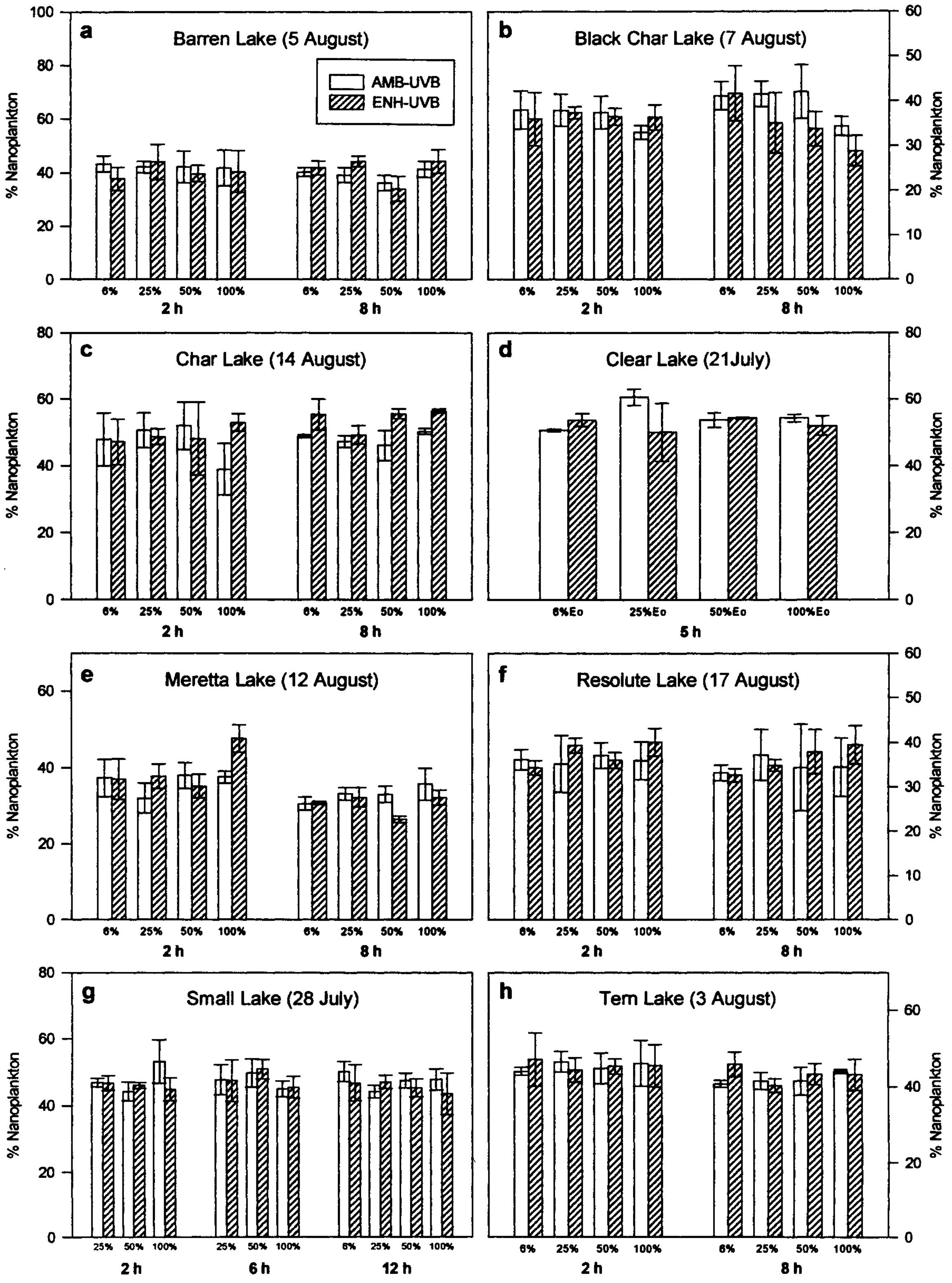

a
Barren Lake (5 August)
b
Black Char Lake (7 August)
AMB-UVB
ENH-UVB
c
Char Lake (14 August)
d
Clear Lake (21July)
e
Meretta Lake (12 August)
f
Resolute Lake (17 August)
g
Small Lake (28 July)
h
Tern Lake (3 August)
% Nanoplankton
0
20
40
60
80
100
0
10
20
30
40
50
60
6%
25%
50%
100%
6%Eo
25%Eo
50%Eo
100%Eo
2 h
5 h
6 h
8 h
12 h

Figure 2-6.

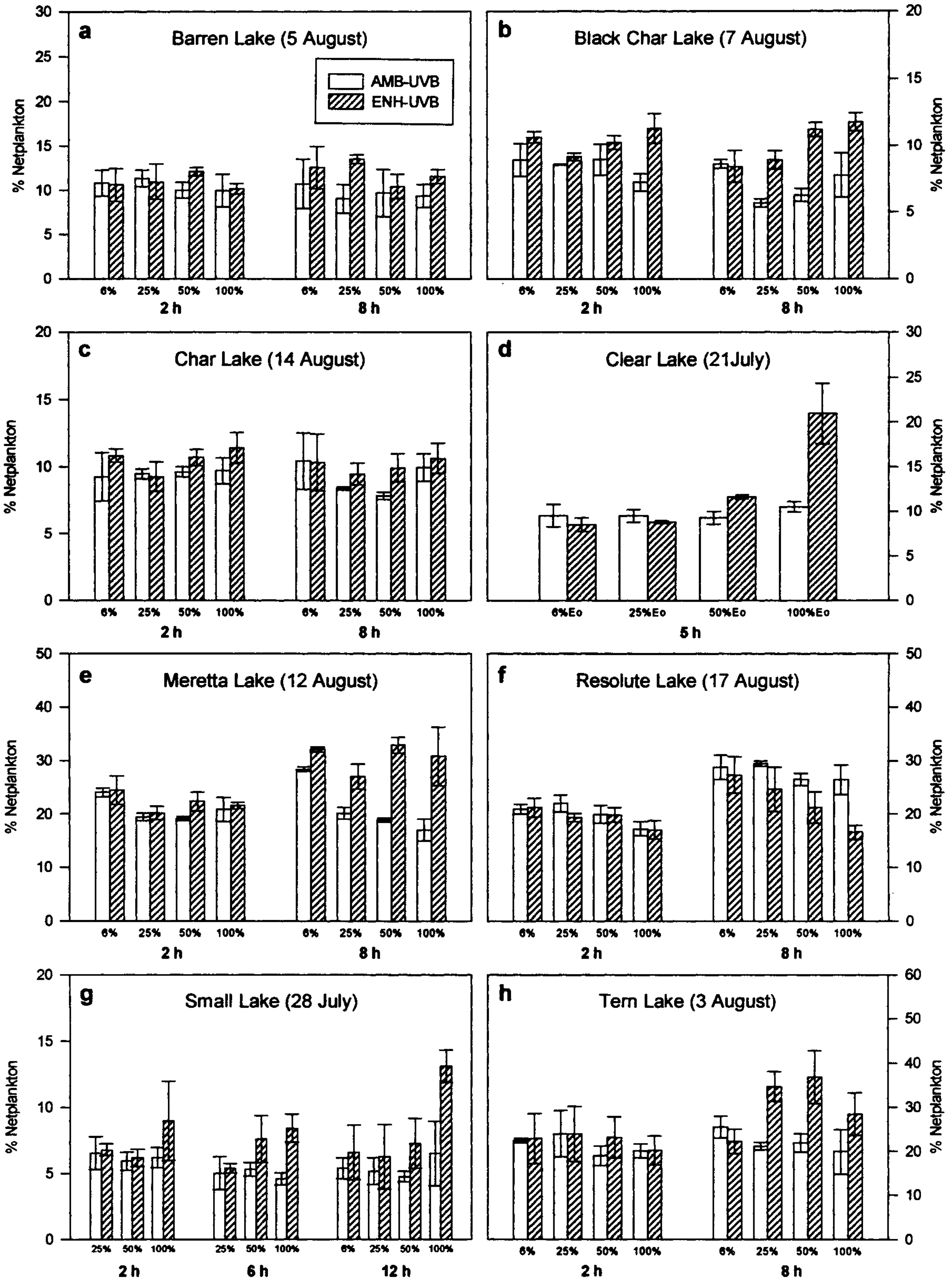

a
Barren Lake (5 August)
AMB-UVB
ENH-UVB
b
Black Char Lake (7 August)
c
Char Lake (14 August)
d
Clear Lake (21July)
e
Meretta Lake (12 August)
f
Resolute Lake (17 August)
g
Small Lake (28 July)
h
Tern Lake (3 August)
% Netplankton
6%
25%
50%
100%
6%Eo
25%Eo
50%Eo
100%Eo
2 h
5 h
6 h
8 h
12 h
0
5
10
15
20
25
30
40
50
60

Figure 2-7.

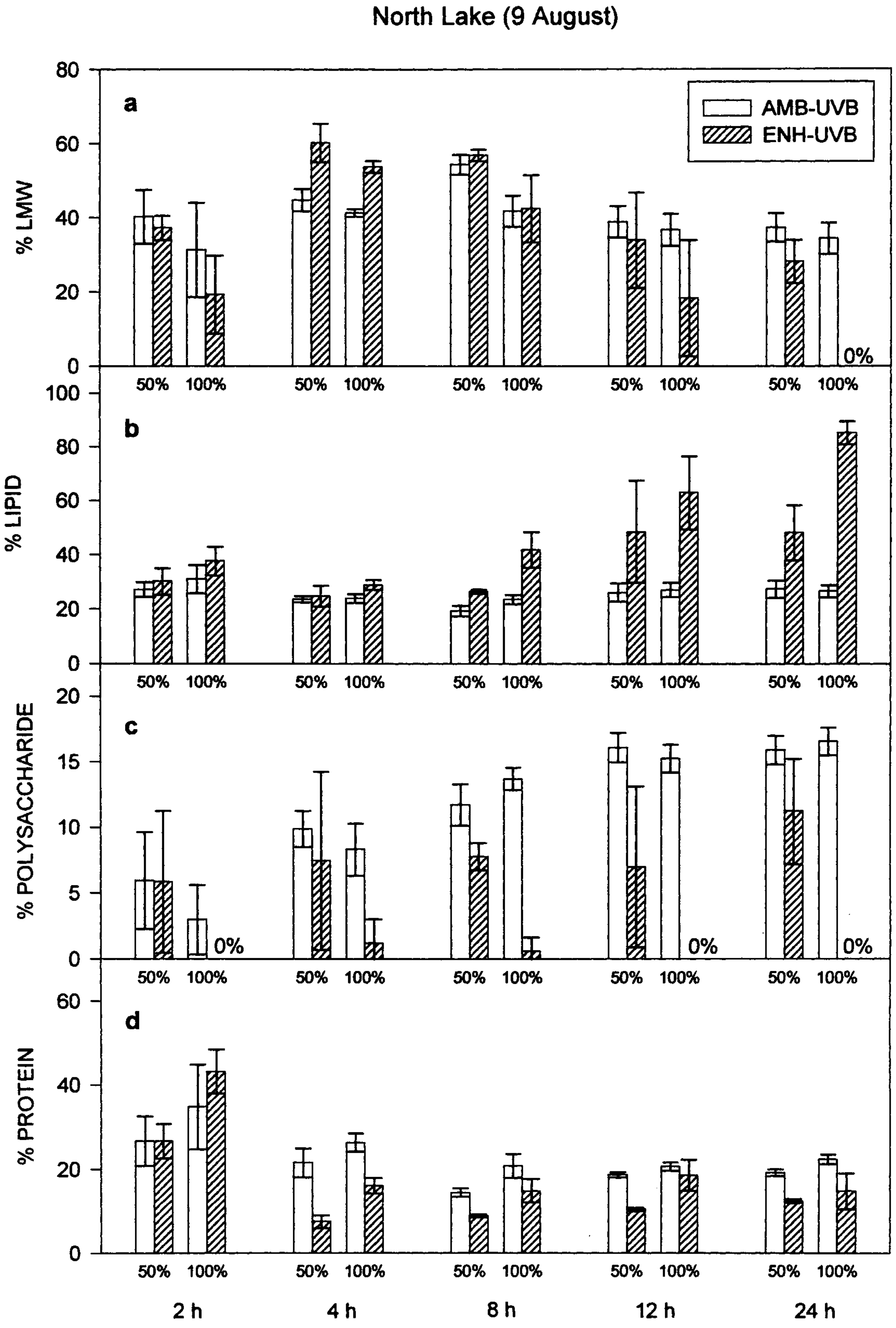

North Lake (9 August)
a
b
c
d
AMB-UVB
ENH-UVB
% LMW
% LIPID
% POLYSACCHARIDE
% PROTEIN
0
20
40
60
80
100
5
10
15
0%
50%
100%
2 h
4 h
8 h
12 h
24 h

Figure 2-8.

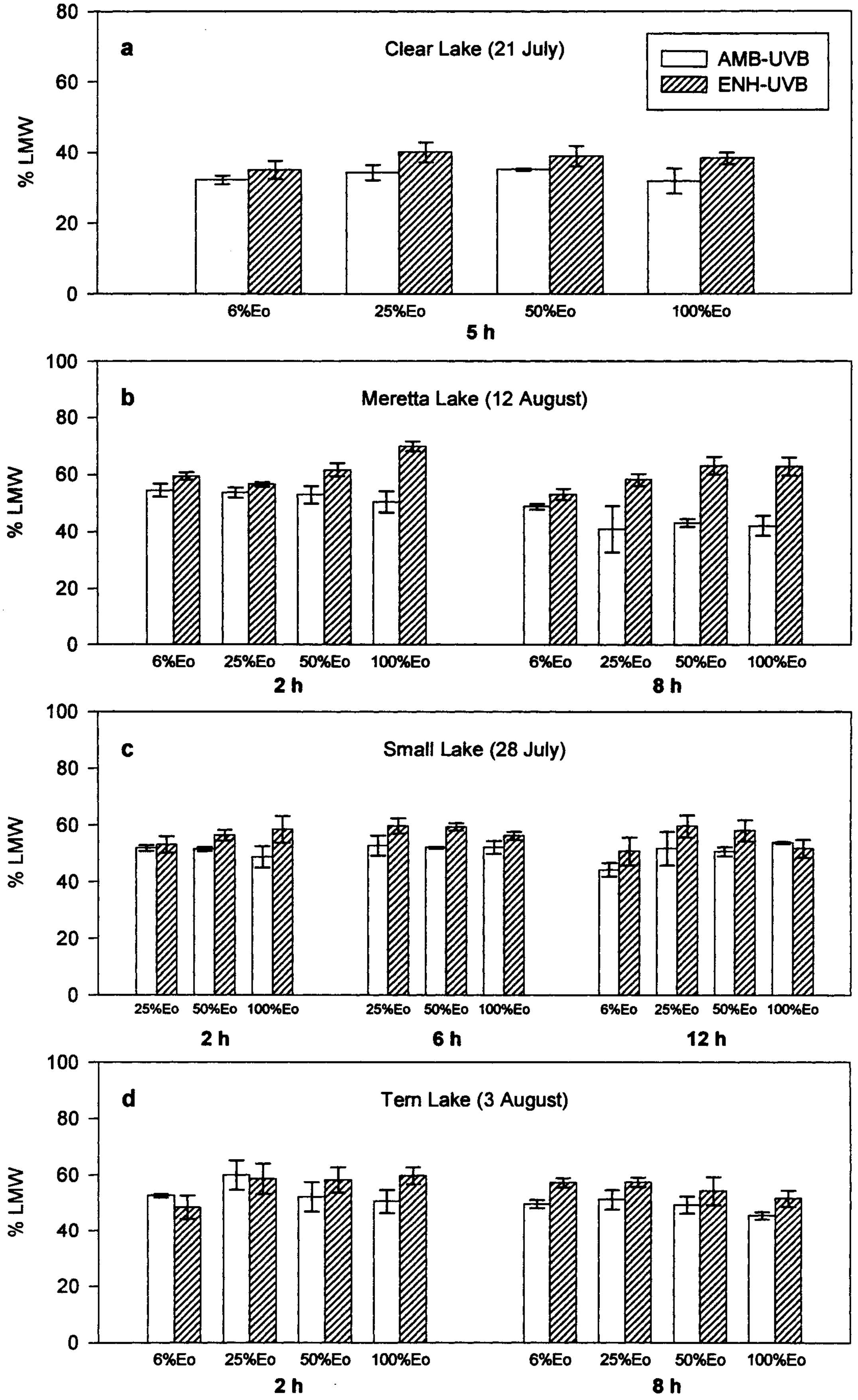

a
Clear Lake (21 July)
AMB-UVB
ENH-UVB
% LMW
0
20
40
60
80
6%Eo
25%Eo
50%Eo
100%Eo
5 h
b
Meretta Lake (12 August)
% LMW
0
20
40
60
80
100
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h
c
Small Lake (28 July)
% LMW
0
20
40
60
80
100
25%Eo
50%Eo
100%Eo
2 h
25%Eo
50%Eo
100%Eo
6 h
6%Eo
25%Eo
50%Eo
100%Eo
12 h
d
Tern Lake (3 August)
% LMW
0
20
40
60
80
100
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h

Figure 2-9.

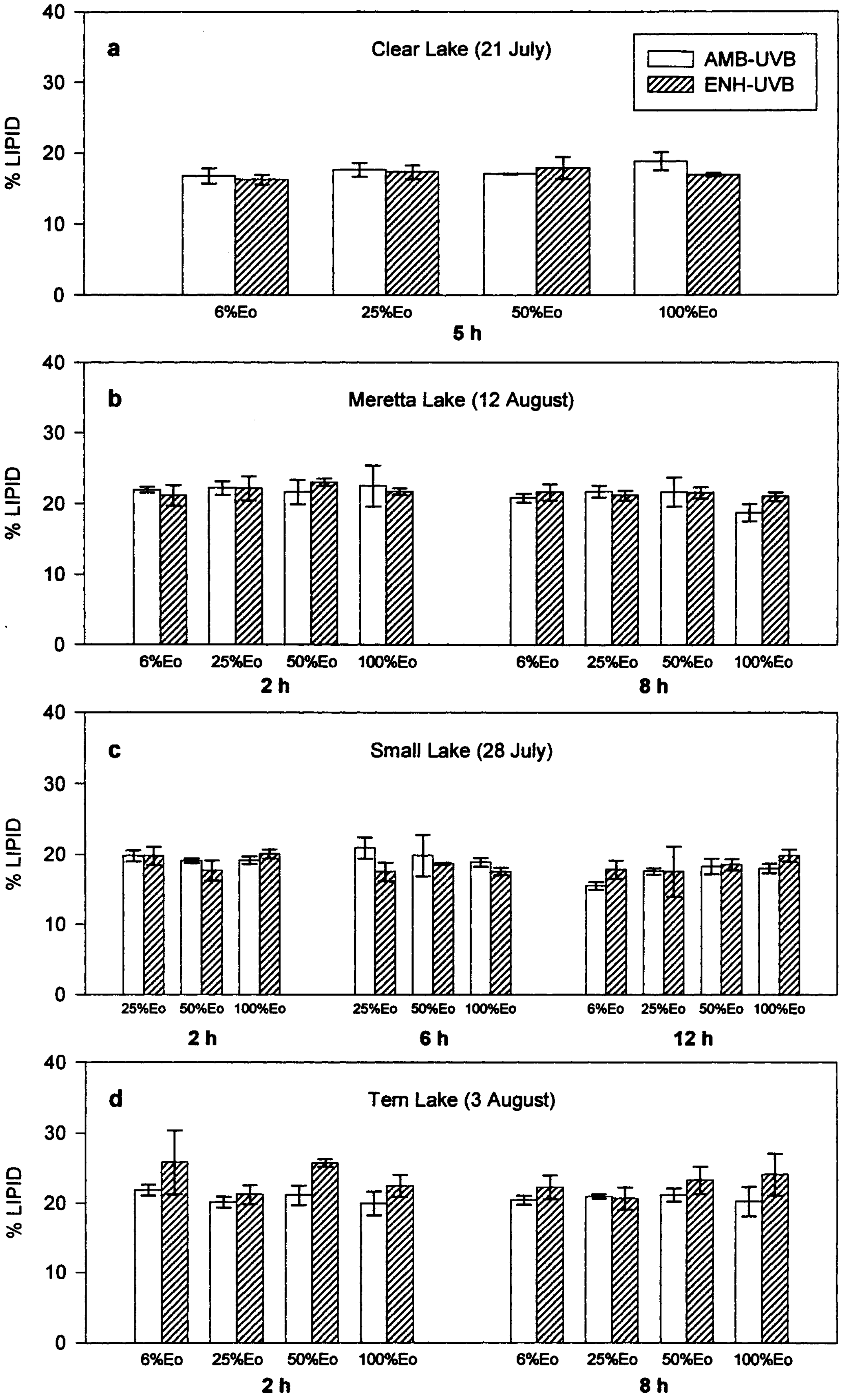
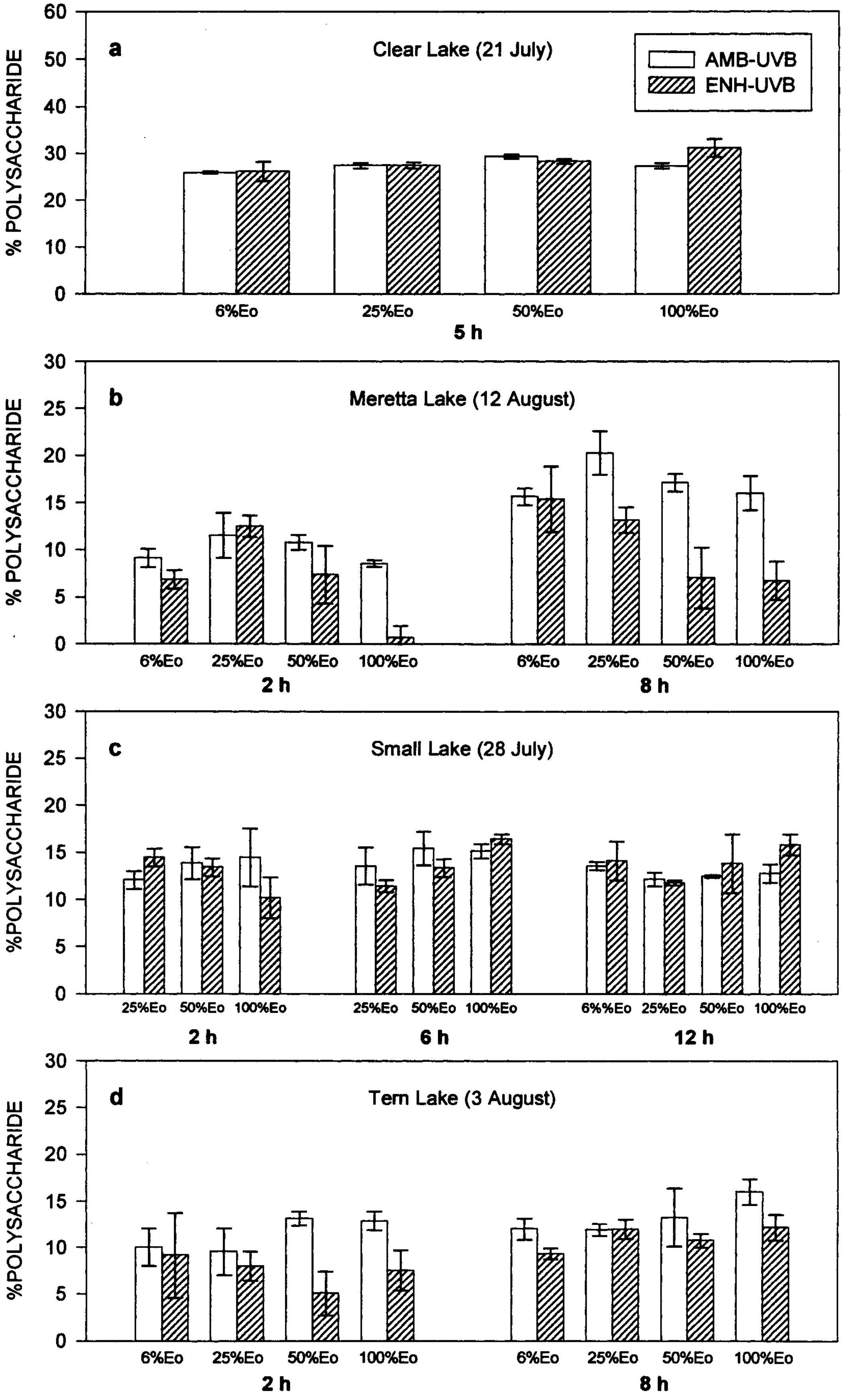

a
Clear Lake (21 July)
AMB-UVB
ENH-UVB
% LIPID
0
10
20
30
40
6%Eo
25%Eo
50%Eo
100%Eo
5 h
b
Meretta Lake (12 August)
% LIPID
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h
c
Small Lake (28 July)
% LIPID
25%Eo
50%Eo
100%Eo
2 h
25%Eo
50%Eo
100%Eo
6 h
6%Eo
25%Eo
50%Eo
100%Eo
12 h
d
Tern Lake (3 August)
% LIPID
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h

Figure 2-10.



a
Clear Lake (21 July)
AMB-UVB
ENH-UVB
% POLYSACCHARIDE
0
10
20
30
40
50
60
6%Eo
25%Eo
50%Eo
100%Eo
5 h
b
Meretta Lake (12 August)
% POLYSACCHARIDE
0
5
10
15
20
25
30
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h
c
Small Lake (28 July)
%POLYSACCHARIDE
0
5
10
15
20
25
30
25%Eo
50%Eo
100%Eo
2 h
25%Eo
50%Eo
100%Eo
6 h
6%%Eo
25%Eo
50%Eo
100%Eo
12 h
d
Tern Lake (3 August)
%POLYSACCHARIDE
0
5
10
15
20
25
30
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h

Figure 2-11.

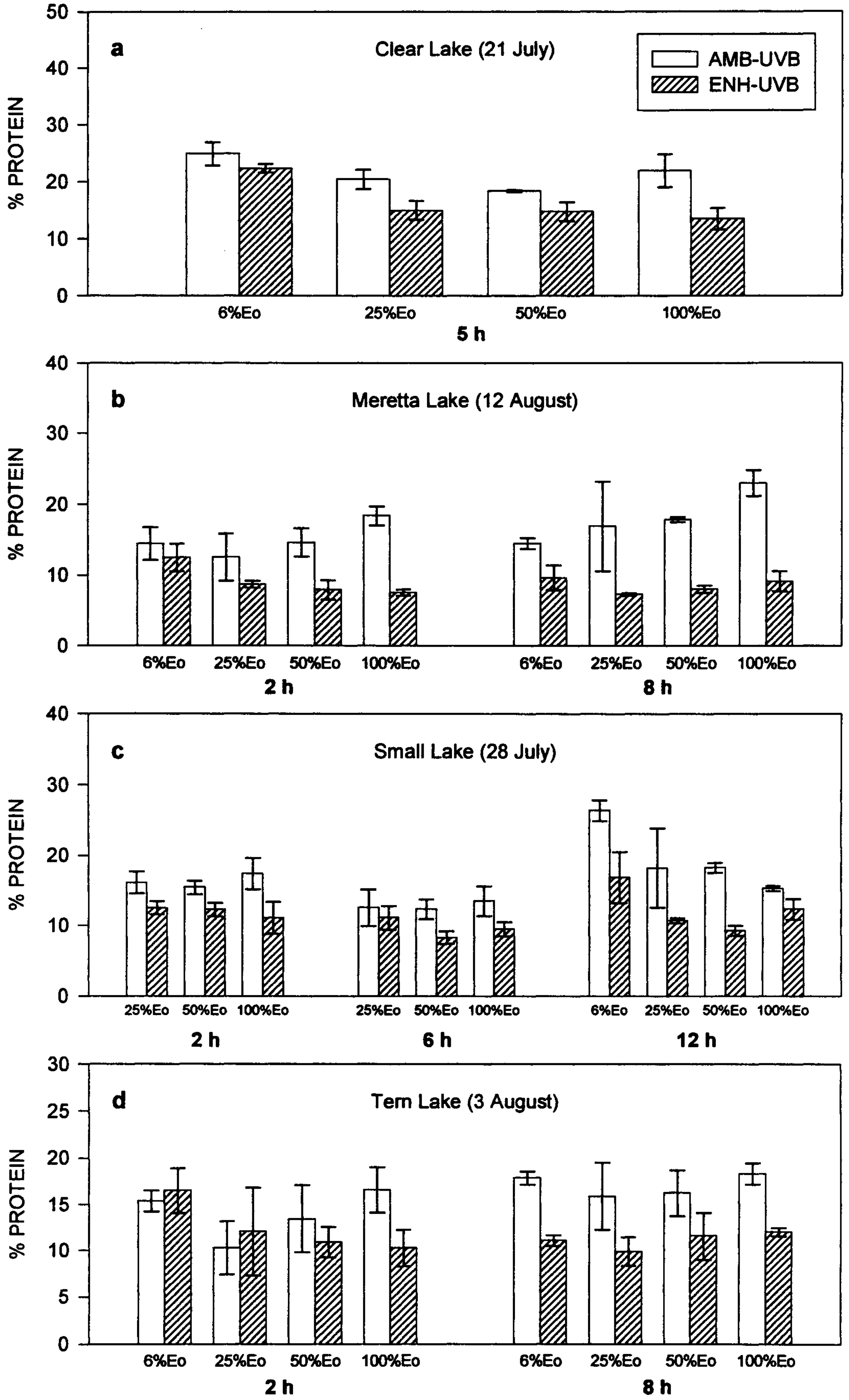

a
Clear Lake (21 July)
AMB-UVB
ENH-UVB
% PROTEIN
0
10
20
30
40
50
6%Eo
25%Eo
50%Eo
100%Eo
5 h
b
Meretta Lake (12 August)
% PROTEIN
0
10
20
30
40
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h
c
Small Lake (28 July)
% PROTEIN
0
10
20
30
40
25%Eo
50%Eo
100%Eo
2 h
25%Eo
50%Eo
100%Eo
6 h
6%Eo
25%Eo
50%Eo
100%Eo
12 h
d
Tern Lake (3 August)
% PROTEIN
0
5
10
15
20
25
30
6%Eo
25%Eo
50%Eo
100%Eo
2 h
6%Eo
25%Eo
50%Eo
100%Eo
8 h

Figure 2-12.

General Conclusion

Conclusions and significance of findings

Ultraviolet-B radiation (UVB; 280 –320 nm) represents the most harmful and mutagenic component of the solar radiation spectrum reaching the Earth's surface. The depletion of the ozone in the stratosphere has raised strong concerns about the effects of increased UVB levels on living organisms, including those inhabiting aquatic environments. However, the extent of the environmental impact has not yet been full realized. Polar aquatic ecosystems, especially in Antarctica, are of particular concern since ozone-related UVB increases have been the greatest in these regions. Over the Arctic, stratospheric ozone thinning shows large interannual variability and UVB levels have been estimated to be 20-40% and 10-20% higher during spring and summer months respectively compared to those for the late 1970s.

Compounding the UVB problem is tropospheric warming due to climate change causing decreased stratospheric temperatures. As a result, more severe ozone depletion is predicted over the Arctic and worldwide recovery of the ozone layer will take longer. In addition to the problems described above, climate change will have an important impact in future levels of underwater UVR in freshwaters by decreasing snow and ice cover duration and altering levels of dissolved organic carbon (DOC), the principal attenuator of ultraviolet radiation in freshwaters. Hence, it becomes important to learn more about the effects of UVR on aquatic organisms and the role of UVR in shaping freshwater ecosystems. However, to date, there is considerable uncertainty with respect to the effects of ozone- and/or climate change-related UVR onto aquatic ecosystems due to the strong variability in UVR responses between and among species as well as the complex combination of direct and indirect impacts of UVR at each trophic level (Perin and Lean 2004). Thus, it has been extremely difficult to predict any future shifts in aquatic ecosystem structure, especially in arctic freshwaters where little information exist on the effects of UVB in these communities.

The research presented in this thesis showed that UVB has diverse and wide ranging effects in arctic freshwaters. The 27-d *in situ* mecocosm experiment in Chapter 1 showed that long-term exposure to a moderate increase in UVB stimulated some biological processes, especially the microbial food web (i.e., heterotrophic bacteria and heterotrophic flagellates) and zooplankton in Two Basin Lake, a relatively high DOC lake of the arctic region. These positive effects may be the result of the photochemical release of low molecular weight organic carbon substrates, inorganic nutrients and/or beneficial trace metals (e.g., iron and manganese) available to organisms. This shift in carbon flow from the conventional food web to the microbial food web could have important consequences in the pelagic communities of these ecosystems, especially on the community structure of higher trophic levels (i.e., zooplankton, invertebrate, and/or fish). For example, a copepod-dominated zooplankton community could be replaced by a cladoceran/rotifer-dominated zooplankton community since cladocerans and rotifers may be better grazers of bacteria and protozoans than copepods.

Most importantly, results from Chapter 1 demonstrate that DOC plays a crucial role in planktonic community response to changes in solar UVB radiation. Waters with high DOC levels, as in Two Basin Lake, can minimize the harmful effects of UVB by protecting the planktonic communities and/or can induce beneficial rather than harmful effects of UVB to a given community. On the other hand, for low-DOC lakes, negative effects of increased UVB may be more important, depending on the photo-adaptive capability of the organisms, since UVB can penetrate deeper and photochemical reactions extend from surface waters to greater depths. Consequently, results from this Chapter should not be extrapolated to low-DOC lakes, which are more commonly found in the Arctic. However, the results from this experiment could become more representative of arctic lakes in the future since, with climate warming, lakes with higher DOC levels are expected to become more common in parts of the arctic region.

In Chapter 2, the effects of enhanced UVB on inorganic carbon uptake and assimilation into low molecular weight compounds (LMW), lipid, polysaccharide and protein were examined. Photosynthetic rates of natural phytoplankton assemblages from nine low-DOC lakes within close geographical proximity were sensitive to UVB increases and harmful effects were dependent not only on the UVB level but also the duration of exposure. This Chapter also demonstrated that the larger phytoplankton size class (i.e., > 20 μm) were more tolerant to enhanced UVB than smaller phytoplankton. These findings conflict with those from several other studies on photosynthetic inhibiton by solar UVR. However, cell size alone may not be a good index of sensitivity to UVB since photosynthetic responses from the two smaller phytoplankton size classes, picoplankton (0.2 - 2 μm) and nanoplankton (2 - 20 μm), were not consistent among all nine lakes. Findings from this Chapter also showed for the first time that UVB affect patterns of cellular carbon into LMW and macromolecular classes (lipid, polysaccharide and protein) in phytoplankton populations of arctic lakes. The most pronounced and consistent UVB impact was a decrease in the relative allocation into protein along with an increase in the relative allocation into LMW. Meanwhile, the proportion of carbon allocated into polysaccharide decreased or did not change. The lipid fraction was the least affected, with no or increased proportion of carbon allocated in this fraction after exposure to UVB.

In summary, results from these short-term assays (≤ 24 h) on phytoplankton productivity in Chapter 2 would suggest that exposure to enhanced UVB levels could be detrimental to phytoplankton living in low-DOC waters and cause a decrease in carbon uptake rates, a shift towards more resistant species/cell sizes and change the biochemical composition/food quality of phytoplankton. However, it is important to consider that other factors, such as water depth and vertical mixing, can modify the final expression of UVB damage. Although the nine lakes had relatively low DOC levels (≤ 2 mg L^{-1}) and were within close geographical proximity, differences in the effects of UVB on total photosynthesis, size distribution or patterns of intracellular photosynthate allocation were observed. This study highlights the importance that variations in the taxonomic/size composition of the phytoplankton community and/or phytoplankton physiological status (i.e., previous light history, photoprotective and repair capabilities) can result in different responses to UVB between individual lakes, regardless of their geographical proximity.

Aside from UVB effects, findings from the thesis demonstrated that phytoplankton biomass and productivity rates of High Arctic lakes are low, most likely as a result of both low water temperatures (< 8 °C) and nutrient (i.e., nitrogen and phosphorus) levels. Calculated volumetric photosynthetic rates were between 0.02 to 1.59 µg C L^{-1} h^{-1} among the 10 High Arctic lakes studied in this thesis, whereas typical summer values are about 8 µg C L^{-1} h^{-1} for temperate lakes (D. Lean, personal communication). Like for other Arctic lakes and sub-Arctic lakes, small cells (< 20 µm) were shown to contribute by more than 80% to total phytoplankton productivity, with less than 20% by netplankton (i.e., > 20 μm). Despite the low photosynthetic rates, the partitioning of carbon into the four main end–products in phytoplankton assemblages of High Arctic lakes has been found to be fairly similar to temperate oligotrophic lakes (e.g., Perin *et al.* 2002). More specifically, the lipid fraction remained the most conservative fraction, with typical values around 20% of newly fixed total carbon. Contrary to many studies in temperate regions, the labeling patterns of the four major end-products in phytoplankton communites from High Arctic lakes showed no consistent trends with light intensity. Planktonic heterotrophic bacterial abundance in Two Basin Lake was between 1-5 x 10^5 cells mL^{-1}, which is typical for oligotrophic lakes (Kalff 2002). Photosynthetic picoplankton abundance ranged from as little as 50 cells mL^{-1} to greater than 5 x 10^4 cells mL^{-1} during ice-free conditions in the summer among the studied lakes. This is much lower than typical values $\geq 10^5$ cells mL^{-1} for oligotrophic temperate lakes (e.g., Tzaras *et al.* 1999).

The basic characteristics of High Arctic lakes are long periods of ice and snow cover, low nutrient levels, low water temperatures (even in the summer), and exposure to pronounced seasonal and daily variations in solar radiation. The planktonic communities of these lakes are less complex and contain fewer species than temperature lakes or cold marine systems. For instance, the zooplankton community greater than 40 μm included only one species of cyclops, two species of cladocerans and one species of rotifers in Two Basin Lake. Consequently, the loss of species sensitive to UVB may lead to rapid changes in these freshwaters systems.

Recommendations for future research

The conclusions of this thesis highlight several areas for further research. It is critical to have a better understanding not only of the influence of solar UVR in High Arctic lakes on organisms, but also on the basic limnological processes and ecosystem functioning in these lakes. This would include the changes in the drainage basin that is further complicated by climate change at the local and regional level.

It is important to consider that the assessment of the response of High Arctic freshwater environments to UVB radiation from stratospheric ozone depletion cannot be isolated from other important environmental changes like climate warming. In addition to possibly changing underwater UVR climate and cause earlier ice breakup or loss of permanent ice in Arctic lakes, increase tropospheric temperatures would also increase water temperatures. Warmer water temperatures could influence the responses of aquatic biota to UVR stress and lead to drastic change at the ecosystem level. For example, Williamson *et al.* (2002) found that, for three zooplankton species, UVB tolerance increased with rising temperatures in species (*Daphnia catawba* and *Leptodiaptomus minutus*) that were highly dependent on photoenzymatic repair (PER) while UVB tolerance decreased in *Asplanchna girodi*, a species with less PER capability. However, very few studies exist on the interactive effects of water temperature and UVR on aquatic organisms, especially in the Arctic where climate warming is predicted to be greater.

In regards to UVR effects, Chapter 1 demonstrates the need for more research to determine the role that UVB has on photochemical reactions with humic substance or other photosensitizing agents in surface waters. If applicable, it would be important to determine if the photoproducts may be beneficial to bacteria and/or phytoplankton through enhancement of substrate and trace nutrient supply or detrimental to organisms thought the release of toxic trace metals, reduced oxygen species or organic moieties such as carbon monoxide and formaldehyde. It is still not known if there is a loss of color across the absorption spectrum when dissolved organic matter (DOM) is exposed to UVB. This would decrease absorbance of humic materials, a process referred to as DOM photobleaching. Furthermore, a long-term *in situ* mesocosm experiment should be done similar to that described in Chapter 1, but in a low-DOC lake of the Arctic. Results would likely differ greatly from those obtained here at Two Basin Lake.

Defence strategies play an essential role for aquatic organisms to cope with UVR. This would be especially the case for low-DOC shallow arctic lakes where UV penetration is great and no refuge is available. Discrepancies in results between the lakes in Chapter 2 would suggest differential tolerance to UVB among the phytoplankton populations. Although defence strategies such as the production of melanin and vertical migration have been studied for arctic daphnia (e.g., Hessen *et al.* 1999; Rautio and Korhola 2002a,b; Rautio *et al.* 2003), much remains to be known about protective and recuperative processes against UVR in arctic freshwater organisms. For instance, mycosporine-like amino acids (MAAs) have been identified in a number of aquatic systems around the world, but the occurrence of these compounds have not yet been determined in arctic plankton communities. Very little is known about repair processes such as those involved in DNA repair for arctic freshwater organisms. UVB damage is likely not temperature sensitive, but repair processes are temperature-dependent (e.g., Vincent and Roy 1993; Buma *et al.* 2001a) Furthermore, it would be important to determine how these defence strategies compare between shallow and deep lakes or between high-DOC and low-DOC lakes.

Aside for the major studies conducted on Char and Meretta lakes between 1968 and 1972 during the International Biological Program (IBP), Canadian northern lakes are still among the most poorly studied lakes of the world. While phytoplankton biomass and productivity of these lakes are low in these lakes, zooplankton and bacterial abundances are still comparable to oligotrophic lakes from warmer temperate regions. One potential food source could be the benthic algae. Welch and Kalff (1974) have estimated that the productivity of benthic algae accounted for about 80% of the annual primary production in Char Lake. This is considerable and one wonders how much of this benthic production is used by protozoans and zooplankton relative to that of phytoplankton.

Benthic algae live at the bottom of lakes and ponds of the Arctic in mats and films. They are dominated by cyanobacteria, especially the nitrogen-fixing genus *Nostoc* and *Scytonema* and filamentous species of the order Oscillatoriales (e.g., Quesada *et al.* 1999). These organisms have been shown to have sophisticated protective mechanisms against high PAR or UVR through vertical migration in the mat and the production of sheath pigments such as scytonemin (e.g., Quesada *et al.* 1999). The excretion or decomposition products of benthic algae may represent an important food source to the rest of the food chain.

Beside the benthic communities, another source of productivity is organic carbon used by bacteria that become food for protozoans and zooplankton. The relative importance of pelagic microbial communities (i.e., heterotrophic bacteria and protozoans) remains largely unknown for High Arctic lakes. Findings from Chapter 1 suggest that the heterotrophic microbial community may represent an important carbon pathway for zooplankton. Thus, further research is much needed on the hetetrotrophic microbial communities of these lakes as well as on their vulnerability to UVB and their photoprotective processes.

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APPENDICES

Appendix A: Physical characteristics of the mesocoms and surrounding lake at TBL (Chapter 1)

Figure headings

Figure A-1. Water temperature (°C ± SD) profile in the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels and the surrounding lake (outside the mesoscosms) on day 3, 10, 17 and 27 of the study period (n = 2, except for lake n = 1).

Figure A-2. Oxygen (mg L^{-1} ± SD) profile in the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels and the surrounding lake (outside the mesocosms) on day 3, 10, 17 and 27 of the study period (n = 2, except for lake: n = 1).

Figure A-3. Conductivity (µS cm^{-1} ± SD) profile in the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels and the surrounding lake (outside the mesocosms) on day 3, 10, 17 and 27 of the study period (n = 2, except for lake n = 1).

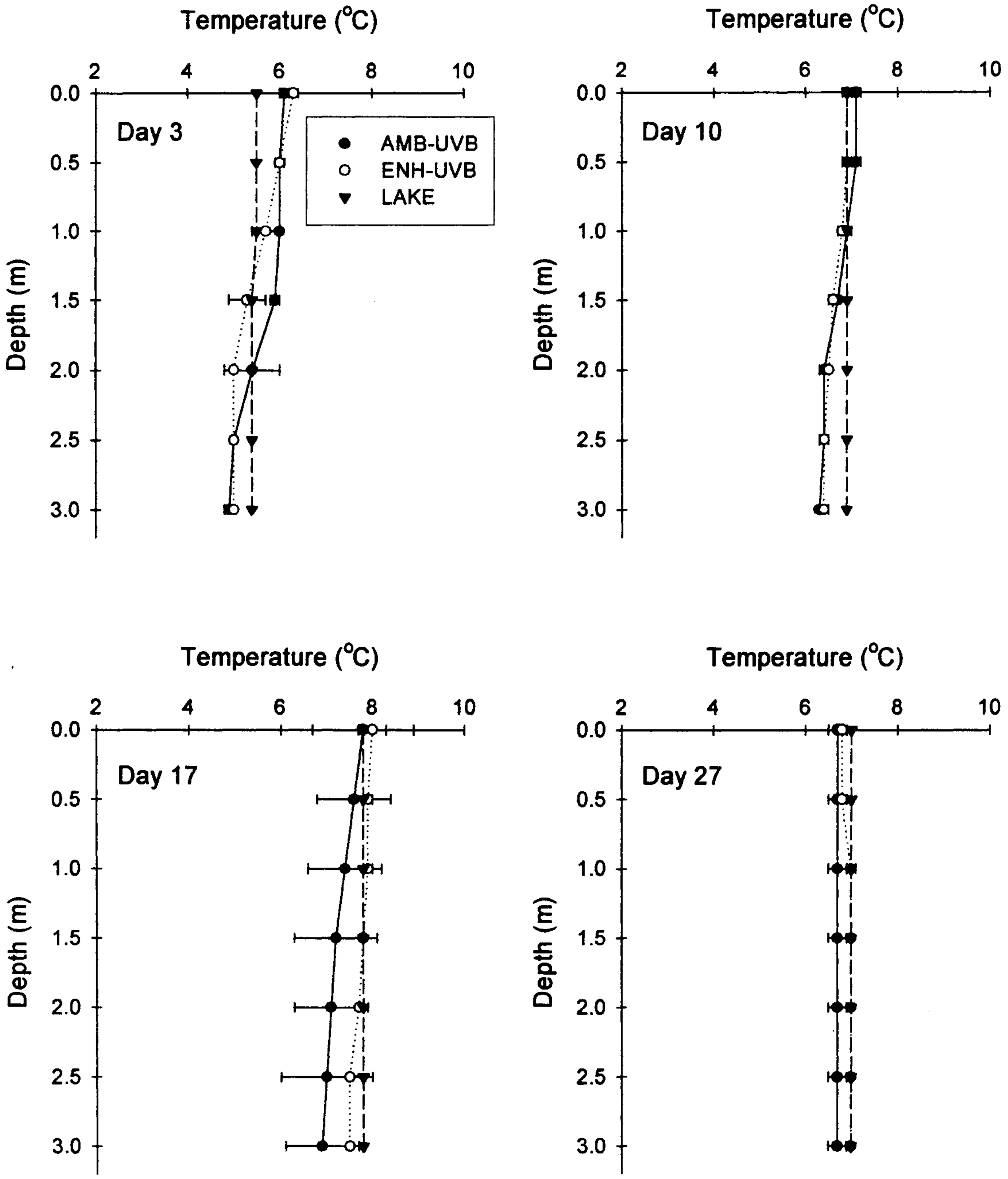

Temperature (°C)
2
4
6
8
10
Depth (m)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Day 3
Day 10
Day 17
Day 27
● AMB-UVB
○ ENH-UVB
▼ LAKE

Figure A-1.

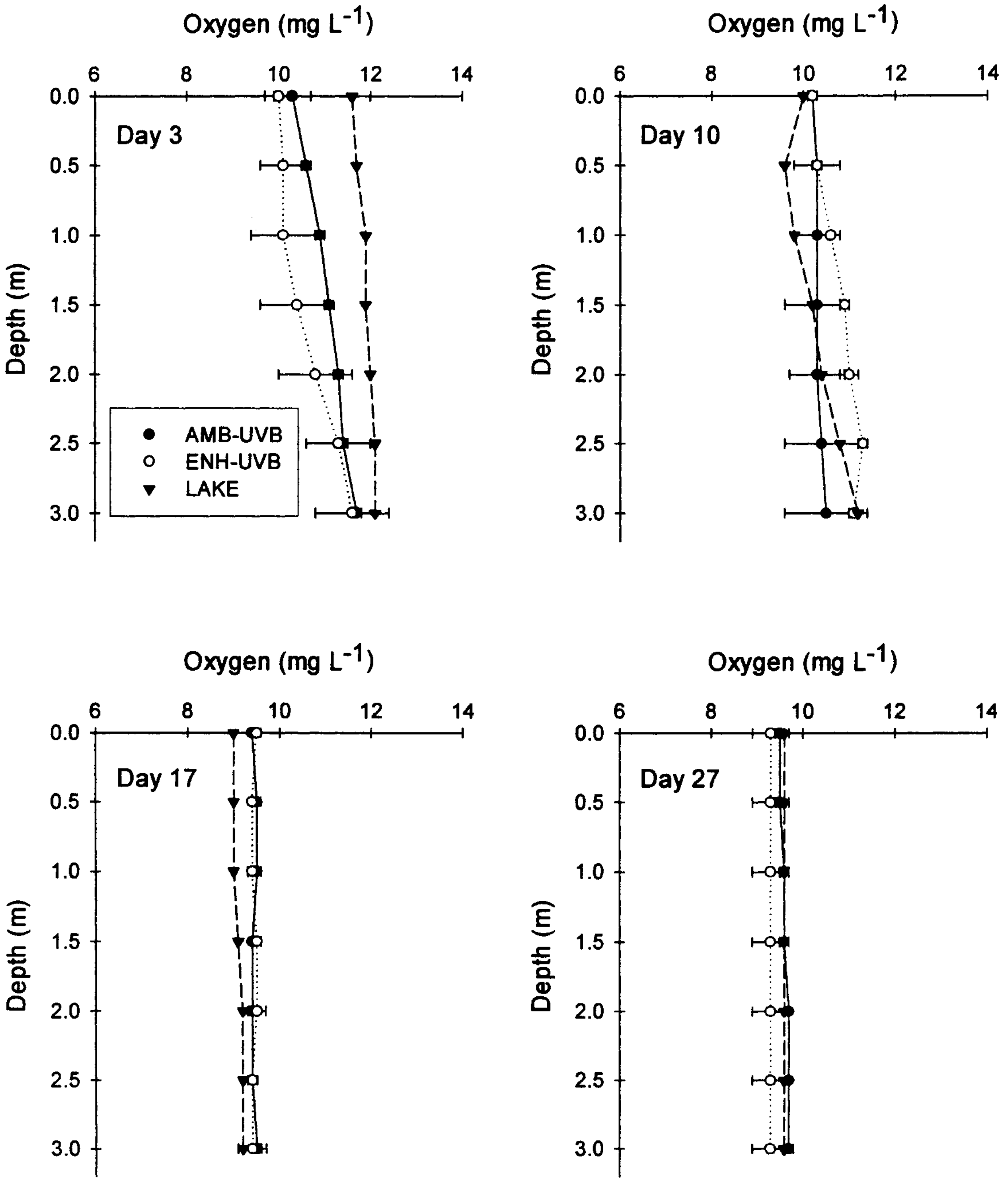

Oxygen (mg L^{-1})
6
8
10
12
14
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Depth (m)
Day 3
● AMB-UVB
○ ENH-UVB
▼ LAKE
Oxygen (mg L^{-1})
Day 10
Oxygen (mg L^{-1})
Day 17
Oxygen (mg L^{-1})
Day 27

Figure A-2.

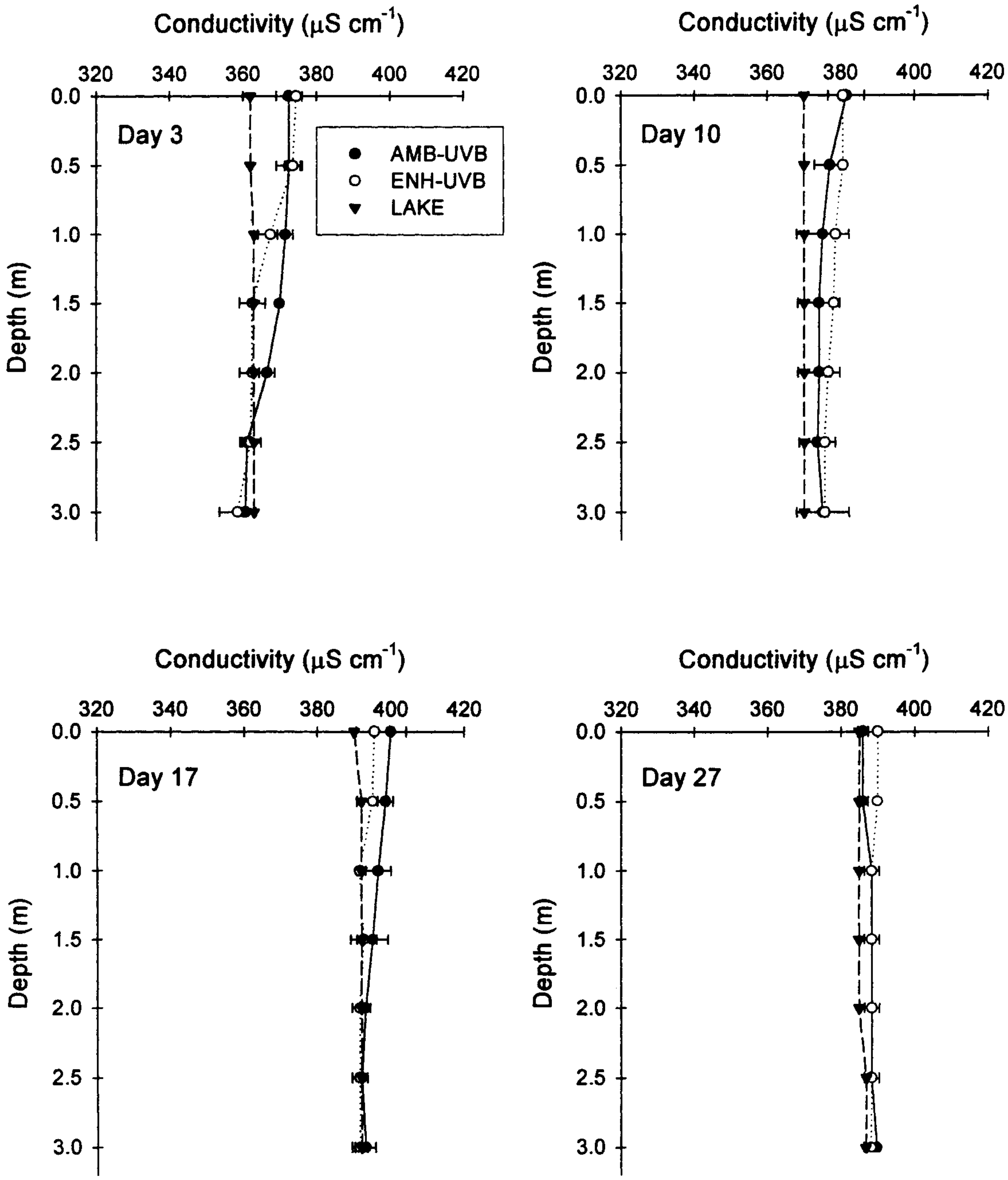

Conductivity (μS cm-1)
320
340
360
380
400
420
Depth (m)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Day 3
● AMB-UVB
○ ENH-UVB
▼ LAKE
Day 10
Day 17
Day 27

Figure A-3.

Appendix B: Physical and chemical characteristics of the mesocosms and surrounding lake at TBL (Chapter 1)

Table B-1. Physical and chemical characteristics of the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels and the surrounding lake over the course of the experiment between 22 July and 15 August 1994. The overall values represent the averages from all sampling dates combined (± SD). Abb: below detection limit (BDL), not applicable (N/A), water temperature (TEMP), conductivity (COND), total phosphorus unfiltered (TPUF), total phosphorus filtered (TPF), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total Kjeldahl nitrogen (TKN), total nitrogen (TN), chlorophyll *a* (CHL *a*), particulate organic carbon (POC), particulate organic nitrogen (PON).

	TEMP (°C)	COND (µS · cm^{-1})	O_2 (mg · L^{-1})	TPUF (µg · L^{-1})	TPF (µg · L^{-1})	SRP (µg · L^{-1})	NO_2 (µg · L^{-1})	NO_2+NO_3 (µg · L^{-1})	NH_3 (µg · L^{-1})
Day 3									
AMB-UVB	5.6 ± 0.5	368 ± 5	11.0 ± 0.5	5.5 ± 0.4	3.1 ± 0.5	0.5 ± 0.2	BDL (<2)	BDL (<10)	BDL (<5)
ENH-UVB	5.5 ± 0.5	366 ± 6	10.6 ± 0.8	6.4 ± 1.0	4.0 ± 0.9	0.3 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
LAKE	5.4 ± 0.1	363 ± 1	11.9 ± 0.2	4.9 ± 1.2	3.7 ± 0.3	0.6 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
Day 9-10									
AMB-UVB	6.7 ± 0.3	376 ± 5	10.3 ± 0.5	8.5 ± 1.6	3.5 ± 1.0	0.4 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
ENH-UVB	6.6 ± 0.2	378 ± 2	10.7 ± 0.4	6.3 ± 1.7	3.1 ± 0.3	0.6 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
LAKE	6.9 ± 0.0	370 ± 0	10.3 ± 0.6	5.4 ± 0.4	4.5 ± 1.3	0.6 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
Day 16-17									
AMB-UVB	7.3 ± 0.7	395 ± 4	9.4 ± 0.1	9.3 ± 1.4	4.3 ± 0.8	0.9 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
ENH-UVB	7.8 ± 0.2	393 ± 3	9.4 ± 0.1	7.1 ± 3.1	3.7 ± 0.4	0.6 ± 0.1	BDL (<2)	BDL (<10)	BDL (<5)
LAKE	7.8 ± 0.0	392 ± 1	9.1 ± 0.1	6.5 ± 0.5	4.0 ± 0.7	0.6 ± 0.0	BDL (<2)	BDL (<10)	BDL (<5)
Day 23-27									
Amb UVB	6.7 ± 0.2	388 ± 2	9.6 ± 0.1	5.6 ± 1.0	4.5 ± 1.7	0.5 ± 0.1	6 ± 3	BDL (<10)	BDL (<5)
Enh UVB	6.9 ± 0.1	389 ± 2	9.3 ± 0.3	5.3 ± 2.5	4.0 ± 1.0	0.5 ± 0.1	2 ± 1	BDL (<10)	BDL (<5)
LAKE	7.0 ± 0.0	386 ± 1	9.6 ± 0.0	5.1 ± 0.5	5.6 ± 0.5	0.8 ± 0.4	2 ± 0	BDL (<10)	BDL (<5)
Overall									
AMB-UVB	*6.6 ± 0.8*	*382 ± 12*	*10.1 ± 0.7*	*7.0 ± 2.0*	*3.8 ± 1.1*	*0.6 ± 0.2*	*N/A*	*BDL (<10)*	*BDL (<5)*
ENH-UVB	*6.7 ± 0.9*	*381 ± 11*	*10.0 ± 0.8*	*6.3 ± 2.1*	*3.7 ± 0.7*	*0.5 ± 0.1*	*N/A*	*BDL (<10)*	*BDL (<5)*
LAKE	*6.8 ± 0.9*	*378 ± 12*	*10.2 ± 1.1*	*5.4 ± 0.9*	*4.3 ± 0.9*	*0.6 ± 0.2*	*N/A*	*BDL (<10)*	*BDL (<5)*

Table B-1 (continued). Physical and chemical characteristics of mesocosms and surrounding lake at TBL (Chapter 1).

	DOC (mg · L^{-1})	DIC (mg · L^{-1})	TKN (µg · L^{-1})	TN (µg · L^{-1})	SiO_2 (mg · L^{-1})	SO_4 (mg · L^{-1})	Ca (mg · L^{-1})	Na (mg · L^{-1})	K (mg · L^{-1})
Day 3									
AMB-UVB	18.7 ± 5.0	34.5 ± 0.3	206 ± 31	226 ± 29	0.97 ±0.02	10.5 ± 0.3	42.5 ± 1.8	52.9 ± 2.2	4.4 ± 0.2
ENH-UVB	13.5 ± 3.2	34.3 ± 0.3	196 ± 27	227 ± 25	1.04 ±0.04	10.4 ± 0.1	42.6 ± 1.4	53.2 ± 1.7	4.6 ± 0.2
LAKE	9.6 ± 2.5	33.9 ± 0.0	181 ± 8	205 ± 6	1.03 ±0.01	10.3 ± 0.0	43.1 ± 1.6	53.9 ± 1.7	4.5 ± 0.0
Day 9-10									
AMB-UVB	10.7 ± 6.9	34.0 ± 0.4	184 ± 7	213 ± 3	1.05 ±0.03	11.0 ± 1.2	44.2 ± 1.7	55.5 ± 2.2	4.6 ± 0.2
ENH-UVB	13.6 ± 6.5	33.3 ± 0.3	183 ± 20	201 ± 20	1.06 ±0.02	11.1 ± 0.8	42.7 ± 1.0	54.0 ± 1.3	4.5 ± 0.2
LAKE	12.6 ± 8.6	33.0 ± 0.3	176 ± 6	190 ± 3	1.03 ±0.04	10.7 ± 1.1	43.5 ± 1.0	55.0 ± 0.9	4.6 ± 0.1
Day 16-17									
AMB-UVB	10.9 ± 6.7	33.6 ± 0.3	204 ± 12	242 ± 15	1.06 ±0.04	10.8 ± 0.7	42.6 ± 2.0	54.0 ± 2.9	4.6 ± 0.3
ENH-UVB	8.2 ± 3.4	34.4 ± 0.9	170 ± 15	203 ± 19	0.96 ±0.06	10.0 ± 1.0	43.9 ± 1.6	55.7 ± 1.9	4.6 ± 0.1
LAKE	5.3 ± 0.6	35.7 ± 0.1	190 ± 1	216 ± 3	0.97 ±0.00	11.8 ± 0.8	42.8 ± 5.9	54.6 ± 7.1	4.5 ± 0.4
Day 23-27									
AMB-UVB	11.0 ± 2.4	35.8 ± 0.4	167 ± 15	206 ± 12	1.01 ±0.01	11.0 ± 0.8	45.8 ± 2.8	58.2 ± 3.5	4.9 ± 0.3
ENH-UVB	11.2 ± 3.9	35.4 ± 0.4	166 ± 17	199 ± 19	0.93 ±0.01	10.1 ± 1.4	45.3 ± 1.1	58.5 ± 1.5	4.9 ± 0.2
LAKE	13.9 ± 5.0	35.5 ± 0.5	164 ± 21	187 ± 23	0.87 ±0.01	10.1 ± 0.1	43.9 ± 1.8	56.2 ± 2.6	4.7 ± 0.4
Overall									
AMB-UVB	*12.8 ± 6.1*	*34.5 ± 0.9*	*190 ± 23*	*222 ± 21*	*1.02 ±0.04*	*10.8 ± 0.8*	*43.8 ± 2.4*	*55.1 ± 3.2*	*4.6 ± 0.3*
ENH-UVB	*11.6 ± 4.6*	*34.3 ± 0.9*	*179 ± 22*	*207 ± 22*	*1.00 ±0.07*	*10.4 ± 0.9*	*43.6 ± 1.6*	*55.3 ± 2.6*	*4.6 ± 0.2*
LAKE	*10.3 ± 5.2*	*34.5 ± 1.2*	*177 ± 13*	*199 ± 15*	*0.97 ±0.07*	*10.7 ± 0.8*	*43.3 ± 2.5*	*54.9 ± 3.1*	*4.6 ± 0.2*

Table B-1 (continued). Physical and chemical characteristics of mesocosms and surrounding lake at TBL (Chapter 1).

	Cl ($mg \cdot L^{-1}$)	CHL *a* ($\mu g \cdot L^{-1}$)	POC ($\mu g \cdot L^{-1}$)	PON ($\mu g \cdot L^{-1}$)	TN:TPUF	POC:PON	DOC:POC	Fe ($\mu g \cdot L^{-1}$)	Mn ($\mu g \cdot L^{-1}$)
Day 3									
AMB-UVB	85.7 ± 0.9	0.7 ± 0.2	213 ± 19	18 ± 1	43 ± 8	12 ± 1	99 ± 8	59 ± 17	6.0 ± 3.6
ENH-UVB	83.3 ± 0.6	0.6 ± 0.3	307 ± 39	31 ± 5	36 ± 6	10 ± 1	44 ± 7	53 ± 11	5.5 ± 1.3
LAKE	82.8 ± 0.1	0.6 ± 0.0	253 ± 11	24 ± 1	44 ± 12	11 ± 0	38 ± 9	65 ± 20	4.2 ± 2.2
Day 9-10									
AMB-UVB	85.0 ± 0.9	0.7 ± 0.2	283 ± 57	29 ± 9	26 ± 5	10 ± 3	40 ± 31	75 ± 15	7.3 ± 2.2
ENH-UVB	85.2 ± 0.6	0.8 ± 0.3	242 ± 45	18 ± 3	33 ± 7	14 ± 1	56 ± 25	63 ± 40	7.3 ± 3.5
LAKE	84.7 ± 0.1	0.4 ± 0.0	221 ± 28	15 ± 4	35 ± 3	15 ± 2	55 ± 32	67 ± 11	4.5 ± 2.5
Day 16-17									
AMB-UVB	85.6 ± 0.5	1.0 ± 0.1	352 ± 70	38 ± 5	28 ± 5	9 ± 1	35 ± 32	89 ± 19	11.1 ± 4.0
ENH-UVB	85.4 ± 1.1	1.0 ± 0.2	288 ± 85	34 ± 10	33 ± 14	9 ± 0	32 ± 18	49 ± 28	6.0 ± 4.1
LAKE	85.1 ± 0.9	0.2 ± 0.0	272 ± 8	27 ± 4	34 ± 2	10 ± 2	19 ± 2	18 ± 24	1.7 ± 1.0
Day 23-27									
AMB-UVB	85.6 ± 0.5	1.1 ± 0.3	317 ± 30	35 ± 3	38 ± 8	9 ± 1	35 ± 11	61 ± 13	6.8 ± 3.5
ENH-UVB	85.6 ± 0.7	0.8 ± 0.2	305 ± 43	33 ± 5	42 ± 12	9 ± 1	39 ± 19	44 ± 16	5.1 ± 1.8
LAKE	80.9 ± 1.1	0.5 ± 0.2	222 ± 7	23 ± 1	37 ± 8	10 ± 1	62 ± 21	26 ± 1	1.5 ± 0.1
Overall									
AMB-UVB	*85.4 ± 0.7*	*0.9 ± 0.3*	*297 ± 67*	*31 ± 9*	*34 ± 9*	*10 ± 2*	*49 ± 33*	*73 ± 19*	*7.9 ± 3.7*
ENH-UVB	*84.9 ± 1.2*	*0.8 ± 0.3*	*285 ± 57*	*29 ± 9*	*36 ± 10*	*10 ± 2*	*43 ± 19*	*52 ± 24*	*6.0 ± 2.8*
LAKE	*83.4 ± 1.9*	*0.4 ± 0.2*	*242 ± 26*	*22 ± 5*	*37 ± 7*	*11 ± 3*	*44 ± 23*	*44 ± 27*	*3.1 ± 2.0*

Table B-1 (continued). Physical and chemical characteristics of mesocosms and surrounding lake at TBL (Chapter 1).

	Mg ($\mathrm{mg \cdot L^{-1}}$)	Al ($\mathrm{mg \cdot L^{-1}}$)	Ba ($\mathrm{\mu g \cdot L^{-1}}$)	Li ($\mathrm{\mu g \cdot L^{-1}}$)	Sr ($\mathrm{\mu g \cdot L^{-1}}$)	Zn ($\mathrm{\mu g \cdot L^{-1}}$)	Cu ($\mathrm{\mu g \cdot L^{-1}}$)	Be ($\mathrm{\mu g \cdot L^{-1}}$)	Co ($\mathrm{\mu g \cdot L^{-1}}$)
Day 3									
AMB-UVB	17.1 ± 0.7	0.02 ±0.01	242 ± 24	17 ± 1	171 ± 7	5 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
ENH- UVB	17.1 ± 0.6	0.03 ±0.01	239 ± 12	16 ± 1	171 ± 7	6 ± 2	BDL (< 1)	BDL(<0.2)	BDL (< 1)
LAKE	17.3 ± 0.6	0.03 ±0.01	240 ± 8	17 ± 1	173 ± 6	5 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
Day 9-10									
AMB-UVB	17.7 ± 0.7	0.02 ±0.00	253 ± 24	17 ± 1	178 ± 7	5 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
ENH-UVB	17.1 ± 0.4	0.02 ±0.00	243 ± 11	16 ± 0	173 ± 4	5 ± 2	BDL (< 1)	BDL(<0.2)	BDL (< 1)
LAKE	17.4 ± 0.4	0.02 ±0.00	247 ± 10	17 ± 1	176 ± 3	4 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
Day 16-17									
AMB-UVB	17.1 ± 0.8	0.03 ±0.01	246 ± 24	16 ± 1	173 ± 8	4 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
ENH-UVB	17.6 ± 0.7	0.02 ±0.01	259 ± 21	16 ± 1	178 ± 6	4 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
LAKE	17.2 ± 2.4	0.02 ±0.01	244 ± 47	17 ± 2	176 ± 23	3 ± 0	BDL (< 1)	BDL(<0.2)	BDL (< 1)
Day 23-27									
AMB-UVB	18.4 ± 1.1	0.02 ±0.00	271 ± 12	17 ± 1	187 ± 11	3 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
ENH-UVB	18.1 ± 0.5	0.02 ±0.01	260 ± 10	18 ± 1	187 ± 5	4 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
LAKE	17.7 ± 0.7	0.02 ±0.00	257 ± 5	17 ± 1	180 ± 8	3 ± 1	BDL (< 1)	BDL(<0.2)	BDL (< 1)
Overall									
AMB-UVB	*17.5 ± 0.9*	*0.02 ±0.01*	*253 ± 22*	*17 ± 1*	*177 ± 10*	*4 ± 1*	*BDL (< 1)*	*BDL(<0.2)*	*BDL (< 1)*
ENH-UVB	*17.5 ± 0.7*	*0.02 ±0.01*	*250 ± 16*	*16 ± 1*	*177 ± 8*	*5 ± 1*	*BDL (< 1)*	*BDL(<0.2)*	*BDL (< 1)*
LAKE	*17.4 ± 1.0*	*0.02 ±0.01*	*247 ± 20*	*17 ± 1*	*176 ± 10*	*4 ± 1*	*BDL (< 1)*	*BDL(<0.2)*	*BDL (< 1)*

Table B-1 (continued). Physical and chemical characteristics of mesocosms and surrounding lake at TBL (Chapter 1).

	Cd ($\mu g \cdot L^{-1}$)	Cr ($\mu g \cdot L^{-1}$)	Mo ($\mu g \cdot L^{-1}$)	Ni ($\mu g \cdot L^{-1}$)	Pb ($\mu g \cdot L^{-1}$)	V ($\mu g \cdot L^{-1}$)
Day 3						
AMB-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
ENH-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
LAKE	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
Day 9-10						
AMB-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
ENH-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
LAKE	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
Day 16-17						
AMB-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
ENH-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
LAKE	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
Day 23-27						
AMB-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
ENH-UVB	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
LAKE	BDL (< 1)	BDL (< 1)	BDL (< 1)	BDL (< 2)	BDL (< 5)	BDL (< 1)
Overall						
AMB-UVB	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 2)*	*BDL (< 5)*	*BDL (< 1)*
ENH-UVB	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 2)*	*BDL (< 5)*	*BDL (< 1)*
LAKE	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 1)*	*BDL (< 2)*	*BDL (< 5)*	*BDL (< 1)*

Appendix C. Calculations

C-1. Chlorophyll *a*

1. For TBL 1994 (Chapter 1):

$$\text{Chl } a\ (\mu\text{g L}^{-1}) = \frac{[(11.64 * E_{663}) - (2.16 * E_{645}) + (0.10 * E_{630})] * V_e}{V_f * l}$$

where: $E_{663, 645, 630}$ = Spectrophotometric absorbance readings at 663, 645 and 630 nm respectively;

V_e = Volume (mL) of acetone extract;

V_f = Volume (L) of water filtered;

l = Light path of cell (cm)

2. For Resolute 1996 (Chapter 2):

$$\text{Chl } a\ (\mu\text{g L}^{-1}) = \frac{\text{Concentration } (\mu\text{g L}^{-1}) \text{ from calibration curve} * \text{Extraction volume (mL)}}{\text{Volume filtered onto GF/F filter (mL)}}$$

C-2. Phytoplankton productivity, size distribution and carbon allocation

1. Phytoplankton productivity:

$$\text{Total Productivity } (\mu g\ C\ L^{-1}\ h^{-1}) = \frac{(S-B) * 1.06 * DIC}{T * t}$$

Where:

S = Activity per mL from the treatment sample (0.2 μm) filter (DPM mL^{-1});

B = Activity per mL from the dark sample (0.2 μm) filter (DPM mL^{-1});

1.06 = Discrimination factor to correct for the ratio of ^{12}C:^{14}C uptake (Steemann Nielsen 1952);

DIC = Dissolved inorganic carbon concentration (μg C L^{-1});

T = Total activity per mL (DPM mL^{-1});

t = Incubation time (h)

2. Size distribution of phytoplankton productivity:

$$\text{(1) Percent contribution of picoplankton (0.2 – 2 μm)} = \frac{(S_{0.2} - S_2) * 100}{S_{0.2}}$$

Where:

$S_{0.2,\,2}$ = Activity per mL from the treatment sample on the 0.2 and 2 μm filters respectively (DPM mL^{-1}).

$$\text{(2) Percent contribution of nanoplankton (2 - 20 μm)} = \frac{(S_2 - S_{20}) * 100}{S_{0.2}}$$

Where:

$S_{0.2,\,2,\,20}$ = Activity per mL from the treatment sample on the 0.2, 2 and 20 μm filters respectively (DPM mL^{-1}).

(3) Percent contribution of netplankton (> 20 µm) $= \frac{S_{20}}{S_{0.2}} * 100$

Where:

$S_{0.2,\,20}$ = Activity per mL from the treatment sample on the 0.2, 2 and 20 µm filters respectively (DPM mL^{-1}).

3. Carbon allocation:

Percent carbon allocation into LMW, lipid, polysaccharide or protein $= \frac{S_{LMW,\,lipid,\,poly\,or\,protein}}{S_{total}} * 100$

Where:

$S_{LMW,\,lipid,\,poly,\,protein}$ = Activity from the treatment sample of the LMW, lipid, polysaccharide and protein fractions respectively (DPM);

S_{total} = Total activity (DPM) = $S_{LMW} + S_{lipid} + S_{poly} + S_{protein}$

C-3. Heterotrophic bacteria, photosynthetic picoplankton and heterotrophic flagellates abundances

1. Heterotrophic bacteria (HB):

$$\text{HB (cells mL}^{-1}\text{)} = \frac{(\text{\# cells on field}) * (A_f / A_m)}{V_f * \text{Dilution factor}}$$

Where:

cells on field = Average number of cells per field (from 20 fields total);

A_f = Area of filter used (mm^2);

A_m = Area of field on the microscope (mm^2) = πr^2, with r = 0.08 mm at 100x

V_f = Volume of water filtered (mL);

Dilution factor = 0.90 or 0.96

2. Photosynthetic picoplankton (PPICO) and heterotrophic nanoflagellates (HNF):

$$\text{PPICO or HNF (cells mL}^{-1}\text{)} = \frac{(\text{\#cells on transect}) * (A_f / A_m)}{V_f * \text{Dilution factor}}$$

Where:

cells on transect = Number of cells per transect (3 transects total);

A_f = Area of filter used (mm^2);

A_m = Area covered on the microscope (mm^2) = transect (mm) * diameter of whole field (0.160 mm);

V_f = Volume of water filtered (mL);

Dilution factor = 0.90

C-4. Heterotrophic bacterial activity

$$\text{Bacterial Activity } (\text{pmol } ^{3}\text{H-TdR L}^{-1}\text{ h}^{-1}) = \frac{(S-B) * 1 \times 10^{12} \text{ pmol mol}^{-1}}{V_f * SA * D * t}$$

Where:

S = Activity of the sample (DPM);

B = Average activity of the formaldehyde-killed controls (DPM);

V_f = Volume filtered (L);

SA = Specific activity of the isotope = 6.5×10^4 Ci mol^{-1} ^{3}H-TdR;

D = Unit conversion factor = 2.2×10^{12} DPM Ci^{-1};

t = Incubation time (h)

C-5. Zooplankton

1. Volume of lake water filtered:

V (m^3) = (depth of haul) · (number of hauls) · (area of square net) · (E)

Where:

Depth of haul = Approx. 3 m;

Number of hauls = Number of vertical hauls = 2

Area of square net = 0.3 m x 0.3 m = 0.09 m^2

E = Filtering efficiency of the square net during vertical tows, calculated as the number of revolutions recorded by the Rigosha meter per metre of the vertical haul, divided by the relative ideal, 11 revs m^{-1}, obtained by hauling the net frame and meter through the same distance. The filtering efficiency (E) for the vertical tows ranged from 0.49 to 1.55 with a mean of 0.67 ± 0.23.

2. Total zooplankton density (TZD):

$$\text{TZD (\#organisms m}^3\text{)} = \frac{\text{Total number of zooplankton counted}}{\text{Volume of lake water filtered (m}^3\text{)}}$$

3. Relative abundance of each zooplankton taxa:

$$\text{Percent abundance of a given taxa} = \frac{\text{Total number of individuals in given taxa}}{\text{Total number of individuals in all taxa}} * 100$$

4. Total zooplankton length (TZL):

TZL (mm) = $\sum$ (mean length of taxa i * relative proportion of taxa i)

Appendix D. All statistical analyses for TBL (Chapter 1)

Table D-1. Repeated-measures ANOVA for the between-subject effects of UVB (ambient and enhanced UVB) and sampling depth (0.5 and 2.5 m) plus related interactions and within-subject effects (DAY and related interactions) on chlorophyll *a* levels ($\mu g\ L^{-1}$). Total of 4 sampling dates (day 3, 9, 16 and 23). Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and NS = not significant.

	DF	Chl *a*
Between-Subjects		
UVB	1	NS
DEPTH	1	NS
UVB * DEPTH	1	NS
Error	4	
Within-Subjects		
DAY	3	*
DAY * UVB	3	NS
DAY * DEPTH	3	NS
DAY * UVB * DEPTH	3	NS
Error	12	

Table D-2. Repeated-measures ANOVA for the between-subject effect of UVB (ambient and enhanced UVB) nested for mesocosms (ENCLO) and within-subject effects (DAY and related interactions) on total phytoplankton productivity (TOTAL; $\mu g\ C\ L^{-1}\ h^{-1}$), percent productivity of picoplankton (%PICO), nanoplankton (%NANO), and netplankton (%NET) and percent ^{14}C-sodium bicarbonate assimilated into low molecular weight (%LMW), lipid (%LIPID), polysaccharide (%POLY), and protein (%PRO). Total of 5 sampling dates (day 4, 8, 12 and 19 and 26), except for size distribution of productivity where there is no day 26. Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and NS = not significant.

	DF	TOTAL	%LMW	%LIPID	%POLY	%PRO	DF	%PICO	%NANO	%NET
Between-Subjects										
UVB	1	*	NS	NS	NS	NS	1	**	*	*
ENCLO (UVB)	2	NS	*	NS	NS	**	2	NS	NS	NS
Error	8						8			
Within-Subjects										
DAY	4	***	**	***	*	**	3	***	**	**
DAY * UVB	4	***	NS	NS	NS	NS	3	NS	*	NS
DAY * ENCLO (UVB)	8	NS	NS	***	NS	NS	6	NS	NS	NS
Error	32						24			

Table D-3. Repeated-measures ANOVA for the between-subject effects of UVB (ambient and enhanced UVB) and depth of water sampled (0.5 and 2.5 m) plus related interactions and within-subject effects (DAY and related interactions) on heterotrophic bacterial abundance (HB; cells mL^{-1}), picocyanobacteria abundance (PPICO; cells mL^{-1}) and heterotrophic nanoflagellate abundance (HNF; cells mL^{-1}). Total of 3 sampling dates (day 3, 16 and 23), except for PICO and HF where there is no day 23. Statistical significance at * p < 0.05, ** p < 0.01, *** p < 0.001 and NS = not significant.

	DF	HB	DF	PPICO	HNF
Between-Subjects					
UVB	1	NS	1	*	*
DEPTH	1	NS	1	NS	NS
UVB * DEPTH	1	NS	1	*	NS
Error	4		4		
Within-Subjects					
DAY	2	***	1	NS	**
DAY * UVB	2	***	1	*	**
DAY * DEPTH	2	*	1	NS	NS
DAY * UVB * DEPTH	2	NS	1	NS	NS
Error	8		4		

Table D-4. Repeated-measures ANOVA for the between-subject effects of UVB (ambient and enhanced UVB) nested for mesocosms (ENCLO) and depth of water sampled (0.5 and 2.5 m) plus related interactions and within-subject effects (DAY and related interactions) on heterotrophic bacterial (HB) activity (measured as tritiated thymidine assimilation rates; pmol ^{3}H-TdR L^{-1} h^{-1}). Total of 4 sampling dates (day 7, 13, 21 and 25), Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and NS = not significant.

	DF	HB Activity
Between-Subjects		
UVB	1	*
DEPTH	1	NS
UVB * DEPTH	1	NS
ENCLO (UVB)	2	NS
Error	10	
Within-Subjects		
DAY	3	***
DAY * UVB	3	***
DAY * DEPTH	3	NS
DAY * UVB * DEPTH	3	**
DAY * ENCLO (UVB)	6	NS
Error	30	

Table D-5. Repeated-measures ANOVA for the between-subject effect of UVB (ambient and enhanced UVB) nested for mesocoms (ENCLO) and within-subject effects (DAY and related interactions) on total zooplankton density (TZD; total number of individuals m^{-3}), total zooplankton mean length (TZML; mm) and the relative abundance of *Cyclops* (adults and nauplii), *Daphnia*, *Diaphanosoma* and *Keratella*. Total of 4 sampling dates (day 6, 13, 20 and 27), Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and NS = not significant.

				Relative Abundance				
	DF	TZD	TZML	*Cyclops* adults	*Cyclops* nauplii	*Daphnia*	*Diaphanasoma*	*Keratella*
Between-Subjects								
UVB	1	**	NS	***	NS	**	**	**
ENCLO (UVB)	2	NS	NS	*	NS	NS	NS	NS
Error	8							
Within-Subjects								
DAY	4	***	**	***	*	***	NS	*
DAY * UVB	4	**	*	**	NS	**	NS	NS
DAY * ENCLO (UVB)	8	NS	NS	NS	NS	NS	NS	NS
Error	32							

Table E-1. Total phytoplankton productivity (μg C · L^{-1} · h^{-1}; TOTAL) and productivity of picoplankton (0.2 – 2 μm; PICO), nanoplankton (2 – 20 μm; NANO) and netplankton (> 20 μm; NET) of water samples from the ambient (AMB) and enhanced (ENH) UVB mesoscosms during short-term (2-3 hours) incubations under subsurface solar radiation on each of the 4 sampling dates (days 4, 8, 12 and 19). Values are based on 3 samples from two replicate mesocosms respectively. ± SD.

	Productivity (μg C · L^{-1} · h^{-1})	
	AMB-UVB	ENH-UVB
Day 4		
TOTAL	0.10 ± 0.01	0.08 ± 0.01
PICO (0.2 - 2 μm)	0.06 ± 0.01	0.04 ± 0.01
NANO (2 - 20 μm)	0.04 ± 0.01	0.03 ± 0.01
NET (> 20 μm)	0.01 ± 0.01	0.01 ± 0.01
Day 8		
TOTAL	0.32 ± 0.05	0.19 ± 0.01
PICO (0.2 - 2 μm)	0.15 ± 0.02	0.08 ± 0.01
NANO (2 - 20 μm)	0.14 ± 0.02	0.10 ± 0.00
NET (> 20 μm)	0.03 ± 0.01	0.02 ± 0.00
Day 12		
TOTAL	0.37 ± 0.11	0.22 ± 0.07
PICO (0.2 - 2 μm)	0.22 ± 0.07	0.10 ± 0.01
NANO (2 - 20 μm)	0.13 ± 0.04	0.10 ± 0.05
NET (> 20 μm)	0.02 ± 0.01	0.02 ± 0.00
Day 19		
TOTAL	0.46 ± 0.22	0.98 ± 0.08
PICO (0.2 - 2 μm)	0.26 ± 0.12	0.57 ± 0.08
NANO (2 - 20 μm)	0.18 ± 0.09	0.31 ± 0.05
NET (> 20 μm)	0.03 ± 0.01	0.10 ± 0.04

Table E-2. Total carbon uptake (μg C · L^{-1} · h^{-1}; TOTAL) and its incorporation into low molecular weight metabolites (LMW), lipid, polysaccharide (POLY) and protein of water samples from the ambient (AMB) and enhanced (ENH) UVB mesocosms during short-term (2-3 hours) incubations at subsurface solar radiation on each of the 4 sampling dates (days 4, 8, 12 and 19). Values are based on 3 samples from two replicate mesocosms respectively. ± SD.

	Carbon Uptake (μg C · L^{-1} · h^{-1})	
	AMB-UVB	ENH-UVB
Day 4		
TOTAL	0.10 ± 0.01	0.08 ± 0.01
LMW	0.04 ± 0.00	0.03 ± 0.01
LIPID	0.02 ± 0.00	0.02 ± 0.01
POLY	0.02 ± 0.01	0.02 ± 0.00
PROTEIN	0.03 ± 0.01	0.02 ± 0.01
Day 8		
TOTAL	0.32 ± 0.05	0.19 ± 0.01
LMW	0.09 ± 0.01	0.06 ± 0.01
LIPID	0.08 ± 0.02	0.05 ± 0.00
POLY	0.07 ± 0.01	0.04 ± 0.01
PROTEIN	0.08 ± 0.01	0.05 ± 0.00
Day 12		
TOTAL	0.37 ± 0.11	0.22 ± 0.07
LMW	0.10 ± 0.03	0.07 ± 0.02
LIPID	0.07 ± 0.03	0.04 ± 0.01
POLY	0.07 ± 0.02	0.04 ± 0.01
PROTEIN	0.12 ± 0.03	0.07 ± 0.02
Day 19		
TOTAL	0.46 ± 0.22	0.98 ± 0.07
LMW	0.14 ± 0.05	0.30 ± 0.05
LIPID	0.12 ± 0.06	0.24 ± 0.05
POLY	0.08 ± 0.04	0.18 ± 0.02
PROTEIN	0.13 ± 0.06	0.26 ± 0.06
Day 26		
TOTAL	0.74 ± 0.11	0.68 ± 0.13
LMW	0.28 ± 0.00	0.21 ± 0.01
LIPID	0.14 ± 0.02	0.14 ± 0.01
POLY	0.15 ± 0.02	0.13 ± 0.01
PROTEIN	0.17 ± 0.01	0.20 ± 0.01

Table E-3. Total zooplankton (> 40 μm) abundance (nb. of organisms m^{-3}; TOTAL) and abundances of each taxonomic group for the ambient (AMB) and enhanced (ENH) UVB treatments on each of the 4 sampling dates (Day 6, 13, 20 and 27). Values are based on 3 samples from two replicate mesocosms respectively. ± SD.

	AMB-UVB	ENH-UVB
Day 6		
TOTAL	4965 ± 2659	5407 ± 994
Cyclops (adults)	3156 ± 2090	2372 ± 549
Cyclops (nauplii)	1386 ± 757	1707 ± 619
Daphnia	119 ± 38	226 ± 85
Diaphanosoma	32 ± 49	92 ± 52
Keratella	272 ± 251	1010 ± 639
Day 13		
TOTAL	6771 ± 1881	7981 ± 2551
Cyclops (adults)	4329 ± 1270	3630 ± 2090
Cyclops (nauplii)	1579 ± 679	1526 ± 757
Daphnia	121 ± 84	997 ± 32
Diaphanosoma	30 ± 41	114 ± 49
Keratella	713 ± 486	1714 ± 251
Day 20		
TOTAL	6406 ± 1645	11180 ± 1376
Cyclops (adults)	2504 ± 634	4429 ± 998
Cyclops (nauplii)	2456 ± 1004	3103 ± 865
Daphnia	390 ± 301	1240 ± 331
Diaphanosoma	70 ± 62	356 ± 170
Keratella	986 ± 588	2053 ± 275
Day 27		
TOTAL	4795 ± 2719	8757 ± 3039
Cyclops (adults)	2548 ± 1852	2631 ± 1292
Cyclops (nauplii)	1009 ± 445	2378 ± 1091
Daphnia	920 ± 571	1597 ± 1032
Diaphanosoma	64 ± 51	243 ± 203
Keratella	254 ± 191	1980 ± 1156

Table E-4. Mean lengths (mm) of each zooplankton taxa and total zooplankton mean length (TZML) in the mesocosms exposed to ambient (AMB) and enhanced (ENH) UVB levels for each of the 4 sampling dates (Day 6, 13, 20 and 27) plus all 4 sampling dates combined. Values are based on 3 samples from two replicate mesocosms respectively (expect for the last column). TZML have been corrected for relative abundance of all taxa. ± SD.

	Day 6		Day 13		Day 20		Day 27		**Overall**
	AMB	ENH	AMB	ENH	AMB	ENH	AMB	ENH	
Cyclop sp.	0.87 ±0.13	0.92 ±0.08	0.86 ±0.04	0.80 ±0.06	0.73 ±0.08	0.72 ±0.06	0.78 ±0.11	0.70 ±0.18	**0.78 ±0.14**
Nauplius	0.25 ±0.03	0.27 ±0.07	0.25 ±0.01	0.26 ±0.08	0.19 ±0.02	0.20 ±0.02	0.20 ±0.02	0.18 ±0.01	**0.22 ±0.05**
Daphnia sp.	1.14 ±0.32	1.16 ±0.20	1.11 ±0.20	1.24 ±0.08	1.29 ±0.12	1.30 ±0.10	1.38 ±0.06	1.30 ±0.09	**1.24 ±0.26**
Diaphanosoma sp.	0.99 ±0.02	1.08 ±0.54	0.97 ±0.49	0.82 ±0.28	1.12 ±0.07	1.02 ±0.10	1.37 ±0.24	1.24 ±0.20	**1.00 ±0.44**
Keratella sp.	0.16 ±0.02	0.17 ±0.05	0.16 ±0.01	0.16 ±0.01	0.16 ±0.02	0.18 ±0.03	0.16 ±0.01	0.17 ±0.01	**0.17 ±0.06**
TMZL	**0.66 ±0.10**	**0.59 ±0.08**	**0.65 ±0.02**	**0.61 ±0.08**	**0.48 ±0.09**	**0.54 ±0.05**	**0.74 ±0.12**	**0.58 ±0.19**	**0.61 ±0.12**

Table E-5. Summary of all variables measured for the two UVB treatments (AMB-UVB and ENH-UVB) and the surrounding lake (outside the mesocoms) during the experimental period. Values represent the average of all the sampling dates combined. ± SD (n = 8 – 30). **Abb:** chlorophyll *a* (Chl *a*), low molecular weight metabolites (LMW), photosynthetic picoplankton (PPICO), heterotrophic nanoflagellates (HNF), total zooplankton density (TZD), total zooplankton mean length (TZML).

	AMB-UVB	ENH-UVB	LAKE
Chl *a* (µg L^{-1})	0.9 ± 0.3	0.8 ± 0.3	0.4 ± 0.2
Phytoplankton Production (µgC L^{-1} h^{-1})	0.4 ± 0.2	0.4 ± 0.4	0.2 ± 0.1
Size fractionation of productivity (%):			
Picoplankton (0.2 - 2 µm)	54 ± 8	48 ± 8	46 ± 14
Nanoplankton (2 - 20 µm)	39 ± 7	42 ± 8	43 ± 11
Netplankton (> 20 µm)	7 ± 2	9 ± 2	10 ± 4
Carbon Allocation (%):			
LMW	31 ± 5	31 ± 4	32 ± 4
Lipid	22 ± 4	22 ± 3	20 ± 3
Polysaccharide	20 ± 3	20 ± 2	21 ± 3
Protein	27 ± 4	27 ± 4	27 ± 3
Bacterial abundance (10^6 cells mL^{-1})	2.9 ± 1.2	3.2 ± 2.0	2.4 ± 1.2
Bacterial activity (pmol ^{3}H-TdR L^{-1} h^{-1})	1.4 ± 0.6	1.6 ± 0.4	0.9 ± 0.4
PPICO abundance (cells mL^{-1})	229 ± 98	136 ± 95	33 ± 32
HNF abundance (cells mL^{-1})	129 ± 60	297 ± 232	115 ± 111
TZD (number of individuals L^{-1})	5.7 ± 2.3	8.3 ± 2.9	19.9 ± 12.4
TZML (mm)	0.63 ± 0.12	0.58 ± 0.11	0.49 ± 0.08
Relative Abundance (%):			
Cyclops (adults)	54 ± 14	39 ± 9	41 ± 11
Cyclops (nauplii)	28 ± 11	27 ± 9	33 ± 13
Daphnia	8 ± 9	12 ± 8	13 ± 7
Diaphanosoma	1 ± 1	2 ± 2	2 ± 2
Keratella	9 ± 7	20 ± 7	11 ± 6

Appendix F. Correlation between unprocessed filters and sums of all fractions for carbon uptake by phytoplankton populations from lakes around Resolute (Chapter 2)

Figure heading

Figure F-1. Degree of association in ^{14}C-activity (disintegration per minute mL^{-1}) between the sums of the derived fractions and unprocessed 0.2 µm Nuclepore filters. Each data point represents the activity of one sample. Pearson correlation coefficient = 0.989; $p < 0.001$; sample size (n) = 240.

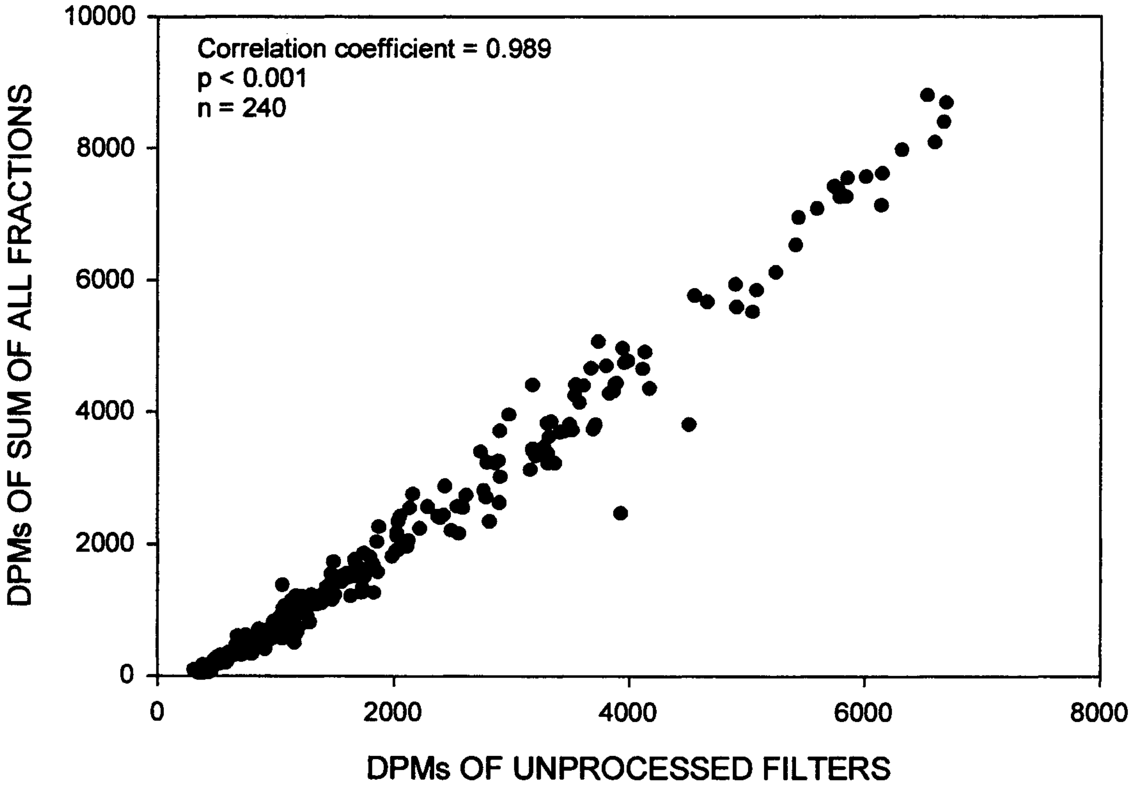

Correlation coefficient = 0.989
p < 0.001
n = 240
DPMs OF SUM OF ALL FRACTIONS
10000
8000
6000
4000
2000
0
0
2000
4000
6000
8000
DPMs OF UNPROCESSED FILTERS

Figure F-1.

Appendix G. Total incident solar radiation, UVA and UVB during the experiments in Chapter 2

Table G-1. Total incident solar radiation (E_o; in µmol photons m^{-2} s^{-1}), UVA (in W m^{-2}) and UVB (ambient and artificially enhanced; in W m^{-2}) measured in the 4 irradiance treatments (i.e., 6, 25, 50 and 100% surface irradiance) at the start and during the incubation period of each lake experiment and their overall mean (± SD) during the study. 1 µmol photons m^{-2} s^{-1} = 0.2174 W m^{-2}.

Lake		E_o (µmol photons m^{-2} s^{-1})				UVA (W m^{-2})				AMB-UVB (W m^{-2})				ENH-UVB (W m^{-2})			
		6	25	50	100	6	25	50	100	6	25	50	100	6	25	50	100
Barren	0 h	25	120	200	400	0.40	1.10	2.25	4.55	0.04	0.09	0.19	0.37	0.06	0.25	0.39	0.71
L.	2 h	50	200	420	840	0.66	1.80	4.05	7.83	0.05	0.15	0.28	0.64	0.10	0.30	0.47	1.00
(5 Aug.)	8 h	15	50	110	200	N/A	N/A	N/A	N/A	0.02	0.05	0.09	0.15	0.07	0.20	0.38	0.64
Black	0 h	50	125	280	540	0.41	1.62	3.00	5.60	0.04	0.12	0.25	0.46	0.12	0.34	0.62	1.15
Char L.	2 h	25	110	210	420	0.45	1.70	2.80	5.30	0.04	0.12	0.23	0.43	0.08	0.32	0.51	0.97
(7 Aug.)	8 h	30	80	150	280	0.20	0.65	1.20	2.25	0.01	0.04	0.08	0.14	0.07	0.23	0.41	0.73
Char L.	0 h	30	120	220	440	0.50	1.80	3.00	5.60	0.04	0.12	0.22	0.39	0.08	0.25	0.49	0.87
(14 Aug)	2 h	40	380	700	1500	0.70	2.60	5.50	11.00	0.05	0.19	0.40	0.78	0.10	0.34	0.64	1.10
	8 h	10	45	90	180	0.11	0.45	1.08	2.00	0.02	0.05	0.08	0.20	0.04	0.18	0.34	0.62
Clear L.	0 h	60	300	750	1100	0.50	2.60	4.95	10.00	0.06	0.18	0.45	0.80	0.11	0.45	0.87	1.53
(21 July)	5 h	12	55	110	220	0.18	0.65	1.18	2.31	0.02	0.06	0.09	0.16	0.07	0.21	0.34	0.58
Meretta	0 h	30	150	260	520	0.50	1.37	2.60	4.90	0.03	0.12	0.20	0.38	0.07	0.34	0.61	1.08
L.	2 h	75	230	420	850	0.90	2.60	4.60	8.80	0.05	0.19	0.33	0.66	0.09	0.34	0.65	1.16
(12 Aug)	8 h	45	150	300	700	0.40	1.05	2.30	4.35	0.01	0.07	0.17	0.31	0.07	0.29	0.52	0.92
North L.	0 h	110	460	775	1500	0.83	3.82	7.20	13.66	0.08	0.34	0.65	1.23	0.30	0.46	0.99	1.74
(10 July)	3 h	105	375	875	1675	1.55	4.25	8.65	16.41	0.11	0.46	0.81	1.58	0.17	0.53	1.15	2.12
	6 h	63	513	825	1400	0.66	3.58	6.35	13.89	0.08	0.33	0.62	1.27	0.11	0.52	1.13	2.03
	12 h	10	65	185	413	0.13	0.67	1.50	3.18	0.01	0.05	0.10	0.21	0.04	0.23	0.46	0.87
	24 h	115	388	788	1500	0.80	3.63	7.38	13.50	0.08	0.27	0.62	1.18	0.07	0.54	1.06	1.84
North L.	0 h	50	350	500	1250	0.74	2.40	4.20	8.70	0.06	0.17	0.34	0.65	0.12	0.41	0.70	1.30
(1 Aug.)	2 h	30	170	300	600	0.60	1.70	3.40	6.50	0.06	0.12	0.30	0.55	0.11	0.29	0.50	0.90
	8 h	30	120	210	440	0.33	1.06	2.20	4.00	0.03	0.08	0.14	0.27	0.09	0.29	0.50	0.86

Table G-1 (continued). Total incident solar radiation, UVA and UVB during the experiments in Chapter 2.

Lake		E_o (μmol photons m^{-2} s^{-1})				UVA (W m^{-2})				AMB-UVB (W m^{-2})				ENH-UVB (W m^{-2})			
		6	25	50	100	6	25	50	100	6	25	50	100	6	25	50	100
North L.	0 h	N/A	N/A	150	360	N/A	N/A	1.95	3.80	N/A	N/A	0.12	0.28	N/A	N/A	0.38	0.75
(9 Aug.)	2 h	N/A	N/A	280	620	N/A	N/A	3.85	7.15	N/A	N/A	0.26	0.49	N/A	N/A	0.46	0.92
	4 h	N/A	N/A	800	1500	N/A	N/A	6.00	12.00	N/A	N/A	0.47	0.87	N/A	N/A	0.58	1.08
	8 h	N/A	N/A	250	550	N/A	N/A	2.30	5.00	N/A	N/A	0.13	0.31	N/A	N/A	0.38	0.74
	12 h	N/A	N/A	29	55	N/A	N/A	0.23	0.43	N/A	N/A	0.01	0.03	N/A	N/A	0.31	0.55
	24 h	N/A	N/A	200	550	N/A	N/A	2.60	5.60	N/A	N/A	0.18	0.41	N/A	N/A	0.33	0.68
Resolute	0 h	40	145	295	575	0.70	2.00	3.60	7.00	0.08	0.20	0.29	0.58	0.12	0.39	0.72	1.32
L.	2 h	60	200	350	710	0.80	2.40	4.00	8.21	0.10	0.25	0.39	0.79	0.21	0.55	0.94	1.72
(17 Aug)	8 h	20	90	150	325	0.25	1.10	2.00	4.00	0.04	0.09	0.16	0.38	0.06	0.21	0.41	0.73
Small L	0 h	45	180	340	650	0.44	1.50	2.85	5.40	0.04	0.12	0.24	0.46	0.08	0.27	0.45	0.84
(28 July)	2 h	22	80	125	245	N/A	N/A	5.60	6.31	0.03	0.06	0.12	0.23	0.08	0.28	0.45	0.82
	6 h	10	33	60	120	0.13	0.60	1.90	2.60	0.01	0.03	0.05	0.11	0.07	0.19	0.32	0.64
	12 h	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Tern L.	0 h	55	220	390	780	0.68	2.35	4.30	7.90	0.07	0.21	0.34	0.62	0.14	0.50	0.80	1.42
(3 Aug.)	2 h	60	225	440	900	0.50	2.10	4.10	7.88	0.05	0.17	0.32	0.62	0.15	0.44	0.88	1.60
	8 h	60	230	480	1200	0.50	1.35	3.30	6.60	0.03	0.10	0.20	0.39	0.09	0.36	0.65	1.19
Overall Mean		*45*	*192*	*352*	*706*	*0.54*	*1.88*	*3.55*	*6.78*	*0.05*	*0.15*	*0.27*	*0.52*	*0.10*	*0.34*	*0.59*	*1.07*
± SD		*28*	*128*	*243*	*455*	*0.30*	*1.02*	*1.94*	*3.74*	*0.03*	*0.10*	*0.18*	*0.35*	*0.05*	*0.11*	*0.24*	*0.42*

Appendix H. Physical characteristics of the nine lakes in the vicinity of Resolute (Cornwallis Island, Nunavut) during summer 1996 (Chapter 2)

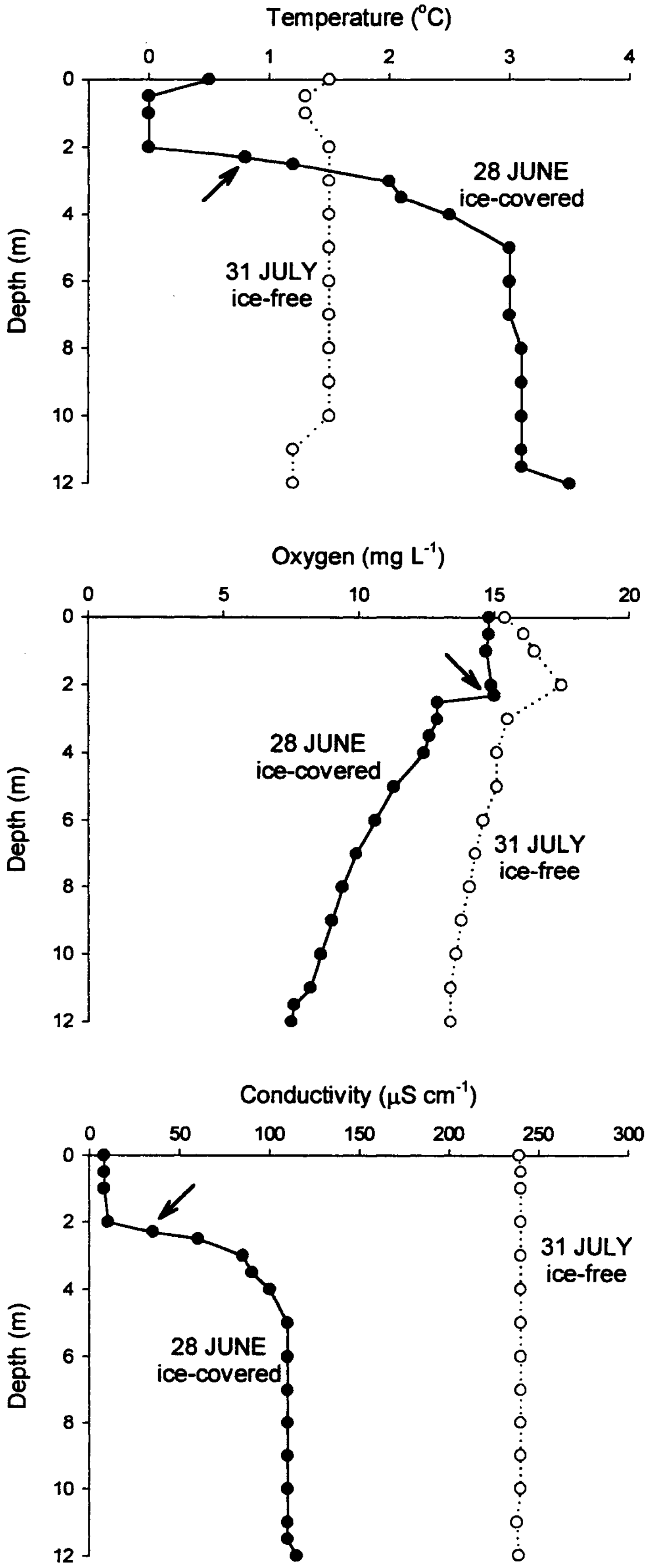
Figure headings

Figure H-1. Profiles of water temperature (°C; top graph), dissolved oxygen (mg L^{-1}; middle graph), and water conductivity (µS cm^{-1}; bottom graph) in North Lake on 28 June (when lake is still ice-covered) and 31 July (when lake is nearly all ice-free). The arrow indicates the ice-water interface on 28 June.

Figure H-2. Water temperature (°C) profiles of Barren, Black Char, Char, Clear, Meretta, Resolute, Small, and Tern lakes measured on the indicated dates during ice-free conditions, except for Small Lake (ice-covered conditions).

Figure H-3. Dissolved oxygen (mg L^{-1}) profiles of Barren, Black Char, Char, Clear, Meretta, Resolute, Small, and Tern lakes measured on the indicated dates during ice-free conditions, except for Small Lake (ice-covered conditions).

Figure H-4. Water conductivity (µS cm^{-1}) profiles of Barren, Black Char, Char, Clear, Meretta, Resolute, Small, and Tern lakes measured on the indicated dates during ice-free conditions, except for Small Lake (ice-covered conditions).



Temperature (°C)
0
1
2
3
4
Depth (m)
0
2
4
6
8
10
12
28 JUNE
ice-covered
31 JULY
ice-free
Oxygen (mg L⁻¹)
0
5
10
15
20
Depth (m)
0
2
4
6
8
10
12
28 JUNE
ice-covered
31 JULY
ice-free
Conductivity (μS cm⁻¹)
0
50
100
150
200
250
300
Depth (m)
0
2
4
6
8
10
12
31 JULY
ice-free
28 JUNE
ice-covered

Figure H-1.

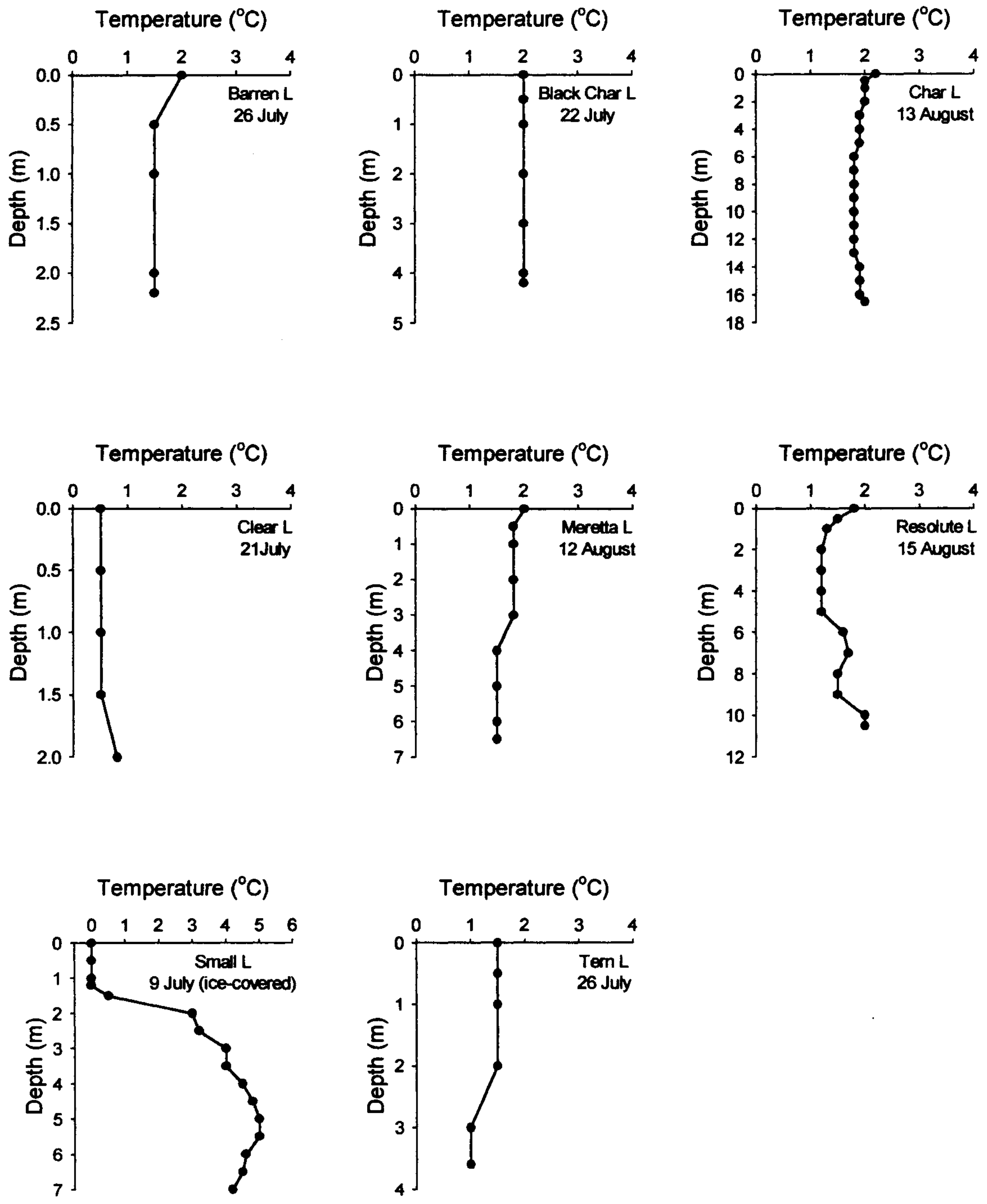

Temperature (°C)
Depth (m)
Barren L
26 July
Black Char L
22 July
Char L
13 August
Clear L
21July
Meretta L
12 August
Resolute L
15 August
Small L
9 July (ice-covered)
Tern L
26 July

Figure H-2.

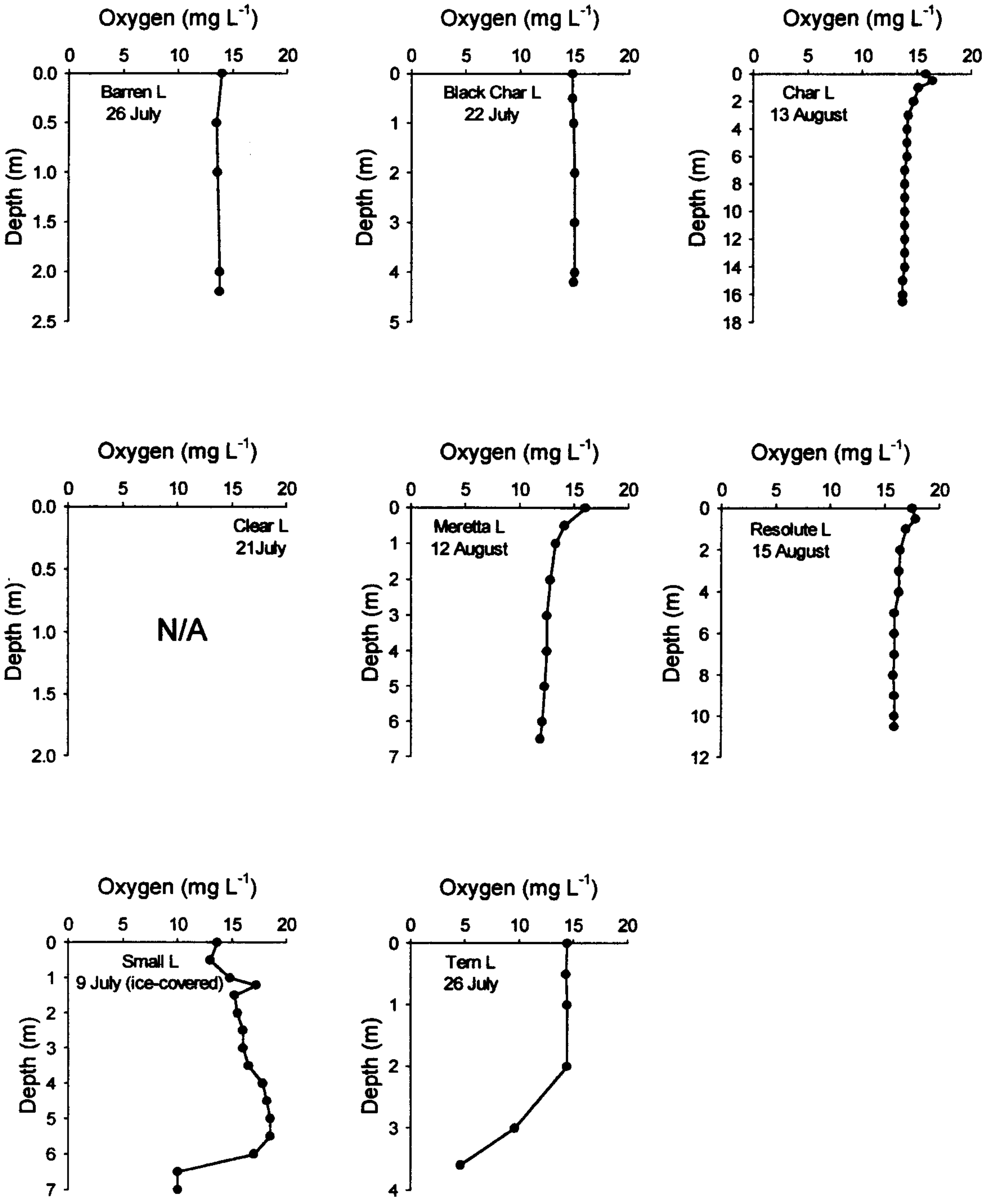

Oxygen (mg L^{-1})
Depth (m)
0
5
10
15
20
Barren L
26 July
0.0
0.5
1.0
1.5
2.0
2.5
Black Char L
22 July
Char L
13 August
Clear L
21July
N/A
Meretta L
12 August
Resolute L
15 August
Small L
9 July (ice-covered)
Tern L
26 July

Figure H-3.

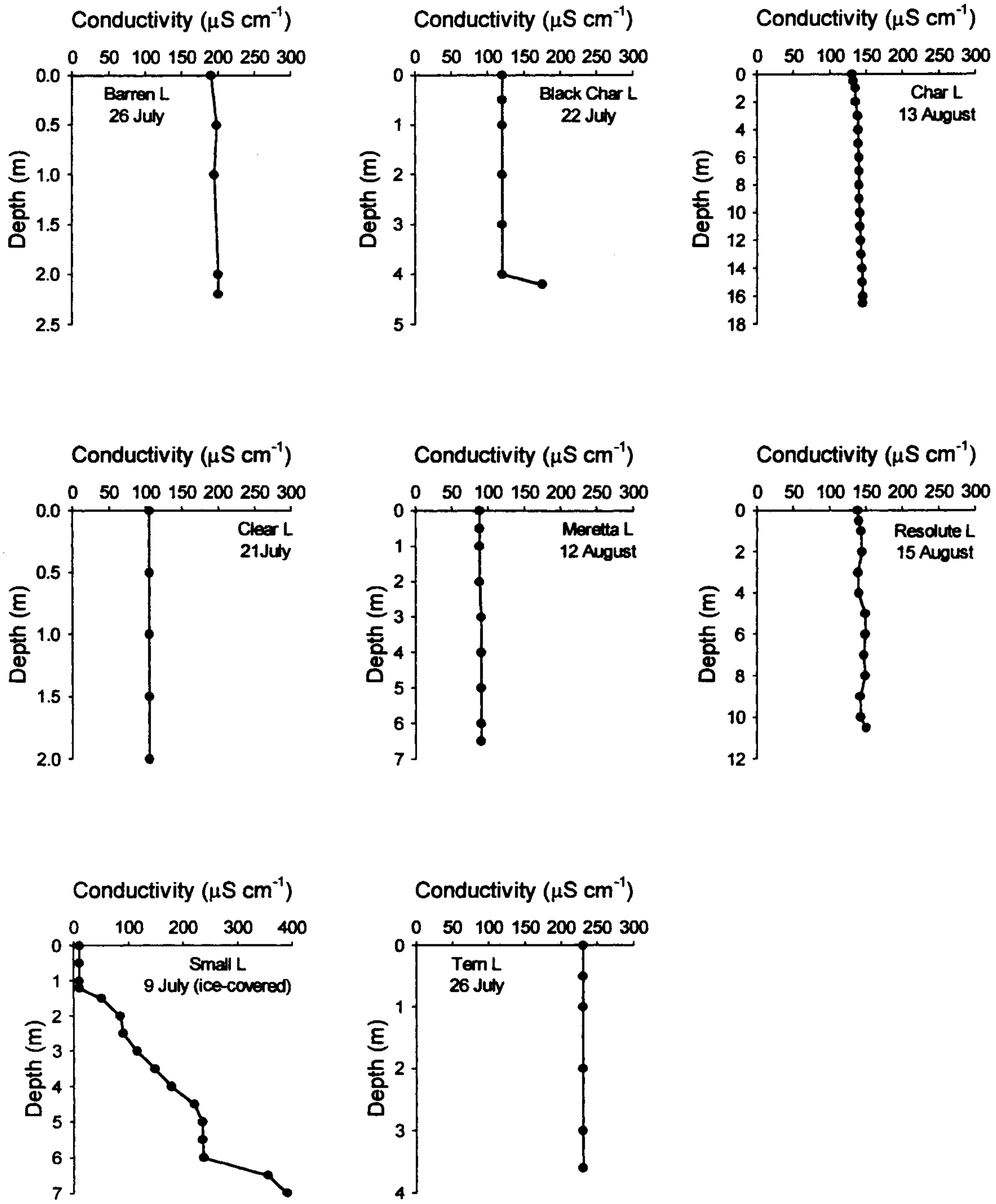

Conductivity (μS cm^{-1})
Depth (m)
Barren L
26 July
Black Char L
22 July
Char L
13 August
Clear L
21July
Meretta L
12 August
Resolute L
15 August
Small L
9 July (ice-covered)
Tern L
26 July
0 50 100 150 200 250 300
0 100 200 300 400
0.0 0.5 1.0 1.5 2.0 2.5
0 1 2 3 4 5
0 2 4 6 8 10 12 14 16 18
0.0 0.5 1.0 1.5 2.0
0 1 2 3 4 5 6 7
0 2 4 6 8 10 12
0 1 2 3 4 5 6 7
0 1 2 3 4

Figure H-4.

Appendix I. Chemical characteristics and DOC profiles of lakes in the vicinity of Resolute (Cornwallis Island, Nunavut) during summer 1996 (Chapter 2)

Figure headings

Figure I-1. Profiles of 25 chemical variables in North Lake on 28 June (when lake is still ice-covered) and 31 July (when lake is nearly all ice-free).

Figure I-2. Dissolved organic carbon (DOC; mg L^{-1}) profiles of Char (filled triangle; 13 August), Meretta (hollow circle; 11 August), North (filled circle; 31 July) and Resolute (hollow triangle; 15 August) lakes during ice-free conditions.

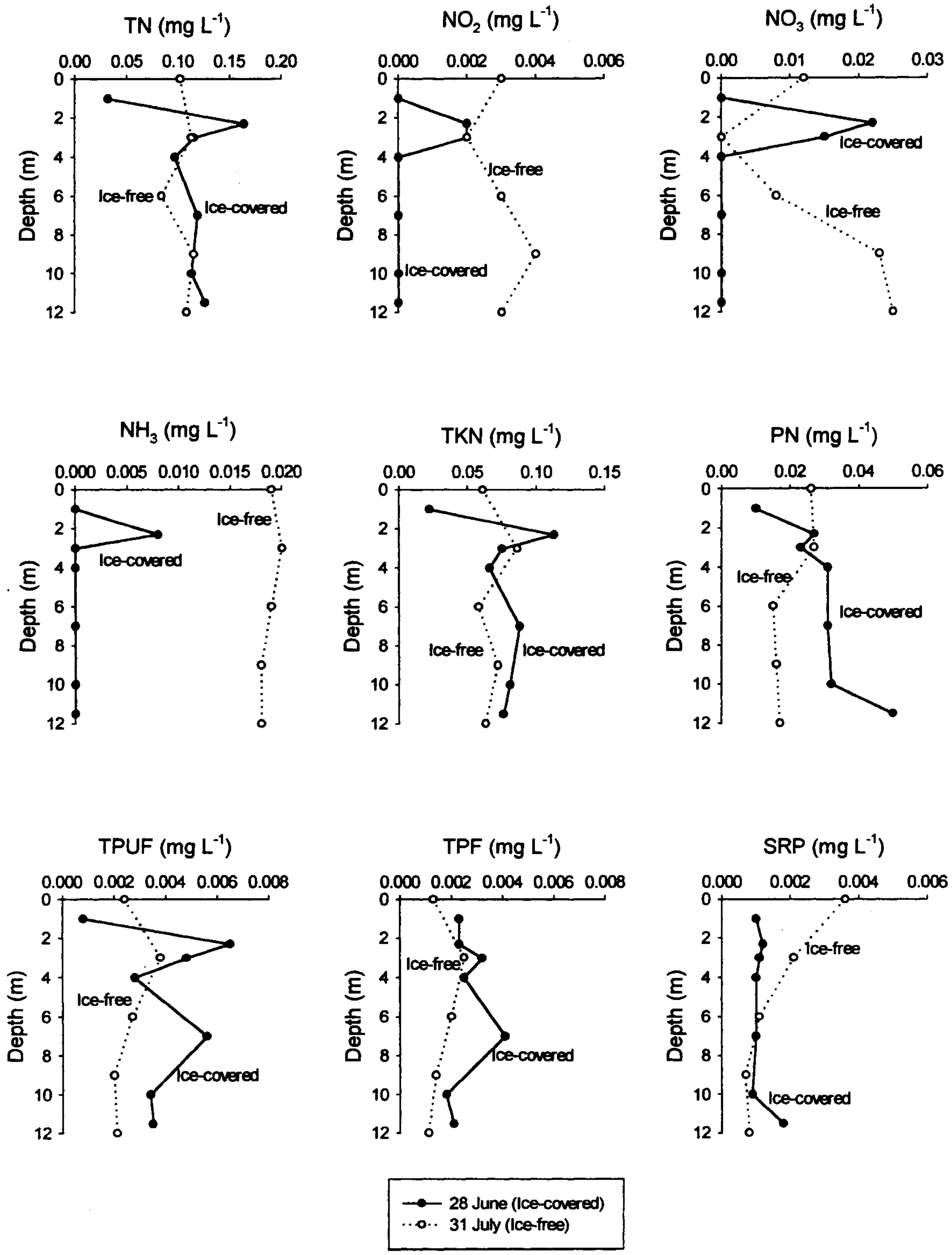

TN (mg L^{-1})
0.00 0.05 0.10 0.15 0.20
NO$_2$ (mg L^{-1})
0.000 0.002 0.004 0.006
NO$_3$ (mg L^{-1})
0.00 0.01 0.02 0.03
NH$_3$ (mg L^{-1})
0.000 0.005 0.010 0.015 0.020
TKN (mg L^{-1})
0.00 0.05 0.10 0.15
PN (mg L^{-1})
0.00 0.02 0.04 0.06
TPUF (mg L^{-1})
0.000 0.002 0.004 0.006 0.008
TPF (mg L^{-1})
0.000 0.002 0.004 0.006 0.008
SRP (mg L^{-1})
0.000 0.002 0.004 0.006
Depth (m)
0 2 4 6 8 10 12
Ice-free
Ice-covered
28 June (Ice-covered)
31 July (Ice-free)

Figure I-1.

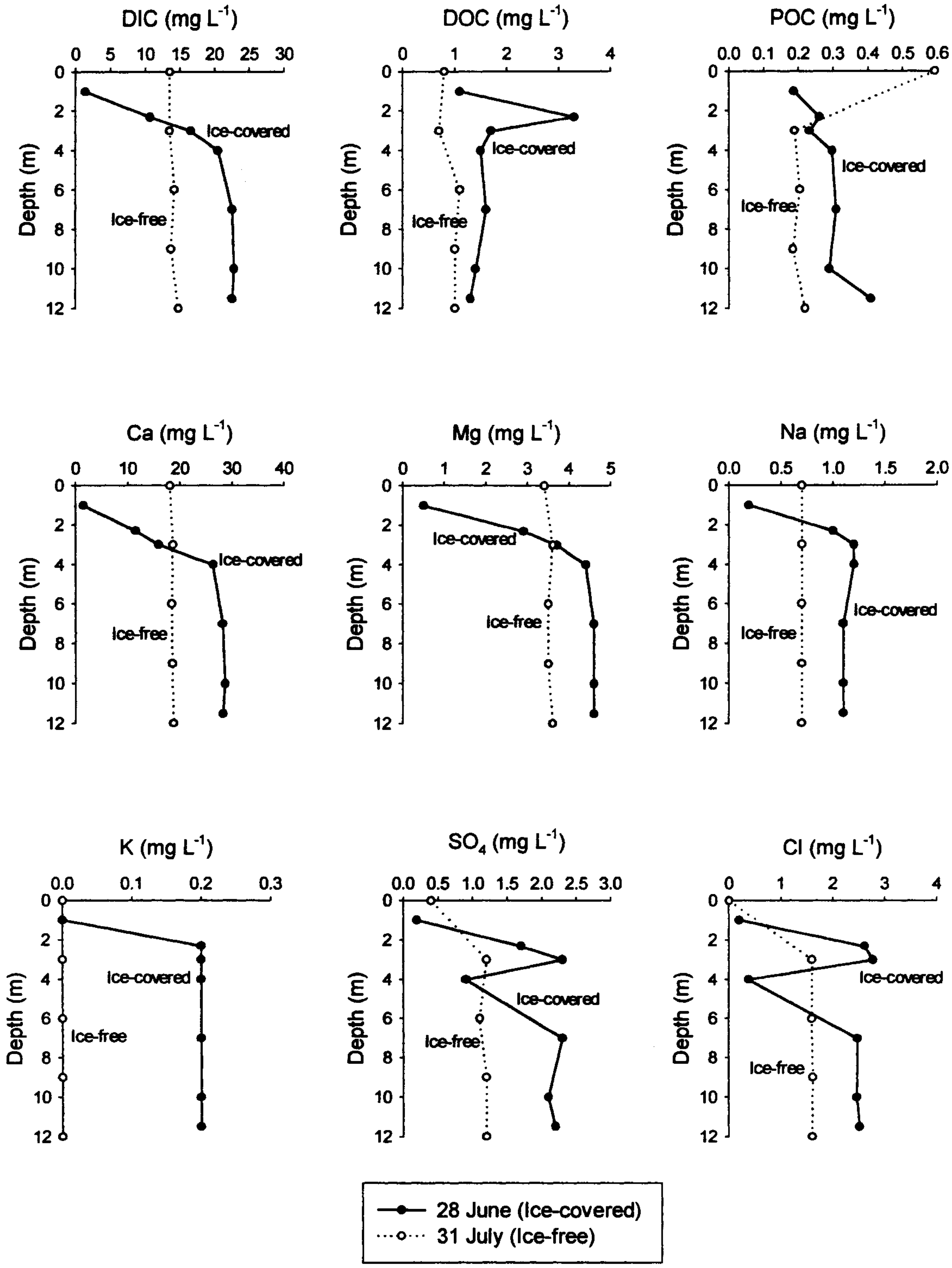


Figure I-1 (continued).

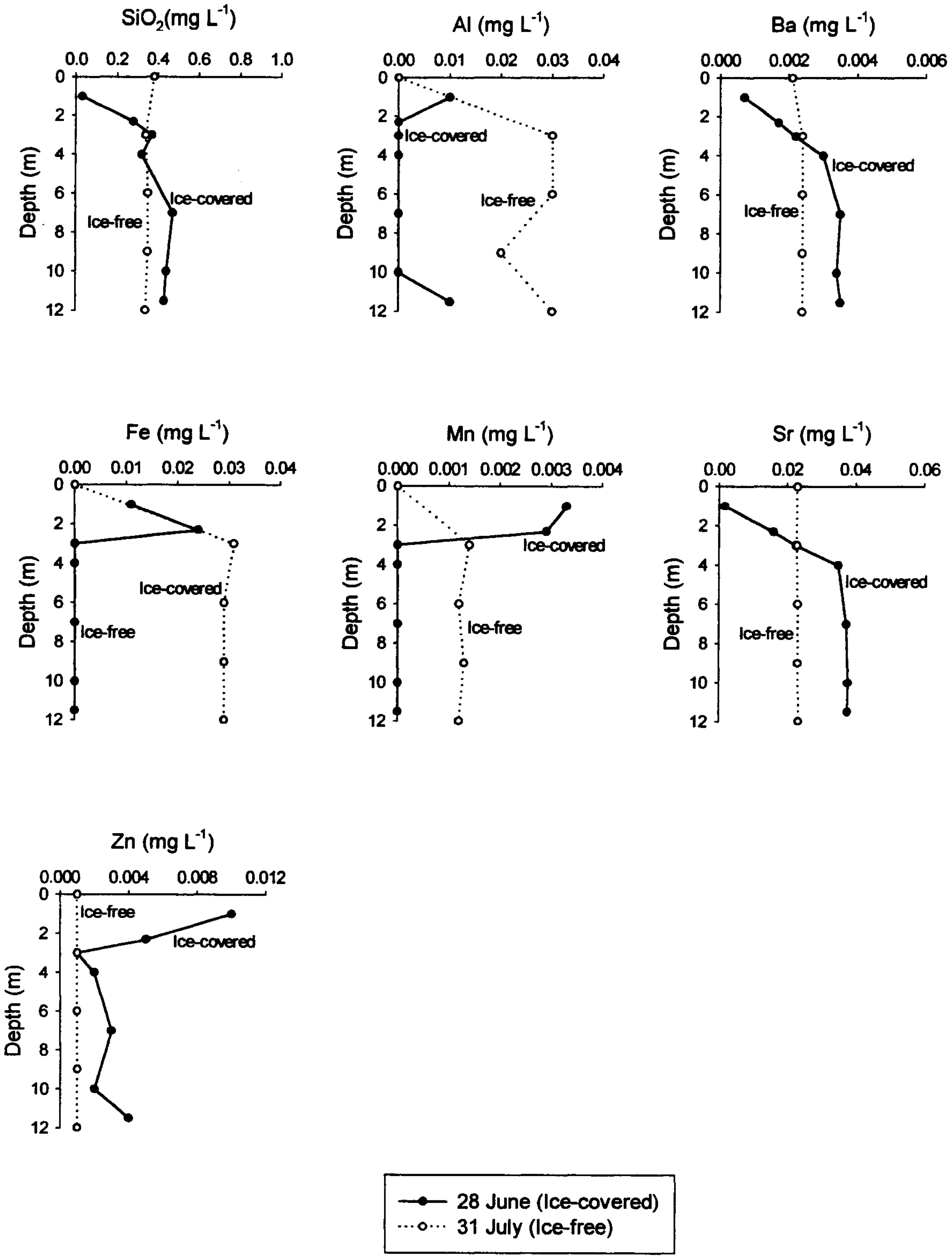


Figure I-1 (continued).

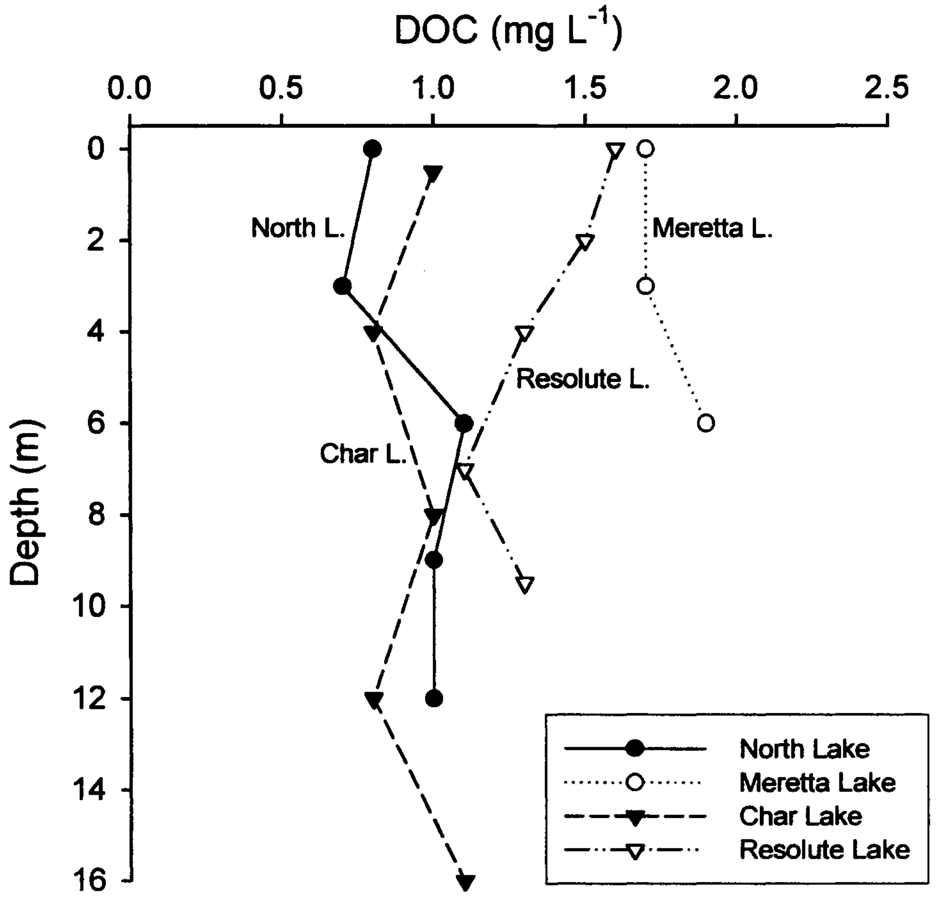

DOC (mg L-1)
0.0
0.5
1.0
1.5
2.0
2.5
Depth (m)
0
2
4
6
8
10
12
14
16
North L.
Meretta L.
Resolute L.
Char L.
North Lake
Meretta Lake
Char Lake
Resolute Lake

Figure I-2.

Table I-1. Depth integrated characteristic of 30 variables for the nine studied lakes during summer 1996. All units are in mg · L^{-1}, unless stated otherwise. **Abb:** below detection limit (BDL), not available (n/a), the"<" symbol indicates that sample was below the detection limit for that particular variable; depth integrated (Depth; meters); chlorophyll *a* (Chl *a*; μg L^{-1}), picocyanobacteria (Pico; cells mL^{-1}), total phosphorus unfiltered (TPUF), total phosphorus filtered (TPF), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), DOC fluorescence in quinine sulphate units (DOCFL; QSU); dissolved inorganic carbon (DIC), total Kjeldahl nitrogen (TKN), total nitrogen (TN), particulate organic carbon (POC), particulate nitrogen (PN). ± SD.

	Barren	Black Char	Char	Clear	Meretta	North	Resolute	Small	Tern
Date	5 August	7 August	14 August	21 July	12 August	9 August	17 August	27 July	2 August
Depth (m)	0.5 – 2.8	0.5 – 3.8	0.5 – 10.0	0.5 – 1.8	0.5 – 6.0	0.5 – 12.0	0.5 – 11.0	0.5 – 5.0	0.5 – 3.0
PH	8.00	7.89	N/a	7.95	n/a	7.90	n/a	8.24	8.16
Chl *a* (μg L^{-1})	0.19 ±0.02	0.67 ±0.04	0.51 ±0.03	0.57 ±0.07	1.09 ±0.02	0.50 ±0.03	1.02 ±0.05	0.63 ±0.02	1.59 ±1.25
Pico (cells mL^{-1})	0.02×10^4	0.01×10^4	3.70×10^4	0.01×10^4	0.05×10^4	0.24×10^4	2.70×10^4	2.00×10^4	0.01×10^4
TN	0.095	0.241	0.123	0.245	0.220	0.125	0.148	0.223	0.116
NO_2	0.002	0.002	0.002	0.002	0.003	0.003	0.004	0.002	0.002
NO_3	0.012	0.008	0.009	0.009	BDL	0.021	BDL	0.010	0.011
NH_3	0.016	0.018	0.016	0.018	0.005	0.015	0.018	0.019	0.017
TKN	0.071	0.201	0.088	0.198	0.185	0.076	0.119	0.172	0.086
PN	0.010	0.030	0.024	0.036	0.035	0.025	0.029	0.039	0.017
TPUF	0.0012	0.0096	0.0021	0.0051	0.0070	0.0017	0.0042	0.0040	0.0017
TPF	0.0007	0.0036	0.0016	0.0043	0.0043	0.0022	0.0018	0.0028	0.0020
SRP	0.0004	0.0004	0.0010	0.0008	0.0008	0.0006	0.0009	0.0030	0.0005
DIC	21.5	13.8	21.2	16.2	13.4	13.5	21.0	20.6	19.8
DOC	1.4	2.0	1.1	2.4	2.0	1.0	1.4	1.9	1.5
DOCFL	8.8	7.4	2.7	5.6	4.9	4.1	3.7	4.8	3.5
POC	0.221	0.285	0.358	0.427	0.274	0.200	0.291	0.368	0.232
TN:TPUF	79	25	59	48	31	74	35	56	68
POC:PN	22	10	15	12	8	8	10	9	14
DOC:POC	6	7	3	6	7	5	5	5	7

Table I-1 (continued). Depth integrated characteristic of 30 variables for the nine studied lakes during summer 1996 (Chapter 2).

	Barren	Black Char	Char	Clear	Meretta	North	Resolute	Small	Tern
Ca	20.9	16.1	32.7	17.8	17.0	18.6	30.9	21.5	18.9
Mg	8.8	4.5	5.2	6.2	4.7	3.6	6.3	8.2	8.2
Na	1.0	1.6	7.9	2.1	5.1	0.7	10.8	7.0	0.9
K	< 0.2	< 0.2	0.8	0.2	0.3	< 0.2	0.8	0.4	< 0.2
SO_4	1.1	1.5	13.6	2.1	4.0	1.1	14.7	2.7	1.0
Cl	2.54	3.39	11.40	3.86	8.08	1.61	18.70	13.50	2.08
SiO_2	0.27	0.23	0.67	0.81	0.13	0.32	0.69	0.91	0.17
Al	< 0.01	< 0.01	0.05	< 0.01	< 0.01	0.02	0.01	< 0.01	< 0.01
Ag	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Ba	0.0009	0.0026	0.0095	0.0059	0.0074	0.0024	0.0133	0.0069	0.0013
Be	< 0.0002	< 0.0002	< 0.0002	< 0.0002	< 0.0002	< 0.0002	< 0.0002	< 0.0002	< 0.0002
Cd	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Co	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Cr	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Cu	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Fe	0.003	0.023	0.072	0.063	0.062	0.019	0.026	0.007	0.016
Li	< 0.001	< 0.001	0.001	< 0.001	< 0.001	0.001	0.002	< 0.001	< 0.001
Mo	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Mn	< 0.0005	0.0005	0.0021	0.0021	0.0028	0.0008	0.0013	0.0019	0.0005
Ni	< 0.002	< 0.002	< 0.002	< 0.002	< 0.002	< 0.002	< 0.002	< 0.002	< 0.002
Pb	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005
Sr	0.0094	0.0257	0.0815	0.0248	0.0393	0.0234	0.0720	0.0379	0.0097
V	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Zn	0.001	0.001	0.002	0.002	0.001	0.002	0.001	0.001	0.001

Appendix J. Optical properties of North Lake (Chapter 2)

Figure heading

Figure J-1. Percent surface irradiance of UVB (280 – 320 nm), UVA (320 - 400 nm) and total incident radiation (mainly PAR) as a function of depth in North Lake, generated from calculated (for PAR) or estimated (for UVB and UVA) attenuation coefficients from equations by Scully and Lean (1994) using DOC and DOC fluorescence (DOCFL) levels (see Table 2-3 for K_{dI} values).

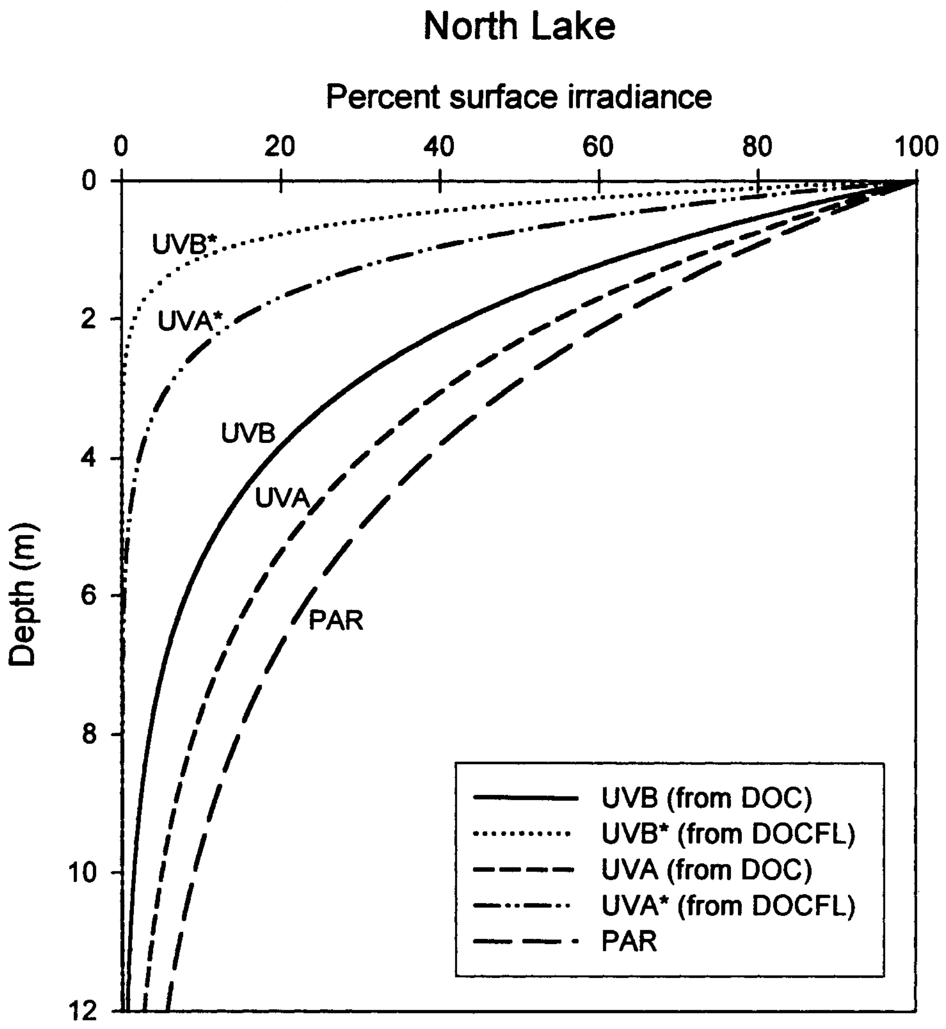

North Lake
Percent surface irradiance
0
20
40
60
80
100
0
2
4
6
8
10
12
Depth (m)
UVB*
UVA*
UVB
UVA
PAR
UVB (from DOC)
UVB* (from DOCFL)
UVA (from DOC)
UVA* (from DOCFL)
PAR

Figure J-1.

Appendix K. Profiles of chlorophyll a and picocyanobacteria of the lakes in the vicinity of Resolute during summer 1996 (Chapter 2)

Figure headings

Figure K-1. Profiles of chlorophyll *a* ($\mu g\ L^{-1}$) in: (a) North Lake on 28 June (filled diamond; when lake is still ice-covered) and 31 July (hollow diamond; when lake is nearly all ice-free) and (b) Char (hollow triangle), Meretta (filled circle), and Resolute (filled square) lakes on the indicated dates during ice-free conditions. The arrow indicates the ice-water interface on 28 June for North Lake.

Figure K-2. Profiles of picocyanobacteria (cells mL^{-1}) in: (a) North Lake on 28 June (filled diamond; when lake is still ice-covered) and 31 July (hollow diamond; when lake is nearly all ice-free) and (b) Char (hollow triangle), Meretta (filled circle), and Resolute (filled square) lakes on the indicated dates during ice-free conditions. The arrow indicates the ice-water interface on 28 June for North Lake.

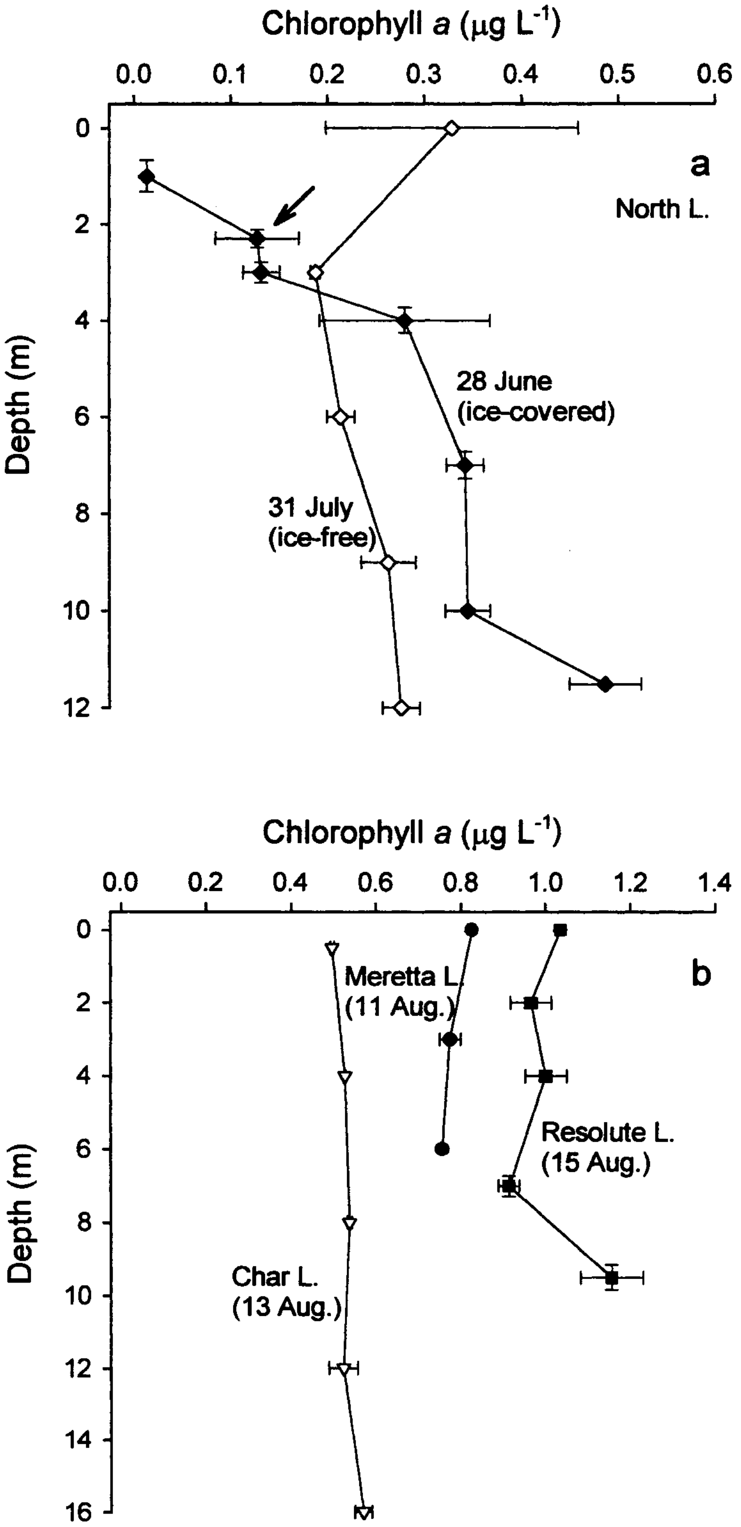

Chlorophyll a (μg L^{-1})
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Depth (m)
0
2
4
6
8
10
12
a
North L.
28 June
(ice-covered)
31 July
(ice-free)
Chlorophyll a (μg L^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Depth (m)
0
2
4
6
8
10
12
14
16
b
Meretta L.
(11 Aug.)
Resolute L.
(15 Aug.)
Char L.
(13 Aug.)

Figure K-1.

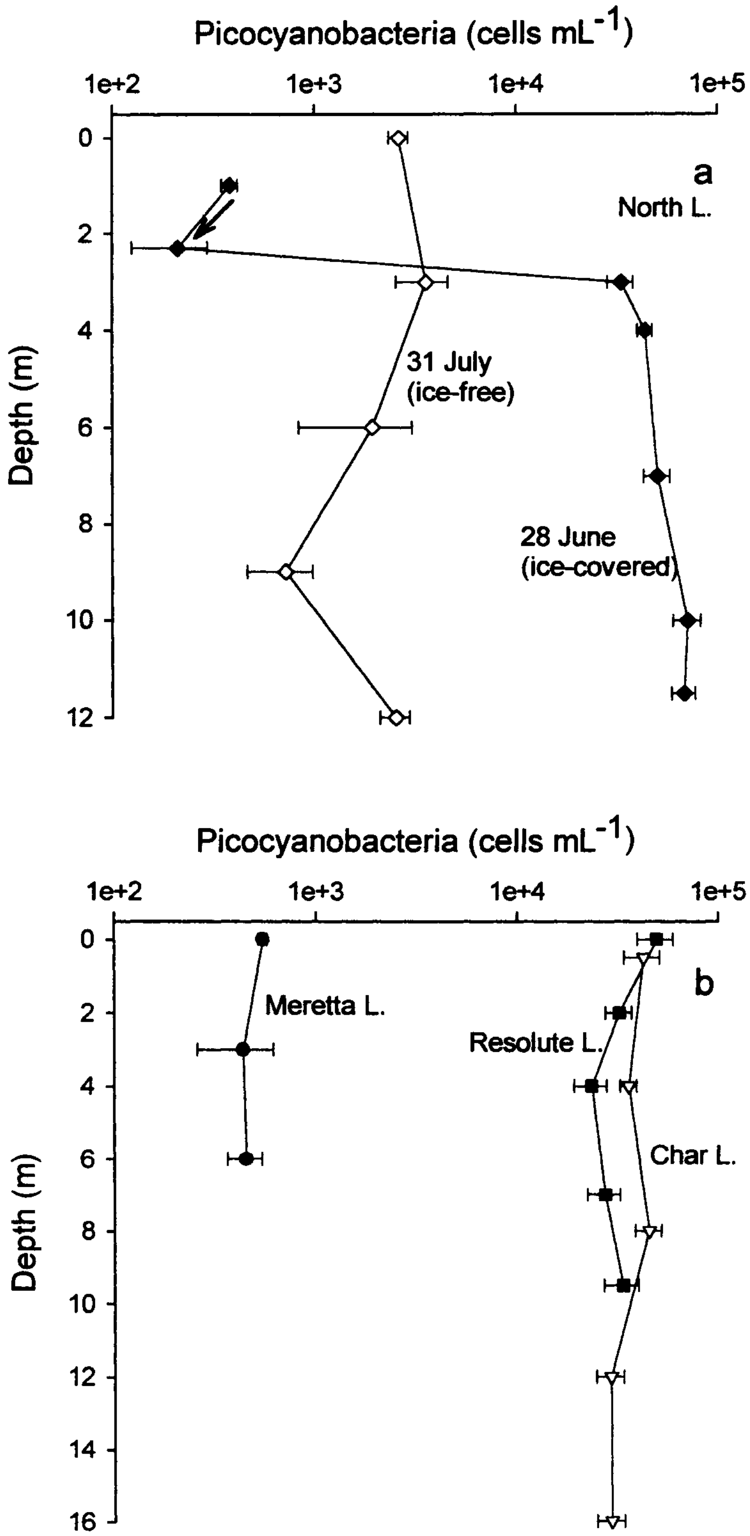

Picocyanobacteria (cells mL^{-1})
1e+2
1e+3
1e+4
1e+5
0
2
4
6
8
10
12
Depth (m)
a
North L.
31 July
(ice-free)
28 June
(ice-covered)
Picocyanobacteria (cells mL^{-1})
1e+2
1e+3
1e+4
1e+5
0
2
4
6
8
10
12
14
16
Depth (m)
b
Meretta L.
Resolute L.
Char L.

Figure K-2.

Appendix L. All statistical analyses for lakes in the vicinity of Resolute (Chapter 2)

Table L-1. Three-way analysis of variance (ANOVA) for the effects of enhanced UVB, time of incubation (T), irradiance levels (E) and their corresponding interactions on total phytoplankton productivity (TOTAL; $\mu g\ C\ L^{-1}\ h^{-1}$), chlorophyll-specific photosynthetic rate (P^B; $\mu g\ C \cdot \mu g\ Chl\ a^{-1} \cdot h^{-1}$), percent productivity of picoplankton (%PICO), nanoplankton (%NANO), and netplankton (%NET) and percent ^{14}C-sodium bicarbonate assimilated into low molecular weight (%LMW), lipid (%LIPID), polysaccharide (%POLY), and protein (%PRO) for all nine lakes. Statistical significance at * $p < 0.005$, ** $p < 0.01$, *** $p < 0.001$, and NS = not significant. Note: 2-way ANOVA for Clear Lake since productivity was measured only once i.e., after 5 hours of incubation (no time effect).

Lake	Effects	DF	TOTAL	P^B	%PICO	%NANO	%NET	%LMW	%LIPID	%POLY	%PRO
Barren L.	UVB	1	NS	NS	NS	NS	**	N/A	N/A	N/A	N/A
	Time	1	**	**	NS	NS	NS	N/A	N/A	N/A	N/A
	Irradiance	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * T	1	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	T * E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * T* E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	Error	32									
Black Char L.	UVB	1	***	***	NS	*	***	N/A	N/A	N/A	N/A
	Time	1	***	***	NS	NS	**	N/A	N/A	N/A	N/A
	Irradiance	3	**	**	*	**	***	N/A	N/A	N/A	N/A
	UVB * T	1	*	*	NS	*	*	N/A	N/A	N/A	N/A
	UVB * E	3	***	***	NS	NS	***	N/A	N/A	N/A	N/A
	T * E	3	NS	NS	NS	NS	*	N/A	N/A	N/A	N/A
	UVB * T* E	3	**	**	NS	NS	***	N/A	N/A	N/A	N/A
	Error	32									

Table L-1 (continued). Two or three-way analysis of variance (ANOVA).

Lake	Effects	DF	TOTAL	P^B	%PICO	%NANO	%NET	%LMW	%LIPID	%POLY	%PRO
Char L.	UVB	1	***	***	**	*	**	N/A	N/A	N/A	N/A
	Time	1	***	***	NS	NS	NS	N/A	N/A	N/A	N/A
	Irradiance	3	***	***	NS	NS	*	N/A	N/A	N/A	N/A
	UVB * T	1	**	**	*	NS	NS	N/A	N/A	N/A	N/A
	UVB * E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	T * E	3	*	*	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * T* E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	Error	32									
Clear L.*	UVB	1	***	***	NS	NS	***	***	NS	NS	***
	Irradiance	3	***	***	*	NS	***	NS	NS	***	***
	UVB * E	3	***	***	**	*	***	NS	NS	**	*
	Error	16									
Meretta L.	UVB	1	***	***	***	NS	***	***	NS	***	***
	Time	1	***	***	NS	***	***	***	*	***	NS
	Irradiance	3	***	***	***	***	***	*	NS	***	**
	UVB * T	1	***	***	NS	**	***	***	NS	**	**
	UVB * E	3	***	***	NS	*	***	***	NS	***	***
	T * E	3	***	***	NS	NS	NS	NS	NS	*	NS
	UVB * T *E	3	***	***	NS	NS	*	*	NS	*	NS
	Error	32									

Table L-1 (continued). Two or three-way analysis of variance (ANOVA).

Lake	Effects	DF	TOTAL	P^B	%PICO	%NANO	%NET	%LMW	%LIPID	%POLY	%PRO
North L. (10 July)	UVB	1	***	***	N/A	N/A	***	N/A	N/A	N/A	N/A
	Time	3	***	***	N/A	N/A	***	N/A	N/A	N/A	N/A
	Irradiance	3	***	***	N/A	N/A	***	N/A	N/A	N/A	N/A
	UVB * T	3	**	**	N/A	N/A	**	N/A	N/A	N/A	N/A
	UVB * E	3	*	*	N/A	N/A	**	N/A	N/A	N/A	N/A
	T * E	9	NS	NS	N/A	N/A	**	N/A	N/A	N/A	N/A
	UVB * T *E	9	**	**	N/A	N/A	**	N/A	N/A	N/A	N/A
	Error	64									
North L. (1 Aug.)	UVB	1	***	***	***	***	***	N/A	N/A	N/A	N/A
	Time	1	***	***	***	***	***	N/A	N/A	N/A	N/A
	Irradiance	3	***	***	***	***	**	N/A	N/A	N/A	N/A
	UVB * T	1	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * E	3	NS	NS	*	*	NS	N/A	N/A	N/A	N/A
	T * E	3	NS	NS	**	***	NS	N/A	N/A	N/A	N/A
	UVB * T *E	3	NS	NS	NS	*	NS	N/A	N/A	N/A	N/A
	Error	32									
North L. (9 Aug.)	UVB	1	***	***	N/A	N/A	N/A	**	***	***	***
	Time	4	***	***	N/A	N/A	N/A	***	***	***	***
	Irradiance	1	***	***	N/A	N/A	N/A	***	***	***	***
	UVB * T	4	NS	NS	N/A	N/A	N/A	***	**	***	***
	UVB * E	1	NS	NS	N/A	N/A	N/A	**	*	***	*
	T * E	4	NS	NS	N/A	N/A	N/A	NS	NS	NS	NS
	UVB * T *E	4	NS	NS	N/A	N/A	N/A	NS	NS	NS	NS
	Error	40									

Table L-1 (continued). Two or three-way analysis of variance (ANOVA).

Lake	Effects	DF	TOTAL	P^B	%PICO	%NANO	%NET	%LMW	%LIPID	%POLY	%PRO
Resolute L.	UVB	1	**	**	NS	NS	***	N/A	N/A	N/A	N/A
	Time	1	***	***	**	NS	***	N/A	N/A	N/A	N/A
	Irradiance	3	***	***	NS	NS	***	N/A	N/A	N/A	N/A
	UVB * T	1	*	*	NS	NS	***	N/A	N/A	N/A	N/A
	UVB * E	3	**	**	NS	NS	NS	N/A	N/A	N/A	N/A
	T * E	3	*	*	NS	NS	NS	N/A	N/A	N/A	N/A
	UVB * T *E	3	NS	NS	NS	NS	NS	N/A	N/A	N/A	N/A
	Error	32									
Small L.**	UVB	1	***	***	NS	NS	***	***	NS	NS	***
	Time	2	***	***	NS	NS	NS	NS	NS	*	***
	Irradiance	2	***	***	NS	NS	***	NS	NS	NS	NS
	UVB * T	2	***	***	NS	NS	NS	NS	*	NS	*
	UVB * E	2	***	***	NS	NS	***	NS	NS	NS	NS
	T * E	4	***	***	*	NS	*	NS	NS	*	NS
	UVB * T *E	4	*	*	NS	NS	NS	**	NS	**	NS
	Error	36									
Tern L.	UVB	1	***	***	***	NS	***	***	***	***	***
	Time	1	***	***	NS	**	***	**	NS	***	NS
	Irradiance	3	**	**	NS	NS	NS	**	*	NS	*
	UVB * T	1	***	***	**	NS	**	NS	NS	NS	**
	UVB * E	3	***	***	NS	NS	*	NS	NS	*	NS
	T * E	3	NS	NS	NS	NS	NS	*	NS	NS	NS
	UVB * T* E	3	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Error	32									

Table L-2. Pearson correlation coefficients between percent ^{14}C-sodium bicarbonate incorporated by picoplankton (PICO), nanoplankton (NANO) and netplankton (NET) under ambient (AMB) and enhanced (ENH) UVB conditions for each lake and when data of all lakes have been pooled together. Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and NS = not significant. n = sample size.

	Lake		PICO	NANO
AMB-UVB	Barren L	NANO	-0.934***	- - -
	(n = 24)	NET	-0.578**	0.247^{NS}
	Black Char L	NANO	-0.950***	- - -
	(n = 24)	NET	-0.254^{NS}	-0.060^{NS}
	Char L	NANO	-0.988***	- - -
	(n = 24)	NET	-0.332^{NS}	0.203^{NS}
	Clear L	NANO	-0.977***	- - -
	(n = 12)	NET	-0.180^{NS}	-0.035^{NS}
	Meretta L	NANO	-0.655**	- - -
	(n = 24)	NET	-0.608**	-0.201^{NS}
	North L	NANO	-0.952***	- - -
	(n = 24)	NET	-0.824***	0.609**
	Resolute L	NANO	-0.716***	- - -
	(n = 24)	NET	-0.680**	-0.024^{NS}
	Small L	NANO	-0.962***	- - -
	(n = 30)	NET	-0.284^{NS}	0.012^{NS}
	Tern L	NANO	-0.701***	- - -
	(n = 24)	NET	-0.678**	-0.048^{NS}
	Overall	_NANO_	_-0.523***_	- - -
	_(n = 210)_	_NET_	_-0.592***_	_-0.376***_
ENH-UVB	Barren L	NANO	-0.966***	- - -
	(n = 24)	NET	-0.548*	0.313^{NS}
	Black Char L	NANO	-0.968***	- - -
	(n = 24)	NET	0.278^{NS}	-0.510*
	Char L	NANO	-0.978***	- - -
	(n = 24)	NET	-0.175^{NS}	-0.032^{NS}
	Clear L	NANO	-0.640^{NS}	- - -
	(n = 12)	NET	-0.794**	0.042^{NS}
	Meretta L	NANO	-0.608**	- - -
	(n = 24)	NET	-0.182^{NS}	-0.670**
	North L	NANO	-0.964***	- - -
	(n = 24)	NET	-0.730***	0.523*
	Resolute L	NANO	-0.388^{NS}	- - -
	(n = 24)	NET	-0.588**	-0.517*
	Small L	NANO	-0.785***	- - -
	(n = 30)	NET	-0.391^{NS}	-0.263^{NS}
	Tern L	NANO	0.072^{NS}	- - -
	(n = 24)	NET	-0.834***	-0.611*
	Overall	_NANO_	_-0.503***_	- - -
	_(n = 210)_	_NET_	_-0.588***_	_-0.404***_

Table L-3. Pearson correlation coefficients between percent ^{14}C-sodium bicarbonate assimilated into low molecular weight (LMW), lipid, polysaccharide (POLY) and protein under ambient (AMB) and enhanced (ENH) UVB conditions for each lake and when data of all lakes have been pooled together. Statistical significance at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and NS = not significant. n = sample size.

	Lake		LMW	LIPID	POLY
AMB-UVB	Clear L	LIPID	-0.528^{NS}	- - -	- - -
	(n = 12)	POLY	0.609^{NS}	-0.130^{NS}	- - -
		PROTEIN	-0.837**	0.076^{NS}	-0.863**
	Meretta L	LIPID	0.132^{NS}	- - -	- - -
	(n = 24)	POLY	-0.783***	-0.337^{NS}	- - -
		PROTEIN	-0.767***	-0.278^{NS}	0.286^{NS}
	North L	LIPID	-0.902***	- - -	- - -
	(n = 30)	POLY	0.056^{NS}	-0.229^{NS}	- - -
		PROTEIN	-0.722***	0.674***	-0.691***
	Small L	LIPID	0.444^{NS}	- - -	- - -
	(n = 30)	POLY	-0.299^{NS}	-0.103^{NS}	- - -
		PROTEIN	-0.852***	-0.710***	-0.112^{NS}
	Tern L	LIPID	-0.185^{NS}	- - -	- - -
	(n = 24)	POLY	-0.721***	-0.287^{NS}	- - -
		PROTEIN	-0.909***	0.126^{NS}	0.447^{NS}
	Overall	*LIPID*	*-0.380****	- - -	- - -
	(n = 120)	*POLY*	*-0.465****	*-0.440****	- - -
		PROTEIN	*-0.791****	*0.374****	*-0.039*^{NS}
ENH-UVB	Clear L	LIPID	-0.121^{NS}	- - -	- - -
	(n = 12)	POLY	0.013^{NS}	0.211^{NS}	- - -
		PROTEIN	-0.718*	-0.305^{NS}	-0.653^{NS}
	Meretta L	LIPID	-0.042^{NS}	- - -	- - -
	(n = 24)	POLY	-0.915***	-0.141^{NS}	- - -
		PROTEIN	-0.341^{NS}	-0.085^{NS}	-0.007^{NS}
	North L	LIPID	-0.878***	- - -	- - -
	(n = 30)	POLY	0.380^{NS}	-0.429^{NS}	- - -
		PROTEIN	-0.417^{NS}	-0.016^{NS}	-0.391^{NS}
	Small L	LIPID	-0.400^{NS}	- - -	- - -
	(n = 30)	POLY	-0.683***	0.007^{NS}	- - -
		PROTEIN	-0.770***	0.032^{NS}	0.235^{NS}
	Tern L	LIPID	-0.497^{NS}	- - -	- - -
	(n = 24)	POLY	-0.405^{NS}	-0.469^{NS}	- - -
		PROTEIN	-0.859***	0.405^{NS}	0.118^{NS}
	Overall	*LIPID*	*-0.784****	- - -	- - -
	(n = 120)	*POLY*	*0.040*^{NS}	*-0.537****	- - -
		PROTEIN	*-0.622****	*0.249**	*-0.108*^{NS}

Appendix M. Total volumetric and chlorophyll-specific phytoplankton photosynthetic rates of the nine lakes in the vicinity of Resolute (Chapter 2)

Table M-1. Total phytoplankton productivity (µg C · L^{-1} · h^{-1}) and chlorophyll-specific photosynthetic rate (P^{B}; µg C · µg Chl a^{-1} · h^{-1}) of all nine lakes after exposure to ambient (AMB) and enhanced (ENH) UVB under 6, 25, 50 and/or 100% of incoming surface irradiance (%E$_o$). ± SD.

Lake		%E$_o$	Total Productivity (µg C · L^{-1} · h^{-1})		P^{B} (µg C · µg Chl *a*$^{-1}$ · h^{-1})	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Barren L. (5 August)	2 h	6	0.06 ± 0.03	0.08 ± 0.05	0.29 ± 0.15	0.40 ± 0.27
		25	0.09 ± 0.03	0.09 ± 0.04	0.48 ± 0.17	0.50 ± 0.20
		50	0.05 ± 0.03	0.04 ± 0.04	0.28 ± 0.17	0.23 ± 0.20
		100	0.08 ± 0.04	0.05 ± 0.01	0.41 ± 0.19	0.26 ± 0.06
	8 h	6	0.05 ± 0.01	0.03 ± 0.00	0.26 ± 0.06	0.18 ± 0.02
		25	0.06 ± 0.01	0.04 ± 0.01	0.32 ± 0.08	0.22 ± 0.05
		50	0.06 ± 0.02	0.04 ± 0.00	0.33 ± 0.11	0.19 ± 0.02
		100	0.03 ± 0.02	0.02 ± 0.01	0.18 ± 0.09	0.09 ± 0.04
Black Char L. (7 Aug.)	2 h	6	0.21 ± 0.05	0.15 ± 0.05	0.31 ± 0.07	0.23 ± 0.08
		25	0.26 ± 0.03	0.22 ± 0.04	0.39 ± 0.05	0.33 ± 0.06
		50	0.29 ± 0.05	0.17 ± 0.03	0.44 ± 0.07	0.26 ± 0.04
		100	0.32 ± 0.05	0.12 ± 0.03	0.49 ± 0.07	0.18 ± 0.04
	8 h	6	0.18 ± 0.01	0.15 ± 0.02	0.27 ± 0.01	0.22 ± 0.04
		25	0.27 ± 0.03	0.11 ± 0.02	0.41 ± 0.04	0.16 ± 0.03
		50	0.30 ± 0.02	0.08 ± 0.01	0.46 ± 0.04	0.11 ± 0.01
		100	0.22 ± 0.04	0.05 ± 0.02	0.33 ± 0.06	0.07 ± 0.03
Char L. (14 Aug.)	2 h	6	0.22 ± 0.07	0.23 ± 0.06	0.42 ± 0.13	0.46 ± 0.12
		25	0.22 ± 0.05	0.21 ± 0.02	0.44 ± 0.10	0.42 ± 0.04
		50	0.16 ± 0.05	0.16 ± 0.02	0.31 ± 0.09	0.31 ± 0.04
		100	0.15 ± 0.04	0.13 ± 0.01	0.29 ± 0.08	0.25 ± 0.01
	8 h	6	0.16 ± 0.03	0.14 ± 0.01	0.32 ± 0.05	0.28 ± 0.03
		25	0.14 ± 0.01	0.10 ± 0.01	0.27 ± 0.02	0.20 ± 0.03
		50	0.12 ± 0.02	0.06 ± 0.00	0.24 ± 0.05	0.12 ± 0.01
		100	0.07 ± 0.01	0.04 ± 0.00	0.14 ± 0.01	0.09 ± 0.00
Clear L. (21 July)	5 h	6	0.30 ± 0.05	0.28 ± 0.06	0.52 ± 0.09	0.49 ± 0.10
		25	0.53 ± 0.05	0.55 ± 0.02	0.94 ± 0.09	0.96 ± 0.04
		50	0.61 ± 0.02	0.50 ± 0.08	1.08 ± 0.04	0.87 ± 0.14
		100	0.47 ± 0.06	0.18 ± 0.08	0.82 ± 0.10	0.32 ± 0.14
Meretta L. (12 Aug.)	2 h	6	0.44 ± 0.01	0.49 ± 0.03	0.40 ± 0.01	0.45 ± 0.03
		25	0.62 ± 0.04	0.53 ± 0.03	0.56 ± 0.04	0.48 ± 0.03
		50	0.53 ± 0.05	0.39 ± 0.04	0.49 ± 0.04	0.36 ± 0.04
		100	0.39 ± 0.07	0.27 ± 0.02	0.35 ± 0.07	0.24 ± 0.02
	8 h	6	0.51 ± 0.02	0.47 ± 0.03	0.46 ± 0.02	0.43 ± 0.03
		25	0.66 ± 0.05	0.30 ± 0.01	0.60 ± 0.05	0.27 ± 0.01
		50	0.53 ± 0.03	0.13 ± 0.03	0.48 ± 0.03	0.11 ± 0.03
		100	0.28 ± 0.03	0.09 ± 0.01	0.26 ± 0.03	0.08 ± 0.01

Table M-1 (continued). Total volumetric and chlorophyll-specific phytoplankton photosynthetic rates (Chapter 2).

Lake		%E_o	Total Productivity (μg C · L^{-1} · h^{-1})		P^B (μg C · μg Chl a^{-1} · h^{-1})	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
North L. (10 July)	3 h	6	0.07 ± 0.01	0.04 ± 0.00	0.50 ± 0.07	0.28 ± 0.02
		25	0.06 ± 0.01	0.04 ± 0.00	0.46 ± 0.07	0.27 ± 0.03
		50	0.05 ± 0.01	0.04 ± 0.00	0.40 ± 0.07	0.26 ± 0.03
		100	0.04 ± 0.00	0.02 ± 0.01	0.31 ± 0.03	0.17 ± 0.06
	6 h	6	0.05 ± 0.01	0.04 ± 0.01	0.35 ± 0.06	0.27 ± 0.04
		25	0.04 ± 0.01	0.03 ± 0.00	0.31 ± 0.07	0.21 ± 0.01
		50	0.05 ± 0.01	0.01 ± 0.00	0.35 ± 0.06	0.05 ± 0.02
		100	0.03 ± 0.00	0.01 ± 0.00	0.23 ± 0.01	0.05 ± 0.02
	12 h	6	0.03 ± 0.00	0.02 ± 0.00	0.20 ± 0.03	0.16 ± 0.02
		25	0.03 ± 0.00	0.01 ± 0.00	0.23 ± 0.03	0.10 ± 0.01
		50	0.03 ± 0.00	0.01 ± 0.00	0.22 ± 0.03	0.09 ± 0.03
		100	0.02 ± 0.00	0.01 ± 0.00	0.14 ± 0.02	0.07 ± 0.01
	24 h	6	0.03 ± 0.00	0.02 ± 0.00	0.21 ± 0.04	0.16 ± 0.04
		25	0.03 ± 0.01	0.01 ± 0.00	0.24 ± 0.04	0.10 ± 0.03
		50	0.03 ± 0.01	0.01 ± 0.00	0.19 ± 0.04	0.09 ± 0.01
		100	0.02 ± 0.01	0.01 ± 0.00	0.13 ± 0.03	0.07 ± 0.02
North L. (1 Aug.)	2 h	6	0.10 ± 0.01	0.06 ± 0.00	0.44 ± 0.04	0.13 ± 0.02
		25	0.09 ± 0.02	0.07 ± 0.01	0.40 ± 0.10	0.09 ± 0.02
		50	0.08 ± 0.02	0.05 ± 0.01	0.36 ± 0.07	0.06 ± 0.01
		100	0.06 ± 0.02	0.02 ± 0.01	0.25 ± 0.07	0.04 ± 0.01
	8 h	6	0.08 ± 0.02	0.06 ± 0.00	0.37 ± 0.09	0.27 ± 0.02
		25	0.08 ± 0.01	0.05 ± 0.01	0.33 ± 0.03	0.20 ± 0.04
		50	0.06 ± 0.00	0.02 ± 0.01	0.28 ± 0.02	0.11 ± 0.05
		100	0.03 ± 0.01	0.01 ± 0.00	0.14 ± 0.03	0.05 ± 0.02
North L. (9 Aug.)	2 h	50	0.17 ± 0.02	0.13 ± 0.01	0.35 ± 0.05	0.26 ± 0.03
		100	0.13 ± 0.04	0.03 ± 0.03	0.26 ± 0.08	0.06 ± 0.05
	4 h	50	0.16 ± 0.01	0.09 ± 0.03	0.32 ± 0.01	0.18 ± 0.07
		100	0.11 ± 0.02	0.05 ± 0.03	0.21 ± 0.03	0.10 ± 0.06
	8 h	50	0.16 ± 0.03	0.07 ± 0.02	0.32 ± 0.05	0.14 ± 0.04
		100	0.11 ± 0.03	0.02 ± 0.01	0.22 ± 0.07	0.04 ± 0.01
	12 h	50	0.15 ± 0.02	0.04 ± 0.02	0.30 ± 0.03	0.07 ± 0.04
		100	0.11 ± 0.00	0.01 ± 0.00	0.22 ± 0.00	0.03 ± 0.01
	24 h	50	0.12 ± 0.01	0.02 ± 0.01	0.23 ± 0.01	0.04 ± 0.02
		100	0.09 ± 0.02	0.00 ± 0.00	0.18 ± 0.04	0.01 ± 0.00

Table M-1 (continued). Total volumetric and chlorophyll-specific phytoplankton photosynthetic rates (Chapter 2).

Lake		%E_o	Total Productivity (µg C · L^{-1} · h^{-1})		P^B (µg C · µg Chl a^{-1} · h^{-1})	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Resolute L. (17 Aug.)	2 h	6	0.40 ± 0.04	0.43 ± 0.06	0.39 ± 0.04	0.42 ± 0.06
		25	0.36 ± 0.08	0.37 ± 0.03	0.35 ± 0.08	0.36 ± 0.03
		50	0.30 ± 0.05	0.27 ± 0.02	0.29 ± 0.05	0.26 ± 0.02
		100	0.19 ± 0.01	0.13 ± 0.02	0.18 ± 0.01	0.13 ± 0.02
	8 h	6	0.35 ± 0.03	0.38 ± 0.06	0.34 ± 0.03	0.37 ± 0.06
		25	0.25 ± 0.05	0.19 ± 0.04	0.24 ± 0.05	0.19 ± 0.04
		50	0.26 ± 0.01	0.09 ± 0.02	0.25 ± 0.01	0.08 ± 0.02
		100	0.15 ± 0.04	0.06 ± 0.01	0.15 ± 0.04	0.06 ± 0.01
Small L. (28 July)	2 h	6	N/A	N/A	N/A	N/A
		25	0.32 ± 0.03	0.27 ± 0.02	0.57 ± 0.06	0.49 ± 0.03
		50	0.33 ± 0.02	0.29 ± 0.04	0.60 ± 0.04	0.51 ± 0.06
		100	0.23 ± 0.03	0.17 ± 0.02	0.41 ± 0.06	0.31 ± 0.03
	6 h	6	N/A	N/A	N/A	N/A
		25	0.28 ± 0.01	0.21 ± 0.04	0.50 ± 0.02	0.37 ± 0.07
		50	0.33 ± 0.04	0.16 ± 0.05	0.59 ± 0.07	0.30 ± 0.09
		100	0.33 ± 0.03	0.08 ± 0.03	0.58 ± 0.05	0.15 ± 0.05
	12 h	6	0.07 ± 0.01	0.05 ± 0.01	0.12 ± 0.02	0.09 ± 0.01
		25	0.19 ± 0.01	0.11 ± 0.01	0.34 ± 0.02	0.21 ± 0.03
		50	0.26 ± 0.01	0.09 ± 0.04	0.46 ± 0.03	0.17 ± 0.07
		100	0.28 ± 0.00	0.05 ± 0.02	0.49 ± 0.01	0.09 ± 0.04
Tern L. (3 Aug.)	2 h	6	0.18 ± 0.01	0.17 ± 0.03	0.11 ± 0.00	0.11 ± 0.02
		25	0.23 ± 0.05	0.18 ± 0.03	0.15 ± 0.03	0.11 ± 0.02
		50	0.23 ± 0.02	0.11 ± 0.02	0.14 ± 0.01	0.07 ± 0.01
		100	0.18 ± 0.04	0.17 ± 0.04	0.11 ± 0.02	0.11 ± 0.03
	8 h	6	0.20 ± 0.03	0.14 ± 0.02	0.12 ± 0.02	0.09 ± 0.01
		25	0.23 ± 0.01	0.12 ± 0.03	0.14 ± 0.00	0.07 ± 0.02
		50	0.22 ± 0.01	0.04 ± 0.01	0.14 ± 0.01	0.02 ± 0.00
		100	0.21 ± 0.05	0.05 ± 0.01	0.13 ± 0.03	0.03 ± 0.01

Appendix N. Absolute and percent productivity of pico-, nano- and netplankton of lakes in the vicinity of Resolute (Chapter 2)

Table N-1. Absolute productivity (μg C · L^{-1} · h^{1}) of picoplankton (0.2 – 2 μm; PICO), nanoplankton (2 – 20 μm; NANO), and netplankton (> 20 μm; NET) for all nine lakes after exposure to ambient (AMB) and enhanced (ENH) UVB under 6, 25, 50 and/or 100% of incoming surface irradiance (%E_o). ± SD.

Lake		%E_o	PICO (0.2 – 2 μm)		NANO (2 – 20 μm)		NET (> 20 μm)	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Barren L. (21 July)	2 h	6	0.025 ± 0.013	0.041 ± 0.029	0.024 ± 0.014	0.028 ± 0.019	0.006 ± 0.002	0.007 ± 0.004
		25	0.042 ± 0.014	0.044 ± 0.021	0.039 ± 0.015	0.041 ± 0.015	0.010 ± 0.004	0.010 ± 0.002
		50	0.026 ± 0.017	0.022 ± 0.020	0.022 ± 0.012	0.016 ± 0.014	0.005 ± 0.003	0.005 ± 0.004
		100	0.038 ± 0.022	0.024 ± 0.003	0.032 ± 0.013	0.021 ± 0.009	0.007 ± 0.002	0.005 ± 0.001
	8 h	6	0.024 ± 0.007	0.015 ± 0.001	0.019 ± 0.004	0.014 ± 0.002	0.005 ± 0.001	0.004 ± 0.001
		25	0.031 ± 0.009	0.017 ± 0.003	0.023 ± 0.006	0.018 ± 0.005	0.005 ± 0.001	0.006 ± 0.001
		50	0.034 ± 0.015	0.020 ± 0.003	0.022 ± 0.006	0.012 ± 0.001	0.006 ± 0.001	0.004 ± 0.000
		100	0.018 ± 0.010	0.007 ± 0.004	0.014 ± 0.006	0.007 ± 0.002	0.003 ± 0.001	0.002 ± 0.001
Black Char L. (7 Aug.)	2h	6	0.111 ± 0.034	0.083 ± 0.041	0.077 ± 0.011	0.052 ± 0.009	0.018 ± 0.004	0.016 ± 0.005
		25	0.141 ± 0.025	0.116 ± 0.026	0.099 ± 0.006	0.081 ± 0.013	0.022 ± 0.003	0.020 ± 0.005
		50	0.159 ± 0.041	0.092 ± 0.014	0.108 ± 0.008	0.064 ± 0.013	0.026 ± 0.003	0.018 ± 0.003
		100	0.195 ± 0.032	0.062 ± 0.015	0.107 ± 0.013	0.042 ± 0.008	0.023 ± 0.001	0.013 ± 0.004
	8 h	6	0.091 ± 0.008	0.073 ± 0.020	0.074 ± 0.004	0.060 ± 0.000	0.016 ± 0.001	0.012 ± 0.004
		25	0.142 ± 0.006	0.061 ± 0.016	0.113 ± 0.019	0.037 ± 0.006	0.015 ± 0.001	0.010 ± 0.001
		50	0.158 ± 0.030	0.041 ± 0.002	0.127 ± 0.008	0.026 ± 0.006	0.019 ± 0.002	0.008 ± 0.001
		100	0.126 ± 0.031	0.029 ± 0.014	0.074 ± 0.010	0.014 ± 0.004	0.016 ± 0.001	0.006 ± 0.002

Table N-1 (continued). Absolute productivity of pico- nano- and netplankton (Chapter 2).

Lake		%E$_0$	PICO (0.2 – 2 µm)		NANO (2 – 20 µm)		NET (> 20 µm)	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Char L. (14 Aug.)	2 h	6	0.095 ± 0.047	0.100 ± 0.044	0.101 ± 0.021	0.106 ± 0.010	0.019 ± 0.003	0.025 ± 0.006
		25	0.089 ± 0.024	0.090 ± 0.013	0.113 ± 0.027	0.103 ± 0.011	0.021 ± 0.005	0.020 ± 0.001
		50	0.062 ± 0.030	0.066 ± 0.023	0.079 ± 0.015	0.076 ± 0.018	0.015 ± 0.004	0.017 ± 0.001
		100	0.079 ± 0.034	0.045 ± 0.004	0.056 ± 0.008	0.067 ± 0.006	0.014 ± 0.003	0.014 ± 0.002
	8 h	6	0.067 ± 0.011	0.049 ± 0.008	0.079 ± 0.012	0.079 ± 0.007	0.017 ± 0.003	0.015 ± 0.004
		25	0.061 ± 0.005	0.042 ± 0.004	0.065 ± 0.005	0.050 ± 0.009	0.012 ± 0.001	0.010 ± 0.001
		50	0.056 ± 0.011	0.021 ± 0.002	0.056 ± 0.013	0.034 ± 0.001	0.010 ± 0.002	0.006 ± 0.000
		100	0.028 ± 0.002	0.015 ± 0.001	0.036 ± 0.004	0.025 ± 0.001	0.007 ± 0.001	0.005 ± 0.000
Clear L. (21 July)	5 h	6	0.119 ± 0.020	0.106 ± 0.019	0.151 ± 0.027	0.152 ± 0.033	0.029 ± 0.007	0.024 ± 0.004
		25	0.159 ± 0.014	0.226 ± 0.048	0.324 ± 0.035	0.275 ± 0.048	0.051 ± 0.007	0.049 ± 0.003
		50	0.227 ± 0.012	0.169 ± 0.029	0.330 ± 0.025	0.269 ± 0.044	0.057 ± 0.007	0.058 ± 0.009
		100	0.164 ± 0.020	0.052 ± 0.033	0.253 ± 0.034	0.093 ± 0.034	0.049 ± 0.004	0.036 ± 0.010
Meretta L. (12 Aug.)	2 h	6	0.170 ± 0.027	0.188 ± 0.036	0.164 ± 0.020	0.181 ± 0.024	0.106 ± 0.004	0.120 ± 0.018
		25	0.302 ± 0.037	0.224 ± 0.019	0.197 ± 0.017	0.200 ± 0.015	0.120 ± 0.011	0.108 ± 0.012
		50	0.228 ± 0.012	0.169 ± 0.032	0.204 ± 0.035	0.138 ± 0.004	0.102 ± 0.007	0.088 ± 0.010
		100	0.161 ± 0.031	0.083 ± 0.016	0.146 ± 0.034	0.127 ± 0.001	0.080 ± 0.010	0.058 ± 0.004
	8 h	6	0.207 ± 0.007	0.174 ± 0.010	0.155 ± 0.015	0.145 ± 0.007	0.144 ± 0.004	0.151 ± 0.011
		25	0.309 ± 0.039	0.122 ± 0.017	0.218 ± 0.013	0.096 ± 0.006	0.132 ± 0.003	0.081 ± 0.005
		50	0.254 ± 0.019	0.051 ± 0.013	0.176 ± 0.016	0.034 ± 0.009	0.100 ± 0.005	0.041 ± 0.008
		100	0.135 ± 0.031	0.032 ± 0.007	0.101 ± 0.002	0.028 ± 0.005	0.048 ± 0.004	0.026 ± 0.004

Table N-1 (continued). Absolute productivity of pico- nano- and netplankton (Chapter 2).

Lake		%E$_o$	PICO (0.2 – 2 μm)		NANO (2 – 20 μm)		NET (> 20 μm)	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
North L. (1 Aug.)	2 h	6	0.050 ± 0.008	0.025 ± 0.002	0.041 ± 0.002	0.027 ± 0.002	0.008 ± 0.001	0.005 ± 0.000
		25	0.047 ± 0.011	0.031 ± 0.010	0.036 ± 0.011	0.031 ± 0.005	0.006 ± 0.001	0.006 ± 0.002
		50	0.039 ± 0.008	0.018 ± 0.003	0.034 ± 0.007	0.028 ± 0.005	0.008 ± 0.002	0.005 ± 0.002
		100	0.027 ± 0.010	0.007 ± 0.006	0.025 ± 0.006	0.008 ± 0.006	0.005 ± 0.002	0.002 ± 0.001
	8 h	6	0.046 ± 0.013	0.033 ± 0.001	0.034 ± 0.009	0.024 ± 0.002	0.003 ± 0.000	0.003 ± 0.001
		25	0.045 ± 0.003	0.023 ± 0.007	0.027 ± 0.005	0.020 ± 0.002	0.003 ± 0.000	0.003 ± 0.001
		50	0.039 ± 0.003	0.012 ± 0.007	0.022 ± 0.002	0.010 ± 0.005	0.003 ± 0.001	0.002 ± 0.000
		100	0.017 ± 0.004	0.004 ± 0.002	0.013 ± 0.003	0.006 ± 0.002	0.002 ± 0.000	0.001 ± 0.000
Resolute L. (17 Aug.)	2 h	6	0.172 ± 0.027	0.193 ± 0.038	0.143 ± 0.007	0.148 ± 0.013	0.083 ± 0.007	0.091 ± 0.009
		25	0.154 ± 0.051	0.153 ± 0.012	0.123 ± 0.018	0.146 ± 0.015	0.079 ± 0.023	0.072 ± 0.006
		50	0.129 ± 0.021	0.119 ± 0.009	0.111 ± 0.020	0.098 ± 0.009	0.060 ± 0.013	0.054 ± 0.005
		100	0.088 ± 0.012	0.057 ± 0.005	0.067 ± 0.008	0.053 ± 0.010	0.032 ± 0.002	0.022 ± 0.002
	8 h	6	0.133 ± 0.021	0.153 ± 0.041	0.117 ± 0.007	0.124 ± 0.018	0.101 ± 0.001	0.103 ± 0.003
		25	0.082 ± 0.020	0.078 ± 0.016	0.092 ± 0.025	0.067 ± 0.012	0.072 ± 0.015	0.048 ± 0.015
		50	0.101 ± 0.028	0.036 ± 0.013	0.088 ± 0.025	0.032 ± 0.003	0.068 ± 0.001	0.018 ± 0.005
		100	0.060 ± 0.026	0.028 ± 0.003	0.051 ± 0.011	0.025 ± 0.005	0.039 ± 0.009	0.011 ± 0.002
Small L. (28 July)	2 h	6	N/A	N/A	N/A	N/A	N/A	N/A
		25	0.147 ± 0.016	0.127 ± 0.004	0.148 ± 0.013	0.129 ± 0.013	0.021 ± 0.006	0.019 ± 0.002
		50	0.166 ± 0.022	0.136 ± 0.014	0.147 ± 0.001	0.132 ± 0.018	0.020 ± 0.001	0.018 ± 0.004
		100	0.092 ± 0.003	0.078 ± 0.004	0.124 ± 0.030	0.077 ± 0.013	0.014 ± 0.002	0.015 ± 0.006
	6 h	6	N/A	N/A	N/A	N/A	N/A	N/A
		25	0.131 ± 0.008	0.099 ± 0.031	0.133 ± 0.017	0.096 ± 0.009	0.014 ± 0.003	0.011 ± 0.002
		50	0.147 ± 0.032	0.069 ± 0.023	0.161 ± 0.005	0.083 ± 0.020	0.017 ± 0.002	0.013 ± 0.007
		100	0.164 ± 0.018	0.039 ± 0.015	0.146 ± 0.012	0.038 ± 0.013	0.015 ± 0.002	0.007 ± 0.002
	12 h	6	0.029 ± 0.006	0.025 ± 0.007	0.033 ± 0.003	0.024 ± 0.002	0.004 ± 0.001	0.003 ± 0.001
		25	0.095 ± 0.005	0.053 ± 0.007	0.084 ± 0.009	0.054 ± 0.009	0.010 ± 0.001	0.007 ± 0.002
		50	0.123 ± 0.012	0.045 ± 0.018	0.122 ± 0.001	0.043 ± 0.018	0.012 ± 0.002	0.006 ± 0.001
		100	0.126 ± 0.013	0.022 ± 0.012	0.132 ± 0.009	0.021 ± 0.010	0.018 ± 0.007	0.006 ± 0.003

Table N-1 (continued). Absolute productivity of pico- nano- and netplankton (Chapter 2).

Lake		$\%E_o$	PICO (0.2 – 2 µm)		NANO (2 – 20 µm)		NET (> 20 µm)	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Tern L.	2 h	6	0.061 ± 0.005	0.051 ± 0.011	0.080 ± 0.001	0.079 ± 0.005	0.041 ± 0.001	0.040 ± 0.015
(3 Aug.)		25	0.071 ± 0.032	0.057 ± 0.003	0.107 ± 0.015	0.081 ± 0.012	0.055 ± 0.008	0.045 ± 0.016
		50	0.083 ± 0.009	0.033 ± 0.006	0.103 ± 0.016	0.047 ± 0.009	0.044 ± 0.008	0.025 ± 0.009
		100	0.062 ± 0.024	0.061 ± 0.018	0.082 ± 0.008	0.078 ± 0.008	0.036 ± 0.007	0.036 ± 0.014
	8 h	6	0.066 ± 0.010	0.046 ± 0.010	0.080 ± 0.015	0.066 ± 0.009	0.050 ± 0.009	0.032 ± 0.006
		25	0.084 ± 0.004	0.030 ± 0.012	0.094 ± 0.008	0.047 ± 0.009	0.048 ± 0.003	0.041 ± 0.007
		50	0.081 ± 0.004	0.007 ± 0.001	0.091 ± 0.010	0.016 ± 0.002	0.048 ± 0.006	0.014 ± 0.004
		100	0.077 ± 0.026	0.016 ± 0.005	0.093 ± 0.022	0.023 ± 0.004	0.041 ± 0.006	0.015 ± 0.000

Table N-2. Percent ^{14}C incorporated by picoplankton (0.2 –2 μm), nanoplankton (2 – 20 μm) and netplankton (> 20 μm) of all nine lakes after exposure to ambient (AMB) and enhanced (ENH) UVB levels under 6, 25, 50 and/or 100% of surface irradiance (E_o). ±SD.

Lake		%E_o	%Picoplankton		%Nanoplankton		%Netplankton	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Barren L. (5 Aug.)	2 h	6	45.96 ± 1.76	51.70 ± 5.74	43.24 ± 2.99	37.70 ± 4.25	10.80 ± 1.49	10.61 ± 1.86
		25	46.63 ± 2.84	44.99 ± 8.13	42.02 ± 2.16	44.04 ± 6.62	11.35 ± 0.96	10.97 ± 2.00
		50	47.90 ± 6.68	48.29 ± 3.51	42.08 ± 6.01	39.59 ± 3.07	10.02 ± 0.90	12.12 ± 0.45
		100	48.33 ± 6.93	49.43 ± 7.22	41.72 ± 6.65	40.40 ± 7.82	9.95 ± 1.85	10.18 ± 0.60
	8 h	6	48.92 ± 3.68	45.62 ± 1.33	40.36 ± 1.59	41.82 ± 2.58	10.72 ± 2.78	12.56 ± 2.37
		25	51.83 ± 2.67	42.18 ± 2.45	39.15 ± 2.76	44.29 ± 2.01	9.02 ± 1.60	13.53 ± 0.48
		50	54.15 ± 5.37	55.53 ± 5.27	36.19 ± 2.84	34.04 ± 4.61	9.66 ± 2.67	10.43 ± 1.37
		100	49.36 ± 3.58	44.24 ± 3.70	41.30 ± 2.96	44.18 ± 4.36	9.34 ± 1.28	11.58 ± 0.08
Black Char L. (7 Aug.)	2 h	6	53.00 ± 5.27	53.36 ± 6.42	38.07 ± 4.27	35.99 ± 6.00	8.93 ± 1.23	10.64 ± 0.42
		25	53.48 ± 3.63	53.42 ± 1.10	37.94 ± 3.62	37.40 ± 1.36	8.58 ± 0.04	9.18 ± 0.27
		50	53.60 ± 4.68	53.21 ± 2.35	37.43 ± 3.71	36.54 ± 1.90	8.96 ± 1.16	10.25 ± 0.50
		100	59.83 ± 2.12	52.37 ± 2.04	32.92 ± 1.54	36.33 ± 2.77	7.26 ± 0.68	11.30 ± 1.10
	8 h	6	50.21 ± 2.79	49.81 ± 5.03	41.15 ± 3.13	41.74 ± 6.15	8.64 ± 0.33	8.45 ± 1.19
		25	52.74 ± 2.58	56.03 ± 7.12	41.59 ± 2.83	35.05 ± 6.74	5.68 ± 0.32	8.92 ± 0.67
		50	51.71 ± 5.88	55.05 ± 3.77	42.01 ± 6.05	33.73 ± 3.85	6.28 ± 0.48	11.22 ± 0.53
		100	57.82 ± 3.79	59.41 ± 3.38	34.41 ± 2.12	28.83 ± 3.35	7.78 ± 1.68	11.76 ± 0.67
Char L. (14 Aug.)	2 h	6	42.83 ± 8.44	42.05 ± 7.17	47.92 ± 7.90	47.11 ± 6.86	9.25 ± 1.81	10.85 ± 0.50
		25	39.95 ± 4.79	42.12 ± 2.25	50.56 ± 5.15	48.62 ± 2.35	9.49 ± 0.38	9.26 ± 1.12
		50	38.42 ± 7.51	41.21 ± 10.96	51.95 ± 7.16	48.09 ± 11.02	9.63 ± 0.36	10.70 ± 0.62
		100	51.38 ± 8.64	35.62 ± 3.73	38.90 ± 7.69	52.95 ± 2.63	9.72 ± 0.96	11.43 ± 1.14
	8 h	6	41.79 ± 0.05	34.26 ± 2.80	48.78 ± 0.50	55.40 ± 4.63	10.43 ± 2.10	10.34 ± 2.09
		25	44.36 ± 1.67	41.35 ± 2.37	47.25 ± 1.77	49.18 ± 2.78	8.40 ± 0.11	9.47 ± 0.80
		50	46.10 ± 4.81	34.46 ± 1.42	46.05 ± 4.53	55.59 ± 1.42	7.85 ± 0.28	9.94 ± 1.04
		100	39.78 ± 1.23	32.90 ± 1.56	50.25 ± 0.88	56.45 ± 0.57	9.97 ± 1.03	10.65 ± 1.12

Table N-2 (continued). Percent productivity of pico- (0.2 – 2 μm), nano- (2 – 20 μm) and netplankton (> 20 μm) in Chapter 2.

Lake		%E$_o$	%Picoplankton		%Nanoplankton		%Netplankton	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Clear L. (21 July)	5 h	6	39.81 ± 1.66	37.70 ± 1.16	50.64 ± 0.40	53.77 ± 1.91	9.55 ± 1.27	8.53 ± 0.77
		25	29.90 ± 1.95	41.13 ± 8.64	60.58 ± 2.44	50.03 ± 8.64	9.52 ± 0.69	8.84 ± 0.17
		50	36.99 ± 2.87	34.09 ± 0.28	53.73 ± 2.21	54.27 ± 0.23	9.29 ± 0.72	11.64 ± 0.23
		100	35.22 ± 0.73	27.00 ± 6.23	54.25 ± 1.23	52.00 ± 2.91	10.53 ± 0.59	21.00 ± 3.36
Meretta L. (12 Aug.)	2 h	6	38.68 ± 5.76	38.56 ± 7.31	37.29 ± 4.94	36.99 ± 5.25	24.03 ± 0.83	24.44 ± 2.63
		25	48.59 ± 3.30	42.07 ± 1.97	31.99 ± 3.96	37.74 ± 3.12	19.42 ± 0.69	20.18 ± 1.21
		50	42.87 ± 3.05	42.51 ± 3.87	38.00 ± 3.38	35.14 ± 3.08	19.13 ± 0.38	22.35 ± 1.77
		100	41.60 ± 1.53	30.77 ± 3.74	37.58 ± 1.63	47.67 ± 3.61	20.82 ± 2.23	21.56 ± 0.67
	8 h	6	40.93 ± 1.56	37.04 ± 0.16	30.64 ± 1.75	30.85 ± 0.42	28.44 ± 0.42	32.11 ± 0.44
		25	46.70 ± 2.44	40.74 ± 4.90	33.17 ± 1.69	32.27 ± 2.53	20.13 ± 1.07	26.99 ± 2.37
		50	48.03 ± 2.45	40.57 ± 0.60	33.13 ± 2.12	26.49 ± 0.89	18.83 ± 0.41	32.94 ± 1.48
		100	47.24 ± 5.81	36.95 ± 3.60	35.77 ± 4.20	32.22 ± 1.92	17.00 ± 2.08	30.83 ± 5.48
North L. (1 Aug.)	2 h	6	50.37 ± 3.05	44.20 ± 1.69	41.80 ± 1.56	46.77 ± 1.83	7.83 ± 1.49	9.03 ± 0.33
		25	52.74 ± 2.70	44.81 ± 5.63	40.07 ± 2.90	45.74 ± 2.09	7.19 ± 0.24	9.45 ± 3.55
		50	47.83 ± 1.44	35.51 ± 2.08	42.69 ± 0.42	54.53 ± 2.48	9.48 ± 1.56	9.95 ± 1.97
		100	46.27 ± 4.79	42.55 ± 2.42	44.42 ± 4.42	47.90 ± 2.61	9.31 ± 0.44	9.55 ± 0.22
	8 h	6	54.96 ± 6.28	54.95 ± 1.77	40.85 ± 6.21	39.88 ± 1.15	4.19 ± 0.67	5.18 ± 0.62
		25	60.01 ± 3.19	49.36 ± 6.29	36.08 ± 3.39	44.06 ± 6.15	3.91 ± 0.29	6.58 ± 0.17
		50	61.14 ± 2.56	49.51 ± 4.64	34.23 ± 1.36	42.44 ± 1.82	4.63 ± 1.32	8.05 ± 2.93
		100	52.29 ± 2.61	37.33 ± 3.12	40.79 ± 1.88	54.22 ± 2.93	6.93 ± 1.24	8.45 ± 0.22

Table N-2 (continued). Percent productivity of pico- (0.2 – 2 μm), nano- (2 – 20 μm) and netplankton (> 20 μm) in Chapter 2.

Lake		%E$_o$	%Picoplankton		%Nanoplankton		%Netplankton	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Resolute L. (17 Aug.)	2 h	6	42.95 ± 2.89	44.48 ± 3.30	36.14 ± 2.23	34.32 ± 1.62	20.92 ± 0.87	21.20 ± 1.77
		25	42.76 ± 5.50	41.36 ± 0.88	35.20 ± 6.38	39.32 ± 1.66	22.04 ± 1.56	19.32 ± 0.79
		50	42.95 ± 1.46	44.06 ± 3.13	37.09 ± 2.90	36.07 ± 1.76	19.96 ± 1.65	19.87 ± 1.38
		100	46.88 ± 5.43	42.92 ± 1.50	35.91 ± 4.24	40.06 ± 3.10	17.21 ± 1.33	17.03 ± 1.73
	8 h	6	37.62 ± 3.27	39.96 ± 4.18	33.16 ± 1.79	32.68 ± 1.48	28.82 ± 2.25	27.36 ± 3.40
		25	33.30 ± 5.19	40.54 ± 4.68	37.24 ± 5.65	34.82 ± 1.27	29.46 ± 0.46	24.64 ± 4.13
		50	39.11 ± 10.47	40.88 ± 6.46	34.40 ± 9.73	37.94 ± 4.96	26.49 ± 1.11	21.18 ± 2.94
		100	39.13 ± 9.32	43.97 ± 4.81	34.44 ± 6.56	39.47 ± 4.31	26.43 ± 2.77	16.56 ± 1.31
Small L. (28 July)	2 h	6	N/A	N/A	N/A	N/A	N/A	N/A
		25	46.56 ± 1.33	46.44 ± 1.93	46.89 ± 1.23	46.78 ± 2.19	6.55 ± 1.25	6.78 ± 0.45
		50	49.86 ± 3.46	47.76 ± 1.49	44.21 ± 2.85	46.06 ± 0.87	5.93 ± 0.68	6.18 ± 0.66
		100	40.54 ± 6.01	46.15 ± 4.79	53.26 ± 6.50	44.88 ± 3.48	6.19 ± 0.75	8.97 ± 3.00
	6 h	6	N/A	N/A	N/A	N/A	N/A	N/A
		25	47.24 ± 3.37	47.15 ± 6.46	47.74 ± 4.51	47.46 ± 6.21	5.01 ± 1.23	5.39 ± 0.34
		50	44.87 ± 4.71	41.44 ± 2.39	49.82 ± 4.29	50.98 ± 2.93	5.31 ± 0.53	7.58 ± 1.78
		100	50.38 ± 2.74	46.05 ± 4.06	45.03 ± 2.30	45.55 ± 3.26	4.59 ± 0.44	8.40 ± 1.06
	12h	6	44.33 ± 2.23	46.59 ± 5.38	50.29 ± 3.00	46.84 ± 5.43	5.38 ± 0.79	6.57 ± 2.07
		25	50.61 ± 1.77	46.56 ± 2.50	44.22 ± 1.90	47.17 ± 1.96	5.17 ± 1.01	6.26 ± 2.45
		50	47.70 ± 1.98	47.36 ± 3.25	47.55 ± 2.28	45.36 ± 2.67	4.75 ± 0.38	7.28 ± 1.90
		100	45.63 ± 4.54	43.34 ± 6.09	47.88 ± 3.12	43.58 ± 6.24	6.49 ± 2.45	13.09 ± 1.21
Tern L. (3 Aug.)	2 h	6	33.59 ± 1.51	30.09 ± 2.82	43.97 ± 1.01	47.07 ± 7.01	22.44 ± 0.50	22.84 ± 5.66
		25	29.54 ± 7.48	31.67 ± 3.83	46.45 ± 2.70	44.37 ± 3.16	24.01 ± 5.23	23.96 ± 6.27
		50	36.25 ± 6.08	31.59 ± 2.74	44.78 ± 3.95	45.26 ± 1.98	18.97 ± 2.23	23.15 ± 4.68
		100	33.79 ± 5.88	34.37 ± 2.31	46.10 ± 6.03	45.45 ± 5.52	20.11 ± 1.58	20.18 ± 3.31
	8 h	6	33.78 ± 2.43	31.89 ± 5.95	40.69 ± 0.89	45.84 ± 3.27	25.52 ± 2.49	22.27 ± 2.80
		25	37.42 ± 2.86	25.08 ± 5.11	41.46 ± 2.19	40.24 ± 1.76	21.12 ± 0.89	34.68 ± 3.40
		50	36.70 ± 2.38	19.96 ± 4.79	41.38 ± 3.65	43.27 ± 2.71	21.91 ± 2.08	36.77 ± 6.00
		100	36.14 ± 4.85	28.45 ± 4.67	43.97 ± 0.53	43.12 ± 4.09	19.89 ± 5.04	28.43 ± 4.85

Appendix O. Carbon uptake and percent carbon allocated into LMW, lipid, polysaccharide and protein (Chapter 2)

Table O-1. Carbon uptake (μg C · L^{-1} · h^{-1}) into low molecular weight metabolites (LMW), lipid, polysaccharide (POLY), and protein by phytoplankton populations from five lakes after exposure to ambient (AMB) and enhanced (ENH) UVB levels under 6, 25, 50 and/or 100% of incoming surface irradiance (E_o). ± SD.

Lake		%E_o	CARBON UPTAKE (μg C · L^{-1} · h^{-1})							
			LMW		LIPID		POLY		PROTEIN	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Clear L. (21 July)	5 h	6	0.11 ± 0.03	0.12 ± 0.04	0.06 ± 0.02	0.06 ± 0.01	0.09 ± 0.02	0.09 ± 0.02	0.09 ± 0.01	0.08 ± 0.01
		25	0.26 ± 0.03	0.30 ± 0.02	0.13 ± 0.01	0.13 ± 0.01	0.21 ± 0.02	0.20 ± 0.01	0.15 ± 0.01	0.11 ± 0.01
		50	0.31 ± 0.00	0.27 ± 0.06	0.15 ± 0.00	0.12 ± 0.01	0.26 ± 0.00	0.19 ± 0.03	0.16 ± 0.00	0.10 ± 0.01
		100	0.20 ± 0.05	0.11 ± 0.04	0.11 ± 0.01	0.05 ± 0.02	0.17 ± 0.03	0.09 ± 0.04	0.13 ± 0.00	0.04 ± 0.01
North L. (9 Aug.)	2 h	50	0.07 ± 0.02	0.06 ± 0.02	0.05 ± 0.00	0.04 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.05 ± 0.01	0.04 ± 0.00
		100	0.04 ± 0.03	0.01 ± 0.01	0.03 ± 0.00	0.02 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.01	0.03 ± 0.00
	4 h	50	0.08 ± 0.01	0.08 ± 0.03	0.04 ± 0.01	0.03 ± 0.01	0.02 ± 0.00	0.01 ± 0.01	0.04 ± 0.01	0.01 ± 0.01
		100	0.05 ± 0.01	0.03 ± 0.00	0.03 ± 0.01	0.02 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.03 ± 0.00	0.01 ± 0.00
	8 h	50	0.12 ± 0.02	0.04 ± 0.02	0.04 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.01 ± 0.00	0.03 ± 0.00	0.01 ± 0.00
		100	0.05 ± 0.03	0.01 ± 0.00	0.03 ± 0.01	0.01 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00
	12 h	50	0.07 ± 0.01	0.01 ± 0.01	0.05 ± 0.01	0.01 ± 0.01	0.03 ± 0.00	0.00 ± 0.00	0.03 ± 0.00	0.00 ± 0.00
		100	0.04 ± 0.01	0.00 ± 0.00	0.03 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.00 ± 0.00	0.02 ± 0.00	0.00 ± 0.00
	24 h	50	0.05 ± 0.01	0.01 ± 0.00	0.04 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.00 ± 0.00	0.03 ± 0.00	0.00 ± 0.00
		100	0.03 ± 0.01	0.00 ± 0.00	0.03 ± 0.00	0.00 ± 0.00	0.02 ± 0.00	0.00 ± 0.00	0.02 ± 0.00	0.00 ± 0.00
Meretta L. (12 Aug.)	2 h	6	0.26 ± 0.02	0.32 ± 0.08	0.11 ± 0.01	0.11 ± 0.02	0.04 ± 0.01	0.04 ± 0.01	0.07 ± 0.01	0.07 ± 0.01
		25	0.33 ± 0.03	0.34 ± 0.03	0.14 ± 0.01	0.13 ± 0.00	0.07 ± 0.02	0.07 ± 0.01	0.08 ± 0.02	0.05 ± 0.01
		50	0.31 ± 0.03	0.23 ± 0.02	0.13 ± 0.01	0.09 ± 0.01	0.06 ± 0.01	0.03 ± 0.02	0.09 ± 0.01	0.03 ± 0.00
		100	0.25 ± 0.14	0.11 ± 0.03	0.10 ± 0.05	0.03 ± 0.01	0.04 ± 0.02	0.00 ± 0.00	0.09 ± 0.05	0.01 ± 0.00
	8 h	6	0.31 ± 0.03	0.31 ± 0.04	0.13 ± 0.02	0.12 ± 0.01	0.10 ± 0.02	0.09 ± 0.03	0.09 ± 0.01	0.06 ± 0.01
		25	0.30 ± 0.12	0.18 ± 0.03	0.15 ± 0.04	0.07 ± 0.01	0.14 ± 0.02	0.04 ± 0.01	0.11 ± 0.01	0.02 ± 0.00
		50	0.27 ± 0.02	0.05 ± 0.03	0.14 ± 0.02	0.02 ± 0.01	0.11 ± 0.00	0.01 ± 0.01	0.11 ± 0.01	0.01 ± 0.00
		100	0.11 ± 0.00	0.01 ± 0.01	0.05 ± 0.01	0.00 ± 0.00	0.04 ± 0.01	0.00 ± 0.00	0.06 ± 0.01	0.00 ± 0.00

Table O-1 (continued). Carbon uptake into LMW, lipid, polysaccharide (POLY), and protein (Chapter 2).

Lake		%E$_o$	CARBON UPTAKE (µg C L^{-1} h^{-1})							
			LMW		LIPID		POLY		PROTEIN	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Small L. (28 July)	2 h	6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
		25	0.18 ± 0.02	0.17 ± 0.01	0.07 ± 0.00	0.06 ± 0.00	0.04 ± 0.01	0.05 ± 0.00	0.06 ± 0.00	0.04 ± 0.00
		50	0.20 ± 0.02	0.18 ± 0.02	0.07 ± 0.01	0.06 ± 0.00	0.05 ± 0.01	0.04 ± 0.00	0.06 ± 0.00	0.04 ± 0.01
		100	0.13 ± 0.03	0.07 ± 0.02	0.05 ± 0.01	0.02 ± 0.00	0.04 ± 0.02	0.01 ± 0.00	0.05 ± 0.01	0.01 ± 0.00
	6 h	6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
		25	0.17 ± 0.02	0.15 ± 0.01	0.07 ± 0.00	0.04 ± 0.00	0.05 ± 0.01	0.03 ± 0.00	0.04 ± 0.01	0.03 ± 0.00
		50	0.22 ± 0.04	0.13 ± 0.03	0.08 ± 0.00	0.04 ± 0.01	0.06 ± 0.02	0.03 ± 0.00	0.05 ± 0.01	0.02 ± 0.01
		100	0.21 ± 0.01	0.05 ± 0.02	0.07 ± 0.00	0.02 ± 0.00	0.06 ± 0.01	0.01 ± 0.00	0.05 ± 0.01	0.01 ± 0.00
	12	6	0.03 ± 0.01	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.01 ± 0.00
		25	0.12 ± 0.02	0.09 ± 0.02	0.04 ± 0.00	0.02 ± 0.01	0.03 ± 0.00	0.02 ± 0.00	0.04 ± 0.01	0.02 ± 0.00
		50	0.16 ± 0.02	0.07 ± 0.03	0.06 ± 0.00	0.02 ± 0.01	0.04 ± 0.00	0.02 ± 0.00	0.06 ± 0.00	0.01 ± 0.00
		100	0.20 ± 0.00	0.03 ± 0.02	0.07 ± 0.00	0.01 ± 0.01	0.05 ± 0.00	0.01 ± 0.00	0.06 ± 0.00	0.01 ± 0.00
Tern L. (3 Aug.)	2 h	6	0.10 ± 0.02	0.06 ± 0.02	0.04 ± 0.01	0.03 ± 0.00	0.02 ± 0.01	0.01 ± 0.01	0.03 ± 0.00	0.02 ± 0.00
		25	0.18 ± 0.03	0.14 ± 0.04	0.06 ± 0.00	0.05 ± 0.01	0.03 ± 0.01	0.02 ± 0.00	0.03 ± 0.01	0.03 ± 0.01
		50	0.14 ± 0.02	0.04 ± 0.01	0.06 ± 0.01	0.02 ± 0.00	0.03 ± 0.00	0.00 ± 0.00	0.04 ± 0.01	0.01 ± 0.00
		100	0.10 ± 0.01	0.09 ± 0.01	0.04 ± 0.00	0.03 ± 0.00	0.02 ± 0.00	0.01 ± 0.00	0.03 ± 0.01	0.01 ± 0.00
	8 h	6	0.13 ± 0.01	0.09 ± 0.00	0.05 ± 0.00	0.04 ± 0.00	0.03 ± 0.00	0.02 ± 0.00	0.05 ± 0.00	0.02 ± 0.00
		25	0.15 ± 0.01	0.08 ± 0.03	0.06 ± 0.00	0.03 ± 0.01	0.03 ± 0.00	0.02 ± 0.01	0.05 ± 0.01	0.01 ± 0.00
		50	0.14 ± 0.02	0.02 ± 0.01	0.06 ± 0.00	0.01 ± 0.00	0.04 ± 0.01	0.00 ± 0.00	0.04 ± 0.00	0.00 ± 0.00
		100	0.09 ± 0.00	0.03 ± 0.01	0.04 ± 0.00	0.01 ± 0.00	0.03 ± 0.00	0.01 ± 0.00	0.03 ± 0.00	0.01 ± 0.00

Table O-2. Percent carbon allocated into low molecular weight metabolites (LMW), lipid, polysaccharide (POLY), and protein by phytoplankton populations of five lakes after exposure to ambient (AMB) and enhanced (ENH) UVB levels under 6, 25, 50 and/or 100% of incoming surface irradiance (E_o). ± SD.

Lake		%E_o	% C in LMW		% C in LIPID		% C in POLY		% C in PROTEIN	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Clear L.	5 h	6	32.2 ± 1.2	35.1 ± 2.5	16.8 ± 1.1	16.3 ± 0.7	25.9 ± 0.3	26.2 ± 2.1	24.9 ± 2.0	22.4 ± 1.9
(21 July)		25	34.4 ± 2.1	40.1 ± 2.8	17.7 ± 1.0	17.4 ± 1.0	27.4 ± 0.6	27.5 ± 0.6	20.5 ± 1.7	15.0 ± 1.6
		50	35.2 ± 0.3	39.0 ± 2.9	17.1 ± 0.1	17.9 ± 1.6	29.3 ± 0.4	28.3 ± 0.5	18.4 ± 0.2	14.8 ± 1.6
		100	31.9 ± 3.5	38.3 ± 1.6	18.9 ± 1.3	17.0 ± 0.3	27.3 ± 0.6	31.2 ± 1.9	21.9 ± 2.9	13.6 ± 0.8
Meretta L.	2 h	6	54.4 ± 2.3	59.5 ± 1.4	22.0 ± 0.4	21.1 ± 1.4	9.2 ± 1.0	6.9 ± 1.0	14.4 ± 2.3	12.5 ± 2.0
(12 Aug.)		25	53.6 ± 1.8	56.5 ± 0.7	22.2 ± 1.0	22.2 ± 1.7	11.6 ± 2.4	12.5 ± 1.2	12.6 ± 3.3	8.8 ± 0.5
		50	52.9 ± 3.2	61.6 ± 2.2	21.7 ± 1.7	23.1 ± 0.6	10.8 ± 0.8	7.4 ± 3.1	14.6 ± 2.0	7.9 ± 1.4
		100	50.5 ± 3.7	69.9 ± 1.6	22.5 ± 2.9	21.8 ± 0.5	8.6 ± 0.4	0.7 ± 1.2	18.4 ± 1.3	7.6 ± 0.4
	8 h	6	48.9 ± 1.0	53.2 ± 1.9	20.9 ± 0.6	21.7 ± 1.2	15.7 ± 0.9	15.4 ± 3.5	14.6 ± 0.8	9.7 ± 1.8
		25	41.0 ± 8.1	58.2 ± 2.1	21.8 ± 0.8	21.2 ± 0.7	20.3 ± 2.3	13.2 ± 1.4	17.0 ± 6.3	7.4 ± 0.2
		50	43.3 ± 1.4	63.2 ± 3.1	21.7 ± 2.1	21.6 ± 0.8	17.2 ± 0.9	7.1 ± 3.2	17.9 ± 0.4	8.1 ± 0.5
		100	42.1 ± 3.5	62.9 ± 3.2	18.8 ± 1.3	21.0 ± 0.6	16.0 ± 1.8	6.8 ± 2.0	23.0 ± 1.8	9.2 ± 1.4
North L.	2 h	50	40.3 ± 7.3	37.3 ± 3.2	27.0 ± 2.7	30.1 ± 4.9	6.0 ± 3.7	5.9 ± 5.4	26.8 ± 5.9	26.8 ± 4.0
(9 Aug.)		100	31.3 ± 12.8	19.3 ± 10.5	30.8 ± 5.2	37.5 ± 5.2	3.0 ± 2.6	0.0 ± 0.0	34.9 ± 10.1	43.2 ± 5.2
	4 h	50	44.8 ± 3.0	60.3 ± 5.2	23.6 ± 1.1	24.7 ± 3.8	9.9 ± 1.4	7.5 ± 6.8	21.6 ± 3.4	7.5 ± 1.5
		100	41.3 ± 1.1	53.8 ± 1.6	23.9 ± 1.6	28.8 ± 1.8	8.3 ± 2.0	1.2 ± 1.8	26.5 ± 2.2	16.2 ± 1.8
	8 h	50	54.4 ± 2.7	56.9 ± 1.5	19.3 ± 1.9	26.4 ± 0.8	11.7 ± 1.6	7.8 ± 1.0	14.6 ± 1.1	8.9 ± 0.4
		100	41.8 ± 4.2	42.6 ± 9.1	23.6 ± 1.6	41.9 ± 6.6	13.7 ± 0.8	0.6 ± 1.1	20.9 ± 2.8	14.9 ± 2.9
	12h	50	38.9 ± 4.2	34.0 ± 12.8	26.1 ± 3.3	48.5 ± 18.8	16.1 ± 1.1	7.0 ± 6.1	18.8 ± 0.6	10.5 ± 0.4
		100	36.8 ± 4.4	18.4 ± 15.6	27.1 ± 2.7	62.9 ± 13.6	15.3 ± 1.1	0.0 ± 0.0	20.8 ± 1.0	18.7 ± 3.7
	24h	50	37.4 ± 3.8	28.2 ± 5.8	27.3 ± 3.2	48.1 ± 10.0	15.9 ± 1.1	11.2 ± 4.0	19.4 ± 0.8	12.4 ± 0.5
		100	34.4 ± 4.2	0.0 ± 0.0	26.6 ± 2.2	85.2 ± 4.4	16.6 ± 1.1	0.0 ± 0.0	22.5 ± 1.1	14.8 ± 4.4

Table O-2 (continued). Percent carbon allocated into low molecular weight metabolites (LMW), lipid, polysaccharide (POLY), and protein (Chapter 2).

Lake		%E_o	% C in LMW		% C in LIPID		% C in POLY		% C in PROTEIN	
			AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB	AMB-UVB	ENH-UVB
Small L. (28 July)	2 h	6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
		25	51.9 ± 1.2	53.2 ± 2.9	19.8 ± 0.8	19.8 ± 1.3	12.1 ± 0.9	14.5 ± 0.9	16.2 ± 1.6	12.5 ± 0.9
		50	51.5 ± 0.6	56.5 ± 1.9	19.1 ± 0.3	17.7 ± 1.4	13.9 ± 1.7	13.5 ± 0.9	15.5 ± 1.0	12.3 ± 1.0
		100	48.9 ± 3.8	58.6 ± 4.7	19.2 ± 0.5	20.1 ± 0.7	14.5 ± 3.1	10.2 ± 2.2	17.4 ± 2.2	11.1 ± 2.3
	6 h	6	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
		25	52.9 ± 3.5	59.8 ± 2.7	21.0 ± 1.5	17.6 ± 0.5	13.6 ± 2.0	11.5 ± 0.7	12.6 ± 2.6	11.1 ± 1.7
		50	52.3 ± 0.3	59.6 ± 1.4	19.9 ± 2.9	18.7 ± 0.1	15.5 ± 1.8	13.4 ± 0.9	12.4 ± 1.4	8.3 ± 0.9
		100	52.3 ± 2.3	56.4 ± 1.5	19.0 ± 0.7	17.6 ± 0.5	15.2 ± 0.8	16.5 ± 0.5	13.5 ± 2.1	9.5 ± 1.0
	12h	6	44.4 ± 2.4	51.0 ± 4.9	15.6 ± 0.6	17.9 ± 1.3	13.6 ± 0.4	14.2 ± 2.1	26.4 ± 1.5	16.9 ± 3.6
		25	51.9 ± 6.0	59.8 ± 3.9	17.7 ± 0.5	17.6 ± 3.6	12.2 ± 0.7	11.8 ± 0.3	18.3 ± 5.7	10.7 ± 0.4
		50	50.8 ± 1.6	58.2 ± 3.8	18.3 ± 1.1	18.6 ± 0.8	12.5 ± 0.2	13.9 ± 3.1	18.3 ± 0.7	9.3 ± 0.7
		100	53.8 ± 0.4	51.9 ± 3.2	18.0 ± 0.7	19.9 ± 0.8	12.8 ± 1.0	15.9 ± 1.1	15.3 ± 0.4	12.4 ± 1.5
Tern L. (3 Aug.)	2 h	6	52.7 ± 0.6	48.5 ± 4.2	21.9 ± 0.8	25.8 ± 4.6	10.0 ± 2.0	9.2 ± 4.6	15.4 ± 1.1	16.5 ± 2.4
		25	59.9 ± 5.3	58.6 ± 5.4	20.1 ± 0.8	21.2 ± 1.3	9.6 ± 2.5	8.0 ± 1.6	10.3 ± 2.9	12.1 ± 4.8
		50	52.2 ± 5.3	58.3 ± 4.5	21.1 ± 1.4	25.7 ± 0.5	13.2 ± 0.8	5.1 ± 2.4	13.5 ± 3.7	10.9 ± 1.6
		100	50.6 ± 4.1	59.7 ± 3.0	20.0 ± 1.7	22.5 ± 1.6	12.9 ± 1.0	7.5 ± 2.2	16.6 ± 2.4	10.3 ± 2.0
	8 h	6	49.7 ± 1.5	57.3 ± 1.7	20.4 ± 0.6	22.3 ± 1.7	12.0 ± 1.2	9.3 ± 0.6	17.9 ± 0.7	11.1 ± 0.6
		25	51.2 ± 3.5	57.5 ± 1.7	21.0 ± 0.3	20.6 ± 1.6	11.9 ± 0.6	12.0 ± 1.1	15.9 ± 3.6	9.9 ± 1.6
		50	49.3 ± 3.0	54.4 ± 5.0	21.2 ± 0.9	23.3 ± 1.9	13.3 ± 3.2	10.8 ± 0.7	16.2 ± 2.5	11.6 ± 2.6
		100	45.5 ± 1.4	51.7 ± 2.9	20.2 ± 2.1	24.1 ± 3.0	16.0 ± 1.4	12.2 ± 1.4	18.3 ± 1.1	12.0 ± 0.5