

# ULTRAVIOLET RADIATION AND ZOOPLANKTON COMMUNITY STRUCTURE FOLLOWING DEGLACIATION IN GLACIER BAY, ALASKA

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**Abstract.** We investigated changes in UV attenuation and macrozooplankton community structure in a set of lakes along a deglaciation chronosequence in Glacier Bay Alaska. Terrestrial succession in the watersheds of these lakes results in increasing dissolved organic carbon (DOC) content over time. Due to the primary role of DOC in controlling UV attenuation in lakes, one would suspect a gradient in UV attenuation and potentially zooplankton community structure in lakes of different ages. Field measurements of UV in seven lakes of different ages revealed that UV attenuation depths (1% of surface irradiance at 320 nm) ranged from 0.6 m in the oldest lake in the set (90 yr old), to more than 14 m in the youngest lake (10 yr old). Zooplankton community structure also changed across lakes of different ages. Patterns of distribution and abundance of the zooplankton both among and within lakes were consistent with the hypothesis that UV influences zooplankton community structure. The major differences in species composition among lakes were the absence of two primarily epilimnetic species (*Asplanchna priodonta* and *Ceriodaphnia quadrangula*) in all but the oldest lake, and the absence of *Bosmina longirostris* in the four youngest lakes. Transplant experiments in which UV radiation was manipulated in situ revealed that all three of these “delayed colonizer” species perish within only a few days when exposed to UV levels found in the surface waters (0.5 m depth) of the youngest lake. The strong dependence of UV radiation transparency on terrestrially derived DOC suggests a linkage between development of terrestrial plant communities within the watershed, changes in lake hydrology, and the early succession of zooplankton communities following deglaciation.

**Key words:** deglaciation; dissolved organic carbon; Glacier Bay, Alaska; lake ontogeny; predation; succession; ultraviolet radiation; zooplankton community.

## INTRODUCTION

In Glacier Bay, Alaska, deglaciation over the past 250 yr has left behind a landscape in which primary terrestrial succession has been studied in some detail (Chapin et al. 1995). The youngest landscapes within the deglaciated area are composed primarily of neoglaciated till, with little or no terrestrial vegetation. Succession proceeds through four generally recognized stages from “black crusts” of lichens, liverworts, blue-green algae, and mosses to sparse herbaceous vegetation that often develops into a continuous mat of the alpine avens (*Dryas drummondii*). Sitka alders (*Alnus sinuata*), willows (*Salix* spp.), and poplar (*Populus trichocarpa*) often accompany the *Dryas*, followed by a stage with dense thickets of alder, and finally a mature forest comprised primarily of Sitka spruce (*Picea sitchensis*) with some western hemlock (*Tsuga heterophylla*).

Within this landscape lies a sequence of lakes ranging in age from only a few years to several hundreds or (outside the deglaciated area) thousands of years. Studies of lake ontogeny along this deglaciation chron-

osequence have established a clear gradient in apparent color (an effective proxy for dissolved organic carbon, DOC) that indicates an increase in DOC concentration with lake age (Engstrom and Fritz 1990). This is consistent with previous observations that the terrestrial vegetation within a watershed plays a major role in determining DOC concentrations in lakes of similar ages (Engstrom 1987, Cronan 1990, Vincent and Pienitz 1997).

Multivariate analyses of the relationship between zooplankton community structure and associated environmental variables in Glacier Bay lakes have revealed that color explains more of the variance in zooplankton community structure than other environmental variables such as pH, presence or absence of fish, or chlorophyll concentration (Olson et al. 1995). A strong relationship between DOC and zooplankton community structure has also been observed in the Adirondack lakes of New York state (Siegfried et al. 1989). The significance and underlying mechanisms of this relationship between DOC and zooplankton community structure are currently unexplained. The identification of causal mechanisms of relationships involving DOC is particularly challenging given the wide

range of regulatory roles that DOC plays in freshwater ecosystems (Williamson et al. 1999b).

One mechanism that may contribute to the relationship between DOC and zooplankton community structure is the ability of DOC to regulate levels of potentially damaging ultraviolet radiation (UVR). DOC is the primary regulator of variation in ultraviolet radiation (UVR) among freshwater lakes of glacial origin (Scully and Lean 1994, Morris et al. 1995, Laurion et al. 1997). In addition, ambient levels of solar ultraviolet radiation (UVR) have the ability to cause intense and selective mortality in freshwater zooplankton communities in north-temperate lakes with low DOC concentrations (Williamson et al. 1994, 1999a). In the deglaciation chronosequence of lakes in Glacier Bay, the implication is that the underwater UVR environment is likely to vary with lake age. This natural gradient in UVR, if it exists, could provide a mechanistic explanation for the observed relationship between DOC and zooplankton community structure.

Here we address several questions related to the potential influence of UVR on colonization by macrozooplankton during early lake ontogeny in Glacier Bay. The first two questions are whether the underwater UVR environment does in fact vary with lake age, and what the differences are in zooplankton community structure in the younger vs. the older lakes. In particular, we ask what species of zooplankton are the primary colonizers in the first decade or so of lake ontogeny. We also ask whether there are species of zooplankton whose ability to colonize and become established may be constrained by high UVR levels in the younger lakes. To address these questions we first measured UVR levels and sampled the zooplankton in a subset of seven lakes (10–90 yr old) in the deglaciation chronosequence in Glacier Bay. All of the lakes that we investigated were “clear” lakes that were no longer subject to glaciofluvial activity or high turbidity from glacial flour. We found that two types of macrozooplankton were present in all of the lakes from youngest to oldest (*Daphnia* spp. and *Cyclops scutifer*). Three species, which we refer to as “delayed colonizers,” were present in the surface waters of the older, lower UVR lakes but were not found in the younger, higher UVR lakes.

Many factors are known to control zooplankton community structure in lakes including temperature (Moore et al. 1996), pH (Brett 1989), food limitation (Lampert 1985), and predation (Brooks and Dodson 1965, Kerfoot 1987), as well as seasonal variation in these factors (Sommer et al. 1986). If UVR is also important in determining the distribution and abundance of zooplankton, we might expect that species of zooplankton that are UV sensitive would “avoid” high UVR habitats. This pattern might express itself as either variation in zooplankton community structure among lakes with different underwater UVR environments, or as variation in zooplankton abundance within lakes by

depth or time of day. We used a combination of sampling across natural UVR gradients in addition to a series of UVR exposure experiments to assess the potential importance of UVR to zooplankton community structure in these Glacier Bay lakes. During the first year we carried out extensive sampling of both high and low UVR habitats in the study lakes to assess the extent of “avoidance” of high UVR habitats by zooplankton. This “natural experiment” included sampling across UVR gradients where UVR varied among lakes with DOC concentration as well as within lakes with depth (surface mixed layer vs. deeper strata) and time of day (day vs. night). In this context, “avoidance” might be attributed to either active behavioral responses or to passive responses related to lower physiological or ecological performance of individuals in high UVR habitats. In either case, a lower abundance in high vs. low UVR habitats was interpreted as being consistent with a UVR avoidance hypothesis.

These “natural experiments” did not permit us to separate UVR effects from the many other factors that are known to be important in determining zooplankton community structure. Thus during the second year we carried out a series of transplant experiments and an additional vertical distribution survey to test the hypothesis that UVR has the potential to inhibit colonization by the three “delayed colonizer” species during early lake ontogeny. The transplant experiments involved collecting the zooplankton from a low UVR lake and incubating them in a high UVR lake. These experiments were carried out in water from the high UVR incubation lake and manipulated only solar UVR in order to permit separation of UVR effects from other effects that might influence zooplankton community structure.

## METHODS

### *Lake characterization and UV environment*

This project was carried out over a two-year period during the spring–summer of 1996 and 1997 in the area of the Wachusett Inlet of Glacier Bay, Alaska, USA (58°56' N, 136°15' W). This area was selected for its history of recent deglaciation. Aerial photographs indicated that there were several young lakes that had been created recently by the melting of the remnant of the Burroughs Glacier in the Bruce Hills area. In addition to these very young lakes, we sampled several older lakes that had been previously sampled between 1987–1989 (Engstrom and Fritz 1990). Lake age along the Glacier Bay fjord is a function of the date of deglaciation, which is known from the observations of scientists, tree-ring chronologies, and extensive photographic records (Lawrence 1958, Engstrom and Fritz 1990). Lakes were selected primarily for their age, but also for ease of access from Wachusett Inlet, as all equipment and instrumentation had to be carried in on foot from the Inlet. The locations of these small (<1

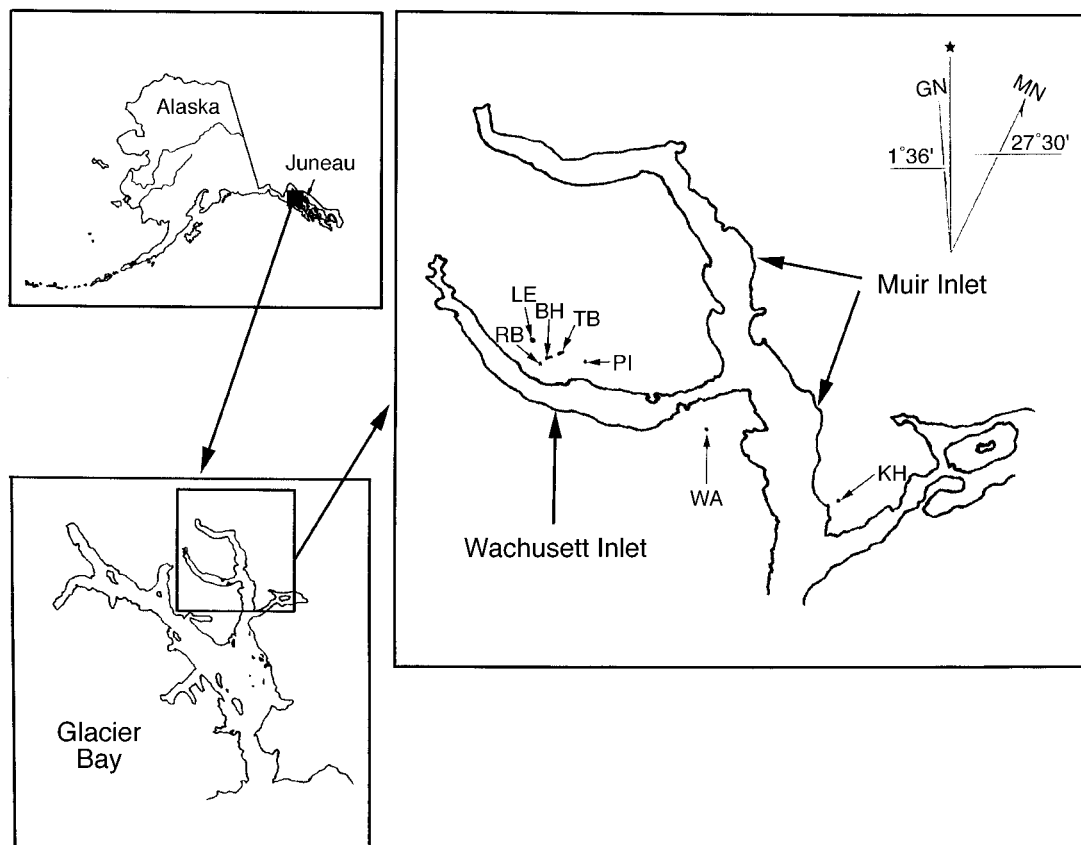


FIG. 1. Location of study lakes in Wachusett Inlet of Glacier Bay, Alaska. Abbreviations for lakes are: BH, Bruce Hills; KH, Klotz Hills; LE, Little Esker; P1, Plateau 1; RB, Round Bruce; TB, Twin Bruce; and W, Wachusett. For scale, the length of Wachusett Inlet traveling down the middle of the channel from end to end is 23 km. In the directional diagram, the star represents true north, GN is grid north, MN is magnetic north, and the arc segments are expressed in units of degrees and minutes.

ha) lakes are given in Fig. 1. The terrestrial vegetation in the watersheds of these lakes conforms nicely to that previously described in the literature for deglaciation chronosequences in Glacier Bay (summarized in the *Introduction*).

All sampling was done from a rubber raft near the center of the lakes. Maximum depths were measured by repeated use of a sounding line. Oxygen-temperature profiles were taken with a hand-held YSI model 55 dissolved oxygen system (YSI, Yellow Springs, Ohio, USA). Underwater UVR was measured with a PUV 501B profiling ultraviolet radiometer (Biospherical Instruments Inc., San Diego, California, USA). The PUV is a medium-bandwidth instrument (8–10 nm full width at half-maximum response) that measures incident solar radiation at four different UVR wavelengths (305, 320, 340, and 380 nm) as well as photosynthetically active radiation (PAR, 400–700 nm). While the PUV does not collect full spectral data, it has been shown to compare favorably with higher resolution spectroradiometers (Kirk et al. 1994, Laurion et al. 1997). DOC measurements were made by Don Morris at Lehigh University with a high temperature Pt catalyst

oxidation method (Morris et al. 1995). Secchi depths were estimated with a 20 cm diameter white and black disk and a view box to reduce reflection at the water surface, while pH was measured with a portable pH meter, generally during midday.

The average exposure to UVR (AEUV, for 320 nm) in the epilimnion of the lakes was calculated in order to estimate the percentage of surface UV irradiance to which an organism is exposed if it circulates freely in the mixed layer. These estimates used the following relationship (Zagarese et al. 1998):

$$AEUV = E_0(1 - e^{-K_d Z})(K_d Z)^{-1} \quad (1)$$

where  $E_0$  is the surface irradiance (here we use 100 in order to provide units as a percentage),  $K_d$  is the diffuse attenuation coefficient as estimated from the PUV profiles each month, and  $Z$  is the depth of the mixed layer. The diffuse attenuation coefficients were measured as the slope of the linear regression relationship between the natural logarithm of downwelling irradiance vs. depth in each lake.

Attenuation depths (1% of surface irradiance) were estimated by dividing 4.605 (the natural log of 100) by

TABLE 1. Physical and chemical characteristics of the seven study lakes as measured during the summer of 1996.

Lake	Lake age (yr)	Max depth (m)	Epilimnion		Temperature (°C)		UV Z1% depth (m)‡	Secchi depth (m)	pH	DOC (mg/L)
			Zmix depth (m)	UV exp (%)†	Epilimnetic	Hypolimnetic				
Klotz Hills§	90	7								
June			3	4	15.3	9.6	0.59	6.4	8.3	3.9
July			3	4	18.1	9.6	0.55	6.9	8.3	4.4
Wachusett§	45	18								
June			3	11	14.5	4.1	1.5	4.8	...	1.8
July			4.5	9	16.7	4.8	1.9	11.3	8.5	2.8
Plateau 1	35	7								
June			3	12	15.4	10.1	1.7	...	8.3	3
July			4	10	16.4	13.3	1.8	6.7	8.4	2.2
Round Bruce	15	6								
June			3	16	14.1	10	2.2	...	8.2	1.6
July			2	23	17	16.7	2.1	...	8.3	2
Bruce Hills	12	8								
June			4	22	14.6	12	4.1	7.3b	8.2	1.1
July			2	44	16.7	16.6	4.7	6.75b	...	1.5
Twin Bruce	12	9								
June			3	32	14.2	6.7	4.6	...	8.3	1.5
July			3	45	16.8	...	7.3	7.6b	...	0.9
Little Esker§	10	6.25								
June			3	65	12.3	9.8	14.7	6.25b	8.5	1.4
July			3	59	14.3	10.8	11.7	6.1b	...	0.7

Notes: The epilimnetic and hypolimnetic temperatures are the temperatures in the middle of the epilimnion and hypolimnion respectively. The epilimnion depth is the surface layer in which the zooplankton were sampled, while the hypolimnion extends from this depth to the bottom. A "b" after the Secchi depth indicates that the disk was on the lake bottom, so the actual Secchi transparency is greater than this. The "June" pH values were taken 30 May 1996, while the July pH values for Bruce Hills and Twin Bruce were taken in July of 1997.

† The UV 320 nm exposure is the percentage of subsurface irradiance to which an organism would be exposed if freely circulating in the epilimnion.

‡ The UV Z1% depth is the depth to which 1% of the incident 320-nm surface irradiance penetrates.

§ Lakes with fish.

the  $K_d$ . In order for attenuation depth estimates to be accurate, two conditions must be met. First, the depth range of the data used to estimate the  $K_d$  must be either greater than the estimated attenuation depth or close to the maximum depth of the water column. Second, the regressions must have high coefficients of determination ( $r^2$ ). If the first condition is not met, extrapolation of regression relationships into deeper strata with potentially different optical properties may render the attenuation depth estimates inaccurate. With one exception, the depth ranges of the data used here to estimate the  $K_d$  values were always either greater than the 1% attenuation depth (for the less UV-transparent lakes), or extended to within a meter of the lake bottom. The one exception was Twin Bruce in July, when the 1% attenuation depth was 7.3 m, and only 7 m of the water column was used in the regression estimate (Table 1). Coefficients of determination for the regression relationships for the  $K_d$  estimates were all 0.99 or better.

The 1% attenuation depth was chosen to be consistent with the phytoplankton literature and the use of 1% PAR as a characterizing depth. While the 1% depth will be correlated with UVR damage potential, it does not itself represent any critical level at which damage starts and stops, as this will be highly variable among species. The choice of the 320 nm wavelength is due to it being on the border of UV-B and UV-A. It thus provides information on the attenuation of both UV-B

and UV-A. Our unpublished data also indicate that 320 nm falls within the wavelength range of peak damage when one considers both the spectral composition of the sunlight and the biological weighting function for zooplankton such as *Daphnia*.

#### Zooplankton sampling and analysis

Zooplankton were collected with a closing "bongo" style plankton net equipped with a 202- $\mu$ m mesh, 30 cm diameter net on one side, and a 48- $\mu$ m mesh, 15 cm diameter Wisconsin style net on the other side, both with a 105-cm length of open mesh between the head ring and the cod end. Previous tests with this net have demonstrated 95–100% collection efficiencies of these nets when towed up to 10 m distance even in eutrophic lakes. Samples were collected from the deepest area of the lake basin during mid-June and mid-July, 1996, from the surface mixed layer (epilimnetic sample), and from just above the bottom to the bottom of the mixed layer (hypolimnetic sample). The dividing depths for the epilimnetic and hypolimnetic samples are given in Table 1 as the epilimnetic depths. Two replicate tows were taken in each stratum during midday, and another set in the middle of the night. Twin Bruce has two basins connected by a very shallow channel, and we sampled only the southwest basin. In June and July of 1997 six of the seven lakes were sampled less rigorously with two replicate full-water-column vertical

TABLE 2. Zooplankton densities (mean no./L of the two strata combined) and diel vertical migration indices (DVM index) for each study lake.

Lake	<i>Cyclops scutifer</i>		<i>Daphnia</i> spp		<i>Bosmina longirostris</i>		<i>Ceriodaphnia quadrangula</i>		<i>Asplanchna priodonta</i>		Limit of detection (L)
	Mean density	DVM index	Mean density	DVM index	Mean density	DVM index	Mean density	DVM index	Mean density	DVM index	
Klotz Hills†											
June	19.08	-6	0.76	-17	1.85	1	0.85	-3	30.34	-10	0.024
July	33.68	1	2.66	7	12.59	-5	13.32	3	18.56	11	0.047
Wachusett§											
June	0.04	0	0.09	1	0.81	0	L	...	L	...	0.006
July	L	...	L	...	1.23	-46	L	...	L	...	0.004
Plateau 1											
June	3.40	-14	2.69	-51	L	...	L	...	L	...	0.014
July	4.01	-18	2.31	-17	6.91	-3	0.06	6	L	...	0.011
Round Bruce											
June	L	...	0.02	2	0.04	0	L	...	L	...	0.004
July	0.01	...	6.92	-31	0.01	0	L	...	L	...	0.014
Bruce Hills											
June	3.40	-14	2.69	-51	L	...	L	...	L	...	0.011
July	1.80	-9	2.52	-10	L	...	L	...	L	...	0.014
Twin Bruce											
June	3.26	-42	0.12	-18	L	...	0.01	1	L	...	0.005
July	6.22	-33	0.05	11	L	...	0.04	-9	L	...	0.014
Little Esker†											
June	0.01	-2	0.02	-2	L	...	L	...	L	...	0.002
July	0.06	1	0.02	-1	L	...	L	...	L	...	0.002

Notes: The DVM index is the percentage of zooplankton sampled in the epilimnion during the day minus the percentage sampled in the epilimnion during the night (see *Methods* for equation used). Negative values are consistent with a UV avoidance hypothesis and indicate downward migration out of the surface waters by day, while positive values indicate upward migration during the day. The limit of detection (L) is given when no organisms were present in the sample volume counted. It indicates the resolution of the counting technique and is the zooplankton density if only a single individual had been observed in the entire counted sample. The blank spaces for the DVM index indicate the absence of adequate data to calculate the index. Note the strong persistence of DVM downward during the day even in lakes without fish.

† Lakes with fish.

tows during midday. Klotz Hills was sampled more rigorously in order to establish whether the three "delayed colonizer" species were found in the topmost surface waters during the day where they would be potentially vulnerable to UVR damage. These Klotz Hills samples were collected in June and July of 1997 at depths of 0–1, 1–2, and 2–5.5 m (maximum depth at time of sampling was 6 m).

Macrozooplankton were counted from the 202- $\mu$ m mesh net samples in a 10 mL Bogorov chamber under a dissecting microscope. A minimum of 200 zooplankton were counted per replicate sample jar (or the full sample) for each lake. In general the equivalent of at least 100 L of lake water was counted, giving a limit of detection (L) for each date, time, and depth of 0.01 zooplankton per liter or lower. The maximum and mean L values for each lake provide an estimate of our ability to detect rarer species in the plankton. Counts of the rotifer *Asplanchna* as well as the cladocerans included females of all ages and sizes. Males were rare or absent. Counts of *Cyclops* represent males, females, and copepodids combined. All zooplankton counts in 1996 were from samples taken with the 202- $\mu$ m mesh net (providing our definition of macrozooplankton), while the zooplankton counts of the vertical distributions of the three delayed colonizers in Klotz Hills in 1997 were from the 48- $\mu$ m mesh to get higher resolution of the

vertical distribution of all life history stages. In general, density estimates from the two nets were very similar in July, but somewhat lower in the 202- $\mu$ m mesh nets during June. Thus in 1996 some of the zooplankton were undoubtedly underestimated, such as neonates of *Asplanchna*, *Bosmina*, and *Ceriodaphnia*, and smaller copepodids of *Cyclops*. Zooplankton identifications were based on several sources (Brandlova et al. 1972, Pennak 1989, Thorp and Covich 1991, De Melo and Hebert 1994, Hebert 1995).

The zooplankton vertical distribution and abundance data from all seven lakes in June and July of 1996 were used to assess the hypothesis that the two zooplankton species that are present in all lakes avoid high UV habitats. One-tailed Wilcoxon paired-sample tests were carried out on the vertical and day–night distributions across all lakes and dates in order to determine whether distributions were consistent with the hypothesis of UV avoidance. The two null hypotheses were: (1) the density of the given species in the daytime epilimnion of the lakes is the same as the corresponding density in the daytime hypolimnion, and (2) the density of the given species in the daytime epilimnion of the lakes is the same as the corresponding density in the nighttime epilimnion. Due to these two species being at or below the limit of detection at certain times (Table 2), sample sizes for the paired-sample tests ranged from 11 to 13.

TABLE 3. Timing, exposure, survival data, and mortality rate coefficients for UV-exposure experiments in Little Esker.

Exp. †	Organism	Start date, time	Exposure			Final survivors per bag				Mortality rate coefficient	
			Duration (d)	UVR (exposure days)	Initial no. per bag	UV shielded		UV exposed		UVR	Other
						Mean	SE	Mean	SE		
1	<i>Asplanchna</i>	27 June, 2030	2.5	1.29	30	23.3	2.05	0.0	0.00	1.26	0.10
3	<i>Asplanchna</i>	8 July, 1830	1.8	0.62	15	7.4	0.47	0.0	0.00	1.11	0.39
1	<i>Bosmina</i>	27 June, 2030	2.5	1.29	30	11.7	1.47	0.6	0.42	1.19	0.38
2	<i>Bosmina</i>	5 July, 2030	1.8	0.55	30	15.8	1.53	5.9	0.68	0.55	0.36
4	<i>Bosmina</i>	11 July, 1300	2.1	0.47	30	19.3	1.35	9.7	1.34	0.33	0.21
3	<i>Ceriodaphnia</i>	8 July, 1830	1.8	0.62	30	24.1	1.83	10.5	1.54	0.46	0.12
4	<i>Ceriodaphnia</i>	11 July, 1300	2.1	0.47	30	26.9	1.15	23.5	1.67	0.06	0.05
5	<i>Ceriodaphnia</i>	20 July, 2100	1.8	0.54	30	21.3	1.53	11.9	1.14	0.32	0.19

Notes: Mortality rate coefficients (per d) are estimated for UVR effects, and for "other" effects (in treatments without UVR). One exposure day is equal to  $8.25 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$  at 320 nm, or one day of UV on a sunny day near summer solstice. For example, experiment 1 lasted 2.5 d, but due to UV attenuation by atmospheric (clouds, aerosols, etc.) and underwater (DOC, etc.) environments, the actual UVR exposure was equivalent to only 1.29 d at the surface.

† Experiment number.

Diel vertical migration (DVM) was examined using the following index that compared the difference between the percentage of zooplankton in the epilimnion during the day vs. the percentage in the epilimnion at night:

$$\text{DVM index} = [100(\text{ED} + 1)/(\text{WD} + 1)] - [100(\text{EN} + 1)/(\text{WN} + 1)] \quad (2)$$

where abbreviations represent zooplankton densities in the epilimnion during the day (ED) or the night (EN), and in the whole water column during the day (WD), or the night (WN). Percentages are used due to concerns about diurnal deficits in zooplankton populations (De Stasio 1993). A positive value indicates upward migration during the day, while a negative value is consistent with a UV avoidance hypothesis and indicates downward migration by day.

#### Zooplankton-UV experiments

Five in situ enclosure experiments that manipulated incident UVR were carried out in Little Esker. Zooplankton for these experiments were collected from Klotz Hills (the only lake that had all three species), isolated in 3 L of Little Esker lake water in gallon-sized polyethylene Bitran bags, and incubated at a depth of 0.5 m for ~2 d. Ten replicate bags for each treatment were suspended in racks covered by either UVR-shielding or UVR-transmitting acrylics. The two acrylics used were OP2 and OP4 (CYRO Industries, Orange, Connecticut, USA), both of which have sharp cutoffs on either side of the solar UVR spectrum. The OP2 blocks most of the UV-B and UV-A radiation (50% transmittance at 410 nm), while OP4 transmits UVR (50% transmittance at 272 nm). The acrylic shields were  $69 \times 36 \text{ cm}$  so that each one could hold two Bitran bags side by side. When filled the bags are  $26 \times 28 \text{ cm}$ , so there are several centimeters of acrylic overhanging each side. The details of the timing and

UVR exposure conditions for each experiment are given in Table 3.

At the end of the incubation period, the number of surviving zooplankton was counted in the field without preservation under a binocular dissecting microscope. UVR treatment effects were assessed using ANOVA. In the experiments in which two species were incubated simultaneously, two-way ANOVAs were used to test for species and UVR treatment effects as well as species by UVR interactions. The magnitude of the decreases in survival due to UVR vs. decreases in survival due to "other" effects (in the UVR-shielded treatments) were compared using two methods. First, mortality rate coefficients were calculated for both UVR-transmitting and UVR-shielded treatments (see Table 3). This was done with the standard exponential equation

$$(N_t = N_0 e^{-kt}) \quad (3)$$

where  $N_0$  is the number of individuals added per bag at the beginning of the experiment,  $N_t$  is the mean number of survivors at the end of the experiment in either the UVR-transmitting or UVR-shielded treatments,  $k$  is the mortality rate coefficient (per d), and  $t$  is the incubation time (d). The mortality rate coefficients in the UVR-shielded treatments provide an estimate of the decrease in survivors due to factors other than UVR, while subtracting the mortality rates in the UVR-shielded treatments from those in the +UVR treatments gives the decrease in survivors attributable to UVR damage. For *Asplanchna* we used a value of 1 for  $N_t$  in the +UVR treatments since there were no survivors in the +UV treatments and  $\ln$  of zero is undefined. This means that the UVR-related mortality rates for *Asplanchna* are underestimated. This approach assumes that rates are additive, and that a constant proportion of the individuals survive per unit time. The second method that we used was to simply calculate the percent

mortality due to UVR throughout the whole experiment in order to examine whether UV response generally increased with dose across the different exposure regimes used in the different experiments. This was done by subtracting the number of survivors in the final experimental treatments (+UVR,  $N_{ic}$ ) from the number of survivors in the final UVR-shielded treatments ( $N_{ic}$ ), and expressing the difference as a percent of the UVR-shielded survivors as follows:

$$\text{percentage mortality} = [(N_{ic} - N_{ic}) (N_{ic})^{-1}] 100 \quad (4)$$

#### *Characterization of experimental UV exposures*

Because we did not have adequate battery power to continuously operate the PUV during the experiments, we took continuous measurements of PAR with a carefully leveled, LI-COR LI-190SA quantum sensor equipped with an LI-1000 datalogger (LI-COR, Lincoln, Nebraska, USA) programmed to record hourly data. Simultaneous side-by-side measurements of solar radiation at 1-min intervals were collected with the LI-COR sensor and the PUV on three different dates (28 June, 21 July, and 26 July 1997) in order to permit intercalibration of the two instruments and a radiative transfer model (Madronich 1993, Biospherical Instruments 1998), using 1997 air calibration factors provided by Biospherical Instruments (San Diego, California, USA).

The mean ratio for daily integrated 320 nm UV:PAR was 0.136 where the units for UV are  $\text{kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$  and the units for PAR are  $\text{mol}/\text{m}^2$ . This ratio varied by <6% between 0830–1730 local time, the period in which 93% of the daily 320 nm energy was recorded during a day near summer solstice (27 June 1997). Incident UVR irradiance was then estimated at 320 nm during the experiments using the LI-COR readings to establish cloud optical depth, and satellite data<sup>3</sup> to establish local column ozone values for the radiative transfer model. Ozone values ranged between 309 and 363 Dobson units throughout the study period (mean = 335). The maximum potential daily UVR exposure at 320 nm expected above the water's surface on a sunny day near summer solstice under the mean ozone levels observed in Glacier Bay (referred to as a 320-nm exposure day, and =  $8.25 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$ ) was also estimated with the radiative transfer model. This was done in order to provide a frame of reference for interpretation of the data for those less familiar with UVR units.

UVR exposure levels in lake incubation experiments were estimated by attenuating the incident irradiance with the vertical attenuation coefficient ( $K_{d320}$ ) calculated from our PUV measurements in the top 0.5 m of Little Esker. We used the standard equation for estimating vertical attenuation (Kirk 1994):

$$E_z = E_0 e^{(-K_d Z)} \quad (5)$$

where  $E_z$  is the underwater irradiance at depth  $Z$ , and  $E_0$  is the incident irradiance just below the surface of the lake.

## RESULTS

### *Lake characterization and UV environment*

The seven study lakes spanned an age range of 10 to 90 yr, with maximum lake depths generally between 6 m and 9 m (Table 1). The exception to this was Wachusett which had a maximum depth of 18 m. During June and July the lakes were generally thermally stratified, with a mixed layer ranging in depth from 2 m to 4 m, and epilimnetic temperatures in the range of 12–15°C in June, warming to the 14–18°C range in July. Hypolimnetic temperatures generally ranged from 4 to 10°C, although in some cases isothermal conditions prevailed as the deeper waters warmed to 16°C or greater (Table 1). The pH of the lakes ranged between 8.2 and 8.5, and all were well-oxygenated. The youngest lakes were generally at or above 90% saturation for oxygen (10 mg/L or greater) down to within a meter or so of the bottom, while even the oldest lake examined here (Klotz Hills) dipped only to 60–70% saturation (6 mg/L or greater) within a meter of the lake bottom. The lakes were influenced by neither glacial runoff nor by the turbidity associated with glacial flour. Consequently, the lakes were clear to lightly stained (higher DOC lakes), with Secchi transparencies ranging between 5 and 11 m or greater. In the younger lakes, the Secchi transparencies were often underestimated as the Secchi disk could be seen even on the bottom of the deepest portions of the lake (Table 1).

As we had anticipated from the earlier color data of Engstrom and Fritz (1990) on a broader range of Glacier Bay lakes, the dissolved organic carbon (DOC) concentrations increased with increasing lake age. The DOC levels ranged from ~1 mg C/L in the youngest lakes to 4 mg C/L in the oldest lake. Corresponding changes in the UV attenuation depths were observed across this chronosequence. The estimated 1% attenuation depths (depth to which 1% of surface irradiance penetrates) for ultraviolet radiation (320 nm) ranged from 0.55 m in the oldest lake, Klotz Hills, to >14 m in the youngest lake, Little Esker (Table 1). This estimated 1% UV depth was about twice as deep as the bottom of the lake basin itself in Little Esker.

The average exposure to 320 nm UV radiation to which a freely circulating organism would be exposed in the epilimnion of these lakes also varied systematically with lake age (Fig. 2). In the oldest lake, an organism would be exposed to only 4% of the 320 nm UV entering the surface waters, while in the youngest lake they would be exposed to ~60% of the surface UV. An abrupt increase in UV exposure levels was observed in the lakes <20 yr old (Fig. 2). The variation in UV exposure in the epilimnion among lakes was due primarily to differences in UV attenuation, and to a

<sup>3</sup> Data available at <http://jwocky.gsfc.nasa.gov>.

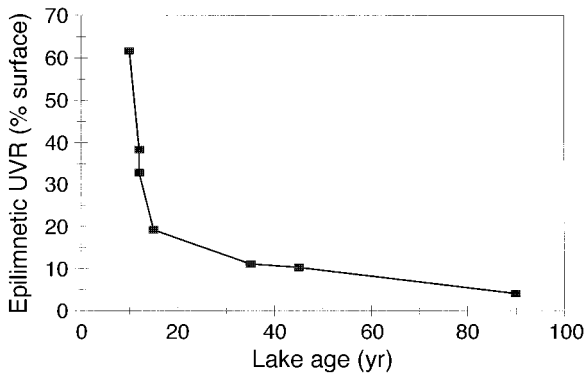


FIG. 2. Mean exposure to UV (320 nm) in the epilimnion of lakes of different ages in the deglaciation chronosequence in Glacier Bay. Exposure levels were estimated based on the assumption that an organism is freely circulating in the epilimnion. Actual exposure levels would be lower if, for example, zooplankton exhibited avoidance of the high UV levels near the surface and spent more time in the lower epilimnion.

lesser extent to differences in epilimnetic mixing depth among lakes (Table 1).

*Zooplankton communities*

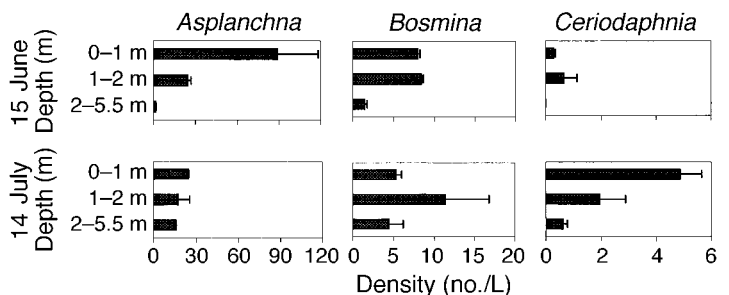
Six species of macrozooplankton were present in the lakes, with species richness declining from five reasonably well-established species in Klotz Hills to only two marginal species ( $\leq 0.06$  individuals/L) in Little Esker (Table 2). The primary species that colonized the lakes during the first 15 yr were the cyclopoid copepod *Cyclops scutifer* and the cladoceran *Daphnia pulicaria*. The oldest lake had well-established populations of *Daphnia dentifera*, two other cladoceran species, *Bosmina longirostris* and *Ceriodaphnia quadrangula*, as well as the large predator rotifer *Asplanchna priodonta*. Both *Cyclops scutifer* and one or the other species of *Daphnia* were present in all seven lakes, although present at extremely low densities ( $< 0.1$  individuals/L) in some of the lakes (Table 2). Although not sampled quantitatively, the presence of fish and benthic crustaceans such as *Gammarus lacustris* and *Eucyclops agilis* were also observed in some of the lakes. Visual observations established that fish (threespine stickleback, *Gasterosteus aculeatus*, and/or Dolly Varden, *Salvelinus malma*) were present in Klotz Hills, Wa-

chusett, and Little Esker. *Daphnia* was most abundant in three of the four lakes that had no fish (Plateau 1, Round Bruce, and Bruce Hills), and was least abundant in the three lakes with fish (Table 2).

Three macrozooplankton species were present in the older, lower UV lakes, but absent or scarce in the younger, high UV lakes. The fact that these species had established populations in only the older lakes leads us to refer to these three species as delayed colonizers. Of these three species, *Asplanchna* was the most restricted in its distribution, being present only in Klotz Hills. *Ceriodaphnia* was present in two other lakes in addition to Klotz Hills, but only at very low densities ( $\leq 0.06$  individuals/L in Plateau 1 and Twin Bruce, Table 2). *Bosmina* was somewhat more aggressive in its colonization of the younger, higher UV lakes, with reasonably well-established populations in Wachusett (about 1 individual/L), and Plateau (up to 6.9 individuals/L), and low density populations in Round Bruce ( $\leq 0.04$  individuals/L, Table 2).

The distributions of *Daphnia* and *Cyclops* were consistent with a UV avoidance hypothesis. Both species were significantly less abundant in the daytime epilimnion of the lakes than in either the nighttime epilimnion or the daytime hypolimnion (Wilcoxon paired-sample tests  $P < 0.05$ ). Interestingly, the diel vertical migration of these two species out of the daytime epilimnion in lakes with no fish (mean DVM index = -22 for *Cyclops* and -21 for *Daphnia*) tended to be stronger than in lakes with fish (mean DVM index = -1 for *Cyclops* and -4 for *Daphnia*, Table 2). The three delayed colonizer species were not abundant enough in the different lakes to carry out the paired-sample tests, but their abundance in the epilimnion during the higher resolution sampling (Fig. 3) and mixed DVM patterns (Table 2) suggest that these latter three species do not exhibit distribution patterns consistent with a UV avoidance hypothesis. In fact, the higher resolution vertical sampling data in Klotz Hills in 1997 indicate that all three delayed colonizers were abundant in the top meter of the water column during the day (Fig. 3). *Asplanchna* was always most abundant in the top meter, particularly in June, while *Ceriodaphnia* was rare at all depths in June ( $< 1$  individual/L), and most abundant in the top meter in July. *Bosmina* was somewhat less epilimnetic than the other two species, but was always present at substantial densities in the top meter.

FIG. 3. Vertical distribution (mean + 1 SE) of the three experimental zooplankton species in Klotz Hills in 1997. Note that, although UVR levels are not particularly high in Klotz Hills, all three species are common in the top 1 m of the water column, suggesting that there is potential for exposure to high UVR in younger, higher-UVR lakes if populations were to become established in these lakes.



### Zooplankton-UV experiments

The 1997 UVR exposure experiments revealed that all three of the delayed colonizers were sensitive to UVR damage. Statistically significant UVR effects were observed in all five experiments, and the interaction effects in the three two-species experiments were also statistically significant ( $P < 0.05$ ). Mortality rate coefficients were in all cases greater for UV effects than for all "other" effects in the UV-shielded treatments (Table 3). Weather in Glacier Bay is often cloudy and the weather during these experiments was no exception. Even during these cloudy periods, statistically significant UV damage was observed after only two days of incubation in the surface waters of Little Esker (Table 3). The maximum daily potential UVR expected above the water's surface on a sunny day near summer solstice under the mean ozone conditions observed in Glacier Bay (335 Dobson units) is  $8.25 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$  at 320 nm. In comparison, the levels of UVR exposure at depth during the experimental periods ranged from 3.84 to  $10.63 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$  at 320 nm, indicating that the equivalent of only a day or less of UVR may be fatal to zooplankton in the surface waters of low DOC lakes such as Little Esker. Moreover, this amount of UVR may be damaging even when spread over several more cloudy days.

The two-way ANOVAs performed on the two-species experiments indicated statistically significant species effects in all three cases ( $P < 0.05$ ; experiments 2, 3, and 4; Table 3). *Asplanchna* was the least UV tolerant of the three delayed colonizers, while *Bosmina* was intermediate in UV tolerance, and *Ceriodaphnia* was the most tolerant (Table 3, Fig. 4). Both *Bosmina* and *Ceriodaphnia* followed a general dose-response relationship, with higher mortality at higher UVR levels, while *Asplanchna* was so sensitive to UVR that it was not possible to look for a dose-response relationship with these data (Fig. 4). Since no *Asplanchna* survived the UV exposure in either experiment, these mortality rate coefficients (Table 3) are most likely underestimated relative to the UVR dose.

### DISCUSSION

#### Lake characterization and UV environment

To answer our initial question, UVR attenuation does vary greatly with lake age in the lakes that we studied in the deglaciation chronosequence in Glacier Bay. UVR penetrated much more deeply in the younger lakes that had low DOC and only sparse vegetation in their watersheds. Older lakes with more well-developed vegetation in their watersheds had more DOC, and lower levels of potentially damaging underwater UVR. This lends further support to the linkage of terrestrial succession to lake ontogeny first described in Glacier Bay lakes by Engstrom and Fritz (1990). Engstrom and Fritz also noted that lake ontogeny has multiple pathways that are regulated largely by watershed hydrology

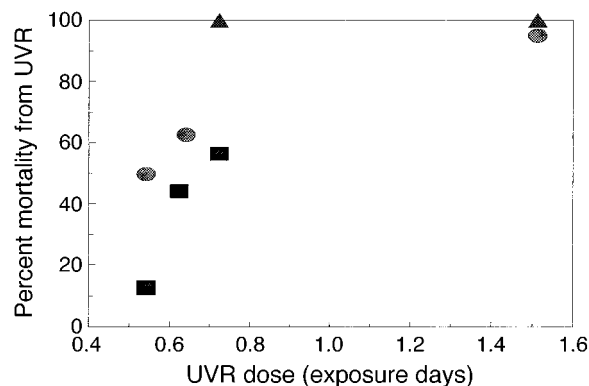


FIG. 4. Percentage mortality from UVR in zooplankton (for entire experimental period) as a function of estimated UVR exposure (320 nm exposure days at 0.5 m depth in Little Esker) in the in situ enclosure experiments. Symbols represent *Asplanchna* (triangles), *Bosmina* (circles), and *Ceriodaphnia* (squares). Zooplankton were incubated in UV-shielded and UV-exposed enclosures for time periods of ~2 d. In all cases, a statistically significant UVR effect was observed ( $P < 0.05$ ), even when incubation periods were short and the skies were cloudy. One exposure day represents the estimated UVR exposure for a sunny day around summer solstice and is equivalent to  $8.25 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$  at 320 nm just above the surface of the lake.

and geology. This is true of the underwater UVR environment as well. For example there are numerous lakes of glacial origin that are thousands of years old that still have very low DOC levels and correspondingly high underwater UVR environments (Morris et al. 1995, Williamson et al. 1996). A somewhat less pronounced example of this in Glacier Bay is Bartlett Lake, which is over 200 yr old, but has a 1% UV 320 nm attenuation depth of 2 m (compare values in Table 1). Many of these older lakes with the lowest DOC and highest UVR are at high elevations where, similar to the situation in the younger lakes in the Glacier Bay chronosequence, there is minimal vegetation in the surrounding watersheds. Others, like Bartlett Lake, are at a lower elevation but have very small watersheds (relative to lake surface area) and hence very low DOC loading from terrestrial sources (Engstrom 1987).

#### Zooplankton communities and UVR

Both experimental and distributional data support the hypothesis that solar UV radiation plays a key role in the distribution and abundance of species both among and within lakes of different ages. Even during cloudy days, ambient levels of solar UVR induced substantial mortality in three zooplankton species that were found to be scarce or absent in the younger, high UVR lakes. While we believe that UVR is not the only factor contributing to the delayed colonization of these three species, the low UVR tolerance combined with the generally epilimnetic nature of these species is strong circumstantial evidence that UVR plays a role in determining colonization by these zooplankton during the

first decades of lake ontogeny in Glacier Bay lakes. Within the two-day experimental time periods, UVR-related mortality rates were higher than all other factors combined, even on cloudy days (Table 3).

The early colonization of Glacier Bay lakes by two other species, *Daphnia pulicaria* and *Cyclops scutifer*, is also consistent with the UVR damage hypothesis. Both of these species exhibited frequent avoidance of the surface waters where UVR levels were high. *Cyclops* is largely hypolimnetic in these lakes, particularly during the day, and thus would not be as exposed to high UVR levels (Table 2). In addition, our previous experiments with *Cyclops scutifer* from lakes in Pennsylvania have shown that this cyclopoid is not only hypolimnetic (D. M. Leech, C. E. Williamson, R. E. Moeller, and B. R. Hargreaves, unpublished manuscript), but also one of the most UVR-tolerant zooplankton species among the many that we have tested (Leech and Williamson 2000).

The situation with *Daphnia* is somewhat more complex. Our previous experiments with UVR tolerance in Pennsylvania lakes suggest that *D. pulicaria* is one of the least tolerant to high UVR (Leech and Williamson 2000). However, in Glacier Bay, *Daphnia* generally exhibited downward migrations during the day, and thus would not be exposed to the high UVR levels in the surface waters (Table 2). One of the interesting aspects of these migrations is that they occurred even in lakes without fish. Diel vertical migrations down to deeper waters during the day in fishless lakes were observed for both *Cyclops* and *Daphnia* (Table 2). Recent studies with *Daphnia* have generally found that fish, or some kairomone from fish or other predators, is necessary to induce vertical migration (Dodson 1988, Dawidowicz et al. 1990, Neill 1990, Tjossem 1990). The persistence of vertical migration in these Glacier Bay lakes without fish (or any important invertebrate predators) strongly suggests that the *Daphnia* are migrating in response to some proximate cue other than fish kairomone. The most likely proximate cue for these migrations is UVR.

A close correlation between water transparency and the amplitude of vertical migration has been demonstrated across a range of lakes for *Daphnia* (Dodson 1990). In addition, *Daphnia* is known to be able to detect UVR (Smith and Macagno 1990). In fact, some recent photophysiological experiments have clearly demonstrated that *Daphnia* is positively phototactic in the presence of visible light, but negatively phototactic in response to UVR (Storz and Paul 1998). The peak sensitivity of *Daphnia*'s UV photoreceptors is actually in the longer wavelength UV-A range. These wavelengths may penetrate to depths >10 m in many lake regions in North America (Williamson et al. 1996). The fact that exposure to natural levels of UVR can kill *Daphnia* within a few days in the surface waters of low DOC lakes (Williamson et al. 1994, Zagarese et al. 1994) suggests that in addition to being a proximate

cue for diel vertical migration, UVR may also be an ultimate factor of some adaptive significance.

The UV experiments have some important limitations to consider. First, the incubation depth of 0.5 m is quite shallow, though not highly unrealistic given that in these small lakes the depth of the epilimnion is often only 2–3 m (Table 1) and a substantial portion of the populations of the three test species occur in the top 1 m of the water column (Fig. 3). Second, the test animals were taken from a relatively low UV lake, so there was little or no potential for acclimation to the higher UV environments in Little Esker. Unfortunately we had no other option for places to collect since Klotz Hills was the only lake that contained all three species of interest.

#### *Other factors controlling zooplankton communities in Glacier Bay lakes*

In addition to UVR, many other factors including dispersal, temperature, food limitation, and predation are also likely to be important in determining the colonization success and community structure of zooplankton in these Glacier Bay lakes. The geographic locations of the lakes are also not random. While our studies were designed to dissect out UVR effects rather than separate out each of multiple "other" factors, the results do suggest that factors other than UVR are important. One example is in the field enclosure experiments where substantial mortality was observed in the three species of delayed colonizers even in the absence of UVR (Table 3). The low nutrient and chlorophyll levels that characterize younger lakes in Glacier Bay (Olson et al. 1995) suggest that food limitation may have contributed to this mortality. In addition, although care was taken during the experiments, some portion of the mortality may also be due to handling zooplankton under the harsh field conditions. Both of these factors may also have stressed the zooplankton and potentially decreased their UVR tolerance.

Food limitation may also explain the presence of both *Daphnia* and *Cyclops* in the surface waters of Little Esker (Table 2). *Daphnia* is known to remain in the surface waters of lakes during times of food limitation (Johnsen and Jakobsen 1987, Flik and Ringelberg 1993), and it may be that food limitation is a stronger proximate stimulus than high UVR in determining the direction and timing of *Daphnia* migration. Although we have no data on food availability for *Daphnia* in Little Esker, the extremely low population densities of *Daphnia* in this lake ( $\leq 0.05$  individuals/L) combined with low egg ratios (no eggs were observed on any of the over 120 *Daphnia* counted in the lake samples in the two years) are consistent with this hypothesis.

Temperature is also likely to be important in these lakes. Higher temperatures offer a distinct demographic advantage to zooplankton that can exploit the warmer surface waters throughout the day (Threlkeld 1980, Or-

cutt and Porter 1983, Stich and Lampert 1984). In the shallow, low DOC lakes in Glacier Bay, temperature and UVR may in fact create strong conflicting selective pressures for zooplankton. The “growing” season for zooplankton in these lakes is short due to the low water temperatures experienced throughout most of the year. During the brief period of only a few months when the surface waters of these lakes warm up, zooplankton that reside in the warmer surface waters during daylight will gain demographically but will also be exposed to potentially damaging UVR.

Predation is also likely to be important to zooplankton community structure in these Glacier Bay lakes. Olson et al. (1995) found that the presence or absence of fish explained a portion of the differences among zooplankton communities in 32 lakes in Glacier Bay, three of which (Klotz Hills, Wachusett, and Plateau) were included in the current study. Our data on a more limited number of lakes support this previous finding. In particular, the abundance of the largest zooplankton species, *Daphnia*, was generally lower in lakes with fish (means 0.02, 0.04 and 1.71 individuals/L) than those without fish (averages 0.09, 2.50, 2.61, and 3.47 individuals/L; Table 2).

On the other hand, predation does not appear to be important in determining the vertical distribution of the macrozooplankton within individual lakes. Diel vertical migration out of the surface waters during the day was at least as common in lakes without fish predators as it was in lakes with fish (Table 2). This may be due to the restricted size of both the depth and the darkness components of the refuge from visual predators in these lakes. In shallow lakes migration to even the deepest waters may not be an effective predator avoidance strategy during the day. Even in deeper lakes such as Wachusett where a more effective depth refuge exists, the long periods of extended daylight at these high latitudes severely restrict the duration of the nocturnal refuge from visual predators in the surface waters. The shallow depths and long days may similarly decrease the effectiveness of vertical migration as a refuge from damaging UV radiation in lakes such as Little Esker where UVR penetrates to the bottom sediments.

Both *Cyclops scutifer* and *Gammarus lacustris* were potentially important invertebrate predators observed in these lakes. We have no quantitative data on *Gammarus*, although we did observe that it was largely benthic, generally absent from our plankton samples, and exhibited increased activity levels in the littoral zone at night. *Cyclops* on the other hand was often abundant, but primarily hypolimnetic (Table 2). For both of these benthic/hypolimnetic species the observed diel vertical migration and distribution patterns of the zooplankton are not consistent with a predator avoidance hypotheses (Table 2).

It is possible that dispersal limitation may contribute to the patterns observed in this study. While we have no data on dispersal, the presence of both partheno-

genesis and resistant resting stages in the delayed colonizer species as well as the presence of abundant migratory waterfowl in the area make dispersal limitation an unlikely explanation for the observed patterns of colonization. The extremely low population densities of zooplankton in several of the younger lakes also support the idea that factors limiting growth, survival, and reproduction may be more important than dispersal limitation. Zooplankton are sparse but present even in proglacial lakes that are still highly turbid from actively flowing glacial meltwater (Koenings et al. 1990), again suggesting that dispersal is not likely a limitation in these lakes.

### Conclusions

In conclusion, we found that the patterns of distribution and abundance of macrozooplankton both within and among lakes in Glacier Bay are consistent with the hypothesis that UVR plays a role in regulating zooplankton community structure in the early stages of lake ontogeny. These findings are consistent with our observations of the distribution and abundance of zooplankton in relationship to UVR in three lakes that we have been studying in some detail in northeastern Pennsylvania (Leech and Williamson 2000). In these Pennsylvania lakes, acid precipitation is a concern and thus it has not been clear whether some of the differences in UVR effects that we have observed among lakes in the past may have been aggravated by such anthropogenic atmospheric pollutants. The Glacier Bay lakes all had uniformly high pH, are much more remote from anthropogenic influence, and still provide strong evidence for UV effects on zooplankton.

The strong predictive relationship between DOC and UVR attenuation in combination with previously observed correlations between DOC and zooplankton community structure suggests that UVR may be a more important factor than previously recognized in determining the distribution and abundance of zooplankton both among and within lake ecosystems. These observations in concert with the rise in DOC with lake age in Glacier Bay provides evidence for directional change in ecosystem structure that is linked biogeochemically to the process of primary terrestrial succession. The rapid revegetation of the newly deglaciated landscape (Reiners et al. 1971, Chapin et al. 1995) and associated edaphic changes—carbonate leaching, humus buildup, nitrogen fixation (Crocker and Major 1955, Bormann and Sidle 1990)—increase the flux of DOC to downstream lakes (Engstrom and Fritz 1990), which transforms the light regime of the water column and allows colonization by UV-sensitive zooplankton, all within a few decades of deglaciation. Despite underlying differences in surface hydrology which may alter the trajectory of individual lakes, this deterministic pattern lends support to the idea that lakes may indeed age in a directional manner, driven in part by autogenic processes that are set in motion with glacial retreat.

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