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Trade-offs in the response of mayflies to low oxygen and fish predation

Frank J. Rahel and Cynthia S. Kolar

Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

Summary. We examined how mayfly larvae (Ephemeroptera, *Callibaetis montanus*) balance the conflicting demands of avoiding both benthic hypoxia and fish predators. Using vertical oxygen and temperature gradients typical of ice-covered lakes, we observed the behavior of mayflies in the presence and absence of fish. In the absence of fish and with adequate oxygen, mayflies spent most of the time on the bottom substrate. As benthic oxygen concentration declined, mayflies increased their activity and moved up in the water column. In the presence of fish and with adequate oxygen, mayflies spent even more time associated with the bottom substrate and reduced their activity levels. As benthic oxygen concentrations declined, mayflies increased their activity and moved up in the water column, but to a lesser extent than when fish were absent. Because of this depression in activity and reluctance to leave the bottom substrate, mayflies endured lower oxygen concentrations in the face of predation threat relative to when fish were absent. Despite this trade-off, benthic hypoxia resulted in increased mortality due to fish predation. Because benthic invertebrates vary in their ability to tolerate hypoxia and in their vulnerability to fish predators, periods of benthic hypoxia could lead to selective predation on some taxa and be an important force structuring benthic invertebrate assemblages.

Key words: Predation – Predator-intimidation – Trade-off – Hypoxia – Ephemeroptera

Behavioral responses to predators or abiotic stresses can have a major influence on the distribution and activity of aquatic organisms. To avoid predators, prey may be forced to switch habitats, seek shelter or restrict activity. Examples of habitat shifts include the vertical migration of zooplankton to avoid fish predators (Lampert 1987), the inshore movement of small fishes during the day

to avoid piscivorous fish (Bohl 1980), and restriction of small fish and invertebrates to the margins of stream pools when predators are present (Cooper 1984; Power 1987). Such habitat shifts can reduce predation risk but may result in reduced growth (Werner et al. 1983). Examples of seeking shelter include hiding under rocks as observed in small fishes and small crayfish (Stein and Magnuson 1976; Rahel and Stein 1988) or moving around seagrass blades to avoid visual detection by predators (Main 1987). Reduction of activity to minimize detection is another common anti-predator behavior (Williams and Moore 1982; Heads 1985; Gilliam et al. 1989). In some cases, microhabitat shifts and reduction in activity can persist for hours after a predator has left an area (Rahel and Stein 1988) or can result from chemical cues without direct contact with the predator (Peckarsky 1980; Sih 1986).

Avoidance of unfavourable temperature and oxygen conditions can also influence the distribution of aquatic organisms. Examples include the emigration of fish assemblages from lakes with low oxygen concentrations into tributary streams with higher oxygen concentrations (Magnuson et al. 1985), the migration of benthic invertebrates to inshore areas with higher oxygen concentrations in stratified lakes with hypoxic hypolimnions (Brinkhurst 1984), and migration of fish and benthic invertebrates out of unfavourable temperature or oxygen conditions (Nagell 1977; Hocutt et al. 1982; Crowder and Magnuson 1982; Suther and Gee 1986).

Increased locomotor activity is another common response of aquatic organisms to stressful conditions. For example, stonefly nymphs and amphipods increase locomotor activity as oxygen levels decrease, apparently in an attempt to find higher oxygen concentrations (Knight and Gaufin 1964; Costa 1967). Fish also increase their activity and move to the water surface when oxygen levels decline to stressful levels (Petrosky and Magnuson 1973; Magnuson et al. 1985).

The above examples indicate that aquatic organisms can respond in an adaptive fashion to the threat of predation and to stressful abiotic conditions. However, or-

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ganisms may be faced with conflicting demands such that avoidance of one factor (e.g. low oxygen) may increase the risk of dying from another factor (e.g. predation). Such conflicts could occur for benthic invertebrates in ice-covered lakes during periods of winter hypoxia in the benthic zone. During extended ice-cover in productive lakes, hypoxia often develops near the bottom substrate and moves progressively upward in the water column (Wetzel 1983). High oxygen concentrations may become restricted to near the ice-water interface (Magnuson and Karlen 1970; Nagell and Brittain 1977) and thus upward migration to this region can allow fish and invertebrates to survive these episodes of hypoxia (Sikorowa 1968; Nagell 1977; Magnuson et al. 1985). However, for benthic invertebrates, movement upward entails leaving the relative safety of bottom substrates and becoming more visible to fish predators (Ware 1973). Furthermore, the increased locomotor activity needed to locate and move to regions of higher oxygen conflicts with the need to reduce activity to minimize detection by fish predators (Wright and O'Brien 1982).

The purpose of our study was to determine how benthic invertebrates balance the conflicting needs to avoid both low oxygen conditions and fish predators in lakes subject to benthic hypoxia during winter ice-cover. Specifically, we looked at how mayflies respond to developing hypoxia in the benthic region with and without fish present. We addressed two questions: 1) does avoidance of low oxygen result in greater risk of predation from fish and 2) are mayflies willing to tolerate lower oxygen conditions when fish predators are present compared to when such predators are absent?

Materials and methods

We monitored the response of mayfly larvae (Ephemeroptera, *Callibaetis montanus*) to declining oxygen concentrations with and without fish present in two sets of experiments. The first experiment (termed the static test) was done in a glass aquaria measuring 25 cm on each side. Sodium sulfite (150 mg/L) was used to deplete the bottom water of oxygen over a 30-min period (Fig. 1). Because surface waters remained well-oxygenated, mayflies were exposed to a vertical oxygen gradient similar to that found in small ponds during winter ice-cover (Wetzel 1983). Other workers using sodium sulfite to reduce oxygen concentrations have found no difference in the response of organisms to hypoxia created by this method or by nitrogen stripping (Wolf and Kramer 1987). Thus the responses we observed should reflect reactions to hypoxia and not other chemical gradients. A screen (0.6 cm mesh) was placed 5 cm above the bottom to provide a benthic refuge from fish predators. Plastic plants rested on the screen and provided some cover for mayflies leaving the benthic refuge. Temperature was uniform throughout the tank and ranged from 8–10 C among trials. Oxygen measurements were made with a Yellow Springs Instruments Model 57 Dissolved Oxygen Meter (Yellow Springs Instruments, Antioch Ohio). The oxygen concentration near the tank bottom was monitored continuously during each trial and a vertical profile was taken at the end of each trial to document the existence of a vertical oxygen gradient.

Mayfly larvae were collected from a Rocky Mountain beaver pond immediately after the ice melted in May, 1987 and were maintained at 8 C prior to the experiments. Each mayfly was used in only one trial. The predators were 12 small brown trout *Salmo*
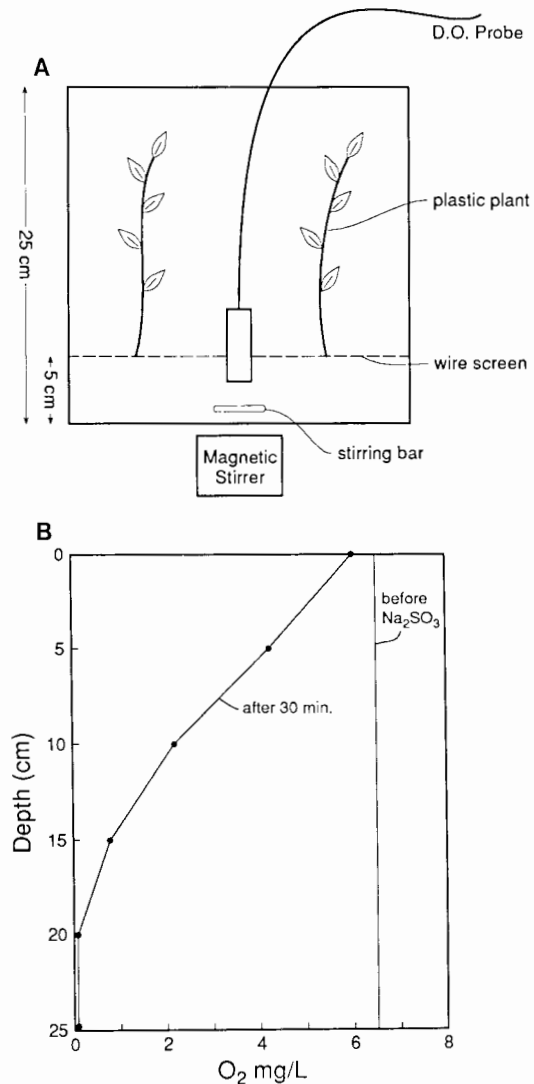
Fig. 1. **A** Chamber used to examine behavioral responses of mayflies to low oxygen and fish predation. A screen placed 5 cm above the bottom provided a benthic refuge from predators. **B** Vertical oxygen gradient 30 min after addition of sodium sulfite. Bottom water was anoxic and a sharp oxygen gradient was present

trutta (60–80 mm total length). Trout were kept in a common tank and fed commercial trout food. Fish were starved for 24 h prior to each experiment and used in only one trial per day. Two fish were randomly selected for each trial.

We began by placing 8 mayflies in the test chamber and allowing them to settle on the bottom. In trials with a predator, two fish were then added to the chamber. All trials lasted 60 min with the first 30 min considered an acclimation period. Mayflies and fish generally resumed normal activity within 5 to 10 min after being placed in the chamber. After 30 min, sodium sulfite was added to the tank for those trials having a low oxygen treatment. The sodium sulfite was added to the bottom of the tank through a tube and caused benthic oxygen concentrations to decline to near 0 mg/L within 5 to 10 min. After a total of 60 min, we recorded the number of mayflies eaten and the proportion of surviving mayflies that were located within the benthic refuge, i.e. within 5 cm of the tank bottom. This procedure provided a conservative estimate of the effect of low benthic oxygen on the vulnerability of mayflies to fish predators because benthic oxygen concentrations in the low-oxygen treatments were only reduced for the last 30 min of the 60 min observation period. To test for the effect of hypoxia
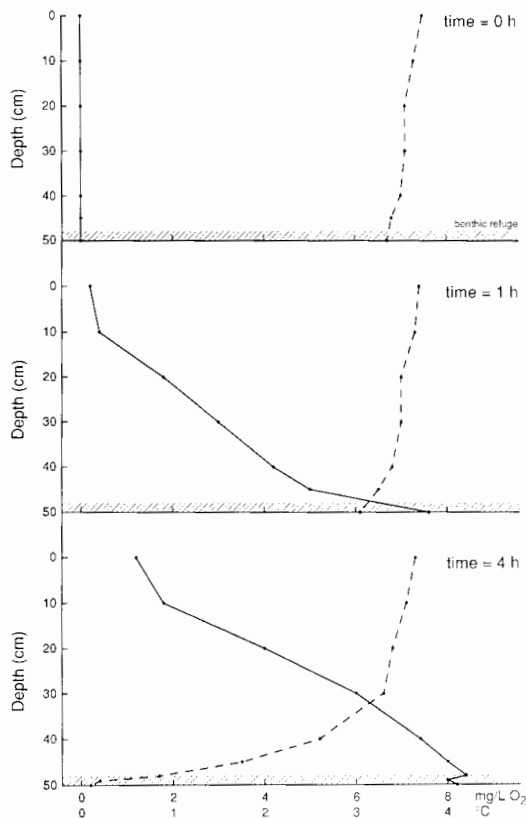
Fig. 2. Vertical temperature and oxygen gradients created by the flow-through system. At time 0, we began with an ice bath and no gradients were present. Next, 4 C water was allowed to flow across the tank bottom. After 1 h, a temperature gradient simulating winter conditions developed with 0 C at the top and 4 C at the bottom. Mayflies were added to the tank at this point. We then removed oxygen from the incoming bottom water and created an oxygen gradient typical of ice-covered lakes with hypoxic water near the bottom substrate and normoxic water near the ice-water surface. —— °C, - - - mg/L O_2

and predators on vertical distribution and activity of mayflies, we used a 2×2 ANOVA design with treatments being benthic oxygen level (high, 6 to 7 mg/L vs low, 0.1 to 0.5 mg/L) and predation threat (fish present vs fish absent). Each treatment combination was replicated 12 times. An arcsine transformation was used for the proportion of mayflies within 5 cm of the tank bottom.

A second set of experiments was done in 1989 using a flow-through system where simultaneous oxygen and temperature gradients were created to simulate the stratified conditions under winter ice-cover. The system relies on density differences due to temperature to maintain a stratified water column and has been described elsewhere (Rahel 1989). Briefly, water is stored in a head tank which also functions as an oxygen stripping column. Water flows by gravity to a chiller tank where it is cooled to 4 C. Next it flows into the experimental tank, which is initially an ice bath at 0 C. The denser, 4 C water flows across the tank bottom and is siphoned out on the other side of the tank. Removing oxygen from the incoming water (by bubbling nitrogen gas through the head tank), results in hypoxic, 4 C water at the tank bottom and well-oxygenated, 0 C water at the top (Fig. 2). These gradients simulate those found in ice-covered ponds and lakes (Nagell and Brittain 1977; Wetzel 1983).

We placed a piece of 0.6 cm mesh screen 2 cm above the tank bottom to create a benthic refuge from predators. A row of plastic aquarium plants rested on the screen and provided cover for mayflies leaving the benthic refuge. Mayfly larvae were collected in May 1989, after the ice melted from the same Rocky Mountain

beaver pond as for the static test and were maintained at 4 C prior to the experiments. Each mayfly was used in only one trial. Predators were 20 small brook trout *Salvelinus fontinalis* (total length 50–60 mm). Trout were held in a common tank and two fish were randomly withdrawn for each trial involving a predator. The trout were fed commercial fish food but were starved for 24 h prior to each trial and used in only one trial per day.

Each trial consisted of a 1 h acclimation period and a 2 h period of gradually declining oxygen concentrations in the benthic region. We began each trial by creating a vertical temperature gradient (0 C at the top and 4 C at the bottom), then placing 10 mayfly larvae on the tank bottom. The mayflies were allowed to acclimate to the tank for 1 h, then observations were made on their vertical distribution and activity. Vertical distribution was recorded as the proportion of mayflies within the benthic refuge (i.e. within 2 cm of the tank bottom). Activity was quantified by counting the number of moves by all mayflies during a 5-min observation period. A move was defined as starting and stopping of a locomotor activity and included swimming in the water column as well as crawling along a substrate.

After the 1-h acclimation period, the oxygen concentration in the benthic region was gradually reduced by bubbling nitrogen through the inflowing water. In treatments with a predator, trout were added at this time. The fish began chasing mayflies within 30 min and were particularly attracted to moving prey. Foraging continued as hypoxia developed, with fish periodically swimming up to the surface waters and then returning to rest near the bottom screen. Each time a mayfly was eaten, we recorded the oxygen concentration within the benthic refuge.

Observations of vertical distribution and activity of the mayflies were made at 15-min intervals over the next 2 h as oxygen concentrations declined. Near the end of the 2-h period, we added small amounts of sodium sulfite (20 mg/L) as suggested by Wolf and Kramer (1987) to reduce the oxygen concentration below the 1 mg/L achieved by nitrogen stripping. We conducted 20 replicates with fish present and 20 replicates with fish absent.

For data analysis, we used analysis of covariance to test for the effects of oxygen concentration and predators on the vertical distribution and activity rates of mayflies (Snedecor and Cochran 1980). Predator presence or absence was the treatment variable and oxygen concentration was the covariate. The regression lines relating the proportion of mayflies within the benthic refuge to oxygen concentration in the presence versus absence of predators had equal slopes. This was also true for the regression lines relating activity rates to oxygen concentration. Prior to data analysis, an arcsine transformation was used on the proportion of mayflies within the benthic refuge and a logarithmic transformation was used on activity rates and oxygen concentration data.

Results

In the static test, both oxygen concentration and the presence of a predator influenced the vertical distribution of mayflies. With high oxygen levels and no fish present, most mayflies (83%) were found within 5 cm of the tank bottom (Fig. 3A). With low oxygen levels in the benthic region and no fish present, mayflies migrated off the tank bottom and only 4% were within 5 cm of the bottom at the end of the 30-min exposure period. No mortality due to low oxygen concentration was observed. When fish were present, mayflies showed an even greater tendency to remain in the benthic refuge when oxygen levels were high (99% of those remaining were within 5 cm of the bottom) and less of a tendency to leave the benthic refuge when oxygen levels were low (30% of those remaining were within 5 cm of the bot-
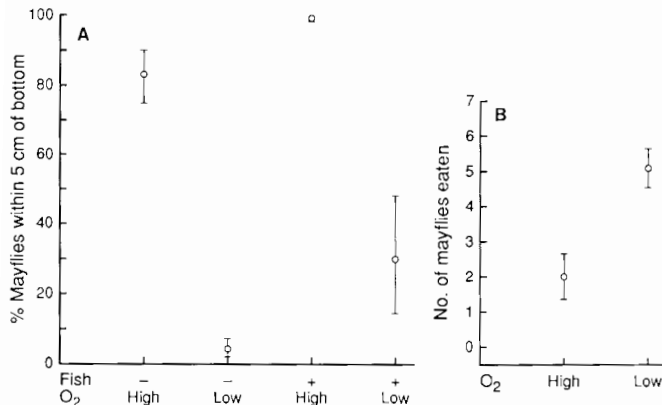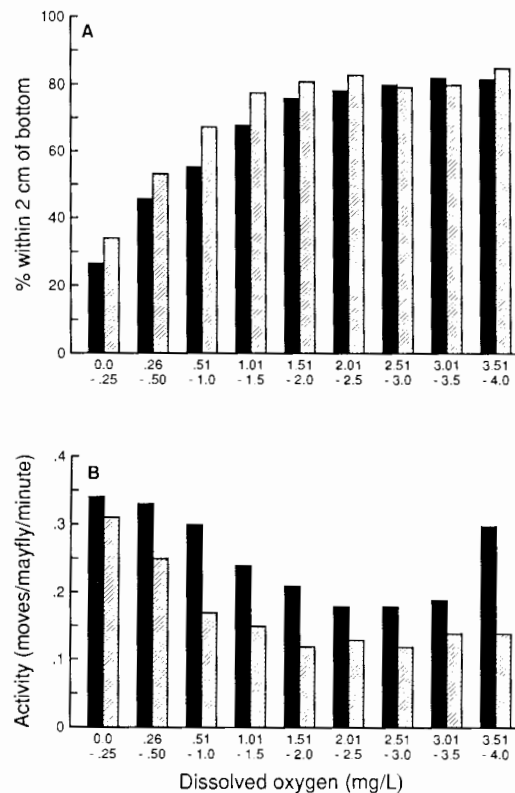
Fig. 3A, B. The vertical distribution of mayflies (A) and the number of mayflies eaten (B) in relation to oxygen concentration and the presence (+) or absence (−) of a predator during the static test. Shown are the mean value±the standard error (n=12). In A, the data represent the proportion of surviving mayflies within 5 cm of the bottom for the treatment where a predator was present

tom). The ANOVA indicated that both oxygen level (F=65.1, 1,44 df, $P<0.001$) and predator presence/absence (F=9.8, 1,44 df, $P<0.01$) had significant effects on the vertical distribution of mayflies. Despite the trends noted above, the interaction term in the ANOVA was not significant (F=0.01, 7,44 df, $P>0.05$). Pairwise comparisons of treatments using Bonferroni t tests (Snedecor and Cochran 1980) indicated that the two treatments with high oxygen concentrations were different from the two treatments with low oxygen concentrations. No other pairwise comparisons were significantly different.

In avoiding low oxygen conditions and moving up off the tank bottom, mayflies became more susceptible to predation by fish (Fig. 3 B). The average number of mayflies eaten in treatments where the benthic oxygen concentration was reduced for the last 30 min was significantly greater than the number eaten in treatments where benthic oxygen concentration remained high (t-test, t=4.04, 22 df, $P<0.001$). In treatments with low oxygen, predation was minimal during the first 30 min (i.e. prior to addition of sodium sulfite) but increased dramatically as oxygen concentrations declined.

In the flow-through test, both oxygen concentration and the presence of fish influenced the distribution and activity of mayflies. Most of the mayflies (80%) remained within the benthic refuge (i.e. within 2 cm of the tank bottom) until oxygen levels declined below 1.5 mg/L (Fig. 4A). This was true whether or not fish were present. Below 1.5 mg/L, there was a decline in the proportion of mayflies within 2 cm of the bottom but for any given oxygen concentration, more mayflies were found near the bottom when fish were present than when fish were absent. Increased use of the benthic refuge in the presence of fish appeared due to avoidance of the upper portion of the tank and not merely the removal of mayflies that strayed above the screen. In many cases, mayflies moved above the benthic refuge but quickly returned to it after being chased by fish. The ANCOVA confirmed that mayflies left the bottom


Fig. 4A, B. The vertical distribution (A) and activity (B) of mayflies in relation to benthic oxygen concentration and the presence or absence of a predator during the flow-through tests. Shown is the mean value for each oxygen concentration (n=20). In A, the data represent the proportion of surviving mayflies within 2 cm of the bottom for the treatment where a predator was present, *Symbols:* ■ no predator, ▨ predator

as oxygen declined (effect of oxygen concentration, F= 404.8, 1,15 df, $P<0.001$), but that a higher proportion of surviving mayflies remained near the bottom when fish were present (effect of predator, F=10.3, 1,15 df, $P<0.01$).

The locomotor activity of mayflies increased as oxygen levels decreased but at any given oxygen concentration, mayflies were less active when fish were present compared to when fish were absent (Fig. 4B). Thus the presence of a predator reduced the activity of mayflies even at low oxygen concentrations when increased activity would be beneficial in locating better oxygen conditions. The ANCOVA confirmed that activity increased with decreasing oxygen levels (effect of oxygen concentration, F=87.2, 1,15 df, $P<0.001$), but that mayflies were less active when fish were present (effect of predator, F=38.9, 1,15 df, $P<0.001$).

As a result of the decreased activity and reluctance to leave the benthic refuge, mayflies endured lower oxygen levels when fish were present relative to when fish were absent. The oxygen concentration at which 50% of the mayflies remained within the benthic refuge was 0.77 mg/L when fish were absent but 0.34 mg/L when fish were present (t-test, t=3.82, df=38, $P<0.001$) and indicates that mayflies endured stressful oxygen conditions in the presence of fish.
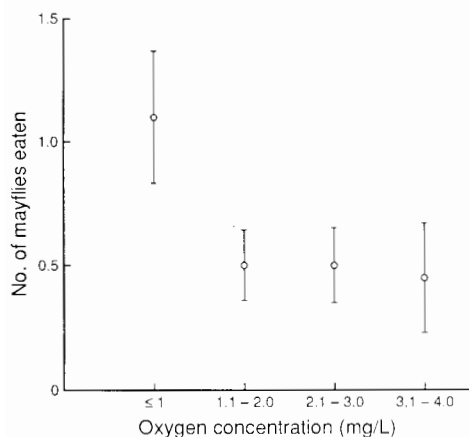
Fig. 5. The number of mayflies eaten per trial in relation to benthic oxygen concentration during the flow-through tests. Shown are the mean value ± the standard error (n = 20)

Despite behavioral changes that reduced the risk of predation, the number of mayflies eaten by fish increased when oxygen concentrations in the benthic zone dropped below 1 mg/L (Fig. 5). Although not quite statistically significant (1-way ANOVA, F = 2.32, 3,16 df, P = 0.08), the trend toward increased predation at low oxygen concentrations agrees with results of the static test and indicates that benthic hypoxia can lead to increased predation risk as benthic invertebrates increase their activity and leave the bottom substrate in search of higher oxygen concentrations.

Discussion

During extended periods of ice-cover in productive lakes, oxygen concentrations often become reduced in the benthic region (Pennak 1968; Wetzel 1983; Rahel 1990). To survive, aquatic macroinvertebrates intolerant of hypoxia would be forced to leave the lake bottom and move up in the water column to better oxygen conditions. Such upward migrations have been reported for two species of mayflies in Swedish ponds (Nagell 1977; Brittain and Nagell 1981) and for *Chaoborus* in a Polish lake (Sikorowa 1968). In our experiments, the mayfly *Callibaetis montanus* also avoided hypoxic conditions with the threshold of avoidance behavior about at 1.5 mg/L dissolved oxygen (Fig. 4). Avoidance involved increased activity and upward migration: behaviors that increased the vulnerability of mayflies to predators such as fish. Thus, activities appropriate for avoiding low oxygen were inappropriate for avoiding predators. Mayflies attempted to balance these conflicting demands by enduring lower oxygen concentrations in the presence of fish. Although benthic hypoxia resulted in increased mortality due to fish predation in our experiments, mortality would have been even greater if mayflies had not made the trade-off of enduring lower oxygen concentrations to remain in the benthic refuge when fish were present.

Increased predation under hypoxic conditions has been noted for other aquatic organisms despite similar trade-offs in hypoxia-avoidance versus predator-avoidance behaviors. For example, small fish responded to hypoxia by increasing the frequency of surface respiration although this entailed leaving submerged vegetation that provided protection from piscivorous fish (Wolf and Kramer 1987). The small fish were caught more quickly when oxygen declined even though their air-breathing frequency declined and cover-use increased in the presence of predators. In a similar study, small fish decreased the rate of air-breathing during hypoxic conditions when an aerial predator (a heron) was present (Kramer et al. 1983). Despite this antipredator behavior, fish were still more vulnerable to the predator at low oxygen concentrations than at high oxygen concentrations. Tadpoles also increased their air-breathing activity at low oxygen concentrations and would thus be more vulnerable to visual predators such as turtles (Feder 1983).

The above studies and our results indicate that under hypoxic conditions, the need to breathe may force aquatic organisms to spend time away from cover and thus increase their vulnerability to predators. Although aquatic organisms may optimize trade-offs between predator avoidance and foraging behavior (Kerfoot and Sih 1987), they appear to have much less flexibility in making trade-offs between predators and stressful oxygen conditions. The consequence of avoiding predators by foraging in suboptimal habitats is reduced growth and fecundity, but the cost of avoiding predators by remaining in anoxic habitats is suffocation and death. Because benthic invertebrates vary in their ability to tolerate hypoxic conditions (Nagell and Fagerstrom 1978; Jacob et al. 1984) and because they also differ in their vulnerability to fish predators (Ware 1973; Cook and Streams 1984) periods of winter hypoxia should lead to selective predation on some macroinvertebrates. Thus interaction of an abiotic factor (winter hypoxia) and a biotic fator (predation) could be an important force structuring benthic invertebrate assemblages in lakes subject to episodes of hypoxia in the benthic region.

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