

## SOLAR ULTRAVIOLET RADIATION AND THE SPAWNING HABITAT OF YELLOW PERCH, *PERCA FLAVESCENS*

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**Abstract.** Dissolved organic carbon (DOC) strongly influences the underwater levels of potentially damaging solar ultraviolet radiation (UVR) in freshwater lakes. Even so, little is known about how DOC-related variation in UVR may influence natural populations and communities in lakes. Past studies of fish recruitment have emphasized the importance of temperature, food limitation, and predation in controlling year-class strength in fish. Here we report that high UVR levels in low-DOC lakes also may modify the spawning depth, hatching success, and thus recruitment of certain freshwater fishes. We examined how UVR influences the spawning habitat and hatching success of yellow perch (*Perca flavescens*) eggs in two lakes with different DOC levels and thus different UVR environments. Yellow perch eggs were incubated at the same depth (0.8 m) in quartz tubes (with mesh ends for water exchange) in both lakes in a modified reciprocal transplant experiment. Solar radiation was manipulated to provide three treatments that included exposure to full solar radiation (quartz alone), shielding from UV-B with wavelength selective filters (Mylar D), and dark controls that removed all wavelengths of solar radiation. All eggs in the light treatments in the high-UVR lake perished, whereas survival to hatching of eggs in all treatments in the low-UVR lake and in the dark controls in the high-UVR lake were  $\geq 96\%$ . Survival time in the high-UVR lake was longer in UV-B-shielded than in fully exposed (quartz) treatments, and eggs collected from the high-UVR lake survived longer than those collected from the low-UVR lake in identical UVR treatments. A survey of natural spawning depths in the two lakes revealed a much deeper spawning depth in the high-UVR lake (median = 3.2 m) than in the low-UVR lake (median = 0.4 m). Deeper spawning depths in the high-UVR lake suggest that yellow perch can avoid direct UVR damage in low-DOC lakes. DOC and hence UVR in lakes may be altered by both anthropogenic and natural disturbances in the surrounding watershed, suggesting that these disturbances may have consequences for the spawning habitat of fish.

**Key words:** dissolved organic carbon (DOC); egg development; fish recruitment; fish spawning depth; *Perca flavescens*; solar ultraviolet radiation (UVR); spawning habitat; temperature; yellow perch.

### INTRODUCTION

Recent concern about stratospheric ozone depletion has increased interest in the role that ultraviolet radiation (UVR) plays in freshwater ecosystems (Williamson and Zagarese 1994, Williamson 1995). In freshwater lakes, variations in UVR intensities among lakes are controlled primarily by dissolved organic carbon concentrations (Kirk 1994, Scully and Lean 1994, Morris et al. 1995). For example, in lakes in different regions of North America, attenuation depths for UVR (1% of surface irradiance) may range from a few centimeters in high-DOC lakes to 10 m or more in some of the lowest DOC lakes (Williamson et al. 1996). DOC concentrations in turn are largely a function of ecosystem processes within the surrounding terrestrial watershed (Engstrom 1987, Rasmussen et al. 1989, Schindler et al. 1992). Thus, independent of any future

changes in stratospheric ozone concentrations, variations in dissolved organic carbon concentrations related to factors such as anthropogenic acidification, modifications in hydrology or land-use patterns in the watershed, and regional climate change may cause substantial changes in the exposure of aquatic communities to underwater UVR (Williamson 1995, Schindler et al. 1996, Williamson et al. 1996, Yan et al. 1996). In spite of this central importance of DOC in determining underwater levels of UVR, little is known about how existing differences in the underwater UVR environment among lakes influence the ecology of aquatic organisms in lakes with different DOC concentrations. Here we examine the implications of different underwater UVR environments for the spawning depth and hatching success of eggs of the yellow perch, *Perca flavescens*, in lakes with different DOC concentrations.

Fish eggs and larvae are highly transparent and frequently occur in shallow waters in both marine and freshwater systems (Hunter and Taylor 1982, Crowder and Crawford 1984), suggesting that these early life

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history stages may be vulnerable to damage by solar UVR. Previous studies with artificial UV lamps and roof-top solar incubators have demonstrated that UV radiation can damage the eggs and larvae of marine fish (Hunter et al. 1979, 1981), as well as damage adult trout in freshwater systems (Little and Fabacher 1994). Quantitative estimates with biological weighting functions have suggested that the damage observed from artificial lamps may occur in nature as well, but the extrapolation of laboratory results to the natural habitat is problematic (Hunter and Taylor 1982, Worrest 1986, Smith 1989). We performed a survey of spawning depths as well as an in situ modified reciprocal transplant experiment in a high-DOC lake and a low-DOC lake to test the hypothesis that differences in natural solar UVR among lakes may influence the spawning habitat and hatching success of yellow perch.

#### METHODS

##### *The study lakes and optical measurements*

Lake Giles is an oligotrophic, low-DOC ( $\approx 1.1$  mg/L) lake located at 41°23' N, 75°06' W, and an elevation of 428 m. It has a surface area of 48 ha, mean depth of 10.1 m, and maximum depth of 24 m. Typical summer epilimnetic chlorophyll values are in the 0.5  $\mu\text{g/L}$  range, Secchi depths are between 13 and 16 m, and pH between 5.2 and 5.4. Lake Lacawac is a mesotrophic, moderate level DOC ( $\approx 4.7$  mg/L) lake located at 41°23' N, 75°18' W, and an elevation of 439 m. Lacawac has a surface area of 21 ha, mean depth of 5.2 m, and maximum depth of 13 m. Typical summer epilimnetic chlorophyll values are in the 2–4  $\mu\text{g/L}$  range, Secchi depths are between 4 and 6 m, and pH between 6.2 and 6.5. Previous sampling with trap nets and gill nets as well as hook and line have produced yellow perch in multiple age classes, demonstrating that both lakes contain reproducing populations of yellow perch. (R. E. Moeller, C. E. Williamson, B. R. Hargreaves, and D. P. Morris, unpublished summary report on the Limnology of the Pocono Comparative Lakes Program core lakes, 1989–1993, available from Lehigh University Libraries through interlibrary loan).

Underwater solar UVR was measured in the two lakes on 27 April 1995 with a Biospherical Instruments PUV-501 (Biospherical Instruments, Inc., San Diego, California, USA). Diffuse attenuation coefficients were estimated from the slope of the linear regression relationship between the natural logarithm of downwelling irradiance vs. depth in the surface waters of each lake. Ambient UVR data were collected with a Biospherical Instruments GUV 521 on a Campbell Scientific CR-10 (Campbell Scientific, Inc., Logan, Utah, USA) data logger located on a weather station near Lake Lacawac. Data were collected at 15-min intervals and integrated over 2 d (the interval at which experiments were checked) throughout the study period (19 April–3 May 1995) to provide a general characteriza-

tion of solar UVR during the experiment. Both of these Biospherical instruments were medium-bandwidth UVR instruments (8–10 nm full width at half-maximum response) that measured four different UVR bands (305, 320, 340, and 380 nm), as well as photosynthetically active radiation (PAR, 400–700 nm). These instruments compare favorably with higher resolution spectroradiometers (Kirk et al. 1994). Irradiance over each 2-d interval at the experimental depth of 0.8 m in each lake was estimated from the GUV data and the corresponding  $K_d$  (diffuse attenuation coefficient) values from the vertical profile data.

##### *The experimental organism*

The yellow perch is a temperate mesotherm that spawns in shallow waters in spring, shortly after ice-out in dimictic lakes such as those in Pennsylvania. Winter minimum temperatures of 6°C or lower for at least 185 d are optimal for gonad maturation (Hokanson 1977). Oocyte growth is synchronous, and each female releases a single large egg mass in a gelatinous ribbon that contains from 7000 to 100 000+ eggs. The width and length of the egg mass are proportional to the number of eggs and the size of the spawning female (Gillet et al. 1995). Spawning occurs at water temperatures of 7°–11°C. Spawning can occur during several weeks in large lakes, but spawning may occur in small lakes for only 1–2 wk in any single locality (Clady and Hutchinson 1975, Hokanson 1977; C. E. Williamson, *personal observation*). In the northeastern United States, yellow perch spawn in early to mid-April, hatch by mid-May, and are found primarily in the surface waters (<2.5–3 m) in the first few weeks of their life. After several weeks the young yellow perch begin to adopt a progressively more demersal or littoral habit, migrating to near-shore habitats (Forney 1980, Post and McQueen 1988, Wahl et al. 1993). Year-class strength may vary by as much as 40-fold among years (Koonce et al. 1977). Individual adults return to the same spawning location within a lake from year to year, and may live for at least 7 yr (Clady 1977). Both yellow perch and its close relative the European yellow perch (*Perca fluviatilis*) are widespread and abundant across north-temperate regions; extensive ecological information is available on both species, making them ideal study organisms (Stevenson 1977).

##### *Transplant experiments with perch eggs*

We examined the potential importance of UVR in determining the spawning habitat of yellow perch in a transplant experiment in two lakes with contrasting UV environments: low-DOC, high-UVR Lake Giles, and moderate-DOC, low-UVR Lake Lacawac (Fig. 1, Table 1). The experimental design was a modified reciprocal transplant. Our preliminary data suggested that perch spawned deeper in the low-DOC lake than in the higher DOC lake. We also suspected that little or no overlap existed in the depth frequency distributions of spawn-

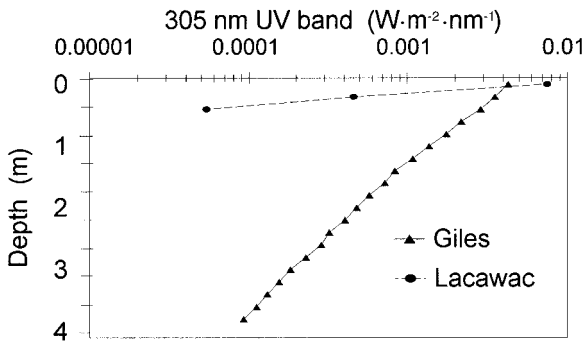


FIG. 1. Vertical profiles of UV-B (305-nm band of PUV-501) irradiance in low-DOC Lake Giles (▲) and moderate-DOC Lake Lacawac (●) in northeastern Pennsylvania, USA on 27 April 1995.

ing between the two lakes, with a breakpoint of  $\approx 0.8$  m. The working hypothesis was that in low-DOC lakes perch could not spawn at the same shallow depths that they do in higher DOC lakes due to the high levels of damaging UVR. We thus set out to test whether eggs could survive in a low-DOC lake at a depth that was close to the maximum depth at which spawning occurred in the higher DOC lake. A conventional reciprocal transplant design was not carried out as it would have incubated eggs at two unrealistic depths: at a much shallower depth than they ever appeared in the low-DOC lake, and at a much deeper depth than they ever occurred in the higher DOC lake.

Recently spawned eggs from both lakes were incubated in 16-mm diameter quartz tubes in both source and target lakes at 0.8-m depths under three different light treatments, generating 12 treatments. The three light treatments included full exposure to solar radiation in quartz tubes alone, a UV-B-shielded treatment in quartz tubes wrapped with Mylar D (23- $\mu$ m thick,

removes most UV-B, 50% transmittance at 316 nm), and a set of dark controls that was shielded from UV-A and PAR as well as UV-B radiation (quartz tubes wrapped with several layers of black polyethylene). All tube ends were covered with 202- $\mu$ m mesh Nitex to permit circulation of ambient water. Each treatment consisted of 100 eggs: 10 eggs per 40-mL quartz tube, with 10 replicates per treatment. The experiment started on 19 April 1996, and egg viability was monitored every 2 d until hatching or death of the eggs. Similar experiments were performed with yellow perch eggs in spring 1994 but with only five replicates, less frequent checking intervals, and only half of the modified reciprocal transplant: eggs collected from Lacawac were incubated in both Lake Lacawac and Lake Giles at a depth of 0.7 m.

*Survey of spawning depths in the two experimental lakes*

We surveyed natural spawning depths of yellow perch on 10 and 18 April 1995, within 1 wk of spawning, on very calm, sunny days, from a boat, with an underwater viewing box and an extendable aluminum pole marked at 1-cm intervals. The entire shoreline of each lake was surveyed and the depth of all perch egg masses recorded.

RESULTS

Ultraviolet radiation was attenuated much more rapidly in Lake Lacawac than in Lake Giles (Fig. 1). The UVR attenuation depths (1% of surface irradiance) in Lake Giles were over an order of magnitude deeper than those in Lake Lacawac (Table 1). For example, the 1% attenuation depths for the longest wavelength UV-B radiation (320 nm) were 4.9 m for Lake Giles and 0.35 m for Lake Lacawac. Although PAR levels

TABLE 1. (A) Diffuse attenuation coefficients ( $K_d$ , m), attenuation depths (depth at which irradiance = 1% of surface value,  $Z_a$ , m), and (B) irradiance for ultraviolet ( $J \cdot m^{-2} \cdot nm^{-1}$ ; 305-, 320-, 340-, and 380-nm bands) and photosynthetically active radiation (PAR, moles  $\cdot m^{-2} \cdot nm^{-1}$ , 400–700 nm) at a depth of 0.8 m in lakes Giles and Lacawac during the experiment (19 April–3 May 1995).

A) Attenuation coefficient/depth										
	Lake Giles					Lake Lacawac				
	305	320	340	380	PAR	305	320	340	380	PAR
$K_d$	1.05	0.939	0.800	0.494	0.201	15.2	13.0	10.1	5.44	0.767
$Z_a$	4.4	4.9	5.8	9.3	23.0	0.30	0.35	0.46	0.85	6.0

B) Total irradiance for each 2-d interval										
Days	Lake Giles					Lake Lacawac				
	305	320	340	380	PAR	305	320	340	380	PAR
0–2	355	3050	6267	11 479	38	0.004	0.19	4	224	25.2
2–4	356	3813	8141	15 022	50	0.005	0.28	6	331	37.0
4–6	520	5510	11796	22 041	76	0.006	0.36	7	429	49.0
6–8	337	4216	9389	17 386	60	0.005	0.32	7	392	45.0
8–10	...†	...	...	...	...	0.005	0.31	7	376	41.7
10–12	...	...	...	...	...	0.002	0.15	3	179	18.8
12–14	...	...	...	...	...	0.002	0.16	3	192	20.3

† Ellipses represent data not collected because the experiment had ended in that lake (all eggs were dead after day 8).

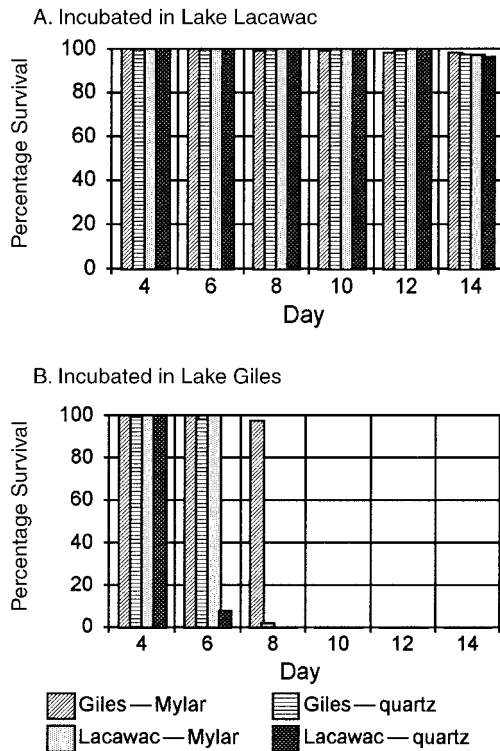


FIG. 2. Mean percentage survival of yellow perch eggs over time when incubated at 0.8-m depth in the four treatments in moderate-DOC Lake Lacawac (A) and low-DOC Lake Giles (B). Note that for each source lake, eggs shielded from UV-B with Mylar survive longer. Survival in all dark control treatments in both lakes (not shown in graph) was  $\geq 97\%$ , and standard errors were  $\leq 2\%$  ( $N = 10$ ) in all experimental and control treatments. No eggs survived in either Mylar or quartz treatments in Lake Giles beyond day 8. The key gives the name of the source lake from which the eggs were collected, as well as the filter treatment (Mylar = UV-B shielded, quartz = UV-B present).

were of a similar order of magnitude in the two lakes at the experimental depth of 0.8 m, UVR levels at this depth in Lake Giles were on the order of 1.5–5 orders of magnitude greater than those at the same depth in Lake Lacawac, with greatest differences in UVR at the shortest wavelengths (Table 1).

In the transplant experiments, survival to hatching was  $\geq 96\%$  for all treatments in Lake Lacawac and all dark controls in Lake Giles, whereas no eggs survived to hatching in any of the four light treatments in Lake Giles (Fig. 2). The timing of the mortality of the eggs also varied among treatments, with longer survival in treatments shielded from UV-B. In the light treatments in Lake Giles, substantial mortality was observed first in the fully exposed Lacawac eggs on day 6, followed 2 d later by virtually complete mortality in the UV-B-shielded Lacawac eggs and the exposed Giles eggs. High mortality in the UV-B-shielded eggs from Lake Giles did not occur until day 10 (Fig. 2). Differences among the four light treatments in Giles were significant (Kruskal-Wallis ANOVA by ranks on time to 50%

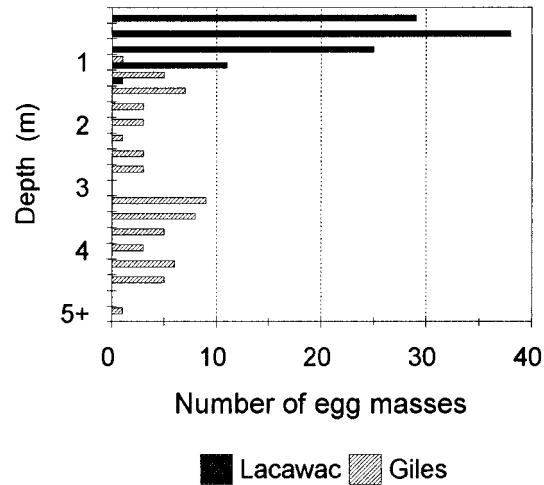


FIG. 3. Depth distribution of yellow perch egg masses in low-DOC Lake Giles (light shaded bars,  $N = 63$  egg masses, median depth = 3.2 m) and moderate-DOC Lake Lacawac (dark shaded bars,  $N = 104$  egg masses, median depth = 0.4 m) in northeastern Pennsylvania, USA in mid-April 1995.

survival (LT50),  $H = 39$ ,  $P < 0.001$ ). Mortality of eggs exposed to damaging solar radiation was evident from the opaque white color of the eggs and the lack of internal structure of the embryos.

Similar data were obtained for the preliminary experiments performed with perch eggs collected from Lacawac in 1994. After 4.4 and 7 d the survival in the UV-B-shielded treatments in Giles was 30 and 0%, respectively, whereas all but 2% of the eggs were dead in the quartz treatments after 4.4 d. Survival in the 1994 Giles controls was 100% after 7 d. The eggs incubated in Lacawac exhibited 98% survival in both shielded and unshielded treatments after 4.4 d, but a uniformly reduced survival of 64–68% in all three treatments after 14 d.

The lake-wide survey of spawning depths in the two lakes revealed that all but one of the 104 egg masses in Lacawac were found in water  $< 1$  m deep (median depth = 0.40 m), whereas in Giles 62 of the 63 egg masses were found deeper than 1 m (median depth = 3.2 m) (Fig. 3). At these median spawning depths, the longest wavelength UV-B (320 nm) irradiance levels are on the order of 5% (Lake Giles at 3.2 m) and 0.5% (Lake Lacawac at 0.40 m) of surface irradiance as estimated from the  $K_d$  values in Table 1.

#### DISCUSSION

Year-class strength in fish is highly variable and determined largely by mortality of early life history stages (May 1974, Magnuson 1991). Starvation, predation, and variation in abiotic factors such as temperature may all contribute to mortality in these early stages (Miller et al. 1988, Luecke et al. 1990, Magnuson 1991, Werner et al. 1993). Our data suggest that UV radiation may be an additional factor to consider

in lakes with low-DOC concentrations. High mortality of yellow perch eggs in the light treatments incubated in Lake Giles reveals that UV-B and longer wavelengths of solar radiation can inflict severe damage when these eggs occur at depths of <1 m in low-DOC lakes, a common spawning depth of yellow perch in many lakes. The  $\geq 96\%$  survival in the (UV protected) dark controls and 0% survival in all the light treatments in combination with the more rapid death of the eggs in the UV-B exposed (vs. UV-B shielded) light treatments would seem to preclude any alternative explanations for this result. All tubes were incubated at the same depth and had mesh-covered ends so water was able to circulate freely through the tubes. While the uniformly reduced survival rates in all of the Lacawac treatments after 2 wk render the 1994 experiments less conclusive, these results are consistent with the hypothesis of damaging UVR in the surface waters of Giles but not Lacawac.

Yellow perch might respond to the negative selective pressures related to potential UVR damage in three ways: UV avoidance by spawning at greater depths, UV protection by manufacturing photoprotective compounds, or post-UV-damage repair by molecular repair mechanisms (Zagarese and Williamson 1994). The deeper spawning depths in Giles vs. Lacawac combined with the high levels of UVR damage observed in the surface waters of Giles in the transplant experiment are consistent with the avoidance hypothesis. The limited data available in the literature are also consistent with the avoidance hypothesis, but no information on UVR is available and other confounding variables such as temperature exist. For example, yellow perch may spawn progressively deeper as summer solstice approaches and ambient UVR increases (*Perca flavescens* in Lochaber Lake, Newsome and Aalto 1987; and *Perca fluviatilis* in Lake Geneva, Gillet and Dubois 1995).

Interestingly, acceptance of the avoidance hypothesis would mean that direct damage from UVR is minimal in nature, and that any disadvantage of UVR is related to other environmental constraints such as increased predation or exposure to colder temperatures at greater depths. Thermal stratification is common in temperate lakes in the spring, and low temperatures can reduce survival and development rates of yellow perch eggs (Hokanson and Kleiner 1974). Our two study lakes showed clear thermal gradients in the top 3 m during the 1995 spawning period, suggesting that the deeper spawning in Lake Giles exposed the eggs to lower temperatures that would slow development and perhaps increase mortality.

The environmental cues that control spawning depth in yellow perch are unknown, but direct detection of UV-B radiation is unlikely given the visual sensory limitations of mature perch. Larval yellow perch have retinal cone photoreceptors with a visual pigment that has an absorption peak at 400 nm (Loew and Wahl 1991), but they lose these cone cells as they mature

and change from planktonic feeders to benthic feeders (Loew et al. 1993, Wahl et al. 1993).

Eggs from Lake Giles survived exposure to UVR longer than those from Lake Lacawac, suggesting that yellow perch populations in the higher UVR environment have responded by increasing either their photoprotective compounds or photorepair processes. Fish eggs are known to contain a variety of photoprotective compounds (Chioccare et al. 1980, Plack et al. 1981) and larvae have the ability to repair photodamage (Kaupp and Hunter 1981). In our experiments, visual examination and spectrophotometric scans of Giles egg masses revealed that the gelatinous matrix and chorion capsules were transparent to visible light and UVR (280–400 nm). We detected UV-B-absorbing compounds by high-pressure liquid chromatography (HPLC) analysis of 55% methanol extracts of embryos dissected from their chorion capsules (following the methods of Karentz et al. 1991), but the quantities (<0.01% of dry mass, assuming peaks were mycosporines with typical molar extinction coefficients) were too low to suggest a UV-protective function. These compounds were present at similar concentrations in both Giles and Lacawac embryos. Thus differences in survival in the two lakes are likely related to different photorepair capabilities between the two populations or to some undetected photoprotective compound.

These conclusions provide useful implications for fisheries management. For example, yellow perch are apparently able to respond both behaviorally and physiologically to avoid or reduce damage from ambient solar UVR. In shallow lakes with very low-DOC behavioral avoidance of high UVR will be difficult or impossible and spawning success will likely be reduced. Extremely shallow, low-DOC systems may not be able to support yellow perch populations due to the lack of a spawning refuge from high solar UVR.

Some important caveats are in order regarding quantitative estimates of UVR damage from DOC levels in lakes. First of all, in addition to DOC quantity, DOC quality, variations in cloud cover, the timing of ice-out, and rapid changes in sun angle may all influence the underwater UVR environment in lakes. Further, the biological response of living organisms to UVR decreases exponentially with increasing wavelength, especially in the UV-B region of the spectrum (Cullen et al. 1992, Madronich 1994). The spectral composition of UVR also changes drastically with depth, largely as a function of DOC concentration (Kirk 1994). Careful photobiological estimates based on species-specific weighting functions, accurate information on the depth distribution of the organisms, and detailed characterization of exposure to incident radiation under conditions of fluctuating environmental solar irradiance are necessary to accurately quantify and compare UVR damage and dose rates.

Our data have demonstrated UV sensitivity under

near-natural conditions, and support previous laboratory experiments on fish, as well as studies that have demonstrated a relationship between the hatching success of amphibian eggs, concentrations of the UV-damage-specific enzyme photolyase, and the intensity of damaging solar radiation in the amphibians' spawning habitats (Blaustein et al. 1994, 1995). More information is needed on how damaging solar radiation may interact with other seasonally and spatially variable factors such as temperature, food supply, and predation, that have previously been demonstrated to be key in regulating recruitment and hence year-class strength in fish populations. Many environmental factors such as climate warming, acid precipitation, and land-use patterns may influence DOC and hence UVR attenuation in lakes. Future changes in underwater UVR levels in freshwater ecosystems will thus be influenced by a variety of natural and anthropogenic environmental disturbances in addition to stratospheric ozone depletion.

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