Environmental Constraints on Spawning Depth of Yellow Perch: The Roles of Low Temperature and High Solar Ultraviolet Radiation

DAVID D. HUFF,† GABRIELLA GRAD, AND CRAIG E. WILLIAMSON

Department of Earth and Environmental Sciences, Lehigh University, 31 Williams Drive, Bethlehem, Pennsylvania 18015-3188, USA

Abstract.—The roles of temperature and ultraviolet radiation (UVR) in determining the spawning success of yellow perch Perca flavescens were investigated in two Pennsylvania lakes with different dissolved organic carbon (DOC) concentrations. In situ incubation experiments were used to manipulate temperature and UVR and to examine hatching time and hatching success. Extensive scuba surveys were used to document actual spawning depths. Differences in the temperature and UVR profiles of the two lakes led to contrasting responses of incubated yellow perch eggs. Higher temperatures in the surface waters of the higher-DOC lake led to hatching times that were 10−26 d shorter than those in the surface waters of the low-DOC lake or in the deeper waters of the higher-DOC lake. The high levels of UVR in the surface waters of the low-DOC lake killed 100% of the eggs before hatching. Ultraviolet radiation had little effect on survival in the higher-DOC lake or in deeper waters of the low-DOC lake. Scuba surveys revealed that spawning in the low-DOC lake occurred at greater depths than previously recognized. Ninety-two percent of the eggs spawned in the low-DOC lake were located at depths greater than 3 m, while 76% of eggs in the higher-DOC lake were spawned in water less than 1 m deep. Temperature and UVR are both important in determining among-lake differences in spawning depths of yellow perch. Yellow perch are able to spawn at shallow depths in higher-DOC lakes, where warmer temperatures accelerate developmental rates and DOC blocks potentially damaging UVR. In low-DOC lakes, yellow perch must spawn at greater depths to avoid UVR damage. Spawning at greater depths may be costly due to the substantially slower developmental rates at lower temperatures. Our data suggest that the conflicting selective pressures of UVR and temperature create an optimal spawning-depth range for yellow perch that differs among lakes as a function of DOC concentration.

Yellow perch Perca flavescens eggs are embedded in a gelatinous, accordion-like matrix, and spawners prefer to entangle egg strands on substrates such as woody debris, submerged macrophytes, and other structures. The duration of the spawning period is variable and can last from 1 to 4 weeks (Hokanson 1977; Thorpe 1977). Magnuson (1991) describes yellow perch as coolwater fish with a preferred temperature range of 20−25°C as adults. They are annual spawners with synchronous oocyte growth during fall through winter, and spawning occurs in spring, when thermal stratification is common in temperate lakes (Hokanson 1977; Reyes et al. 1992; Sandström et al. 1995).

In large lakes (>500 ha; Fee et al. 1996), wind-driven mixing reduces temperature gradients, but in smaller lakes, pronounced vertical gradients in temperature and solar ultraviolet radiation (UVR) can lead to variation in quality of spawning habitat with depth. Seasonal variations in temperature have been demonstrated repeatedly to be important in the spawning success of yellow perch (Hokanson and Kleiner 1974; Hokanson 1977; Clady 1976; Gillett and Dubois 1995), and cold temperatures are known to contribute both to longer development time and to decreased hatching success (Hokanson and Kleiner 1974). However, little attention has been given to the importance of vertical temperature gradients to yellow perch spawning success either within or among lakes. Similarly, there is evidence that UVR can lead to high mortality rates of yellow perch eggs incubated in the surface waters of lakes with low dissolved organic carbon (DOC) levels (Williamson et al. 1997), but there is little information about how the potential for UVR damage in surface waters may interact with vertical thermal gradients to alter the spawning success of yellow perch.

Dissolved organic carbon can strongly influence the thermal structure of small lakes (<500 ha; Fee et al. 1996) by decreasing the mixing depth as DOC increases. Dissolved organic carbon also has a strong influence on potentially damaging UVR.
(Morris et al. 1995) by attenuating UVR penetration, particularly that of the more damaging shorter wavelengths. This suggests that the vertical gradients in temperature and UVR within a lake where yellow perch spawn may be influenced by the DOC concentration of that lake. Knowledge is scarce about the possible constraints or benefits that DOC variations confer on fish spawning depths in either high- or low-DOC lakes. Though the avoidance of high-UVR strata in the surface waters of low-DOC lakes by spawning yellow perch is understood, the tendency of yellow perch in higher-DOC systems to avoid spawning at greater depths, where UVR causes no damage (Williamson et al. 1997), is less clearly understood. One possible explanation is that warmer temperatures in the surface waters create a beneficial environment that accelerates developmental rates and thus shortens hatching times.

Here we use a series of in situ incubation experiments and spawning-depth surveys to examine the potential importance of both temperature and UVR in determining the spawning depth of yellow perch in small lakes for which wind-driven mixing is minimal. Given that yellow perch prefer to spawn near their natal sites (Aalto and Newsome 1990), spawning site fidelity may be used as a proxy for the optimum range of spawning depths. We propose that differences in the vertical profiles of temperature and UVR in these small lakes may contribute to defining optimal spawning habitats at intermediate depths that will vary among lakes as a function of DOC concentration.

Methods

Study lakes.—Lakes Giles and Lacawac are located at an elevation of about 430 m in the Pocono Lakes Region of northeast Pennsylvania. Lake Giles (41°23′N, 75°06′W) has a surface area of 48 ha, a mean depth of 10.1 m, and a maximum depth of 24 m. The lake is oligotrophic and is characterized by low DOC levels (average, 1.1 mg/L). Typical Secchi depths range from 10 to 15 m, and pH is approximately 5.3. Lake Lacawac (41°23′N, 75°18′W) has a surface area of 21 ha, a mean depth of 5.2 m, and a maximum depth of 13 m. Lake Lacawac is mesotrophic, with higher DOC (average, 4.7 mg/L) than Lake Giles. Typical Secchi depths in this lake range from 4 to 6 m, and pH is approximately 6.3. Both lakes are dimictic; ice-out dates usually occur near the beginning of April for Lake Lacawac and about 1 week later for Lake Giles (R. E. Moeller, C. E. Williamson, B. R. Har-
Figure 1.—Positions of experimental sites and survey transects in lakes Lacawac and Giles, Pennsylvania, where the effects of ultraviolet radiation and temperature on yellow perch spawning and egg viability were studied. Artificial substrates were placed in the immediate vicinity of the experimental sites.

Parent egg sac with visible embryo) and dead eggs (milky-white egg sac with no distinct embryo visible) were recorded for each tube at each site. Tubes were removed when the eggs in each tube either hatched or died. We also measured dissolved oxygen two or three times per week at the experimental sites.

The percentage of eggs that survived to hatching in each tube was calculated, and the data were averaged for the four tubes at each site. The percentage data were then arcsine transformed and used in two-factor analyses of variance to determine if either UVR or depth affected hatching success.

Scuba surveys of yellow perch spawning depths.—Scuba surveys of the depth distribution of egg masses were performed on 23–27 April 1999 in Lake Lacawac and on 10–13 May 1999 in Lake Giles. Divers swam underwater transects along the bottom from shore toward the center of
Ultraviolet radiation was attenuated at a much higher level at Lake Giles than at Lake Lacawac (8.7°C at 8 m depth) than in Lake Giles (7.7°C at 15 m). The low value of 5.5 mg/L at 8 m in Lake Lacawac was measured on 26 May 1999; before this measurement, dissolved oxygen at 8 m never fell below 8.6 mg/L.

Both lakes were thermally stratified during the course of the yellow perch spawning season; mean temperatures during incubation generally ranged higher in Lake Lacawac (8.7°C at 8 m to 13.3°C at 0.5 m) than in Lake Giles (7.7°C at 15 m to 11.0°C at 0.5 m; Table 2). Incubating eggs in both lakes developed during a period of rising temperatures (Figure 2). Time to hatching was substantially shorter in the warmer surface waters of Lake Lacawac (9 d) than in the cooler waters in the other treatments, including those in Lake Giles (19–35 d; Table 2).

In Lake Lacawac, there was no significant effect of either depth ($F_{1.7} = 2.8$, $P = 0.18$) or UVR ($F_{1.7} = 0.4$, $P = 0.55$) on hatching success (Table 2). In Lake Giles, significant effects on hatching success were found for depth ($F_{2.11} = 126.7$, $P < 0.001$), UVR ($F_{1.11} = 87.8$, $P < 0.001$), and the depth × UVR interaction ($F_{2.11} = 133.9$, $P < 0.001$) (Table 2).

The scuba surveys revealed that spawning occurred at much greater depths in low-DOC, high-
**FIGURE 2.** Water temperatures at experimental depths in (A) Lake Lacawac and (B) Lake Giles, Pennsylvania, during the yellow perch spawning season in spring 1999. Twenty-four-hour moving averages are shown for temperatures recorded at 15-min intervals at both sites. In Lake Lacawac, temperatures increased at a rate of 0.40°C/d at 0.5 m and 0.02°C/d at 8.0 m. In Lake Giles, temperatures increased at a rate of 0.37°C/d at 0.5 m, 0.18°C/d at 6.0 m, and 0.03°C/d at 15.0 m.

**FIGURE 3.** Yellow perch egg depth distributions from spawning surveys performed in Lake Giles, which is characterized by low dissolved organic carbon (DOC) levels, and higher-DOC Lake Lacawac during spring 1999.

UVR Lake Giles than was previously appreciated from boat surveys. The median spawning depth in Lake Giles was between 5 and 6 m (Figure 3). The shallowest locations of egg masses in Lake Giles were between 2 and 3 m (8%), while the deepest locations were below 10 m (9%). Maximum spawning depths determined from boat surveys in Lake Lacawac were 1.25 m (n = 25; median = 0.75 m) in 1997 and 1.45 m (n = 50; median = 0.54 m) in 1998. The percentage of egg masses found at depths less than 1 m in Lake Lacawac was 80% in 1997 and 82% in 1998 (authors’ unpublished data). In the 1999 scuba survey, most spawning (76%) was observed over the 0–1-m depth interval in Lake Lacawac (Figure 3). Results of the scuba surveys in Lake Lacawac confirmed that boat surveys were probably sufficient for detecting all the egg masses in the previous years. Collectively, these data indicate that Lake Lacawac eggs were primarily spawned in the 0–1-m depth interval, whereas in Lake Giles, egg masses were distributed at much greater depths and over a much wider depth range (Figure 3).

The artificial spawning substrates placed at the SE and NE sites in Lake Giles showed that no egg masses were spawned at 0.5 m. Heavy spawning occurred at the intermediate depth (6 m), with 18 and 25 egg masses found per substrate, and only one egg mass and four egg masses were found on the two substrates at 15 m.

**Discussion**

Previous work with yellow perch eggs has demonstrated that natural levels of solar radiation can damage eggs spawned in the surface waters of low-DOC lakes (Williamson et al. 1997). Although these studies reported prolonged survival times when solar UV-B radiation was reduced with Mylar-D filters in comparison to unshielded treatments, eventually all of the eggs in the shielded treatments died before hatching. The Mylar D used for the UV-B shield in these studies cuts only 60% of solar UV-B energy (280–320 nm; Williamson et al. 2001); only with the total removal of sunlight (with black plastic) was substantial survival of yel-
low perch eggs observed. Thus, Williamson et al. (2001) did not determine which wavelengths of solar radiation were ultimately responsible for this mortality: UVR or high-intensity, short-wavelength blue light. The high survival rates observed in our shallow, UVR-shielded treatments in Lake Giles demonstrate that UVR, not the longer wavelengths of high-intensity, visible light, is responsible for the mortality. We have also shown that yellow perch spawn to a depth of 14 m, a behavior that the boat surveys of Williamson et al. (1997) could not detect.

Our in situ experiments demonstrated that UVR is a definitive factor in determining the upper tolerance of spawning depth in low-DOC Lake Giles. Ultraviolet radiation also seemed to reduce survival to hatching in the shallow waters of high-DOC Lake Lacawac, although this trend was not statistically significant. We are not certain why the hatching success of yellow perch eggs was lower in Lake Lacawac than in Lake Giles, but many factors may be involved. The two egg masses in the experiments came from two different females, but both originated from Lake Giles. The viability of the egg masses used in the Lake Lacawac experiment may have been lower. Transfer of eggs from one lake to another may have also reduced hatching success because of increased mechanical damage, change in water chemistry, or change in temperature from lake to lake.

Perhaps more importantly, our study demonstrates the potential tradeoffs between the strong effects of UVR on survival in surface waters and the development-retarding effects of lower temperatures deeper in the water column of small lakes. Both the experimental data and the egg depth survey data suggest that these conflicting selective pressures define an intermediate depth range that can be referred to as the optimal spawning depths (OSD; Figure 4). The OSD will vary as a function of the DOC concentration of a lake due to the light-absorbing properties of the chromophoric components of dissolved organic matter (CDOM). The OSD will be closer to the surface and narrower in depth span in higher-DOC lakes than in lower-DOC lakes for two reasons. First, high CDOM absorbs and reduces UVR to levels that will minimize potential damage in the surface waters (Tables 1, 2). Second, rapid absorption of solar energy by CDOM and the consequent heating of the surface waters will cause a shallower and steeper thermocline in higher-DOC lakes (Fee et al. 1996). This warmer, shallower, more UVR-protected, mixed layer will in turn create greater selective pressures on yellow perch to spawn near the surface, as occurs in Lake Lacawac (Figures 3, 4). In low-DOC lakes, potentially damaging UVR will penetrate more deeply into the water column and reduce survival of eggs that are spawned near the surface (Tables 1, 2). In addition, the low levels of CDOM will lead to greater penetration of solar energy into the water column and...
consequently a deeper, cooler mixed layer with a more gradual thermocline. Such conditions will create a deeper OSD that spans a wider depth range in low-DOC lakes, such as Lake Giles (Figures 3, 4).

Because yellow perch exhibit demic behavior by returning to their natal sites to spawn (Aalto and Newsome 1990), these selective pressures would necessarily exert a strong influence on spawning depth. For example, a pair of yellow perch that are introduced to a high-UVR lake might spawn randomly at first (because their natal site is in another lake), but the only offspring that would survive to reproduce would be those with a natal site deep enough to avoid egg damage from UVR. This would establish a spawning site for subsequent generations. Changes in water chemistry would give a slight advantage to yellow perch that happen to spawn at slightly greater (or shallower) depths and so on.

Clearly, temperature and UVR are not the only factors that regulate the spawning depth of yellow perch. This study is just a first effort to assess two of the many possible components of the vertical habitat gradient in lakes. Other potentially important components of the vertical habitat gradient include the availability of suitable spawning substrate, exposure to predators, and oxygen levels.

The relative capability of woody or other rough substrate to reduce transport of eggs to harmful locations could lead to a tendency for yellow perch to show substrate-selective spawning (Dorr 1982; Aalto and Newsome 1993). Strong winds provide a potential mechanism for blowing yellow perch eggs ashore. Clady and Hutchinson (1975) observed this phenomenon in Oneida Lake, New York. Yellow perch eggs were not exposed to this situation in Lake Lacawac or Lake Giles because these lakes have a relatively small fetch. Could the lack of spawning at shallow depths in Lake Giles be due to the lack of appropriate spawning substrates? Visual surveys indicated that fallen trees and other appropriate spawning habitats were available but not used in the surface waters of Lake Giles. The data from our artificial spawning substrates support our conclusions from visual surveys that spawning substrate is not limited at shallow depths in this lake.

Oxygen is another important component of the vertical habitat gradient in lakes. Placement of the eggs so that the accordion-like strands are extended over woody structures also ensures that eggs remain well-oxygenated (Reyes et al. 1992). Low oxygen could play a role in compressing the OSD of yellow perch toward the surface layers of higher-DOC lakes because photosynthetically active radiation is reduced and decomposition rates are higher, and thus net oxygen consumption is higher. Although our oxygen data indicate lower oxygen levels in the deeper waters of Lake Lacawac, two factors suggest that oxygen does not explain the observed patterns in hatching success and timing. First, the primary oxygen gradient observed was with depth in Lake Lacawac, but egg survival was higher at greater depths than at shallow depths. Second, other than the UVR-related mortality, the major difference in hatching among depths was in development time, not survival; this result is most likely related to temperature (Hokanson and Kleiner 1974).

The empirical basis for the temperature curves drawn in Figure 4 is from experimental laboratory hatching data (Hokanson and Kleiner 1974). Although hatching success was higher in colder Lake Giles, the harmful effect of colder temperature is still a useful component of the model. Longer development times induced by lower temperatures could have various consequences for yellow perch. Production of copepod nauplii, one of the primary foods of yellow perch larvae in the study lakes (R. E. Moeller, C. E. Williamson, B. R. Hargreaves, and D. P. Morris, Lehigh University, unpublished report; Dina Leech, Lehigh University, personal communication), shows a decreasing trend in density from ice-out in the spring to early summer. Copepod nauplii are an important early food source for yellow perch larvae in other lakes as well (Fisher and Willis 1997). The decline in copepod nauplii during the period of larval development illustrates how the timing of larval production may “mismatch” the production of their principal food source (Cushing 1990). Declining food supplies may slow larval growth and cause the larval period to be extended, thus increasing the possibility that predators will consume vulnerable larvae. Subtle variability in larval predation and starvation rates are difficult to estimate, but are likely to exert a greater effect on recruitment than does catastrophic mortality (Houde 1989). In nature, slowly developing eggs are also exposed for a longer duration to such dangers as transport to poor locations by water currents and mechanical damage.

To date, the influence of DOC-induced changes in water transparency on yellow perch spawning has been largely neglected. Many studies report yellow perch spawning depths, but few studies report water transparency (Newsome and Aalto...
1987; Zeh et al. 1989; Gillett and Dubois 1995). Similarly, many studies have demonstrated the importance of seasonal changes in temperature (Forney 1971; Koonce et al. 1977; Henderson 1985), but none have examined vertical temperature gradients. Recent evidence suggests that changes in climate and land use are altering DOC, with consequences for the vertical thermal and optical gradients in lakes (Schindler et al. 1992; Fee et al. 1996; Williamson et al. 1996). We suggest that more attention to variations in temperature, UVR, and other components of the vertical habitat gradient of small lakes as modified by DOC can provide useful insights into variations in fish spawning behavior.

Acknowledgments

We thank Mark Olson and Don Morris for very thorough and helpful reviews of the manuscript, Daria Mochan, Kelly Maloney, and Danielle Karpelou for assistance in the field, and Dina Leech for extracting copepod data from the Pocono Comparative Lakes Program database. Thanks go to Bruce Hargreaves for providing UVR data from the Lacawac weather station and to Wreck’s and Reef Dive Shop for generously providing scuba supplies and technical expertise. We also thank the Lacawac Sanctuary and The Blooming Grove Hunting and Fishing Club for their cooperation in this project and for access to the lakes. Bathymetric maps in Figure 1 were digitized from maps shown in a 1993 unpublished report by R. E. Moeller, C. E. Williamson, B. R. Hargreaves, and D. P. Morris of Lehigh University. This work was supported by National Science Foundation grants DEB-9509042, DEB-9973938, and DEB-0210972, and is a contribution to Lehigh University’s Pocono Comparative Lakes Program.

References


