# Role of Hypoxia in Limiting Diel Spring and Summer Distribution of Juvenile Yellow Perch (*Perca flavescens*) in a Prairie Marsh[1]

Iain M. Suthers[2] and John H. Gee

*Department of Zoology, University of Manitoba, Winnipeg, Man. R3T 2N2*

Suthers, I. M., and J. H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Can. J. Fish. Aquat. Sci. 43: 1562–1570.

Comparative field and laboratory data on the distribution-limiting levels of dissolved oxygen (DO) for yearling yellow perch (*Perca flavescens*) is presented. At Blind Channel, Delta Marsh, Manitoba, diel fluctuations in DO concentrations began by June, approximately 6 wk after ice-off. By early July severe hypoxia (≤1.5 ppm DO) first occurred in the cattail habitat close to the substrate at dawn, and by early August severe hypoxia extended throughout the cattail bed. Using wire minnow traps, juvenile perch persisted within the cattails close to the substrate in June. In early July, juvenile perch occupied the submerged macrophyte – open water habitat, away from the cattail and hypoxia. Significant diel changes in horizontal distribution were evident at one site, where fish avoided severe hypoxia in the cattail bed overnight but returned during the day, as there was little alternative cover and when DO levels were not lethal. In situ survival experiments demonstrated decreased survival close to the substrate, in the cattail, and overnight compared with overday, reflecting the distribution of low DO. Survival increased 27% over the control by bubbling oxygen into holding cages. In a two-chambered normoxic/hypoxic tank, perch demonstrated a preference for cover, and avoidance of hypoxia at 1.5–3.0 ppm DO. The habitat choice of juvenile yellow perch in Delta Marsh is a compromise between the cattail, with favorable predator/prey conditions, and hypoxia.

Les auteurs présentent des données comparatives, obtenues sur le terrain et en laboratoire, sur la distribution des teneurs limitantes en oxygène dissous (OD) pour des perchaudes (*Perca flavescens*) d'un an. Dans le chenal Blind de Delta Marsh (Manitoba), les fluctuations nycthémérales de la concentration en OD ont débuté en juin, environ 6 sem après la fonte des glaces. Au début de juillet, on notait pour la première fois une importante hypoxie (≤1,5 ppm OD) à l'aube dans l'habitat à typhas, à proximité du substrat; au début d'août cette hypoxie s'étendait à toute la zone à typhas. L'utilisation de trappes à ménés métalliques a permis de noter que les perchaudes juvéniles demeuraient dans les typhas, près du substrat, en juin. Au début de juillet, les poissons occupaient l'habitat d'eau libre à macrophytes submergés, loin des typhas et des conditions hypoxiques. Des variations nycthémérales significatives de la distribution horizontale ont été notées en un endroit où les poissons évitaient les conditions hypoxiques sévères des typhas au cours de la nuit, mais y retournaient durant le jour car il y avait peu de couvert disponible et les concentrations de OD n'y étaient pas mortelles. Des essais de survie *in situ* ont montré une baisse de la survie à proximité du substrat dans la zone à typhas; cette baisse était plus importante la nuit que le jour, ce qui reflète la distribution des faibles teneurs en OD. Le taux de survie a pu être accru de 27 %, comparativement à celui des témoins, en diffusant de l'oxygène dans les cages. Au cours de ces essais en cuves à deux compartiments (conditions normales et hypoxie) les perchaudes ont préféré le couvert et évité une hypoxie de l'ordre de 1,5–3,0 ppm de OD. L'habitat choisi par les perchaudes juvéniles de Delta Marsh représente un compromis entre la zone à typhas où les conditions prédateurs–proies sont favorables et l'hypoxie.

*Received August 7, 1985*
*Accepted April 22, 1986*
*(J8379)*

*Reçu le 7 août 1985*
*Accepté le 22 avril 1986*

Habitat criteria for juvenile freshwater fish include predator risk, prey abundance, presence of competitors, temperature, and other factors (e.g. Crowder et al. 1981; Hall and Werner 1977; Keast et al. 1978). Werner et al. (1983) demonstrated with centrachids a tradeoff between prey availability and predator risk in habitat choice. Habitat choice is a compromise among many factors, including the interaction of physical and biological effects. The potential for low dissolved oxygen (DO) to strongly interact with the biological factors has rarely been considered (Rudstam and Magnuson 1985), and yet hypoxia is a pervasive phenomenon in many aquatic communities. Severe hypoxia in potholes and small eutrophic lakes caused by collapse and subsequent decomposition of large algal blooms (e.g. Nicholls et al. 1980) results in catastrophic mortality of fishes in midsummer, as well as mortality due to nocturnal hypoxia and subsequent avian predation (Kushlan 1974; Tramer 1977). These accounts described a characteristic sequence of mortality, related to the species' physiological and morphological adaptations for breathing the surface film or air-breathing (Gee 1980). An obvious, but often ignored, initial behavioral response to hy-

---

[1] Contribution No. 136 of the University of Manitoba Field Station (Delta Marsh).

[2] Present address: Department of Biology, Dalhousie University, Halifax, N.S. B3H 4J1.

poxia is movement to habitats of higher DO (Hochachka 1980).

Seasonal changes in vertical distribution and survival of fish in relation to low DO (and high temperature) occur in stratified lakes, where by midsummer the hypolimnion may become anoxic (Clady 1976; Engel and Magnuson 1976; Vigg 1980; Rinne et al. 1981; Rudstam and Magnuson 1985). Horizontal DO gradients, resulting from sewage effluent or natural causes, also affect fish and invertebrate distribution (Odum and Caldwell 1955; Alabaster 1959; Birtwell et al. 1983). Magnuson et al. (1985) showed that vertical and horizontal fish distribution under ice was a function of low DO and high $CO_2$. Northern pike (*Esox lucius*) can avoid low DO in late winter (Casselman 1978), and juvenile pike are attracted to traps with an aerated discharge under the ice (Johnson and Moyle 1969). Hypoxia and fish scarcity may be correlated but the underlying mechanisms are difficult to establish in the field (Whitmore et al. 1960) because of other interacting factors (prey distribution, light levels). Rarely are these hypotheses tested with in situ survival experiments (Odum and Caldwell 1955; Klinger et al. 1982; Birtwell et al. 1983). Comparative laboratory and field studies on the effect of low DO on fish distribution are essential to resolve these interacting effects, particularly with respect to a changing diel regime. Alabaster and Robertson's (1961) study is unique in using a large outdoor tank to study diel effects of temperature, DO concentrations, and light levels on fish activity and distribution, though the results were inconclusive.

Our objectives were to describe (1) the temporal and spatial variation in DO, temperature, and vegetation and (2) the associated distribution of yearling yellow perch (*Perca flavescens*) in Delta Marsh. We demonstrate experimentally how amounts of DO and cover affect fish distribution and survival in the laboratory and in the field. Delta Marsh is one of the largest freshwater marshes in North America and surprisingly little is known of its fish populations. The marsh is a nursery ground for juvenile northern pike, carp (*Cyprinus carpio*), spottail shiner (*Notropis hudsonius*), fathead minnow (*Pimephales promelas*), and brook stickleback (*Culaea inconstans*). The marsh is potentially hypoxic due to the abundance of decaying vegetation and submerged macrophytes, but during the spring it provides fish with cover, protection from storms, and a more abundant invertebrate food resource compared with the adjacent Lake Manitoba.

## Materials and Methods

### Study Area

Research was conducted from the University of Manitoba Field Station, Delta Marsh (50°11′N, 98°23′W), situated on the southern shore of Lake Manitoba. Data were collected at Blind Channel, a former bed of the Assiniboine River. It is a shallow (1-m maximum depth), 8-km meandering channel lined with cattail (*Typha* spp.) and bullrush (*Scirpus* sp.). The only connection to Lake Manitoba is via a narrow cut, midway along the channel. Average water levels in Blind Channel vary by ±15 cm due to wind-generated seiches on Lake Manitoba. Water chemistry is similar to that of the lake (pH 8.0–8.5, brackish, ≥1500 mg total dissolved solids·L$^{-1}$) and turbid, particularly in spring but clearing by early summer (Tudorancea and Green 1975).

Two sites (A and B) were selected on the basis of accessibility and presence of large stands of cattail vegetation. Cattail was selected over stands of bullrush, as yellow perch were more abundant in the former (Suthers 1984). In June and July there was a greater percent cover of submerged macrophytes in the open water habitat at site A than at site B. Site A at the northern extremity of Blind Channel was comparable with a backwater, with little current and abundant macrophytes (*Myriophyllum* sp., *Potamogeton* spp., and *Utricularia* sp., Table 1), while site B was midway along the channel, with sparse submerged macrophytes (chiefly *P. pectinatus*) and slight current due to wind seiches.

TABLE 1. Percent cover of submerged macrophytes at station 3 (open water habitat) in 1983 during the periods of yellow perch abundance ($n = 20$ counts ± SD). Early June values included dead plants from the previous summer.

| Period | Site A | Site B |
|---|---|---|
| Early June | 51.5±29.4 | 3.3±5.7 |
| Late June | 31.6±35.8 | 1.8±2.2 |
| Early July | 64.3±41.0 | 31.8±28.1 |
| Late July | —[a] | 61.0±34.8 |

[a]Not recorded, approximately 100%.

### Sampling Procedures

The DO regime and fish distribution were determined at sites A and B in 1982 along four replicate transects selected at random from a total of 10 set perpendicular to the shore, approximately 25 m apart. Each transect was composed of four stations. Station 1 was approximately 2 m into the cattail bed in 30–40 cm of water, station 2 was at the edge of the cattail in 40–50 cm of water, station 3 was 2–3 m offshore in 50–60 cm of water, and station 4 was almost midchannel in 70–80 cm of water. At each station a rod supported two wire minnow traps (42 cm long; 21 cm diameter) with one at the water surface and one at the substrate. For 3 d four transects were selected and traps set in the morning (07:00–10:00) and then examined that evening (19:00–22:00) when a new set of four transects was selected. These times were intended to approximate midpoints of the diel DO fluctuation, thus generally trapping over a high DO and a low DO time of day. This procedure was repeated the following week at site B. The 3-d sampling intervals at each site were repeated over four sampling periods during the summer: 8–18 June, 6–16 July, 27 July – 6 August, and 17–26 August.

For each trap, DO and temperature were recorded and fish were counted before release 500 m away. DO was recorded using a YSI oxygen meter (model 57) and calibration was checked after each transect. Comparison with the Winkler method indicated close agreement (±4%). There were five levels of treatment for each site: sampling period (4), day (3), time of day (2), station (4), and depth (2) with four replicate transects. DO was analysed for each site with a five-way factorial analysis of variance (ANOVA). Nearly all factors and interactions were significant and only the six largest sums of squares are discussed.

The catch per trap was expressed as a proportion of each morning's or each evening's total catch. This removed the effect of larger catches overday than overnight (Suthers 1984) and greater abundance in early June than early July. Homogeneity of variance was attained using an arcsine, square-root transform of this proportion. The distribution of yellow perch [illegible] analysed for each site using the larger, bottom trap catches [illegible] early June and early July sampling periods in a four-way [illegible] (period (2), day (3), time of day (2), by station (4)). [illegible] 1983, five transects were maintained at each site with [illegible] stations per transect (omitting station 4 in midchannel). [illegible] temperature, and catch were recorded at each trap at [illegible] 10:00, 16:00, and 22:00 for 2 d at each site during six [illegible] periods during the summer: 16–26 May, 30 May – [illegible] 11–17 June, 26 June – 6 July, 19–27 July, and [illegible] August. DO was analysed for each site in a five-way [illegible] ANOVA (period (6), day (2), time of day (4), station [illegible] depth (2)) with five replicate transects). A continuous 24-h [illegible] of temperature and DO (YSI model 56) was obtained at [illegible] 1–3 at site A during 1983.

The abundance of yearling yellow perch was lower in 1983 [illegible] 04:00 and 10:00 catch and the 16:00 and 22:00 catch [illegible] combined to give an "overnight" and an "overday" catch, comparable with 1982. Catches were converted to proportions [illegible] and an identical analysis was applied to the larger [illegible] trap catch, omitting the May and August sampling [illegible] (period (4), day (2), time of day (2), station (3), and [illegible] (5)).

### Experimental Manipulations in the Field

[illegible] fish were trapped amongst the cattail by early July, and experimental manipulations were used to determine if fish could survive in the cattail habitat at that time. Caged fish were [illegible] at site A in mid-July 1983 for two days and two nights [illegible] two replicate transects composed of stations 1, 2, and 3, [illegible] and bottom. Each cage (a minnow trap, corked at both [illegible]) contained five perch with the top cage just below the [illegible] surface. Fish were caught from Blind Channel in trap[illegible] within 24 h of the experiment. At approximately 10:00, DO, temperature, and number of live fish were recorded, the [illegible] restocked with new fish, and reexamined at 22:00.

To determine if the level of DO affected survival in the cattail, the oxygen regime was manipulated over two days and two nights in early July 1983 under three treatments: oxygenated ($O_2$ bubbled), hypoxic ($N_2$ bubbled), and control. The experimental design was identical to the experiment described [illegible] except that station 3 was omitted. Oxygen and nitrogen were supplied from cylinders lying in a nearby dinghy to airstones in the bottom trap. To reduce large-scale mixing with surrounding water, a small plastic sheet was placed under the bottom trap and over the surface trap. After each 12-h period, DO and number of live fish were recorded. Analysis of the [illegible] survival (arcsine transformation) involved a four-way [illegible] ANOVA (time of day (2), treatment (3), station (2), [illegible] (2)).

Analyses of variance were performed using the Statistical Analysis System (SAS 1982) and differences in the *F* statistic were considered significant at the 5% level ($p < 0.05$). Taylor's power law (Elliott 1977) was applied to determine a suitable transformation and checked using Cochran's test. Comparison of [illegible] means was performed using Duncan's multiple [illegible]

### Laboratory Experiments

Yearling yellow perch (6–10 cm fork length) were caught in [illegible] in July 1982 and maintained at 12°C in a 12 h [illegible] photoperiod on frozen brine shrimp (maintenance [illegible]) until January 1984, when the fish were acclimated to 18°C over 4 wk to approximate June water temperatures in the marsh.

The test chamber was a 120 × 26 × 15 cm clear acrylic plastic tank with an intake at each end, draining at the centre from holes in the sides and bottom (Scherer and Nowak 1973). Deoxygenated water (generated by bubbling nitrogen through a 200-L drum) flowed to one side of the test-chamber while the opposite side remained normoxic. Flow rates of about 0.8 cm·s$^{-1}$ (approximately 10 L·min$^{-1}$ at each end) yielded distinct conditions of DO in the two halves of the tank through which fish swam without impediment. To simulate conditions in the marsh, the hypoxic side contained cover (weighted black plastic strips), the normoxic side being bare. DO was monitored (YSI model 57) with the probe next to the hypoxic side inlet. A clear plastic sheet covered the surface to prevent atmospheric exchange. The tank was illuminated by a row of incandescent bulbs with a diffusing screen (35 klx at the surface) under a 12 h light : 12 h dark photoperiod, and also illuminated continuously by four infrared lamps (400 nm). Observations were made on a school of eight fish, acclimated to the test tank for 3 d. Using a Sony video camera with a Vidicon sensor tube, and a Sony SL 5400 VCR, the number of fish on the hypoxic side (with cover) were counted every 30 s for 15 min·h$^{-1}$ over two control and two experimental nights (alternated, using the same school). The experimental nights involved lowering DO 1.5 ppm·h$^{-1}$, starting at midnight, from saturation (9.2 ppm) to 0.6 ppm at 06:00. After the incandescent lights came on the count was repeated at 07:00 and DO was returned to saturation by 13:00 at the same rate.

## Results

### Dissolved Oxygen and Temperature Regimes

DO concentrations varied considerably in time and space within the study area. Using DO (1982) as the dependent variable, the six largest sums of squares explained almost 75% of the total variance (Table 2). Distance from the cattail ("station") was the most important single factor at sites A and B, the lowest DO being in the cattail and increasing offshore to station 4. DO recorded in the evening was greater than the morning ("time of day"), and also greater at the surface than at the substrate ("depth"). Generally, mean DO was higher and more variable at site A than at site B (Table 2, total SS). Daily water temperature changed ±2° about the mean but increased seasonally from 9.5°C in late May to 22°C by August. Extreme conditions were recorded in late summer, with temperatures on occasion as high as 27°C and 18 ppm DO (200% saturation). The 1983 DO analysis (Table 2) for sites A and B also showed greater DO offshore, but "period" accounted for a larger proportion of the variance, as six periods were sampled during the 1983 summer (which was comparatively warm and dry). DO was highest in the midafternoon (16:00 > 22:00 > 10:00 > 04:00). Significant diel fluctuations in DO occurred from mid-June onwards (site A) and early July onwards (site B) compared with earlier, more uniform conditions.

Severe hypoxia (≤1.5 ppm DO) was first evident in early July at the station 1 bottom trap position at dawn. By early August severe hypoxia extended throughout the cattail bed for most of the day. Stations 3 and 4 never became hypoxic (1.5–3.0 ppm). These patterns in DO and temperature regimes are summarized in a series of continuous recording traces (Fig. 1) from May, June, and July 1983 at site A. In May, DO

TABLE 2. Six factors with the largest sums of squares of a five-way ANOVA with DO as the dependent variable at sites A and B during 1982 and 1983. All are significant at $p \leq 0.005$

| Source | df | Site A |  | Site B |  |
|---|---|---|---|---|---|
|  |  | SS | % total SS | SS | % total SS |
| 1982 |  |  |  |  |  |
| Period | 3 | 1 235 | 9.5 | 695 | 8.6 |
| Period × replicate day | 6 | 394 | 3.0 | 104 | 1.3 |
| Time of day | 1 | 2 992 | 23.0 | 1 679 | 20.7 |
| Station | 3 | 3 618 | 27.8 | 2 221 | 27.3 |
| Depth | 1 | 1 218 | 9.3 | 903 | 11.1 |
| Period × depth | 3 | 164 | 1.6 | 301 | 3.7 |
| Residual | 576 | 2 048 | 15.7 | 1 161 | 14.0 |
| Total | 767 | 13 028 | 100.0 | 8 124 | 100.0 |
| 1983 |  |  |  |  |  |
| Period | 5 | 8 842 | 38.7 | 2 788 | 18.6 |
| Time of day | 3 | 2 263 | 9.9 | 2 475 | 16.5 |
| Period × time of day | 15 | 685 | 3.0 | 671 | 4.5 |
| Station | 2 | 3 019 | 13.2 | 3 164 | 21.1 |
| Depth | 1 | 2 481 | 10.8 | 1 403 | 9.4 |
| Time of day × depth | 3 | 921 | 4.0 | 339 | 2.3 |
| Residual | 1151 | 1 579 | 6.9 | 1 952 | 13.0 |
| Total | 1438 | 22 873 | 100.0 | 14 987 | 100.0 |

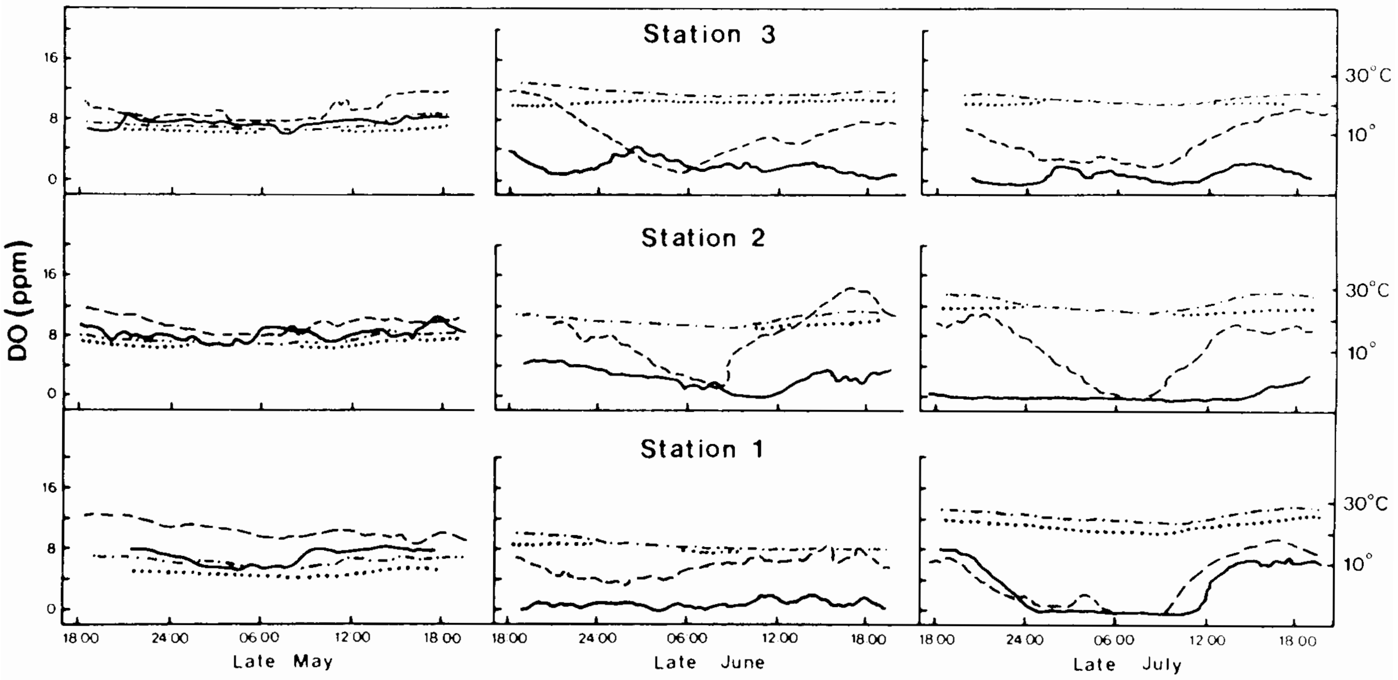

FIG. 1. DO (solid lines) and temperature (dotted lines) traces from a continuous recorder at site A, 1983, at top and bottom traps. Top and bottom temperatures are dot–dash and dotted lines, respectively; top and bottom DO values are dashed and solid lines, respectively.

conditions were uniform both spatially and temporally, but in June and July, DO increased with distance from shore and from the substrate and with increasing diel fluctuations.

## Yellow Perch Distribution

Most perch were found in the bottom trap and were less abundant in 1983, as shown by a comparison of the mean catch per 12 h per trap ($n$ = number of traps set):

| Trap location | Top | Bottom |
|---|---|---|
| 1982 ($n = 768$) | 0.429 | 4.701 |
| 1983 ($n = 1200$) | 0.020 | 0.342 |

Generally, bottom trap catches were greater amongst the cattail than open water in early June, but in early July, yellow perch began to move offshore, and by August, catches were smaller and mostly at open water stations.

The four-way ANOVA of the 1982 proportion of catch in the bottom traps showed two significant effects at site A and four at site B (Table 3). These results indicate the following. A seasonal shift in distribution was demonstrated at both sites by significantly larger catches at station 1 in early June relative to early July when there were larger catches at station 2. A daily shift in distribution was evident at site B over both periods by significantly larger catches at station 1 overday than overnight

TABLE 3. Significant factors of a four-way ANOVA with proportion of yellow perch caught in the bottom trap as the dependent variable at sites A and B during 1982 and 1983 (**$p \leq 0.005$).

| Source | df | Site A |  | Site B |  |
|---|---|---|---|---|---|
|  |  | SS | $F$ | SS | $F$ |
| 1982 |  |  |  |  |  |
| Station | 3 | 1.3350 | 18.7** | 1.4694 | 17.8** |
| Period × station | 3 | 1.5736 | 22.0** | 0.7942 | 9.6** |
| Day × station | 6 | 0.1153 | 0.8 | 0.5649 | 3.4** |
| Time of day × station | 3 | 0.0351 | 0.5 | 0.4835 | 5.9** |
| Residual | 142 | 3.3859 |  | 3.9599 |  |
| Total | 189 | 7.1563 |  | 8.2227 |  |
| 1983 |  |  |  |  |  |
| Period × station | 3 | 1.7428 | 3.73** | 1.8116 | 5.00** |
| Residual | 192 | 14.9576 |  | 11.5999 |  |
| Total | 239 | 18.8234 |  | 15.8641 |  |

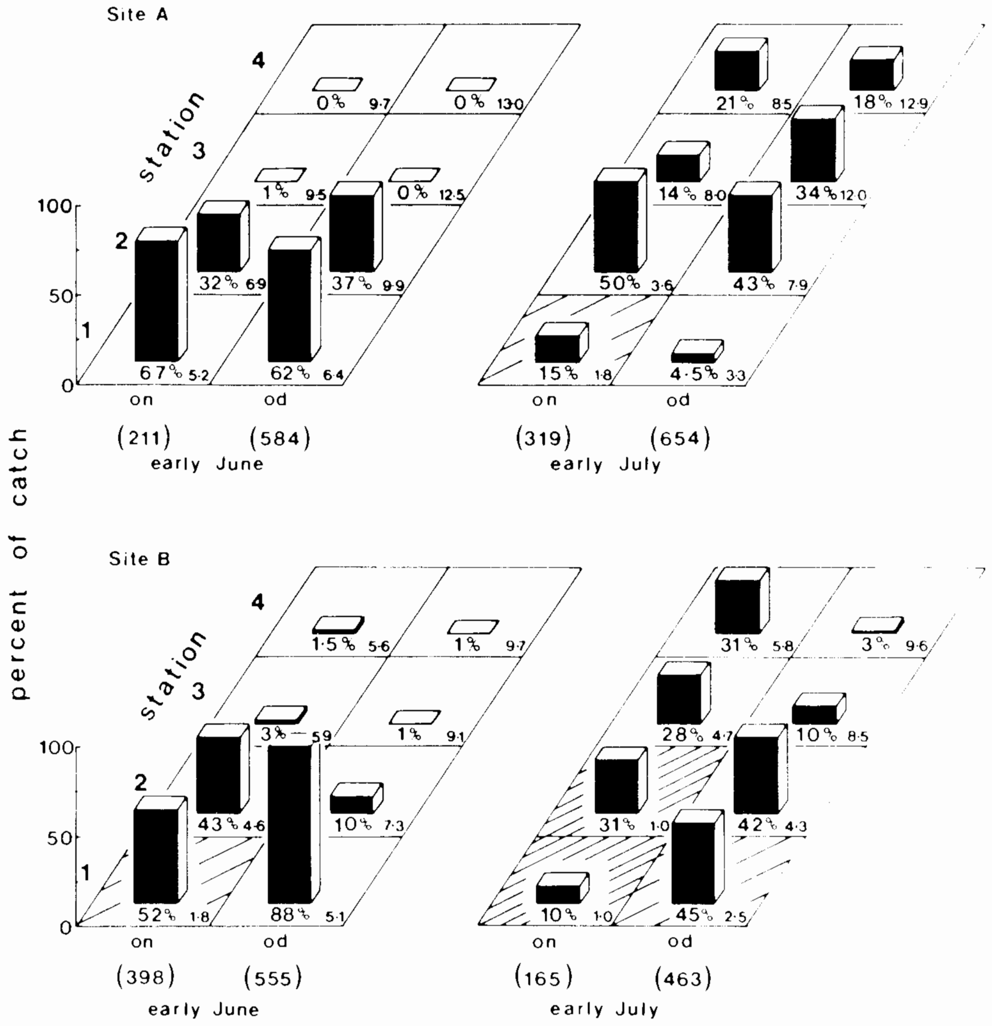

FIG. 2. Percent of each overnight and each overday bottom trap catch ($n$ = 12) for yearling yellow perch in early June and early July 1982 at sites A and B. Total overnight and overday catch for the 3 d and four replicate transects are in parentheses. Corresponding average DO measurement is beside each column. Shaded, severely hypoxic (<1.5 ppm): hatched, hypoxic (1.5–3.0 ppm); on, overnight catch 09:00–21:00; od, overday catch 21:00–09:00. Duncan's multiple range test ranked the period × station means for sites A and B and the time of day × station means for site B as follows. A: June 1 > July 2 = June 2 > July 3 > July 4 > July 1 > June 3 = June 4; B: June 1 > July 2 > June 2 = July 1 = July 3 = July 4 > June 4 = June 3; B: overday 1 > overnight 2 = overday 2 = overnight 1 > overnight 3 = overnight 4 = overday 3 = overday 4.

TABLE 4. Mean percent survival ($n = 4$) of five yellow perch (±SE) caged overday (10:00–22:00) and overnight (22:00–10:00) at stations 1, 2, and 3 at both depths. Mean DO after each 12-h treatment is shown. Daily $O_2$ regime is that of mid-July 1983. Mean water temperature is 24.2°C

| Station | Overnight<br>% survival | Overnight<br>DO (ppm) | Overday<br>% survival | Overday<br>DO (ppm) |
|---|---|---|---|---|
| 3 surface | 100 | 6.2 | 95 (±5) | 9.8 |
| substrate | 80 (±20) | 3.6 | 90 (±10) | 4.8 |
| 2 surface | 0 | 4.2 | 85 (±10) | 9.5 |
| substrate | 0 | 0.8 | 25 (±25) | 1.8 |
| 1 surface | 0 | 0.4 | 0 | 6.7 |
| substrate | 0 | 0.2 | 5 (±5) | 1.6 |

TABLE 5. All significant factors in a four-way ANOVA with the proportion of surviving yellow perch as the dependent variable near site A in early July 1983, overday and overnight under three treatments: control, hypoxic, and oxygenated (Fig. 3). (*$0.01 < p < 0.05$; **$p < 0.01$).

| Source | df | SS | *F* |
|---|---|---|---|
| Time of day | 1 | 3.45 | 14.01** |
| Treatment | 2 | 11.48 | 23.32** |
| Time of day × treatment | 2 | 1.78 | 3.61* |
| Station | 1 | 1.91 | 7.74** |
| Depth | 1 | 3.40 | 13.80** |
| Residual | 66 | 16.25 | |
| Total | 89 | 41.63 | |

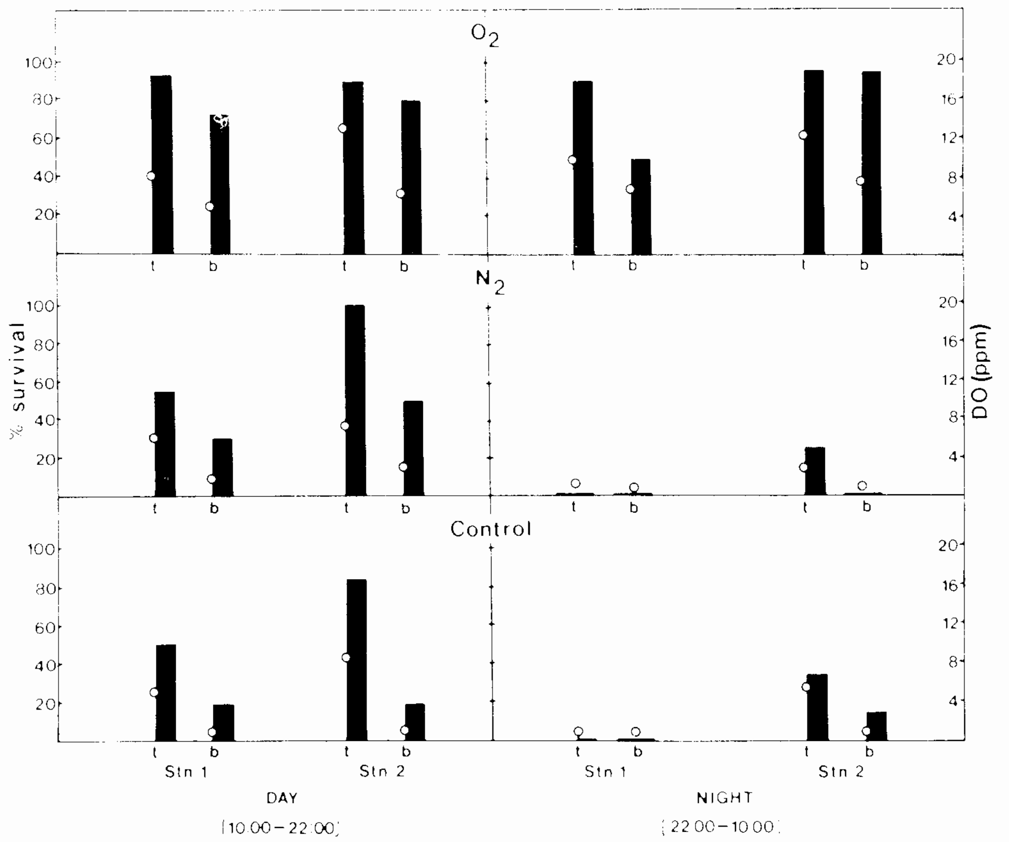

FIG. 3. Average percent survival ($n = 4$) of five yellow perch caged overday and overnight at stations 1 and 2 at both depths under three treatments: oxygen bubbled, nitrogen bubbled, and control. Average DO after each 12-h treatment is shown by an open circle. The environmental DO regime ("control") is that of early July 1983, with average water temperature of 25°C. Duncan's multiple range test ranked the treatment × time of day means as follows: $O_2$ day = $O_2$ night > $N_2$ day > control day > $N_2$ night = control night.

(Fig. 2). There were also significant day to day shifts in distribution and a slight but not significant period effect on diel distribution ($p = 0.08$) at site B (Table 3).

Analysis of the 1983 proportion data also showed a significant seasonal change in the fish distribution (Table 3), with significantly less fish caught in the cattail habitat in early July. The combined morning and evening catches were low, yet there was some indication of a changing diel distribution in July, as fish were caught at station 1 during the day, but not overnight.

The average DO corresponding to each average catch indicates that yellow perch are present where DO may increase to no more than 2.0–3.5 ppm. Perch are absent when mean DO was 1.5 ppm or less at the time of sampling.

## In Situ Survival Experiments

The survival of caged fish also reflects the distribution of low DO. Yellow perch survived overnight only at the open water station (station 3) in the control transects during mid-July (Table 4). However, during the day most individuals survived at station 2 in the surface trap, fewer surviving in the bottom trap, and none surviving at station 1. Although high DO con-

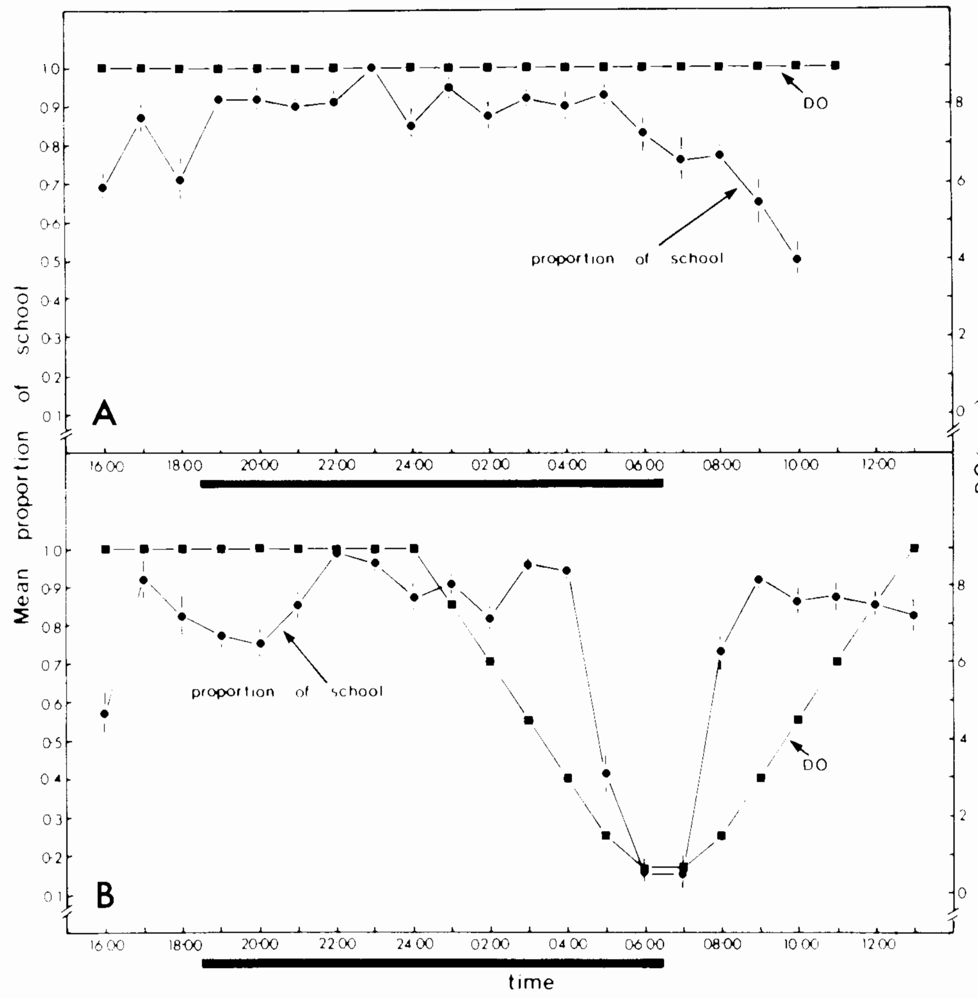

FIG. 4. Average proportion ($n$ = 30 counts) of the school of eight fish on the hypoxic side (with cover) over two replicate runs under a day/night regime. (A) Control; (B) increasing and decreasing hypoxia; lights off at 18:15 and on at 06:15. Vertical lines indicate 95% confidence limits.

centration was recorded for the station 1 surface trap by evening (Table 4), lethal levels of DO were present in the late morning, contributing to the total mortality of yellow perch. Thus, by mid-July, stations 1 and 2 were uninhabitable overnight.

In the manipulated DO experiments the four factors and the interaction term (time of day × treatment) were significant (Table 5). There was significantly greater survival in the surface trap and at station 2 than at station 1 (Fig. 3). Survival under the oxygen-bubbled treatment during day and night was significantly greater than the nitrogen-bubbled and control transects, and in the two latter treatments, survival was significantly greater overday than overnight.

### Laboratory Experiments

Yellow perch demonstrated a marked preference for cover throughout the day and night (Fig. 4A). During increasing hypoxia (Fig. 4B), fish avoided the hypoxic side with cover when DO fell to between 3.0 and 1.5 ppm and returned under increasing DO at the same concentration during daylight conditions.

## Discussion

Diel fluctuations in DO concentrations develop at Delta Marsh during summer such that by late June, severe hypoxia (≤1.5 ppm) occurs at dawn amongst the cattail. Catches of yearling yellow perch indicated seasonal and diel shifts in distribution between the preferred cattail and open water habitats. It is proposed that these changes in distribution are a direct result of severe hypoxia and the growth of alternative cover in the open water habitat.

### Yellow Perch Distribution

The marked seasonal movement away from cattail in midsummer and the high mortality of yellow perch caged in the cattail at this time directly parallel spatial and temporal changes in DO concentrations. This seasonal change in distribution is directly comparable with avoidance by fish, in some eutrophic lakes, of the anoxic hypolimnion in late summer (e.g. Clady 1976; Engel and Magnuson 1976; Vigg 1980). In addition, growth of submerged vegetation in the offshore open water habitat by early July offered alternative cover without the same conditions of hypoxia. Werner et al. (1983) established that cover was a major factor affecting the distribution of juvenile bluegill sunfish (*Lepomis macrochirus*), offering protection from predators, despite greater foraging success in the open water. In Blind Channel, northern pike were the predominant fish predator enhancing continuous, not diel, preference for cover. Predatory aquatic insects were abundant in Blind Channel but their effect on yellow perch is unknown.

Juvenile yellow perch feed predominantly on zooplankton (particularly Cladocera), aquatic insect larvae, and to a lesser extent chironomids during the spring and summer (Keast and Welsh 1968; Keast 1977; Kelso and Ward 1977; Paszkowski and Tonn 1983; I. M. Suthers, pers. obs.). At both sites in 1983, activity trap estimates of zooplankton abundance in early June were two orders of magnitude greater in cattail than in open water (I. M. Suthers, unpubl. data). Thus, in Blind Channel, the cattail habitat provides cover and, at least during June and July of 1983, a more abundant food resource. Yet the suitability of this habitat is compromised as shown by the survivorship of caged fish which was due to hypoxia demonstrated by the manipulated DO regimes. Bubbling oxygen amongst caged fish greatly increased survival even under the most hypoxic conditions.

A changing diel distribution of fish in direct response to diel variations in DO has not been conclusively demonstrated in other studies, as there are often other interacting factors such as light level and temperature (Vigg 1980; Rinne et al. 1981). In this study, there was a diel change in distribution away from the cattail habitat at night and returning during the day in both early June and July at site B but not at site A in 1982. Site A, at the end of Blind Channel, had warm, still conditions, a faster decay of the dead cattail with more variable DO concentrations but with luxuriant growth of submerged macrophytes in the open water habitat. In early July, hypoxia was avoided by inhabiting this alternative cover. At site B, hypoxic conditions developed overnight during early June and early July, but the only substantial cover (particularly in early June) was amongst the cattail. Consequently, yellow perch tended to return there during the day with increased light level and predator activity and higher DO levels. This site is midway along Blind Channel, permitting slight two-way water movement by wind-generated seiches. Here, the movement of more turbid lake water possibly retarded growth of submerged macrophytes, and also swept away detritus leaving little cover in the open water habitat (Table 1). These conditions were modelled in the laboratory, which showed that while cover was the main habitat requirement, yellow perch distinctly avoided water at 3.0–1.5 ppm, in accordance with the field data. Alabaster and Robertson (1961) demonstrated in four trials in an outside tank that adult yellow perch avoided DO concentrations at 6.7, 3.0, 2.3, and 1.9 ppm (23°C). These values are all higher than incipient lethal DO levels, which for post-young-of-the-year yellow perch (10–25°C), using a variety of techniques, were below 1 ppm (Burdick et al. 1957; Doudoroff and Shumway 1970; Petit 1973; Gee et al. 1978).

Field observations of juvenile and adult yellow perch in lakes have shown crepuscular increases in activity (Craig 1977; Kelso and Ward 1977), often associated with an onshore movement in the evening and offshore in the morning (Hasler and Bardach 1949; Hasler and Villemonte 1953; Scott 1955; Emery 1973; Engel and Magnuson 1976). This is contrary to the diel movement at site B, which is argued to be in response to hypoxia. There is no evidence for a light-induced onshore/offshore migration at site A, as minnow trap catches show cover to be the major requirement during the day and night in early June, when there was no hypoxia. Direct observation of this was not possible due to low visibility in June and the dense emergent vegetation. There were no marked temperature gradients of any magnitude, and the water is hard and well buffered, reducing gradients in pH and free $CO_2$. Shelford and Allee (1913) and Hoglund (1961) argued that in the field, fish may detect $CO_2$ and thus avoid low DO concentrations.

Brook stickleback caught with yellow perch also exhibited a seasonal shift offshore, as well as a change in diel distribution in July by moving both horizontally and vertically away from severe hypoxia. Complete avoidance of the station 1 bottom trap was evident when mean DO was below 1 ppm at time of sampling, and was associated with an increased surface trap catch (Suthers 1984).

### Factors Modifying Level of DO Avoidance

The precise level of DO that limits yellow perch distribution in Delta Marsh cannot be determined from field data. The DO regime preceding each 12-h sampling can only be inferred from the DO reading at each trap, and from the continuous recording (Fig. 1), which shows a general decrease from 21:00 to 06:00. The rate and exent of this decrease depends not only on habitat but would vary daily and spatially with microhabitat variation in DO level. Consequently, regressions of mean station 1 catch on mean DO concentration at sites A and B explained only 62 and 40% of the catch variance, respectively. Yellow perch may make brief feeding forays into the hypoxic cattail by exploiting microhabitats with elevated DO concentrations. Both Coulter (1967) and Dendy (1946, cited in Doudoroff and Shumway 1970) gillnetted fish in severely hypoxic benthic regions, presumably feeding. Centrachids were found with food items in their gut that could only have been obtained by foraging in the hypoxic hypolimnion (Dendy 1956; Hanson and Qadri 1984). Microhabitat variation in DO concentration could depend on patches of photosynthetic $O_2$ production and consumption amongst the cattail. Microzones of high DO may also occur around bubbles produced by photosynthesis that are trapped under algae and displaced patches of periphyton. Exploitation of these microzones by fishes would involve both a physiological (activity level, heart rate, ventilatory rate and amplitude) and a behavioral response to environmental cues (sunlight, vegetation, odor). For example, exploitation of high oxygen microzones at the ice–water interface due to cracks and bubbles was observed in mudminnows and brook stickleback under simulated ice conditions (Klinger et al. 1982; Magnuson et al. 1982). In a naturally anoxic hot-spring, Odum and Caldwell (1955) observed fish to exploit eddies where DO had increased slightly.

The hypothesis that changes in distribution of yellow perch are a direct result of severe hypoxia and the growth of alternative cover in the open water habitat is supported by simulation of these events in the laboratory, the in situ survival experiments, and consideration of crepuscular behavior and other factors. The diel shift in distribution is not a periodic, predictable migration but an avoidance of low DO concentrations that can occur between spring normoxic conditions and midsummer anoxia. The optimality tradeoff between prey and predator distribution (Werner et al. 1983) now appears as one between favorable predator/prey conditions and hypoxia. Assessment of juvenile fish utilization of the productive littoral zone as nursery areas, or as refugia in predation studies, should be made in the context of a temporally varying environment.

## Acknowledgements

This study was supported by University of Manitoba Graduate Fellowship to I.M.S. and the Natural Sciences and Engineering Research Council of Canada to J.H.G. The support of R. M. R. Barclay, J. M. Shay, and the staff of the University of Manitoba Field Station (Delta Marsh) is appreciated, and the permission of the Portage Country Club to conduct research on their property is acknowledged. We thank B. J. Hann, J. Mathias, D. Punter, F. J. Ward, and K. T. Frank for earlier criticisms of the paper. E. G. Scherer and R. McNichol assisted with the laboratory work and B. J. Beaver, K. Y. Dyke, and F. I. Schneider assisted in the field.

## References

Alabaster, J. S. 1959. The distribution of dissolved oxygen and fish in a sewerage effluent. J. Anim. Ecol. 28: 283–291.

Alabaster, J. S., and K. G. Robertson. 1961. The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (*Rutilus rutilus* (L)), bream (*Abramis brama* (L)) and perch (*Perca fluviatilis* L). Anim. Behav. 9: 187–192.

Birtwell, I. K., G. L. Greer, M. D. Nassichuk, and I. H. Rogers. 1983. Studies on the impact of municipal sewerage discharged onto an intertidal area within the Fraser River estuary, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1170: 55 p.

Burdick, G. E., H. J. Dean, and E. J. Harris. 1957. Lethal oxygen concentrations for yellow perch. N.Y. Fish Game J. 4: 92–101.

Casselman, J. M. 1978. Effects of environmental factors on growth, survival, activity, and exploitation of northern pike. Am. Fish. Soc. Spec. Publ. 11: 114–128.

Clady, M. D. 1976. Decline in abundance and survival of three benthic fishes in relation to reduced oxygen levels in a eutrophic lake. Am. Midl. Nat. 97: 419–432.

Coulter, G. W. 1967. Low apparent oxygen requirements of deep-water fishes in Lake Tanganyika. Nature (Lond.) 215: 317–318.

Craig, J. F. 1977. Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. J. Fish Biol. 11: 161–166.

Crowder, L. B., J. J. Magnuson, and S. B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38: 662–668.

Dendy, J. S. 1956. Bottom fauna in ponds with largemouth bass only and with a combination of largemouth bass plus bluegill. J. Tenn. Acad. Sci. 31: 198–207.

Doudoroff, P., and D. L. Shumway. 1970. Dissolved oxygen requirements of freshwater fishes. Fish. Tech. Pap. FAO United Nations 86: 291 p.

Elliot, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. No. 25 (2nd ed): 160 p.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario Lakes. J. Fish. Res. Board Can. 30: 761–774.

Engel, S., and J. J. Magnuson. 1976. Vertical and horizontal distributions of coho salmon (*Oncorhynchus kisutch*), yellow perch (*Perca flavescens*), and cisco (*Coregonus artedii*) in Pallette Lake, Wisconsin. J. Fish. Res. Board Can. 33: 2710–2715.

Gee, J. H. 1980. Respiratory patterns and anti-predator responses in the central mudminnow *Umbra limi*, a continuous facultative air-breathing fish. Can. J. Zool. 58: 819–827.

Gee, J. H., R. F. Tallman, and H. S. Smart. 1978. Reactions of some great plains fishes to progressive hypoxia. Can. J. Zool. 56: 1962–1966.

Hall, D. J., and E. F. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan Lake. Trans. Am. Fish. Soc. 106: 545–555.

Hanson, J. M., and S. U. Qadri. 1984. Feeding ecology of age 0 pumpkinseed (*Lepomis gibbosus*) and black crappie (*Pomoxis nigromaculatus*) in the Ottawa River. Can. J. Zool. 62: 613–621.

Hasler, A. D., and J. E. Bardach. 1949. Daily migrations of perch in Lake Mendota, Wisconsin. J. Wildl. Manage. 13: 40–51.

Hasler, A. D., and J. R. Villemonte. 1953. Observations on the daily movements of fishes. Science (Wash., DC) 118: 321–322.

Hochachka, P. W. 1980. Living without oxygen: closed and open systems in hypoxic tolerance. Harvard University Press, Cambridge. 181 p.

Hoglund, L. B. 1961. The reactions of fish in concentration gradients. Rep. Inst. Freshwater Res. Drottningholm 43: 1–147.

Johnson, F. H., and J. B. Moyle. 1969. Management of a large shallow winterkill lake in Minnesota for the production of pike (*Esox lucius*). Am. Fish. Soc. 98: 691–697.

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environ. Biol. Fishes 2: 53–70.

Keast, A., J. H. Harker, and D. Turnbull. 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). Environ. Biol. Fishes 3: 173–184.

Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25: 1133–1144.

Kelso, J. R. M., and F. J. Ward. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. J. Fish Res. Board Can. 34: 1655–1669.

Klinger, S. A., J. J. Magnuson, and G. W. Gallepp. 1982. Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) for low oxygen in winter. Environ. Biol. Fishes 7: 113–120.

Kushlan, J. A. 1974. Effects of a natural fish kill on the water quality, plankton, and fish population of a pond in the Big Cypress Swamp, Florida. Trans. Am. Fish. Soc. 103: 235–243.

Magnuson, J. J., A. L. Beckel, K. Mills, and S. B. Brandt. 1985. Surviving winter hypoxia: behavioral adaptations of fishes in a northern Wisconsin winterkill lake. Environ. Biol. Fishes 14: 241–250.

Magnuson, J. J., J. W. Keller, A. L. Beckel, and G. W. Gallepp. 1982. Breathing gas mixtures different from air: an adaptation for survival under the ice of a facultative air-breathing fish. Science (Wash., DC) 220: 312–314.

Nicholls, K. H., W. Kennedy, and C. Hammett. 1980. A fish-kill in Heart Lake, Ontario, Canada associated with the collapse of a massive population of *Ceratium hirudinella* (Dinophyceae). Freshwater Biol. 10: 553–562.

Odum, H. T., and D. K. Caldwell. 1955. Fish respiration in the natural oxygen gradient of an anaerobic spring in Florida. Copeia 1955: 104–106.

Paszkowski, C. A., and W. M. Tonn. 1983. An experimental study of foraging site selection in young-of-the-year yellow perch, *Perca flavescens*. Environ. Biol. Fishes 8: 283–292.

Petit, G. D. 1973. Effects of dissolved oxygen on survival and behaviour of selected fish of Western Lake Erie. Bull. Ohio Biol. Surv. 4(4): 1–76.

Rinne, J. N., W. L. Minckley, and P. O. Bersell. 1981. Factors influencing fish distribution in two desert reservoirs, Central Arizona. Hydrobiologia 80: 31–42.

Rudstam, L. G., and J. J. Magnuson. 1985. Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. 42: 1178–1188.

SAS 1982. SAS user's guide: statistics. SAS Institute Inc., Cary, NC. 584 p.

Scherer, E., and S. Nowak. 1973. Apparatus for recording avoidance movements of fish. J. Fish. Res. Board Can. 30: 1594–1596.

Scott, D. C. 1955. Activity patterns of perch, *Perca flavescens* in Rondeau Bay of Lake Erie. Ecology 36: 320–327.

Shelford, V. E., and W. C. Allee. 1913. The reactions of fishes to gradients of dissolved atmospheric gases. J. Exp. Zool. 14: 207–266.

Suthers, I. M. 1984. Role of dissolved oxygen in limiting diel and summer distribution of yellow perch in a prairie marsh. M.Sc. thesis, University of Manitoba, Winnipeg, Man. 63 p.

Tramer, E. J. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. Am. Midl. Nat. 97: 469–478.

Tudorancea, C., and R. H. Green. 1975. Distribution and seasonal variation of benthic fauna in Lake Manitoba. Verh. Int. Ver. Limnol. 19: 616–623.

Vigg, S. 1980. Seasonal benthic distribution of adult fish in Pyramid Lake, Nevada, U.S.A. Calif. Fish Game J. 66: 48–58.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.

Whitmore, C. M., C. E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrachid fishes to low oxygen concèntrations. Trans. Am. Fish. Soc. 89: 17–26.