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Reproduction and Distribution of Fishes in a Cooling Lake: Wisconsin Power Plant Impact Study

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FOREWORD

Ths U.S. Environmental Protection Agency (EPA) was designed to coordinate our country's efforts toward protecting and improving the environment. This extremely complex task requires continuous research in a multitude of scientific and technical areas. Such research is necessary to monitor changes in the environment, to discover relationships within that environment, to determine health standards, and to eliminate potentially hazardous effects.

One project, which the EPA is supporting through its Environmental Research Laboratory in Duluth, Minnesota, is the study "The Impacts of Coal-Fired Power Plants on the Environment." This interdisciplinary study, centered mainly around the Columbia Generating Station near Portage, Wis., involves investigators and experiments from many academic departments at the University of Wisconsin and is being carried out by the Environmental Monitoring and Data Acquisition Group of the Institute for Environmental Studies at the University of Wisconsin-Madison. Several utilities and State agencies are cooperating in the study: Wisconsin Power and Light Company, Madison Gas and Electric Company, Wisconsin Public Service Corporation, Wisconsin Public Service Commission, and Wisconsin Department of Natural Resources.

Spatial and temporal patterns during reproductive and early life history of fish were studied in a man-made cooling lake. Fish initially colonized the lake when it was filled with water from the Wisconsin River. Observations suggest a decline of species diversity in the fish community caused by upper lethal tempertures, absence of colonization by warm-water, lake-dwelling species, and lack of recruitment for certain species.

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ABSTRACT

Spatial and temporal patterns during reproduction and early life history of fishes were studied in a manmade cooling lake. Lake Columbia, impounded in 1974, near Portage, Wisconsin, has an area of 190 ha, a mean depth of 2.1 m, and a 15 C temperature gradient derived from the thermal efluent of a 527-MW fossil-fueled generating station which began operation in 1975.

The lake was initially colonized by fishes when filled with Wisconsin River water. Observations suggest a decline of species diversity of the fish community due to: (1) direct action of upper lethal temperatures, (2) absence of colonization by warm-water, lake-dwelling species, and (3) lack of recruitment for certain species.

Spatial and temporal patterns of spawning of black crappie (*Pomoxis nigromaculatus*) were altered by a rapid rise in water temperatures following plant start-up after a 3-week shutdown. Water temperatures above expected spawning temperatures reduced available spawning area and induced aggregation of sexually mature black crappie at coolest available temperatures. Elevated temperatures subsequently shortened the spawning season, induced resorption of ova, and caused loss of secondary sexual characteristics.

A second generating unit began operation in February 1978. Spawning of black crappie and white bass (*Morone chrysops*) occurred 1 month earlier during the spring of 1978 than in 1977.

Species abundance of larval fish catches was greater in 1978 when the spawning season was not unusually abbreviated, as in 1977. After initially drifting with water current, juvenile stages of sunfish (*Lepomis* sp.) and gizzard shad (*Dorosoma cepedianum*) responded to changes in the thermal gradient by horizontal and vertical shifts in abundance.

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SECTION 1

INTRODUCTION

Impoundment of a man-made cooling lake provides an opportunity for development of a recreational fishery. Thermally elevated areas of a cooling lake can increase angler utilization by concentrating fishing effort and extending seasonal angler use in temperate climates (McNurney et al. 1977). Because the cooling lake is a relatively small man-made system it has greater potential and flexibility for recreational fishery management than many systems.

Fish management strategies of stocking or fish harvest for temperate lakes based on surface area or morphoedaphic characteristics will not be valid for lakes substantially altered by thermal input. The elevated thermal conditions of cooling lakes create temporal and spatial limiations for organisms native to nearby lakes. Growth (Bennett and Gibbons 1974), distribution (Merriman and Thorpe 1976), and reproduction (Bennett and Gibbons 1975, Kaya 1977) are modified in thermally altered areas. Lake Columbia, located at the Columbia Generating Station near Portage, Wisconsin, provides an opportunity for research and development of management strategies specifically for cooling lakes in the Great Lakes region.

As a subproject of an assessment of a developing cooling lake ecosystem (Lozano et al. 1978), this study of fishes concerned the reproductive responses of adults and distributional patterns of adult, larval, and early juvenile forms in Lake Columbia. The objectives were: (1) determine changes in species composition of the fish population; (2) delineate temporal and spatial limits of fish reproduction; and (3) determine distributional patterns of larval and early juvenile fishes.

SECTION 2

STUDY SITE

Lake Columbia, Columbia County, Wisconsin, is a 190-ha closed-cycle cooling reservoir for a fossil-fuel generating plant owned by Wisconsin Power and Light Co. The cooling reservoir was created within dikes over a peat sedge meadow. The lake was first filled in June 1974, but the water levels gradually declined until the lake was refilled in November 1974. Water levels were then maintained through March 1975 when testing of the 527-megawatt (MW) Columbia I unit began. Columbia II, a second 527-MW unit, began operating in February 1978.

A central baffle dike constructed of gravel separates the east and west arms of the reservoir (Figure 1). Dike slopes are covered with rock rip-rap. Water depth is between 1.9 and 2.4 m, with an average depth of 2.1 m. To compensate for leakage and evaporative loss, water from the Wisconsin River is pumped at rates up to 52 m^3/min into a settling basin before entering the main body of the reservoir.

Water is removed from the reservoir at the intake channel and pumped through the power-plant condensers where temperatures are raised about 15 C. Effluent water flows from the outfall channel and circulates around the center baffle dike back to the intake channel in approximately 5 days. Water is pumped through the power plant condensers at a rate of 750 m^3/min. Current velocity and water temperature decline exponentially as water flows from outfall to intake channel (Figure 2). Current velocity increases as flow is constricted near the settling basin and intake. During periods of power-plant shutdown, isothermal conditions exist. Water temperatures measured in the settling basin were 5 to 6 C cooler than intake temperature. January to July variations in water temperature between outfall and intake are shown in Figure 3.

Lake configuration and shallow depth causes vertical mixing and results in little thermal or chemical stratification. Except for temperature and current (Figure 2), there are no consistent horizontal gradients of physical and chemical parameters (Andren et al. 1976).

Partially decomposed peat and detrital material cover the bottom of the lake except near the south end where it was removed during construction. Macrophyte surveys during 1975 indicated that production declined rapidly during the first summer of operation and was restricted to areas near the intake in subsequent summers (Lozano et al. 1978).

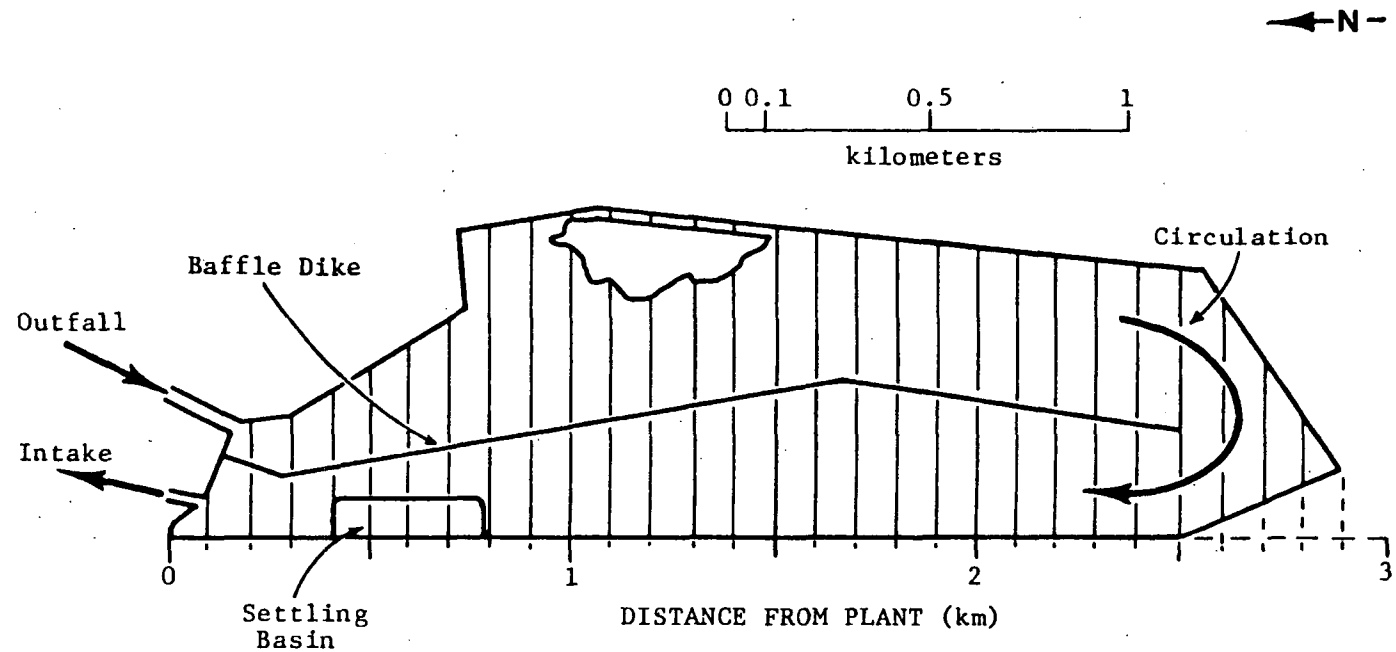


Figure 1. The cooling lake at the Columbia Generating Station.

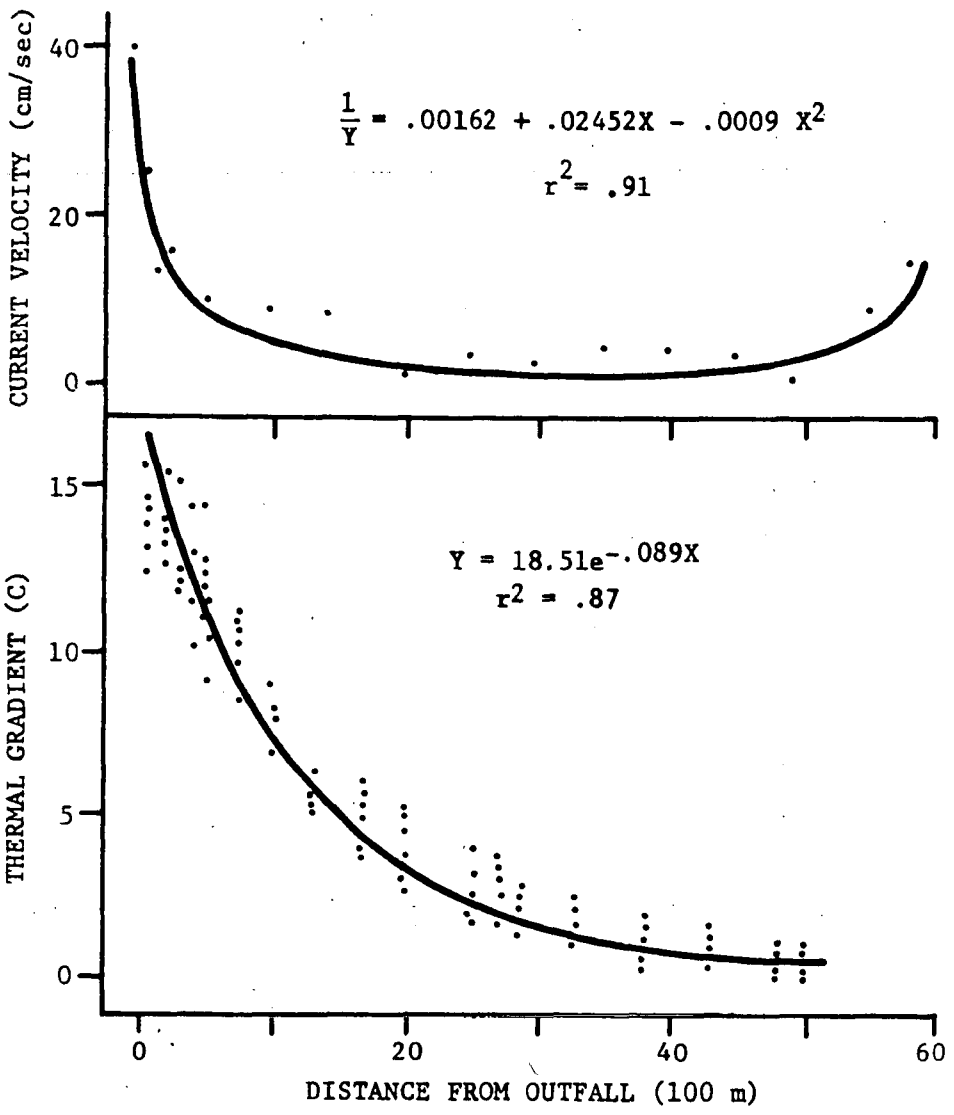


Figure 2. Water current velocity and thermal gradient in the cooling lake.

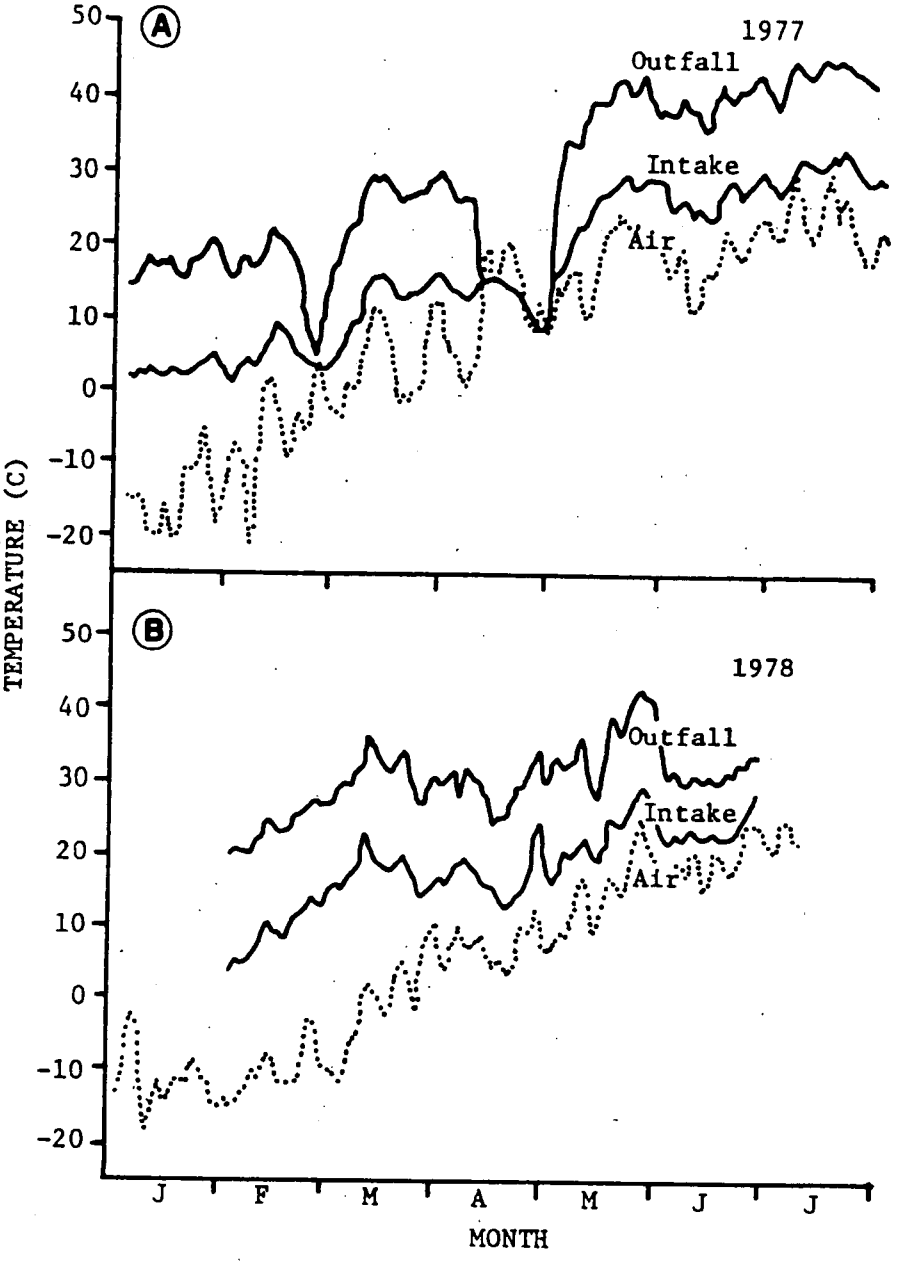


Figure 3. Mean daily power plant water intake, outfall, and air temperature during the first 6 months of 1977 and 1978.

SECTION 3

RELATIVE ABUNDANCE OF FISHES

INTRODUCTION

New impoundments are known for the dramatic changes they cause in fish communities after filling. Studies suggest these changes can be attributed to changes of biotic and abiotic characteristics of the impoundment (Jenkins and Morais 1971). In the cooling lake environment, the effects of the unique thermal regime are imposed on these expected changes in the fish community. Therefore, the first objective was to determine if changes in species composition of the fish population occurred with time.

The fish community was initially established in Lake Columbia by colonization from the Wisconsin River and its backwaters. A drain culvert connected the lake with an adjacent marsh and permitted fish to enter during construction. Following the filling of the lake in 1975 the Wisconsin Department of Natural Resources (WDNR) introduced largemouth bass in an effort to establish a warm-water sport fishery.

METHODS

Composition of the fish community and the relative abundance of adults at locations in Lake Columbia were assessed using fyke nets. Fyke nets were constructed with 32-mm stretch mesh nylon webb, and equipped with a 15.2-m lead, 1.8-m frames, and five 0.75-m diameter hoops. Nets were set perpendicular to shore for 24 h with regular sampling stations at 0.5, 1.3, 2.2, 3.8, 4.5, and 5.5 km from the outfall (Figure 1). Fish were identified, measured for total length, and weighed.

Water temperatures were measured at 0.5, 1.0, 1.5, and 2.0-m depths when nets were set and raised. Recording thermographs were used during spring and summer in 1977 and 1978 to continuously monitor diel temperature changes. Current velocities were measured using an electromagnetic water current meter.

The number of fish per fyke net set--catch per effort (CPE)--was used as a measure of the relative abundance of fish species over time. Two hundred thirty-four fyke net sets were completed on 49 sampling dates from July 1975 through May 1978. Mean quarterly CPE was calculated from monthly catches from December to February, March to May, June to August, and

September to November. Species diversity of the fish population in quarterly fyke net catches was calculated using the Shannon and Weaver (1963) general index of diversity ($\bar{H}$) . Percent similarity was calculated between each quarterly catch and the catch from the first quarter of 1975 using the following formula:

$$PP_k = \frac{2 - \Sigma P_{i,1} - P_{i,k} \times 100}{2}$$

where

$P_{i,1}$ = the proportion of species i in the first quarter;

$P_{i,k}$ = the proportion of species i in the k-th quarter.

RESULTS

During the sampling period, 24,403 fish were caught in fyke nets. Thirty species of fish were represented in the catch.

The Shannon-Weaver diversity index suggests a decline in diversity of quarterly catches that started in the winter of 1975-76 and continued through the fall of 1976 (Figure 4). In fall 1976 only 34% of the catch was similar to that of summer quarter 1975. In the fall quarter of 1976 black bullhead (*Ictalurus melas*) made up 71.5% of the catch, the highest percent for a single species of all quarterly samples. Pumpkinseed sunfish (*Lepomis gibbosus*) and black crappie (*Pomoxis nigromaculatus*) were at low levels in fall 1976, while northern pike (*Esox lucius*) were absent from catches following a die-off in summer 1976. Species diversity did not return to 1975 levels.

Changes in the diversity of fyke net catches can be attributed to a decline of CPE for some species and numerical dominance by others. The mean quarterly CPE of centrarchids in Lake Columbia (Figure 5A) indicates that the abundance of pumpkinseed sunfish declined somewhat between July 1975 and August 1977. The mean CPE for white bass (*Morone chrysops*) (Figure 5B) was high in the winter quarter samples and decreased during the study period. Bluegill (*Lepomis macrochirus*) catches increased dramatically, showing the first peak during fall 1976 and a second during summer 1977. Gizzard shad (*Dorosoma cepedianum*) CPE increased from none caught during the first quarter to a CPE >5 in 1977 (Figure 5B).

Bluegill and gizzard shad length frequencies indicate successful growth and reproduction in the new lake environment, as evidenced by increased CPE. Length frequencies of bluegill suggested an increase of fish <150 mm in length by June 1976. The increased contribution from bluegill <150 mm corresponds with the quarter in which bluegill CPE began to increase (Figure

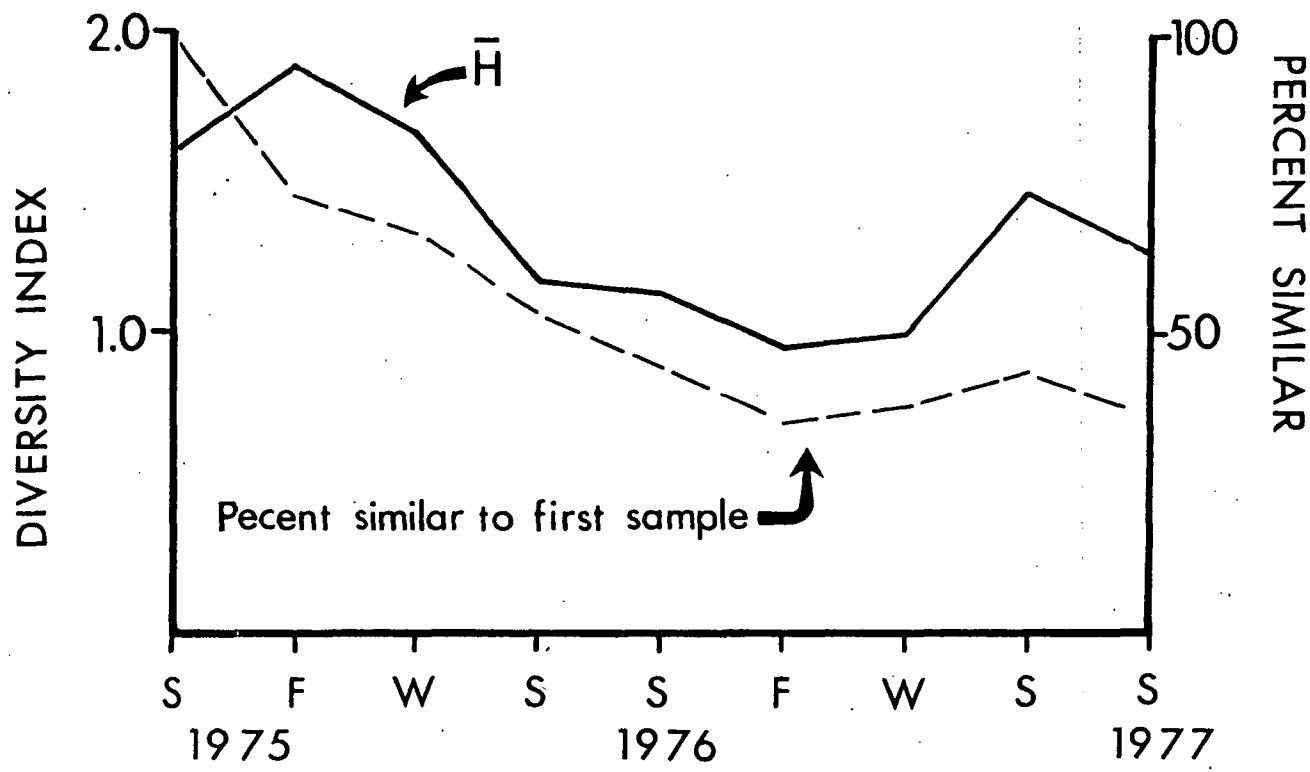


Figure 4. Shannon-Weaver diversity index ($\bar{H}$) and percent similarity to first sample of quarterly fyke net catches in Lake Columbia.

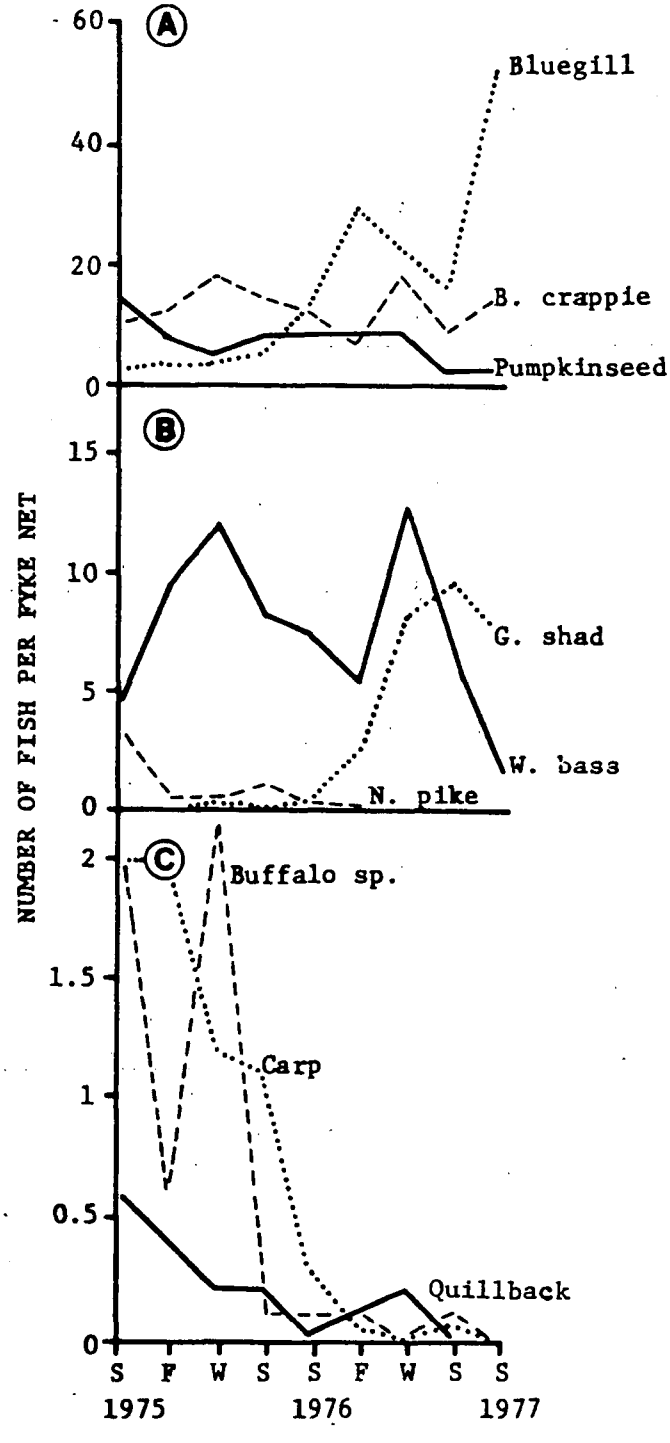


Figure 5. Mean catch per effort in fyke nets during quarterly sampling periods in Lake Columbia.

5A). Length frequencies of gizzard shad show an increasing abundance of smaller shad in January 1977 that also corresponds with dramatic increases in CPE during the winter quarter of 1977 (Figure 5B).

Length frequencies of black crappie and white bass suggest limited recruitment (Figure 6). Examination of scale samples showed that the length frequency modes were different year classes (Lozano et al. 1978). Black crappie length frequency modes were made up of the 1973 and 1974 year classes. The largest mode of white bass was the 1974 year class (Figure 6B). Year classes strongly represented in length frequencies of black crappie and white bass were from years prior to power plant operation.

Other fish species common to the Wisconsin River were found in Lake Columbia. The relationship between changes in relative abundance, final temperature preferenda, and upper incipient lethal temperatures of the most abundant species in fyke net catches is shown in Figure 7. Yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) made up <0.5% of the catch in all quarters. Species at low abundance that have decreased in CPE include quillback (*Carpoides cyprinus*), smallmouth buffalo (*Ictiobus bubalus*), and carp (*Cyprinus carpio*) (Figures 5C,7). Minnow trap catches indicated fathead minnows (*Pimephales promelas*) and mud minnows (*Umbra limi*) were abundant when the plant began operation in March 1975, but abundance was reduced by July. The mean quarterly CPE of northern pike declined 99% between the first and third year of the study. Northern pike disappeared from catches during the summer quarter of 1976 (Figure 5B). On 17 July 1976, 97 dead northern pike were found along the middle dike of the lake. Water temperatures were high (>29.6 C at all depths), dissolved oxygen was low (2.5 ppm), and wind conditions were calm prior to the time that the dead fish were observed. Bluegill abundance increased more than eight-fold between the first and third years (Figure 7).

DISCUSSION

The decline in species diversity of fyke net catches can be attributed to: (1) an absence of colonization by warm-water, lake-dwelling species; (2) direct action of upper lethal temperatures; and (3) lack of recruitment for certain species. The lack of colonization by warm water fishes is expected since the cooling lake is similar to the biological communities of an island. In this case its geographic isolation from other warm water communities reduces the chance of natural colonization. In addition, colonizing species must survive water temperatures near 30 C in summer and be able to acclimate to water temperatures near 0 C in winter during shutdowns.

Thermal characteristics of Lake Columbia were important in structuring the fish community through the direct action of upper lethal temperatures. The rapid disappearance of fathead minnows can also be attributed to high water temperatures. Fathead minnows acclimated to 30 C prefer high temperatures of 26.5 to 30.3 C, but exposure to 33 C has been found to be lethal (Cherry et al. 1977). The observed kill of northern pike eliminated a large piscivorous mesotherm that is an important predator in temperate

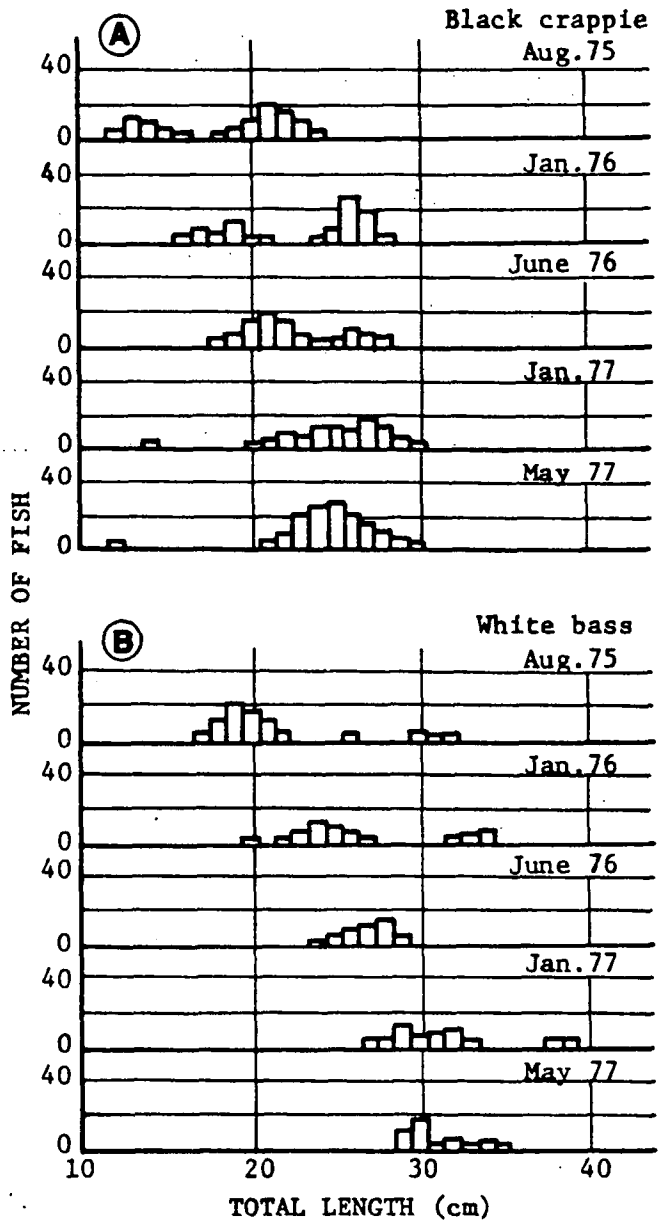
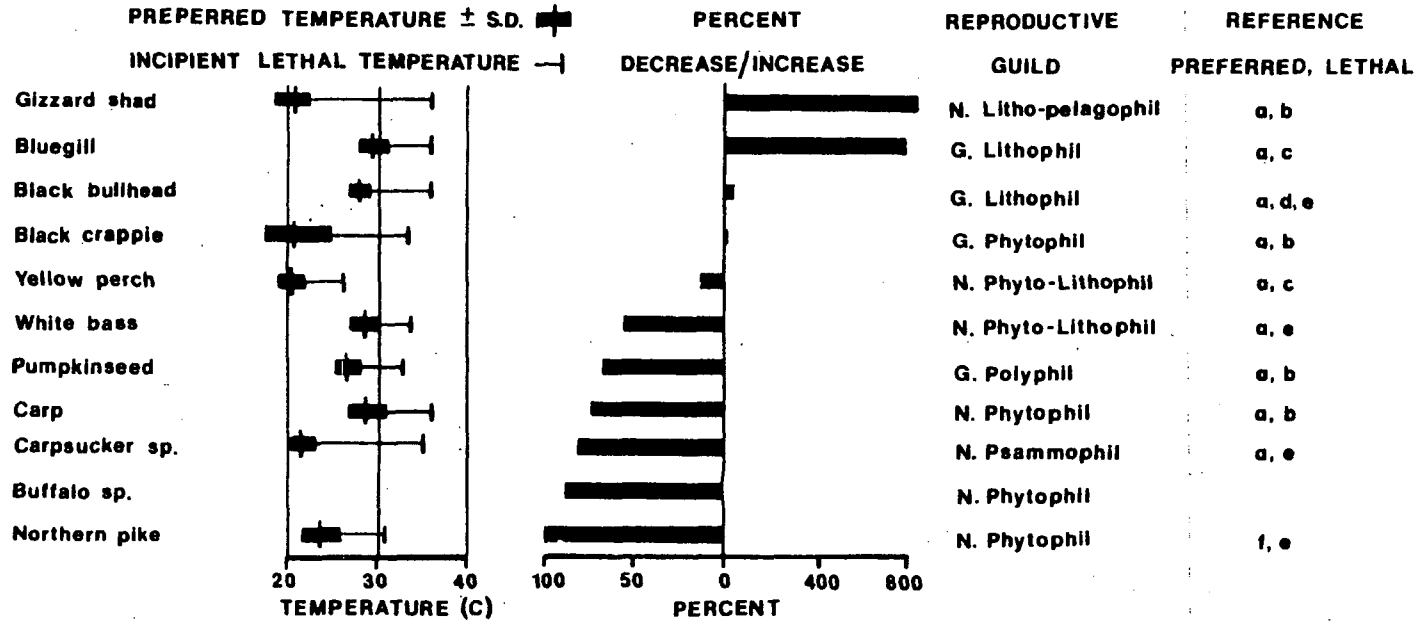


Figure 6. Length frequency distributions of black crappie and white bass, 1975-77.



N = nonguarding spawners
G = guarding spawners

Figure 7. Percent increase or decrease in abundance of selected fishes in Lake Columbia. Preferred and upper incipient lethal temperatures of fish are from other sources (Reutter and Herendorf 1974, Brungs and Jones 1977, Cherry et al. 1977, Coutant 1977, Cvancara et al. 1977). Reproductive guilds are from Balon (1975a).

lakes with similar morphometric characteristics. Northern pike have a laboratory final preferendum of approximately 24 C and an upper incipient lethal temperature of 30.8 C LD_{50} (Cvancara et al. 1977), approximately equal to 29.6 C observed prior to the fish kill. Bluegill, which have a final preferendum of 30.5 C and a 7-day upper lethal temperature of 36 C (Cherry et al. 1977), increased more than eight-fold. Species that increased in abundance had final preferenda ranging from 20.5 to 30.5 C and upper lethal temperatures $\geq$33 C. Other species with relatively high upper lethal temperatures, such as white bass (LD_{50} = 33.5 C; Cvancara et al. 1977) and carp (LD_{50} = 36 C; Brungs and Jones 1977) decreased in abundance. This suggests that other factors were important in determining the abundance of some species.

The lake habitat changed rapidly with increased water temperature, water depth, and the disappearance of macrophytes when the power plant began operation. Subsequent recruitment of bluegill and the apparent lack of success by pumpkinseed changed the centrachid complex from numerical domination by pumpkinseed to numerical domination by bluegill. Bluegill feed higher in the water column and in many cases the major components of the diet are chironomid larvae and zooplankton, while pumpkinseed feed on benthic prey such as mollusks and isopods associated with macrophytes (Werner et al. 1977, Keast 1978). The abundance of chironomid larvae (Kromery 1976), lack of macrophytes (Lozano et al. 1978), and minimum summer water temperatures near 30 C indicate that the bluegill is well adapted to the cooling lake habitat.

The lack of recruitment by black crappie, white bass, and other species with decreases in CPE is not readily explained by final preferenda or upper incipient lethal temperatures (Figure 7). Rapid growth (Lozano et al. 1978) of black crappie (final preferendum 21.7 C), northern pike (*Esox* sp.; 24 to 26 C), pumpkinseed (27.7 C), and white bass (28 to 30 C) (Coutant 1977) suggests that species with a wide range of optimal growth temperatures were able to find adequate food and temperature suitable for growth in the heterothermal lake. The lack of recruitment may result from natural variation in year class strength or inhibited reproduction due to exposure to high temperature, such as observed for trout (Kaya 1977) and yellow perch (Hokanson 1977).

Species which increased in abundance tended to have reproductive characteristics in common (Figure 7). The reproductive guilds described by Balon (1975a) indicate that species with increasing CPE tended to be nest guarding lithophils, species utilizing gravel or sand spawning substrates. Species such as carp, buffalofish, and northern pike declined more than 50% in abundance and belong to the nonguarding phytophil guild which utilizes flooded vegetation as a spawning substrate (Figure 7). The spawning of carp and northern pike is inhibited by the lack of flooded vegetation (Balon 1975a, June 1978). In this case, in Lake Columbia, water temperatures would indirectly inhibit spawning by causing macrophytes to disappear in areas of higher temperatures.

In conclusion, the decline of species diversity resulted from a lack of colonization by warm-water fish species, mortality caused by water tempera-

tures exceeding upper lethal temperatures of some species, and a lack of recruitment by other species. Bluegill are well adapted for the cooling lake because of their relatively high thermal preferendum, planktivorous diet, ability to forage in open water habitat and presence of suitable spawning habitat. Species with limited recruitment tended to belong to similar reproductive guilds, usually nonguarding phytophils.

SECTION 4

REPRODUCTION OF FISHES

INTRODUCTION

Thermal requirements for reproduction of a species are one of the primary limits to distribution and abundance (Alderdice and Forrester 1968, Hokanson 1977). Temperature and photoperiod are environmental factors important in the recrudesence of gametogensis of many teleosts (De Vlaming 1972, 1974, Schrech 1974, Hokanson 1977). The unique thermal regime in the cooling lake creates temperatures during winter and early spring at or above those associated with the initiation of spring spawning. The thermal gradient was expected to determine the spatial and temporal location of spawning within limits of photoperiod control. Thus, the second objective was to study the temporal and spatial limits of reproduction within Lake Columbia. White bass and black crappie were selected for study because adults were growing well but did not appear to be producing young.

METHODS

Temporal Patterns of Reproduction

Temporal patterns of reproduction were determined by monitoring the maturity of white bass and black crappie from the initiation to the completion of spawning during the springs of 1977 and 1978. The percent gonad weight of total body weight or gonadosomatic index (GSI = gonad wt/total fish wt x 100) was calculated as a measure of maturity at 2-week intervals starting in February 1977. Sampling intervals were shortened as fish became more sexually mature. Fish were removed from 24-hr fyke net sets, subsampled within specific size classes, and frozen on dry ice. During 1977, length strata were 200 to 300 and 250 to 350 mm for black crappie and white bass, respectively. During 1978 the lengths were 250 to 350 and 300 to 400 mm for black crappie and white bass, respectively.

Samples of 10 to 15 fish of each sex per date were frozen for dissection. Remaining fish were classified according to eight stages of maturity (Bagenal and Braum 1971) and released. Specimens were taken to the laboratory where total length and total weight were measured. Gonads were then removed, blotted for 1 min on an absorbent towel, and weighed to the nearest 0.01 g. When fish were abundant, equal numbers were selected from stations

0.1 to 2.9 km (warm side) and 3.0 to 6.0 km (cool side) from the outfall (Figure 1).

Spatial Patterns of Reproduction

Spatial limiations of spawning relative to the thermal gradient were examined during the springs of 1977 and 1978. Relative abundance of sexually mature fish at various locations in Lake Columbia was determined by fyke nets as previously described. Abundance of adults recorded as CPE was regressed on mean water temperature at station of capture and station location in km from the outfall. Differences between distributions described by least square linear regression were tested by comparing slopes of the lines (Snedecor and Cockran 1967). For nonlinear distributions, observed CPE in 0.5 C intervals was compared to the expected CPE using the two sample Kolmorgorov-Smironov test (Siegel 1956).

Thermal exposure of adult black crappie was estimated from equations describing distribution of adults and the thermal gradient. The least squares linear regression of $\log_e$ mean water column temperature (N = 4) on station location (N = 20) was used to describe the decline in water temperature. The regression equation was then used to generate predicted mean water column temperature ($\hat{T}$) for station locations at 0.1 km intervals on a daily basis. Predicted mean water temperature values of each station ($\hat{T}$) were then adjusted by adding the difference between the mean intake temperature of a given day and the mean intake temperature predicted by the regression.

Mean intake temperatures were calculated by integration of water temperatures recorded by Ryan thermographs located 0.5 km from the intake. Temperature records were integrated using a Hewlett-Packard model 9107A calculator and digitizer. Missing data during 1977 were replaced by daily mean intake temperatures provided by the Columbia Generating Station and Wisconsin Power and Light, Inc. Daily mean intake temperatures were calculated from readings taken at 4-h intervals at the Columbia I intake.

The regression fit of mean water temperature on station was an exponential function:

$$\hat{T} = 14.16e - 0.049X$$

$$r^2 = 0.98$$

where

$\hat{T}$ = predicted mean water column temperature at the station;

X = a given station (1 to 60) at 0.1 km intervals from 0.1 to 6.0 km from the outfall.

Median and interquartile limits of the thermal exposure are those mean water column temperatures corresponding with 25, 50 (median), and 75% levels of the black crappie distribution. Percent levels of distribution were calculated by the summation of predicted values from equations describing fyke net catches of sexually mature fish.

Gamete Viability

Black crappie gamete viability was tested. Testes of three males were removed, blotted dry, and held in petri dishes floating in a water bath at 22 C in an insulated ice chest. Ova of three females were then stripped separately into petri dishes and fertilized with spermatozoa from two different fish. Several drops of water were added and ova were allowed to sit 5 min. Embryos were then moved to floating incubation cups with nitrex mesh bottoms for transport to the laboratory. At the laboratory embryos were incubated at room temperature (19 to 20 C). Water from Lake Columbia was replaced in the incubation bath twice daily. Microscopic examination of selected embryos was made during incubation. When hatching began, ova were fixed for 5 min in a 4% glacial acetic acid and 0.7% NaCl solution and preserved in 5% buffered formalin for later examination of embryos (Bagenal and Braum 1971). About half of the ova in one incubation chamber were allowed to hatch and held in an aquarium. The randomness of hatching success in each of 10 incubation cups was tested using the multiple runs tests (Siegel 1956).

RESULTS

Temporal Patterns of Reproduction

From 10 to 30 April 1977, the Columbia I generating unit shut down for maintenance. This resulted in a rapid decrease followd by an increase in water temperatures, which in turn altered the temporal placement and duration of spring spawning. During the shutdown water temperatures in the lake were isothermal. Although the Columbia I generating unit did shut down between 6 and 16 April 1978, changes in water temperature and its effects on the temporal placement of spawning were minimized by the operation of the Columbia II generating unit (Figure 3).

Mean GSI of female (Figure 8A) and male white bass increased steadily during spring 1977 until power plant shutdown in early April and then declined slightly between 3 and 29 April. During the shutdown a slight decline in GSI suggested spawning was occurring prior to plant start-up, but no running ripe females, spent females, or spawned ova were found in the nets. When power plant operation resumed 1 May 1977 the decrease in mean female GSI from 12.2 on 29 April to 1.9 on 11 May coincided with an increase in water temperatures (Figure 8A). By 11 May, only 12 days later, white bass ovaries were completely spent, and in an advanced stage of resorption.

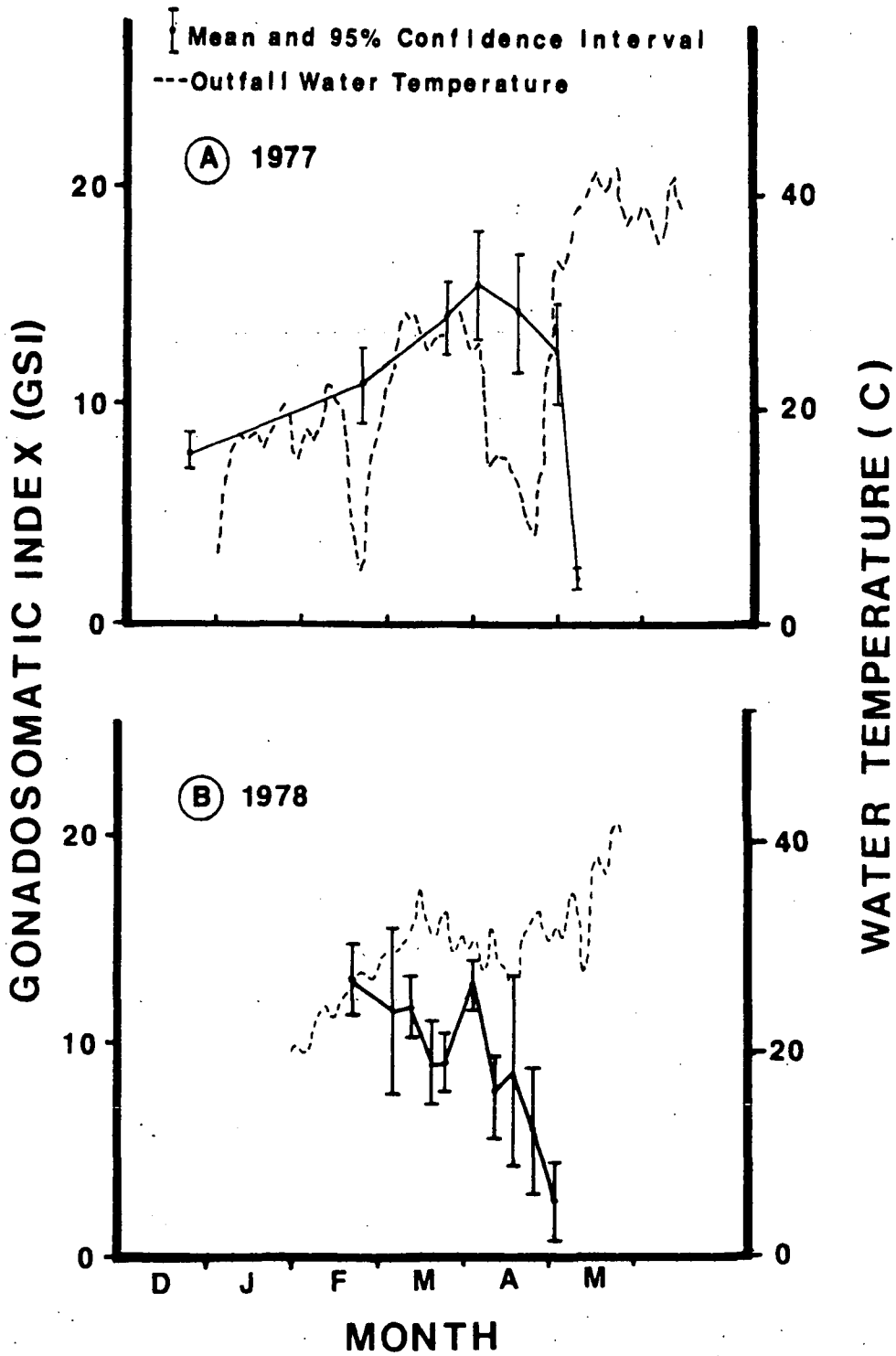


Figure 8. Mean gonadosomatic index (GSI) of female white bass during the spring of 1977 and 1978.

During the spring of 1978 a decline of female white bass GSI began at least 36 days earlier and lasted 28 days longer than during 1977. Mean GSI of female white bass decline from 13.1 on 25 February to 2.4 on 3 May 1978 (Figure 8B). Mean GSI of male white bass also declined from 4.7 on 15 March to 0.5 on 3 May 1978.

The GSI of black crappie during the spring of 1977 increased and declined similar to the GSI of white bass in 1977. Male black crappie mean GSI was highest on 16 April and declined to a low on 11 May after resumption of plant operation. Mean GSI of female black crappie continued to increase during April shutdown to 6.4 and then declined sharply to 3.9 after the power plant resumed operation (Figure 9A). The decline of female mean GSI coincided with a rise in lake water temperatures when the generating plant returned to operation 1 May. The resulting decrease in GSI accounted for only 38% loss of mean ovary weight while most of the remaining ovarian weight was resorbed. Ovaries of most black crappies contained atretic ova and yolk material in which ova were not readily discernable. Between 29 April and 11 May male black crappies lost most of the melanistic color pattern typical of breeding adult male crappies.

The decline of mean GSI of female black crappie in 1978 began 30 days earlier in the spring and lasted 25 days longer than in 1977. Mean GSI of female black crappie was highest on 28 March at 8.2 and subsequently declined to 2.2 on 3 May 1978 (Figure 9B). Mean GSI of male black crappie was highest on 1 April 1978 at 0.98 and lowest at 0.42 on 3 May 1978.

Spatial Patterns of Reproduction

Shutdown and resumption of power plant operation did not significantly affect white bass distribution. The mode of distribution at 3.8 km from the intake accounted for 85% of the total catch prior to the shutdown (Figure 10A), 58% of the total during the shutdown (Figure 10B), and 43% of the total after shutdown (Figure 10C). The mean CPE at stations sampled during shutdown and after resumption of plant operation was not significantly different using the Kolmorgorov-Smironov two sample frequency test ($p > 0.05$). White bass did not aggregate at spring or summer final preferenda temperatures (Reutter and Herdendorf 1974), but remained most abundant 3.8 km from the intake (Figure 10). The distribution of sexually mature white bass was similar during the spring of 1978, with a mode 3.8 km from the intake and fewer fish near the intake and outfall.

Black crappie distributions responded to water temperature changes caused by power plant shutdown and the return of the plant to operation. Prior to the shutdown black crappie aggregated in warmer water 6 km from the power plant intake ($r^2 = 0.34$, $p < 0.05$, Figure 11A). During the 3-week power plant shutdown the aggregation of black crappie dispersed under ambient water temperature conditions. A regression of number of black crappie caught during the shutdown on station location did not have a slope significantly different from zero ($r^2 = 0.003$, $p > 0.05$, Figure 11B). The return of the thermal input into Lake Columbia on 1 May 1977 following a 3-

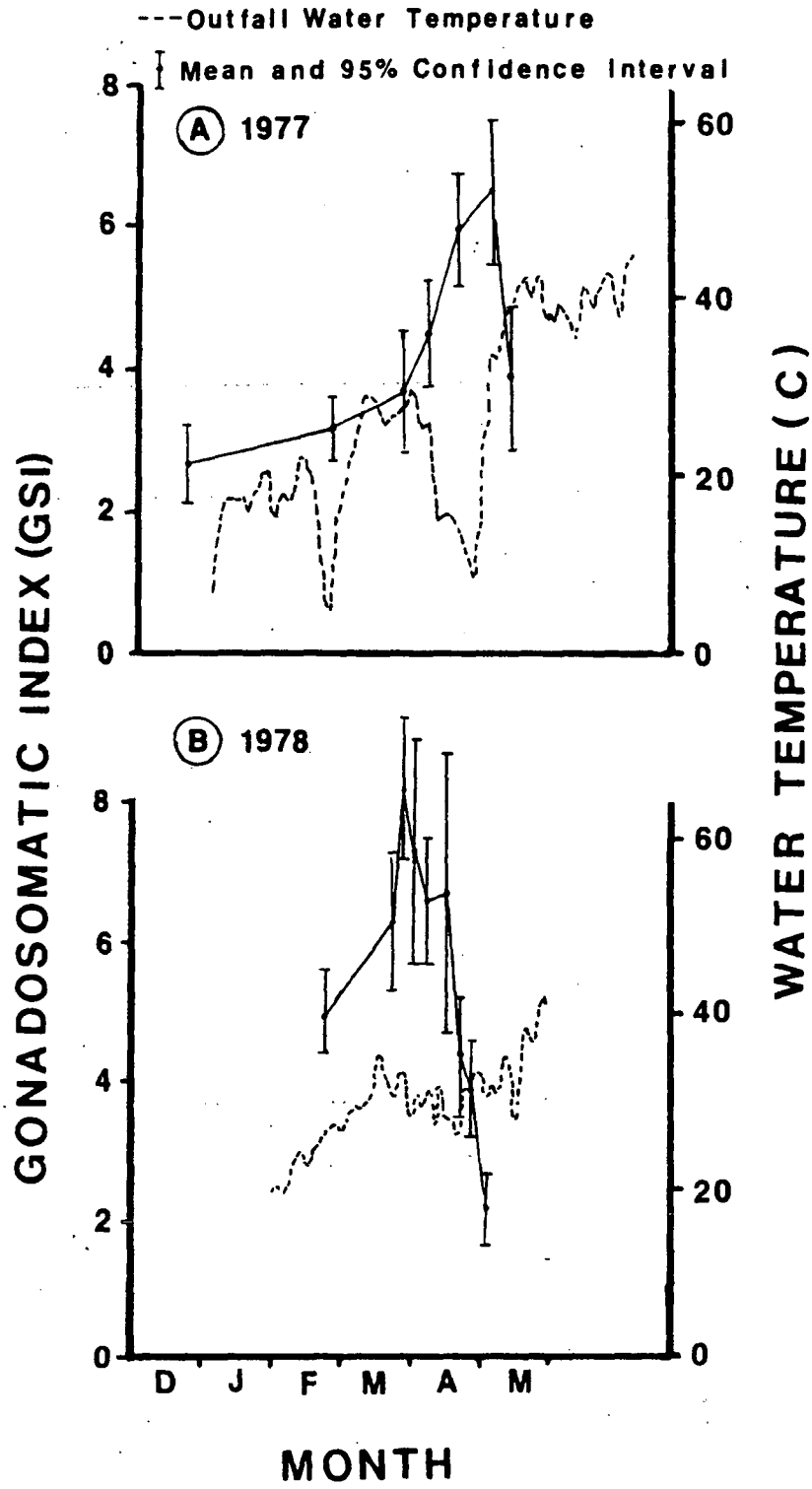


Figure 9. Mean gonadosomatic index (GSI) of female black crappie during the springs of 1977 and 1978.

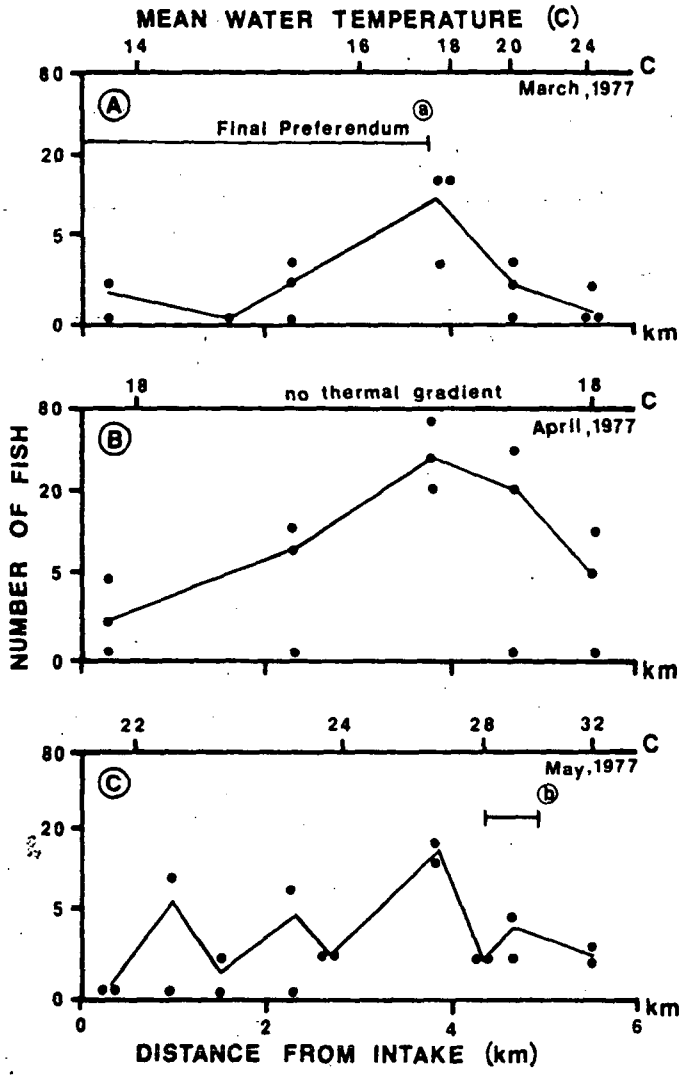


Figure 10. White bass distribution during presence and absence of thermal gradient during the spring of 1977. Final temperature preferenda for spring (a) and summer (b) are from Reutter and Herdendorf (1974).

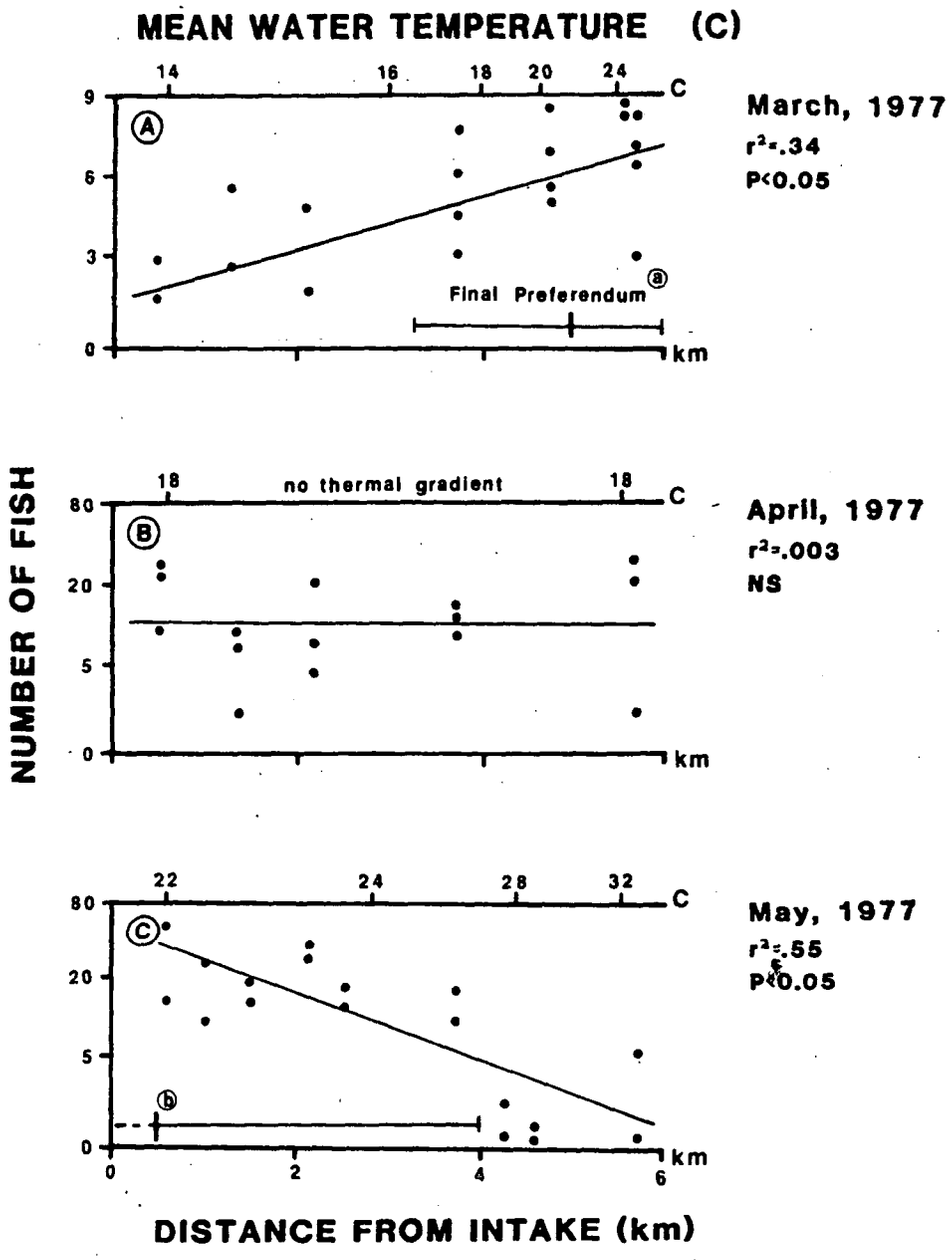


Figure 11. Black crappie distribution during presence and absence of thermal gradient during the spring of 1977. Final temperature (± 1 standard deviation) preferenda for spring (a) and summer (b) are from Reutter and Herdendorf (1974).

week power plant shutdown resulted in a rise of water temperatures and the spatial redistribution of spawning black crappie. As indicated by the negative slope of the regression, fish were more abundant near the intake at cool water temperatures after the shutdown ($r^2 = 0.55$, $p < 0.05$, Figure 11C). Black crappie were more abundant during March at water temperatures included in the spring final preferendum ± 1 SD and during April at summer final preferendum ± 1 SD.

In constrast to the 1977 distribution of black crappie the 1978 distribution had a single mode with little change throughout the reproductive period. The mode of black crappie remained 2.5 to 3.0 km from the intake.

The 1977 movement of sexually mature black crappie toward cooler temperatures coincides with a rapid increase in temperature, decrease in GSI, and decline in available spawning area. Available spawning area was identified as lake surface area with water temperatures ranging from 14.4 to 20.0 C. Black crappie are expected to spawn at these temperatures (Goodson 1966; Schneberger 1972). The surface area of the lake with water temperatures suitable for spawning declined precipitously after the resumption of power plant operation (Figure 12A). During 1978 when thermal input was not interrupted, the percentage of area within expected spawning temperature fluctuated near 50% for 20 days and then declined as seasonal temperatures increased (Figure 12B).

The precipitous decline of available spawning area during 1977 resulted because water temperatures rose rapidly above expected spawning temperatures (Figure 13). The rising water temperatures and declining available spawning area ultimately resulted in exposure of the black crappie population to temperatures above expected spawning temperatures. The thermal exposure of a black crappie population distributed as described are shown in Table 1. Thermal exposure during 9 to 13 May 1977--9 days after the resumption of thermal input--had median and interquartile limits (25%, median, 75%) of 24.8, 25.2, and 26.0 C, respectively. These temperatures are substantially above the range of expected spawning temperatures of 14.4 to 20.0 C. Despite the movement of black crappie into cooler water in response to increased thermal input, interquartile limits of thermal exposure exceeded the range of expected spawning temperatures.

Gamete Viability

Relatively high thermal exposure of black crappie before and during 1978 spawning (Table 1) did not result in reduced gamete viability when tested by artificial fertilization. Of the 5,746 black crappie embryos incubated to test gamete viability, 74% reached the near-hatch stage. A check of sperm viability in water under a microscope indicated > 90% of sperm were highly mobile. The percent hatch in each of 10 incubating chambers did not deviate significantly ($p < 0.05$) from random when tested using a one sample runs test (Siegel 1956). Much of the embryo mortality could be attributed to fungal growth among the large number of embryos

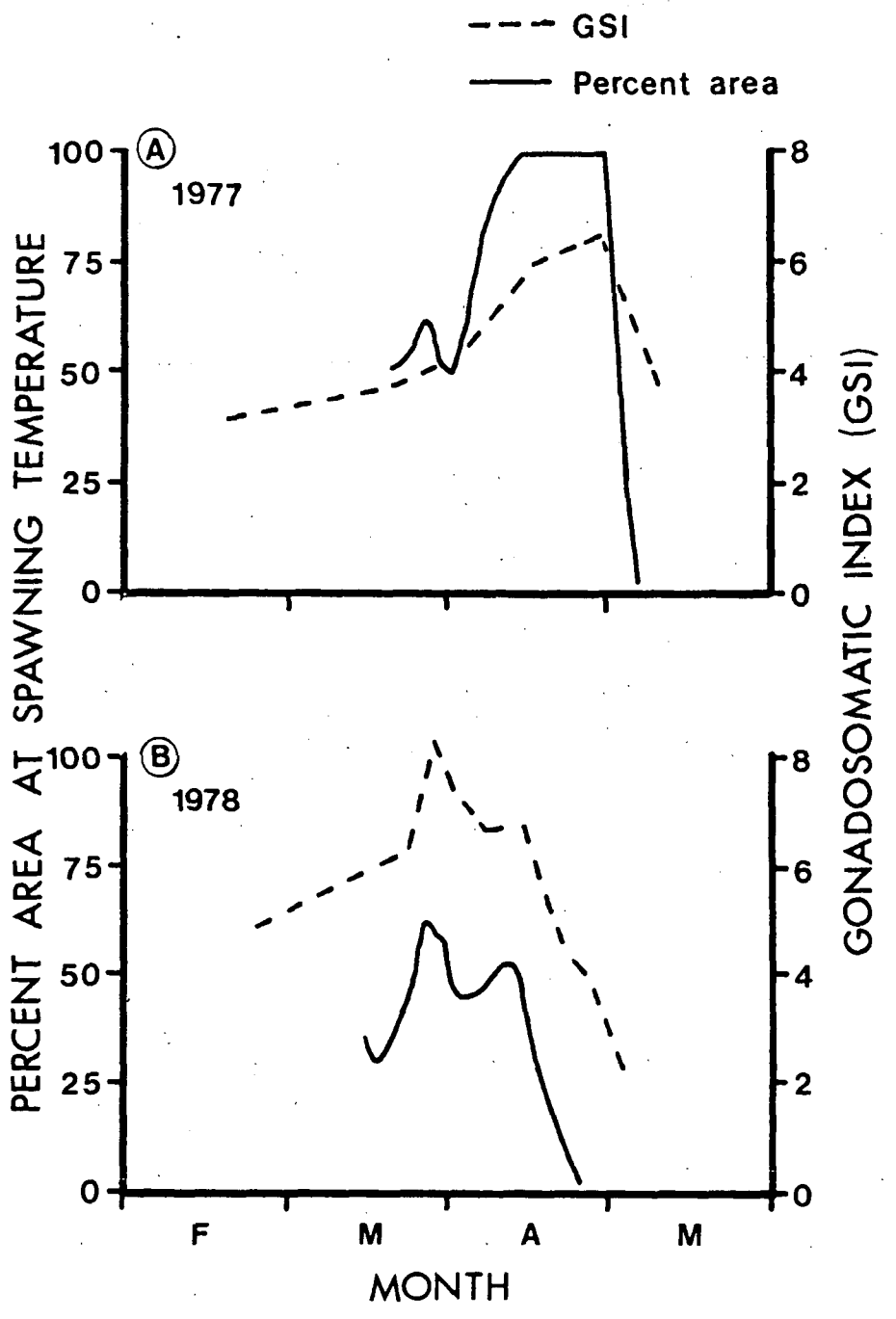


Figure 12. Mean gonadosomatic index (GSI) of female black crappie during the springs of 1977 and 1978 and the percent of surface area of Lake Columbia with water temperatures in the range of expected spawning temperatures of black crappie (14.4 to 20.0 C).

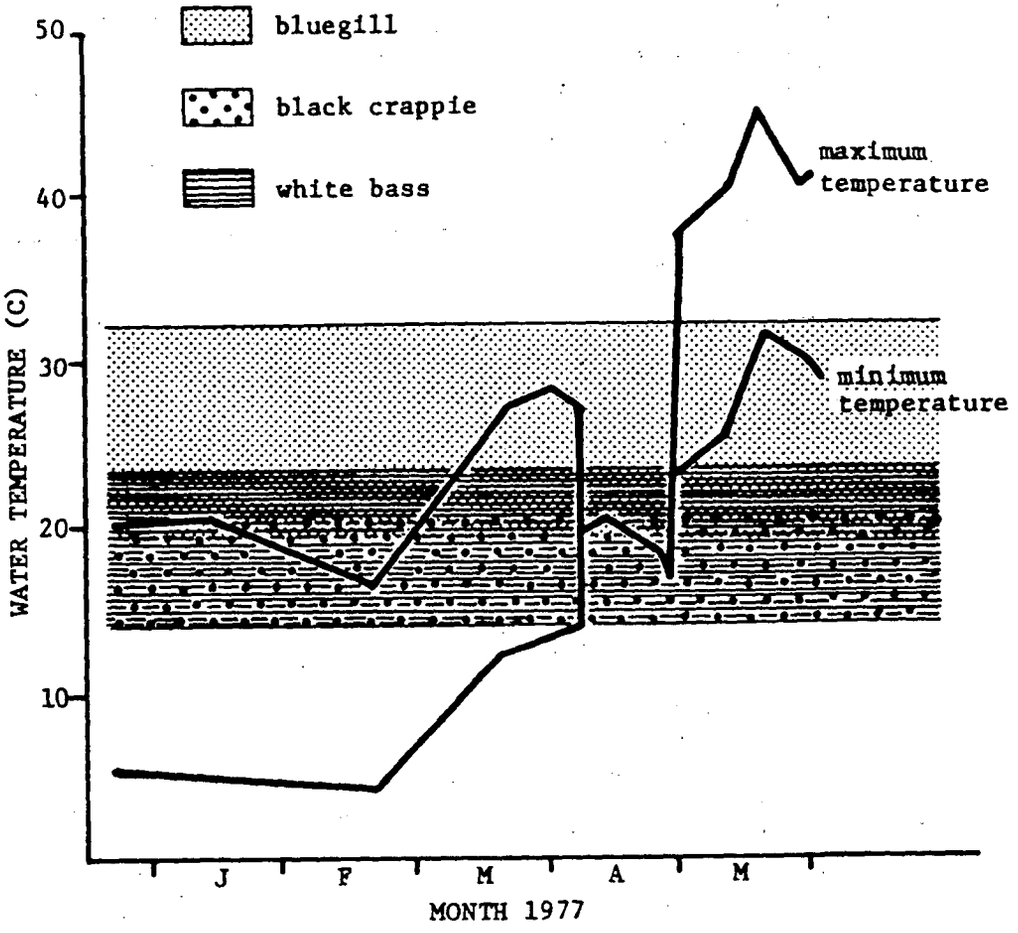


Figure 13. Minimum and maximum water temperatures in Lake Columbia during the spring of 1977 and expected spawning temperatures of selected species.

incubated in a confined system such as that used. A portion of the embryoes were allowed to hatch. Swim-up fry developed that did not appear deformed.

TABLE 1. EXPECTED SPAWNING TEMPERATURES BASED ON VALUES IN LITERATURE AND OBSERVED SPAWNING TEMPERATURES FOR BLACK CRAPPIE IN LAKE COLUMBIA

Temperature (C)	Reference/Date
Expected (Range)	
17.8 --- 20.0	Schneberger (1972)
14.4 --- 17.8	Goodson (1966)
Observed (25% interquartile, median, 75% interquartile) (1977)	
14.9-18.0-21.6	Before shutdown (19 March to 8 April)
20.6-21.0-21.8	After shutdown (3 to 8 May)
24.8-25.2-26.0	After shutdown (9 to 13 May)
Observed (25% interquartile, median, 75% interquartile) (1978)	
19.8-21.1-23.0	Before spawning (13 to 30 May)
18.6-19.8-21.5	During spawning (31 March to 16 April)
22.6-23.8-25.3	After spawning (17 April to 3 May)

DISCUSSION

Spatial limitations were imposed by the heterothermal environment of the cooling lake on the spawning distribution of black crappie, but the response of white bass was not as well defined. The observed aggregation during spawning of black crappie at median temperatures of 21.0 and 19.8 C during 1977 and 1978 (Table 1), respectively, was near the spring final preferendum (Figure 11) of 21.0 C (Reutter and Herdendorf 1974). The aggregation at a spring final preferendum that approximates optimum temperatures for reproduction (17.8 to 20 C) (Schneberger 1972) would be a reproductive advantage. However, in the cooling lake a subsequent rise in water temperature stimulated spawning, reduced available spawning area, and induced aggregation of black crappie at coolest available water temperatures.

The observed distribution of black crappie before spawning in 1977 and early in the spawning season of 1978 resulted in an estimated thermal exposure at the upper limits of expected spawning temperatures. Spawning was initiated at higher temperatures than expected based on literature values. Yellow perch held at elevated thermal regimes in the laboratory initiate spawning earlier and at higher temperatures (Hokanson 1977). The slightly higher spawning temperatures observed may be the stimulus needed to overcome the inhibiting effects of slighly shorter photoperiods of early

spring and an elevated thermal exposure. Spawning at low temperatures can be inhibited by insufficient gonadotropin levels (Hoar 1969). Perhaps a similar inhibition due to low levels of gonadotropin may occur as a result of an elevated thermal exposure. Plasma levels of gonadotropin and spermatogenesis in the goldfish (*Carassuis auratus*) are maximal at 17 to 24 C and inhibited at water temperatures near 30 C (Gillet et al. 1977).

Gonadotrophic hormones are associated with the production of gonadal sex steroids which are involved in the development of secondary sexual characteristics (DeVlaming 1974). Melanistic pigmentation, a secondary sexual characteristic of male black crappies, was well developed during spawning. The rapid loss of melanistic pigmentation observed in male black crappie at elevated temperatures was analogous to the reduced male secondary sex characteristics of male fathead minnows held at an elevated water temperature of 30 C (Brungs 1971).

Female black crappies exhibited resorption of ova during 1977, indicating that thermal limits of spawning were exceeded. The relative importance of spawning and resorption of white bass ovaries could not be evaluated for white bass because ovaries changed from partially spent to an advanced stage of resorption within 12 days. Resorption of residual ova amounted to about 50% of total fecundity of white bass in a thermally unaltered reservoir (Ruelle 1977). Shrode and Gerking (1977) found the thermal limits of oogenesis of the eurytherm *Cyprinodon ns. nevadenis*, a desert pupfish, were even narrower than the limits for successful hatching of eggs exposed to temperature stress after spawning. The observed physiological changes of black crappie, and white bass were similar to those described for golden shiner (*Notemigonus crysoleucas*) exposed to elevated temperatures under laboratory conditions (DeVlaming and Paquette 1977). Female golden shiner had atretic oocytes and significantly smaller GSI after 11 days of continuous exposure to 27 C. Partial loss of gonad weight and resorption of remaining ova in female black crappie were similar to observations by Kaya (1977) for brown trout (*Salmo trutta*) inhabiting a thermally elevated environment.

Expected spawning temperatures of black crappie were exceeded by minimum water temperatures during 1977, but spawning temperatures of more thermally tolerant bluegill were not exceeded (Figure 13). A review of percid temperature requirements (Brungs and Jones 1977, Hokanson 1977) revealed that the range of expected spawning temperatures in percids corresponded closely with embryo tolerance limits. If a similar relationship exists for black crappie, embryos incubating at temperatures above expected spawning temperatures would be above upper tolerance limits. Developing embryos of bluegill, a species with successful reproduction in the cooling lake, would be more temperature tolerant based on their broad range of spawning temperatures (Figure 13). Large temperature increases induced spawning and at the same time reduced the area having temperatures below expected upper lethal temperatures of embryo and larval stages.

Upon hatching, fry metabolize the yolk sac and subsequently become sufficiently mobile to move into the water column and limnetic zone (Faber 1967, Werner 1969, Amundrud et al. 1974). Grunion (*Leuresthes tenuis*)

larvae were not able to metabolize the yolk at 27 C. Ehrlich and Muszynski (1981) suggested that this was due to breakdown of proteolytic enzymes. Such ultimately lethal effects of an elevated thermal history experienced by larvae may be more important than directly lethal effects of high temperatures (Rosenthal and Alderice 1976).

Temporal patterns of reproduction were modified by thermal input to the cooling lake. Spawning of black crappie occurred approximately 1 month earlier in 1978 than in 1977. In 1978, the decline of GSI and presence of black crappie fry indicated spawning was initiated by the end of March, 30 days earlier than in 1977. In a heated reservoir black crappie fry were captured 44 days earlier under conditions of themal input (Ruelle et al. 1977) than under ambient conditions. The GSI of white bass was at a maximum 36 days earlier in 1978 than in 1977. June (1978) found little year-to-year variability between peak spawning dates of 17 species of fish in Lake Oahe, South Dakota, a thermally unaltered reservoir. The mean calendar day of peak white bass spawning activity in Lake Oahe, South Dakota, had a standard deviation of only 4.1 days from 1964 to 1971 (June 1978). Earlier spawning in Lake Columbia in 1978 can be attributed to a further elevated thermal regime due to the operation of the Columbia II generating unit which began in February 1978 (Figure 3).

Following resumption of power plant operation in the spring of 1977 there was rapid warming. This resulted in an unusually abbreviated duration of spawning activity for white bass because this species may not be adapted to the warmer water temperatures. The rapid warming restricted white bass spawning to < 11 days. Mean duration of white bass spawning has been reported as 25 to 28 days (Horrall 1961, Ruelle 1977). The eurythermal bluegill, which spawns intermittently during early spring and summer (Breder and Rosen 1966), showed continued recruitment during the spring of 1977. Fox (1978) found that the English bullhead (*Cottus gobio* L.) spawned only once per year in northern England and intermittently in the longer spawning season available in southern England. In this case, the adaptive advantages of temporally intermittent and one-time reproductive strategies hypothesized by Pianka (1976, 1978) may be extended to spring spawning strategies. Although there are advantages to both strategies, the extreme abbreviation of spawning season for a species that is adapted to spawn for a mean duration of 25 to 28 days might considerably reduce the chances of having a number of individually successful cohorts.

The increase in water temperatures during 1977 induced spawning in many species and temporally compressed the successional appearance of larval fish. Spawning and subsequent dispersal of larval fish into the limnetic zone results in the successional appearance of predator and prey species (Amundrud et al. 1974). A shortened spawning period, induced by sharply increasing water temperature, disrupted seasonal succession and may modify predator-prey relationships and change competitive interactions.

In summary, a rapid rise in water temperatures following a 3-week power plant shutdown during 1977 stimulated spawning, reduced available spawning area, and induced aggregation of black crappie at coolest available water temperatures. Elevated water temperatures subsequently induced resorption

of black crappie ova, loss of secondary sexual characteristics, and were probably near upper lethal temperatures of embryo and larval stages. A temporally shortened spawning season was associated with a rapid rise in water temperatures, while additional thermal input by the Columbia II generating unit caused spawning to occur 30 days earlier in the spring.

SECTION 5

DISTRIBUTION OF LARVAL FISHES

INTRODUCTION

Larvae of many spring spawning fishes initially disperse into limnetic waters (Faber 1967, Werner 1969, Netsch et al. 1971, Amundrud et al. 1974, Kelso and Ward 1977) and later aggregate as juveniles in littoral areas which have higher water temperatures. Juvenile fishes exhibit thermoregulatory behavior in the laboratory (Cherry et al. 1977) and after reviewing temperature preference data of fish Coutant (1977) concluded that laboratory and field results were reasonably consistent. During the development of thermoregulatory behavior, increasing mobility probably facilitates the ability of individual juveniles to thermoregulate. However, little is known about the thermal responsiveness of pelagic larvae and early juveniles of fish when distributed in the limnetic zone. Therefore, an objective of this study was to describe distributional responses of pelagic larvae and juvenile fish to changes in the thermal gradient. Certain abiotic factors--i.e., temperature--are correlated with year-class strength of some fish populations (Kramer and Smith 1962, Koonce et al. 1977).

Larval white bass and black crappie were not captured in sufficient numbers to interpret distribution patterns. Gizzard shad and bluegill, two species whose populations increased in the cooling lake, were studied to determine how the larval forms respond to the dynamic heterothermal environment of the cooling lake. Gizzard shad are surface spawners, their ova settle to rock and gravel substrates, while bluegill are a nest guarding species that utilize sand and gravel substrates (Balon 1975a). The larvae of both species have pelagic behavior soon after hatching.

Additional observations were designed to investigate factors affecting the relative abundance of larval fish. The time of capture, depth of capture, station location, and diel movement patterns were examined.

METHODS

Distribution of Larval Fishes

Abundances of larvae and early juveniles in Lake Columbia were used to measure reproductive success of fishes in the cooling lake. The limnetic area of the lake was sampled from May to July 1977 using paired Miller

samplers (Miller 1961) towed from the ends of a 6.6-m boom mounted across a 6.1-m flat-bottom aluminum boat. Samplers were towed along transects marked by lights. Samplers were equippped with collecting cups and conical nets 90 cm in length with 0.25, 0.59, or 0.96-mm aperature mesh nitrex, depending on the date and the size of fish. Miller samplers were assumed to filter all water encountered (Miller 1961, Noble 1970).

Tows to assess horizontal distribution patterns were made at a depth of 0.5 m between 1900 and 2400 h central standard time (CST). Towing began approximately 0.5 h after sunset in 1977 and 1 h after sunset in 1978. Sampling transects in 1977 were 1.0 km long for sampling dates between 12 and 20 May and 2.0 km thereafter. All transects completed in 1978 were 1.0 km in length.

Clear plexiglass traps equipped with lights, a modification from previous designs (Breder 1960, Casselman and Harvey 1973), were used to collect larval fish in 1977. The traps were 30 x 30 x 15 cm with two funnels opening to an area of 30 x 27.7 cm. The traps had a 0.1 amp light bulb in a 270 ml jar mounted on the trap with electrical wiring to a 6 volt dry cell on a styrofoam float. The traps were set at 30 cm depth for 2 h between 2100 and 2300 h.

Larval and juvenile fish were preserved in the field in 10% formalin and later placed in 5% buffered formalin. In the laboratory, specimens were counted and identified under a binocular dissecting scope according to larval keys and descriptions (May and Gassaway 1967, Siefert 1969, Meyer 1970, Hogue et al. 1976). Balon's (1975b) developmental terminology was used. Random subsamples of not more than 60 specimens per sample in 1977 and not more than 30 specimens per sample in 1978 were measured for total length. Larvae $\leq$ 15 mm were measured to the nearest 0.1 mm with an ocular micrometer and those > 15 mm were measured to the nearest mm on metric graph paper.

Horizontal distributions of *Lepomis* sp. and gizzard shad are reported with respective mean water temperature at capture and by location of capture in km from outfall. Logarithmic transformations of data were performed to normalize variances (Cassie 1971). Least squares linear regression and second order polynomial fit of number of fish on station location (km) and temperature were used to describe horizontal distribution patterns. Abundance of larval and early juvenile fish per m^3 on different dates illustrates the relative abundance over time. Water temperatures at which fish were captured were compared to all water temperatures sampled to determine whether fish aggregated in respect to temperature on each sample date. Median and interquartile ranges of the temperature at which fish were captured are compared to the median, interquartile range and range of water temperatures where sampling took place on the sample date. Median total length of larval and early juvenile fish between two groups of one or more stations were compared using the Mann-Whitney U test (Sokal and Rohlf 1969).

Factors Affecting Relative Abundance

Factorial designs were used to analyze the diel vertical movements of larval and early juvenile fish. On 18 to 20 May 2 x 4 x 4 factorial design observations were conducted with two depths, four stations, and four times of day during a 24-h sampling period to determine the importance of these factors. Samples were collected at 0.5 and 1.2 m depth using methods described earlier. Sampling times were noon, 1200 h; evening, 2100 h; midnight, 2400 h; and morning, 0500 h (CST). Similar factorial observations with two depths, three stations, and three times of day were conducted on 29 to 30 May to examine the behavior of larger early juvenile fish. Gizzard shad catches collected at various strata were tested for heterogeneity using the G-test (Sokal and Rohlf 1969).

Gizzard shad catches were examined to determine whether 0.5-m deep samples collected 0.5 h after sunset were adequate to describe the horizontal distribution. Evening catches at 0.5 m depth were compared to total number caught at 0.5 and 1.2 m at each station during the 24-h sampling period. Comparisons were made to determine whether different conclusions could be drawn with the additional information.

Effects of water temperature on diel vertical movements were examined using a factorial design with 2 days, three depths, and four time periods. Samples were collected between 1.5 and 2.0 km from the outfall on two consecutive dates with different water temperatures. Samples were collected with Miller samplers at 0.5, 1.0, and 1.5-m depths. Midpoints of sampling times were 1700, 1900, 2100, and 2400 h CST. Results of the factorial design were tested for heterogeneity using the G-test (Sokal and Rohlf 1969). Two regression lines fitted to subsets of the data were compared according to Snedecor and Cochran (1967).

RESULTS

Distribution of Larval Fishes

Species abundance was greater in 1978 than in 1977 (Table 2). The mean number of taxa per sample date in 1978 was 5.4 and 2.1 in 1977. The 1977 larval fish catches were dominated by *Lepomis* sp., accounting for 24%, and gizzard shad, accounting for 76% of the total catch (Table 2). The number of larval fish/m^3 declined throughout the 1977 sampling period (Figure 14A). Larval fish sampling was initiated within 12 days of the resumption of power plant operation. Resumption of operation induced rapid gonad weight loss in adult black crappie and white bass, but no larval or early juvenile stages of either species were captured. During 1978, larval fish increased to 24.2 larval fish/m^3 by 14 April and then declined (Figure 14B). In 1978 gizzard shad dominated all samples and accounted for 96% of the total catch (Table 2). Although sampling extended from 28 March to 5 June 1978, 97% of the *Morone* sp. captured during 1978 were captured

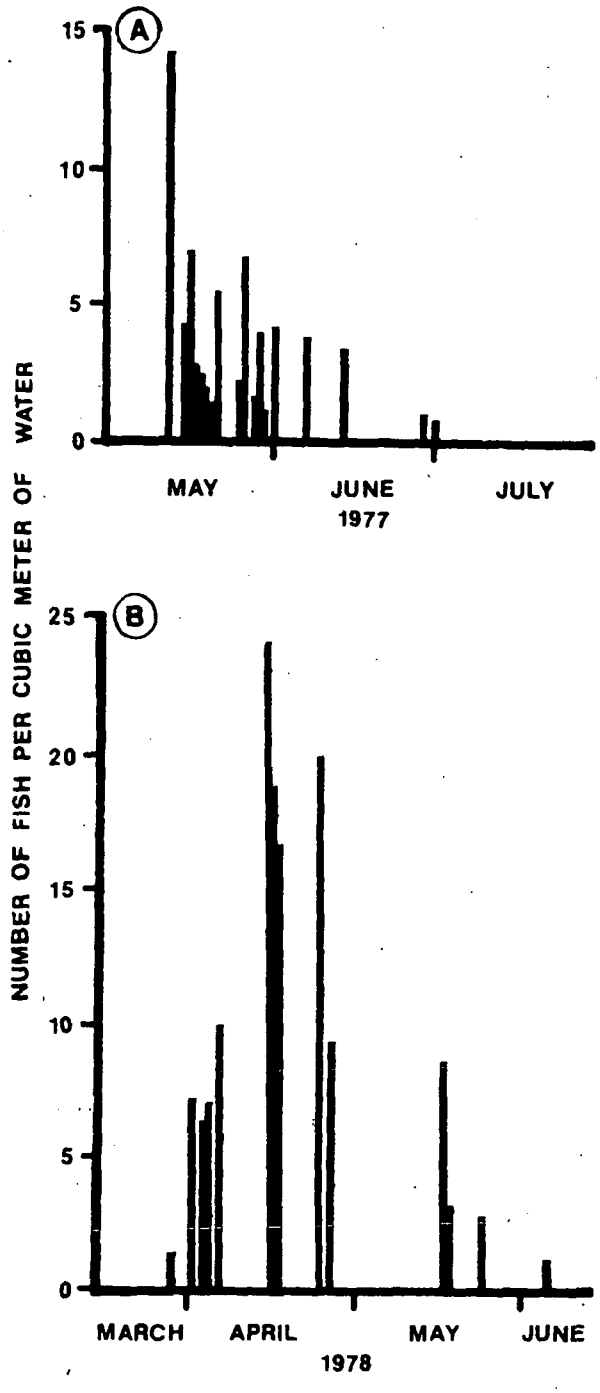


Figure 14. Number of larval and early juvenile fishes per cubic meter of water sampled by Miller sampler during the springs of 1977 and 1978.

between 28 March and 16 April. Eighty-six percent of the black crappie were caught between 4 and 24 April 1978.

TABLE 2. NUMBER OF LARVAL AND JUVENILE FISHES CAUGHT IN LIGHT TRAPS AND MILLER SAMPLERS, 1977-78

Species	Light Trap (1977)	Miller Tow (1977)	Miller Tow (1978)
Morone sp.			119
Lepomis sp.	6,727[a]	1,627	232
Pomoxis sp.		2	160
Micropterus sp.	1		16
D. cepedianum	644	5,246[b]	16,298[c]
I. natalis			1
I. punctatus			3
C. carpio	47		28
N. spilopterus			7
Cyprinidae	11	2	33
Catostomidae	18		18
Atherinidae	1		
Unknown			17

[a]67% captured between 10 and 15 June.
[b]62% captured between 12 and 21 May.
[c]68% captured between 14 and 26 April.

The median water temperature at locations where *Lepomis* sp. and gizzard shad were caught during 1977 was near 30 C. The median temperature of capture for *Lepomis* sp. ranged from 28.1 to 30.9 C during the spring of 1977, while the temperatures during sampling ranged from 24.5 to 40.0 C (Figure 15A). The median temperature of capture of gizzard shad ranged from 29.6 to 31.3 C, while temperatures of effort ranged from 25.1 to 40.2 C (Figure 15B). Median temperature of capture of *Lepomis* sp. and shad during June 1977 was below 30 C. This reflects a lower thermal preference at later stages of development or increased ability to avoid temperatures > 30 C.

Spatial patterns of distribution of juvenile fish changed as ambient temperatures influenced the thermal gradient of the lake. On 25 to 27 May 1977, when the temperature gradient ranged from 29.9 to 42.8 C, *Lepomis* sp. were more abundant 5.0 to 6.0 km from the outfall where the coolest temperatures were available (Figure 16A,B). Under conditions of lower ambient temperatures on 10 June, when the gradient ranged from 24.6 to 37.5 C, the mode of distribution moved to 1.5 to 2.0 km from the outfall (Figure 16C). Location of the mode coincided with water temperatures between 29 and 31 C (Figure 16D). A mid-June rise in air temperatures resulted in lake

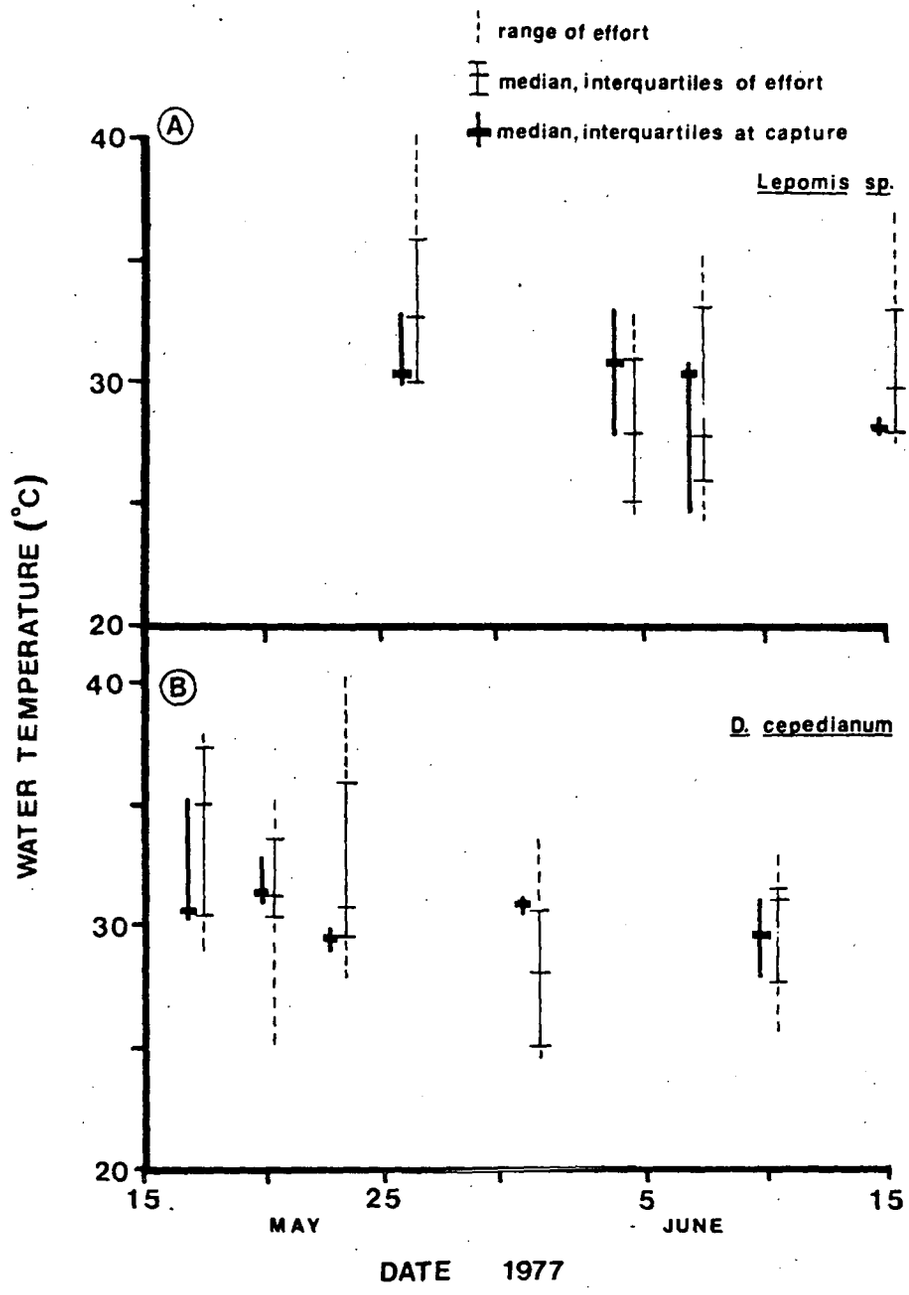


Figure 15. Expected median and interquartile limits of water temperature based on distribution of sampling effort and the observed temperature at location of capture of larval and early juvenile periods of *Lepomis* sp. and gizzard shad during 1977.

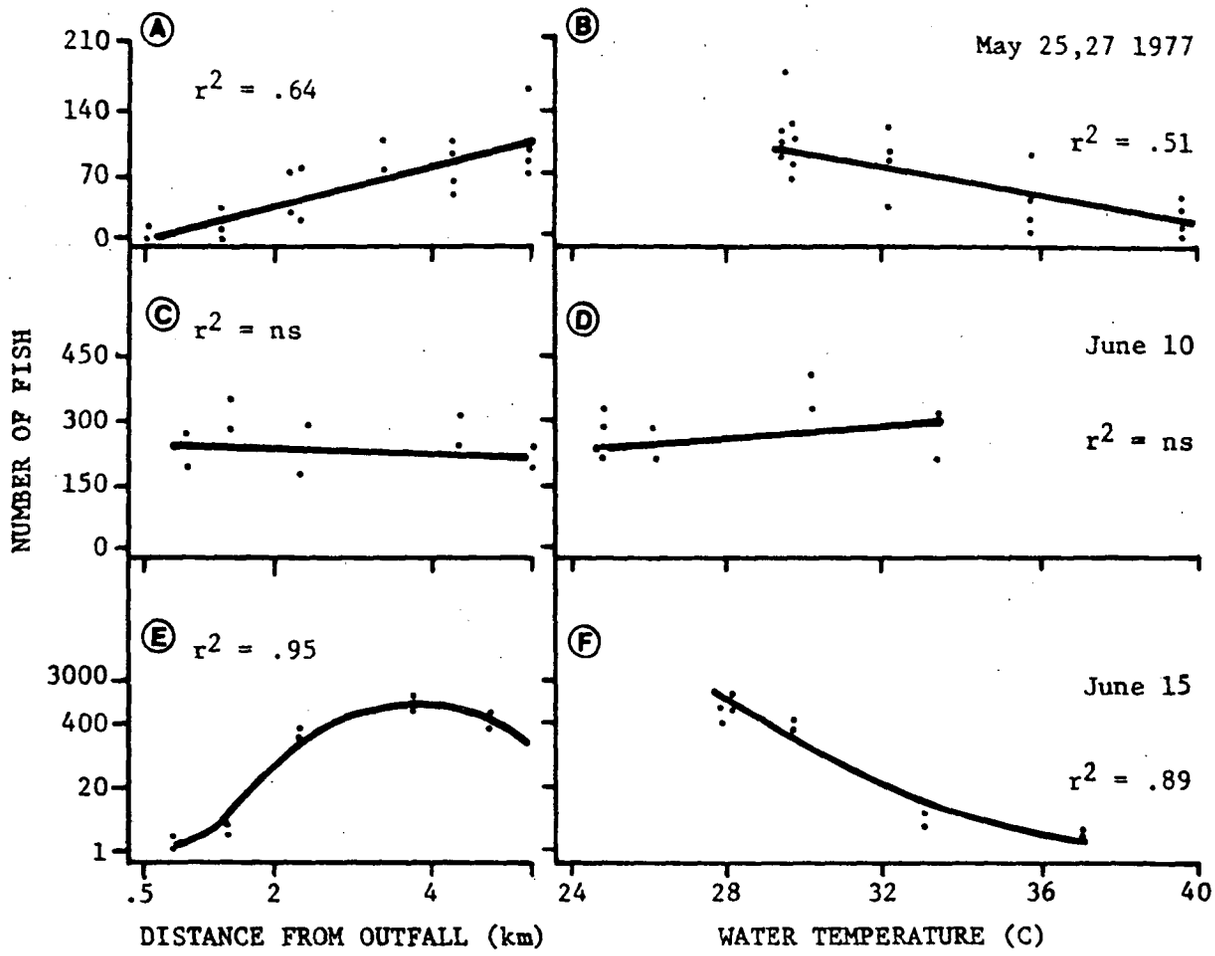


Figure 16. Abundance and temperature at location of capture in light traps for larval and early juvenile *Lepomis* sp. during the spring of 1977.

temperatures of 27.4 to 40.6 C and a concurrent reduction of juvenile *Lepomis* sp. abundance in areas near the outfall (Figure 16E). The mode then returned to an area at a greater distance from the outfall (3.0 to 5.0 km) with 28.1 C water temperature (Figure 16F).

Changing distribution patterns may reflect increasing mobility at more advanced stages of development. Median length of *Lepomis* sp. was greater at warm stations near the outfall for 10 of 11 dates when significant differences existed (Mann-Whitney U test, $p < 0.05$). The one exception was 27 May 1977 when recruitment of smaller larvae to catches occurred. Median length of *Lepomis* sp. was greater at warm stations near the outfall for 10 of 11 dates when significant differences existed (Mann-Whitney U Test, $p < 0.05$). The one exception was May 27, 1977 when recruitment of smaller larvae to catches occurred. Median length of *Lepomis* sp. at warm stations significantly decreased from 5.6 mm on 18 May to 4.8 mm on 27 May (Mann-Whitney U test, $p < 0.05$). During periods of recruitment to light traps, significantly greater abundance (Figure 16A) and larger median lengths at greater distance from the outfall (Mann-Whitney U test, $p < 0.05$) indicate an initial down-current drift. Subsequent changes in modes of abundance and larger median length near the outfall indicate movement by *Lepomis* sp. in the pelagic stage.

Early juvenile gizzard shad responded to temperature changes in the cooling lake environment by changing relative abundance. The mode of relative abundance of gizzard shad caught in Miller samplers was located further from the outfall on 17 and 18 May (Figure 17A, B) and then shifted to the outfall on 29 May. The shift of abundance mode to warm stations near the outfall on 29 May (Figure 17C, D) coincided with a change from significantly larger shad at cool stations on 19 May to significantly larger shad near the outfall on 29 May (Mann-Whitney U test; $p < 0.01$) (Figure 18). On 19 May 46% of the total shad catch was $\leq$ 10 mm length, suggesting recent hatching and recruitment to the gear (Figure 18A). On 29 May 96% of the shad catch near the outfall was $\geq$ 30 mm length, while only 29% of the cool station shad catches were $\geq$ 30 mm (Figure 18B). Samples of 7 to 14 June indicated that the mode of abundance of juvenile gizzard shad had returned to stations toward the middle of the lake (Figure 17E). Shad distribution observed during June, similar to that described for *Lepomis* sp. (Figure 16E), was most abundant 2.0 to 4.0 km from the outfall, an area of low surface current velocities (2 to 4 cm/sec) and temperatures of 28 to 31 C (Figure 17F).

The median length of gizzard shad caught in 1978 was greater at down-current stations during the peak reproductive period, suggesting that drift was an important factor in determining distribution patterns of early larval stages. The period of peak reproductive activity occurred between 14 and 16 April 1978 when 68% of the gizzard shad were caught (Table 2). Median length of gizzard shad ranged from 4.8 mm on 4 to 6 April to 5.1 mm on 24 to 26 April, with significantly larger fish at down-current stations for three groups of 32 Miller samples (Mann-Whitney U test, $p < 0.05$). Approximately 1 month after peak reproductive activity, larval gizzard shad had a median length of 5.1 mm with significantly larger fish at warm stations (Mann-Whitney U test, $p < 0.05$). The median length at warm stations was 5.3 mm

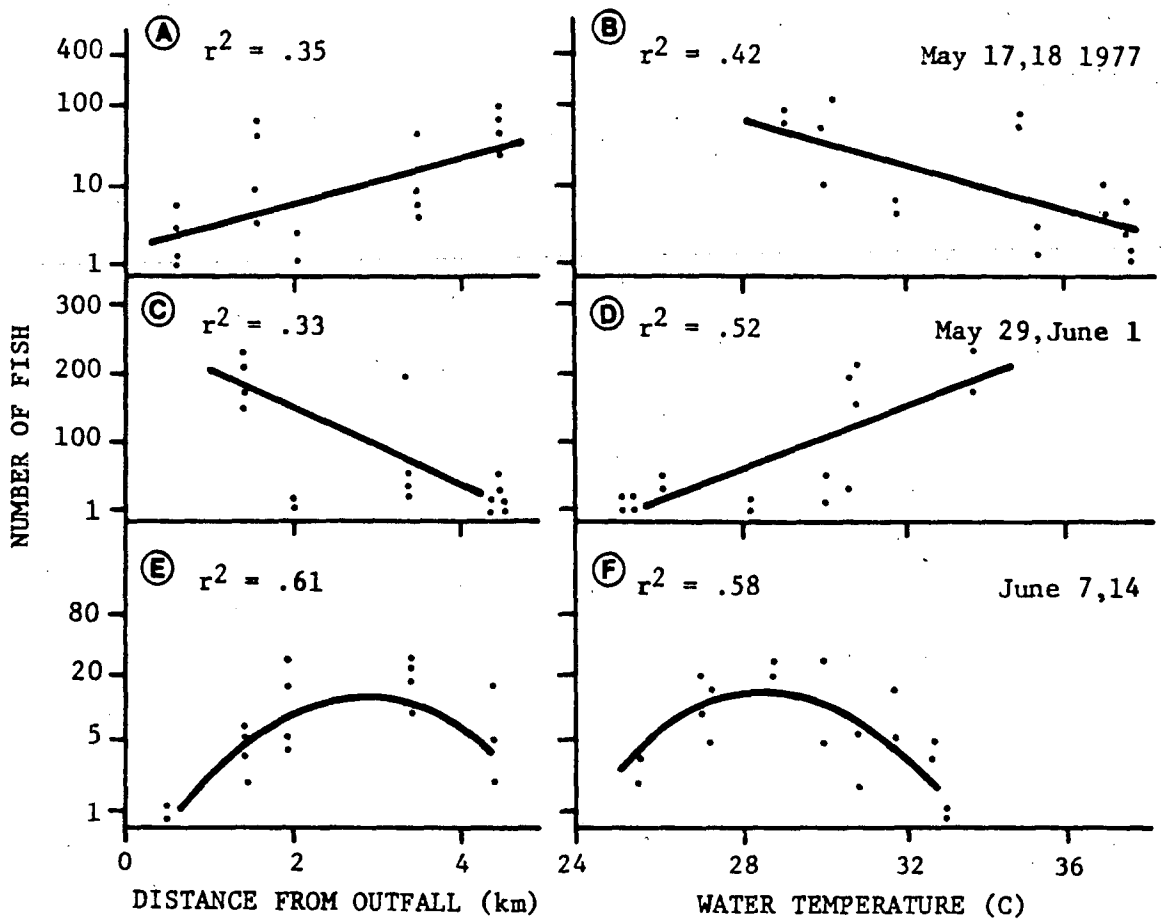


Figure 17. Abundance and temperature at location of capture in Miller samplers for larval and early juvenile gizzard shad during the spring of 1977.

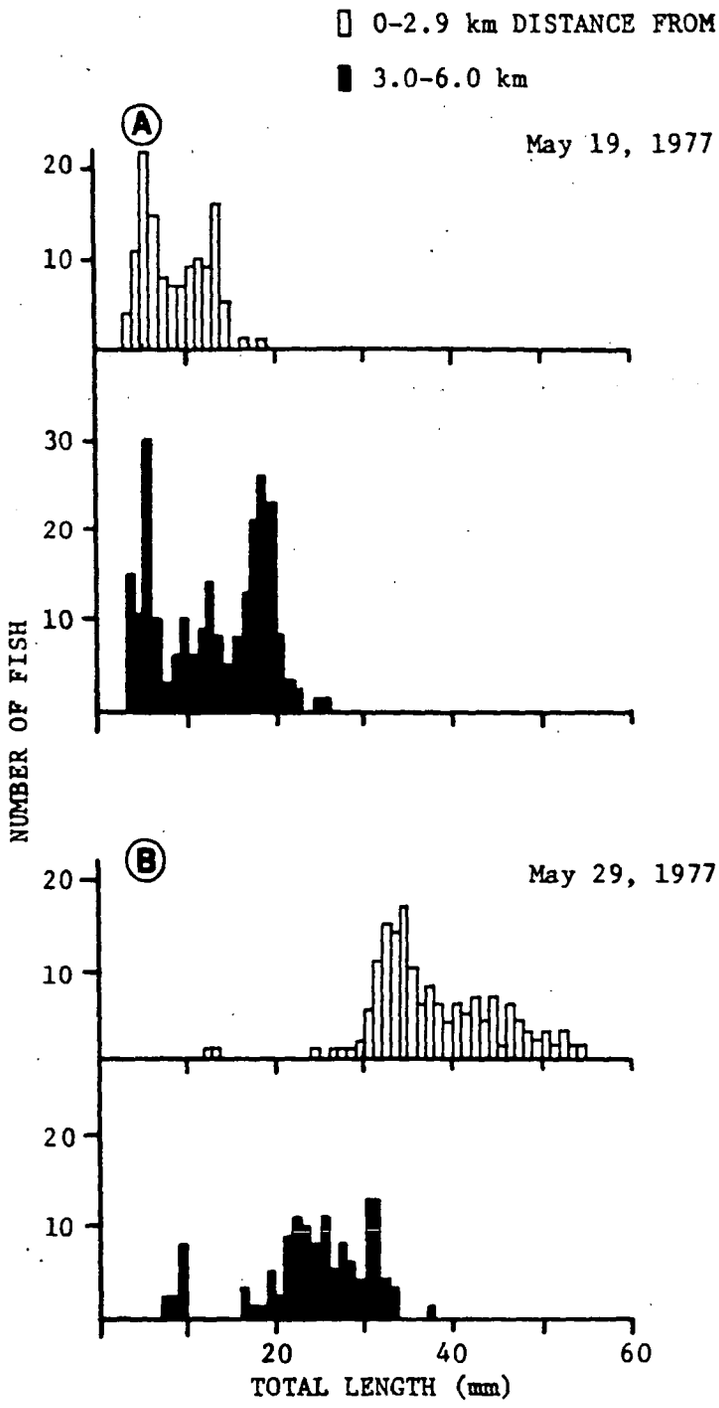


Figure 18. Length frequency of gizzard shad captured at warm stations (0.1 to 2.9 km from outfall) and cool stations (3.0 to 6.0 km from outfall) on 19 and 29 May 1977.

with 20.5% $\geq$ 10 mm. Only 1.9% of the fish caught at cooler down-current stations were $\geq$ 10 mm length.

Factors Affecting Relative Abundance

Several factors influenced the distribution of larvae and early juveniles and therefore the validity of results. Field observations were conducted to test the effects of depth, station, and time of day at which the samples were collected.

The number of gizzard shad caught on 18 to 20 May was not independent of depth, station, or time of day. The observations had highly significant G-test statistics for combinations of depth, station, and time of day ($p < 0.01$, Table 3). The median length of gizzard shad caught on 19 May was 12.0 mm ($N = 358$) for all stations. The time x depth independence term was significant (Table 3), indicating that the abundance of gizzard shad at 0.5 and 1.2 m was not independent of time of sampling. Gizzard shad were more abundant during the evening (2100 h) at 0.5 m depth than at 1.2 m depth (Figure 19A). Seventy-three percent of the gizzard shad caught in the evening were caught at 0.5 m depth. Fourteen percent of the catch at noon were at 0.5 m depth, while the remaining 86% were caught at 1.2 m depth (Figure 19A). The time x station independence term was significant, indicating that abundance at stations changed with time of sampling. Abundance at all stations was low during the noon (1200 h) sample, composing only 10% of the total catch. The lack of independence between depth and station was influenced by the large percentage (30%) of total catch captured

TABLE 3. THE G-STATISTIC VALUES PARTITIONED ACCORDING TO THE HYPOTHESIS TESTED FOR THREE FACTOR DIEL VERTICAL MIGRATION OBSERVATIONS, 18 TO 20 AND 29 TO 30 MAY 1977

Date	Hypothesis tested	df	G	Significance
18 to 20 May 1977	Time x depth independence	3	101.22	**
	Time x station independence	9	8307.98	**
	Depth x station independence	3	135.18	**
	Time x depth x station interaction	9	8001.68	a
	Time x depth x station independence	24	542.10	**
29 to 30 May 1977	Time x depth independence	2	79.80	**
	Time x station independence	4	98.80	**
	Depth x station independence	2	3.60	ns[b]
	Time x depth x station interaction	4	27.60	**
	Time x depth x station independence	12	209.80	**

** $p < 0.01$.
[a]See Sokal and Rolf (1969, p. 607) and Kullback (1959, p. 171).
[b]ns Not significant at $p < 0.05$.

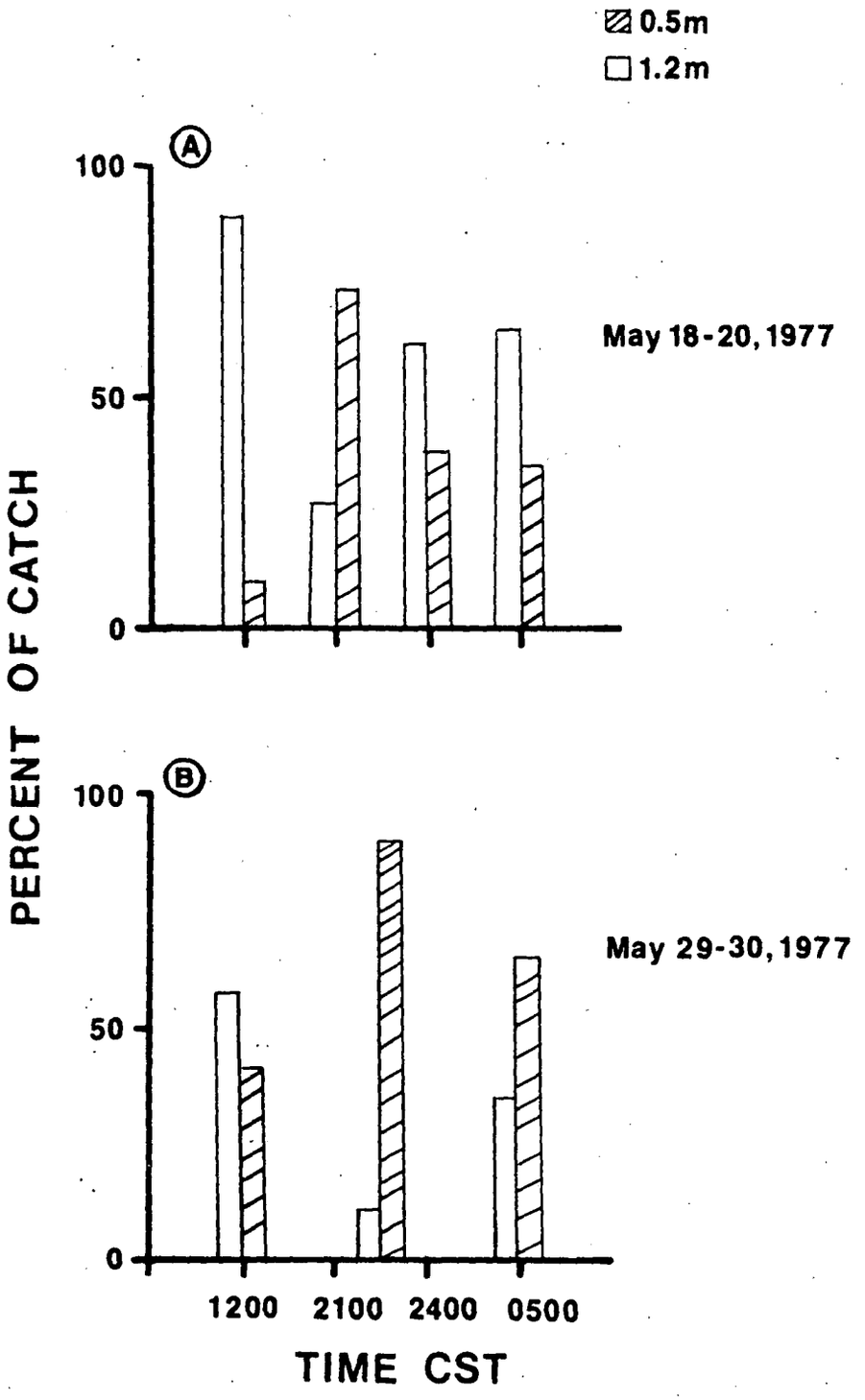


Figure 19. Percent of gizzard shad caught at 0.5 and 1.2 m at different times of day on 18 to 20 and 29 to 30 May 1977.

in 0.5-m depth samples at the station located at the greatest distance from outfall. The significant time x depth x station interaction term indicates that the abundance of gizzard shad at a given depth can be expected to differ with station and the time of day the sample was collected.

Observations with a similar factorial design were conducted on 29 to 30 May to determine if early juvenile stages responded to depth, station, and time factors in the same pattern. The median total length of gizzard shad during the study was 32.0 mm (N = 290). Observations had significant G-values for time x depth, time x station, and the interaction term ($p < 0.01$, Table 3). Eighty-six percent of the total catch occurred during the evening to midnight sampling and 3% were captured during the noon sample. Fish caught at the 0.5-m depth accounted for 91% of the evening to midnight sample (Figure 19B).

To examine the effects of using shad abundance at a depth of 0.5 m as a measure of relative abundance, catches were compared to distribution patterns determined by summation of 0.5 and 1.2-m samples. Evening samples on 18 May 1977 at the 0.5-m depth indicated greater abundance as distance increased from the outfall. A similar pattern of abundance emerged when the percentages of catch collected at 0.5 m depth during the evening were compared to percentages of total catch collected at 0.5 and 1.2 m depth in a 24-h period (Figure 20A). The same conclusion was reached for 29 May after two depths and three time periods were pooled (Figure 20B). Therefore, relative abundance, as determined by 0.5-m deep samples, appeared to adequately describe horizontal distribution.

Although 0.5-m deep samples collected during the evening minimized the effects of diel vertical movements and adequately described horizontal distributions they were not adequate during thermal stratification with elevated surface temperatures. For example, samples collected during the evening of 24 May 1978 (Figure 21A) indicated consistently low abundance near the outfall (Figure 21B). Two 1.5-m depth samples collected near the outfall had a higher abundance (Figure 21B). The 1.5-m samples shown by open circles in Figure 21B taken near the outfall at 30.4 C had catches similar to other samples taken at that temperature (Figure 21C), although the samples were spatially separated by 1 km.

The lower abundance of larval fish observed at the 0.5-m depth at warm stations was partially due to reduced abundance of larval gizzard shad completing upward vertical migration. A total of 2,400 larval gizzard shad and 28 other specimens, including *Pomoxis* sp., *Micropterus* sp., Cyrinidae, and Catostomidae, were caught during the study of vertical migration on 17 and 18 May 1978. Due to declining ambient air temperatures from late afternoon through the night, the 0.5-m deep water temperatures ranged from 28.0 to 30.8 C on the cool day (17 May) and 31.5 to 34.9 C on the warm day (18 May).

Partitioning of the G-test statistic used to analyze the factorial design for vertical migration indicated gizzard shad catches were not independent of 2 days, three depths, and four time periods of collection (Table 4). The significant time x depth term ($p < 0.01$, Table 4) indicates

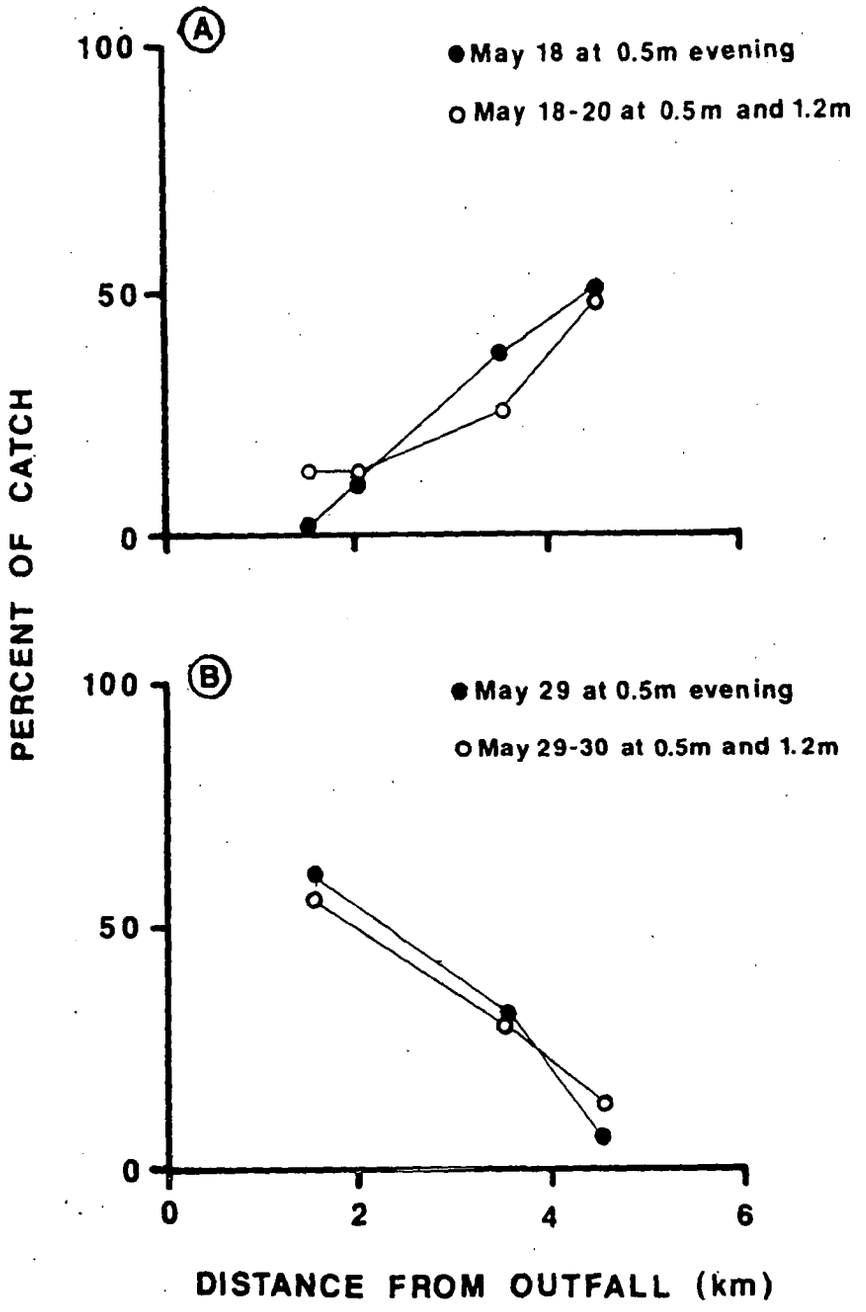


Figure 20. Percent of gizzard shad catch at each station for 0.5 m-depth in the evening using Miller tows and for sum of catches at 0.5 and 1.2 m during a 24-h period on 18 to 20 and 29 to 30 May 1977.

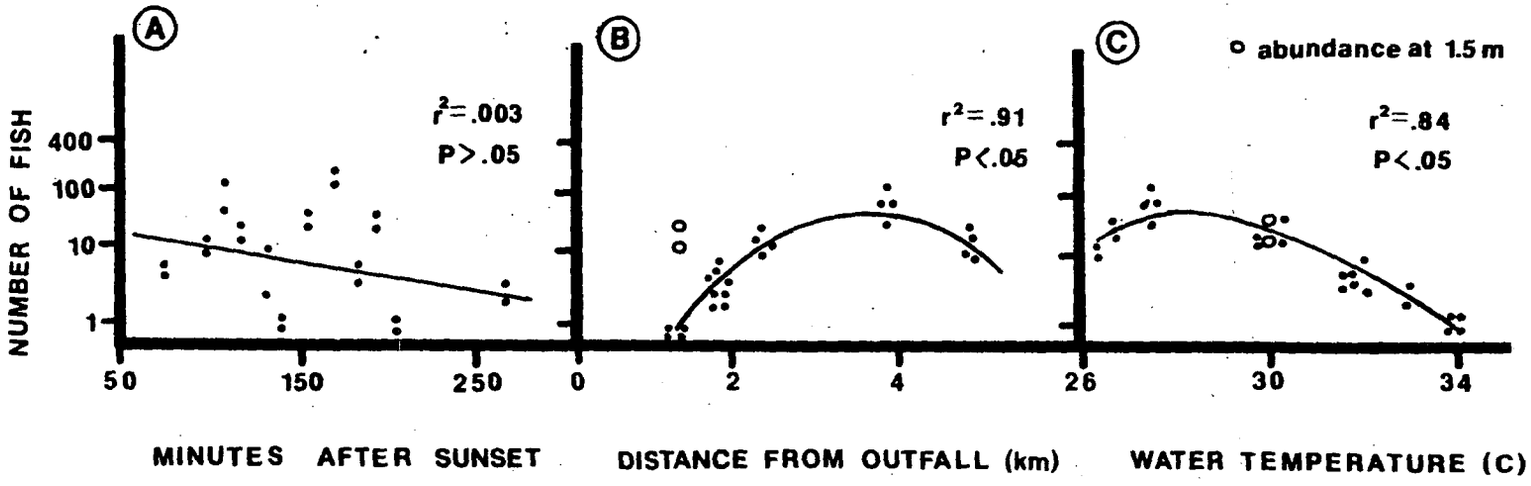


Figure 21. Abundance of larval gizzard shad at time (minutes after sunset), location (km from outfall), and temperature of capture on 24 May 1978. (Sample at 0.5 m unless otherwise noted.)

the abundance at three depths sampled changed during the sampling times (Figure 22). Lack of independence between time x day and depth x day indicates a significant difference ($p < 0.01$) between catches on the cool day and warm day. Shad catches at the 0.5 and 1.0-m depths increased more rapidly on the cool day (black dots) after 1900 h than on the warm day (regression slope, $p < 0.05$; Figure 22A, B). Water temperatures at the 0.5 and 1.0-m depths declined to 31.5 C on the warm day, but abundance did not increase at the 2400-h sampling period (open circles, Figure 22A, B). The number of larvae captured on the warm day at the 1.5-m depth during the 1700 and 1900-h sampling times was less than the number captured on the cool day (Figure 22C). Catches collectd at 2100 and 2400 h at 1.5 m depth with temperatures ranging from 29.6 to 30.3 C appeared similar to catches from the cool day (Figure 22C). Warm day catches of gizzard shad were 35 to 55% of total catches collected at respective depths on the previous cool day. Abundance of larval gizzard shad completing upward vertical migration was reduced when water temperatures were > 31 C.

TABLE 4. THE G-STATISTIC VALUES PARTITIONED ACCORDING TO THE HYPOTHESIS TESTED FOR THREE FACTOR OBSERVATIONS ON THERMAL SUPPRESSION OF VERTICAL MIGRATION, 17 TO 18 MAY 1978

Hypothesis tested	df	G	Significance
Time x depth independence	6	259.2	**
Time x day independence	3	28.2	**
Depth x day independence	2	12.4	**
Time x depth x day interaction	6	120.0	**
Time x depth x day independence	17	419.8	**

**$p < 0.01$.

DISCUSSION

Miller samples were expected to be effective in sampling larval forms of fish inhabiting open water in Lake Columbia. Larval stages of bluegill (Werner 1969), pumpkinseed sunfish (Faber 1967), black crappie (Amundrud et al. 1974), white bass, and gizzard shad (Netsch et al. 1971) inhabit the limnetic zone of a lake. Largemouth bass fry were not expected to be effectively sampled since they inhabit the nearshore area during larval and juvenile stages (Elliot 1976).

The vertical distribution pattern of gizzard shad in May 1977 suggests that gizzard shad undergo diel vertical migration and are more abundant near the surface at night. This observation could be partially explained by gear avoidance of gizzard shad during the day. Noble (1970) found that visual

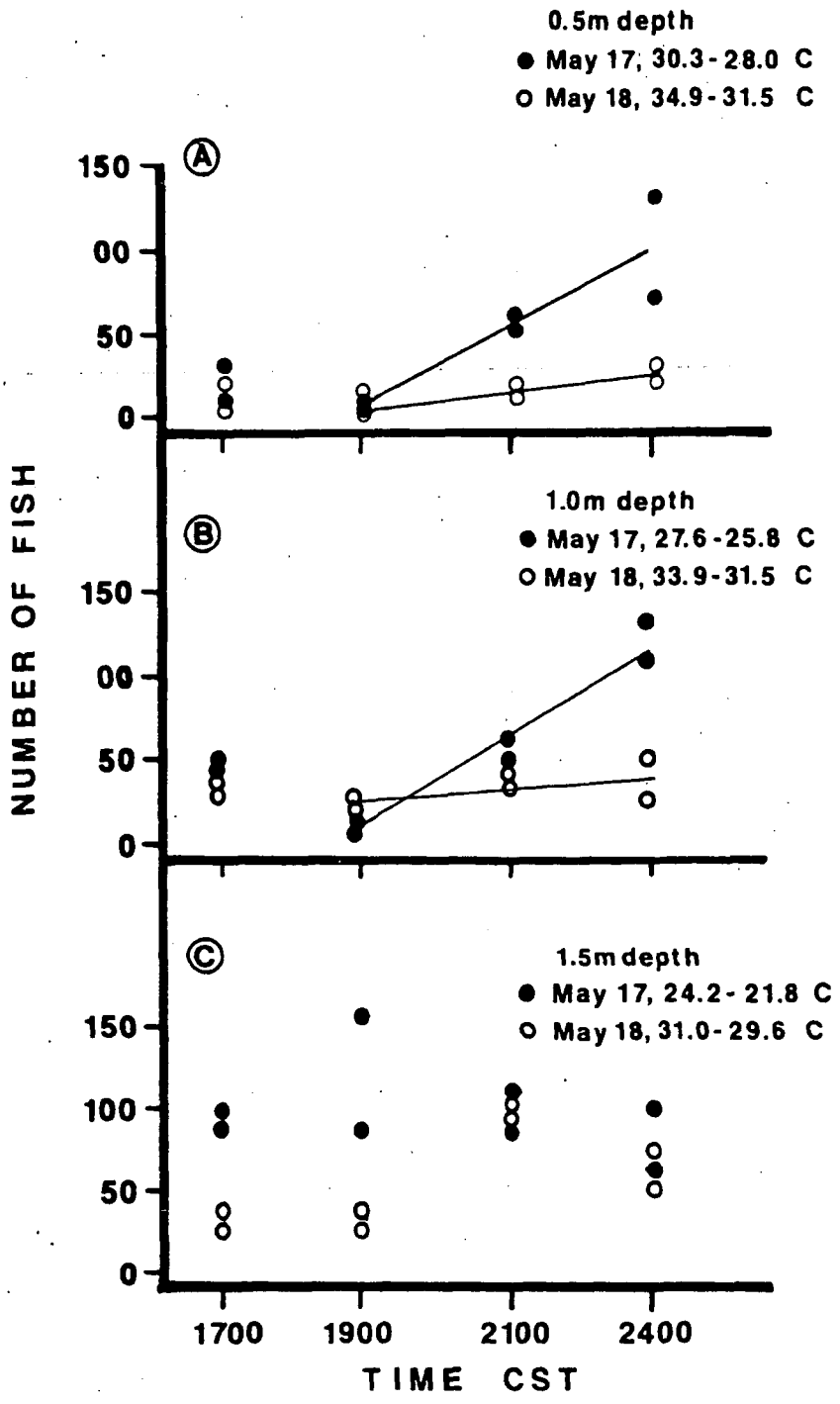


Figure 22. Number of gizzard shad caught at 0.5, 1.0, and 1.5 m depth at cool temperatures (30.3 to 21.8 C) on 17 May and warm temperatures (34.9 to 29.6 C) on 18 May 1978. Samples were collected 1.5 to 2.0 km from the power plant outfall in Lake Columbia, Wisconsin.

cues were an important factor in the ability of yellow perch fry to avoid Miller samplers. The greater percentage of the total catch of each station taken at noon at 1.2 m depth indicated diel vertical migration (Figure 19). Storck et al. (1978) found gizzard shad to be concentrated at the surface during the day and dispersed at night in the turbid upper parts of a reservoir. Acoustic records, trawl catches, and meter net catches of gizzard shad in a reservoir with low turbidity showed abundant but widely dispersed gizzard shad in the upper 10 m at night and tightly schooled concentrations at a 10-m depth during the day (Netsch et al. 1971).

The vertical migration of larval and early juvenile fish in lentic and lotic waters is common for a number of fish species, but the adaptive value is unknown. McLaren (1963) hypothesized that diel vertical movements in zooplankton have a bioenergetic advantage. Zooplankton achieve improved growth efficiency when they feed in surface waters and digest at deeper, cooler water. An analogous hypothesis was proposed by Brett (1971) to explain the diel movement of young sockeye salmon (*Oncorhynchus nerka*) from the thermocline to the surface at night. Diel movements may be advantageous under conditions such as those shown in Figure 22 when temperature differences as great as 6.2 C exist between 0.5 and 1.5 m depth. Thermal stratification was usually limited because even slight winds vertically mixed the shallow lake.

Suppression of vertical migration by elevated temperatures during thermal stratification reduced abundance of gizzard shad at 0.5 and 1.0 m after 1900 h. Marcy (1976) found that caged juvenile American shad (*Alosa sapidissima*) migrated downward (40 cm) as temperatures increased to near 30 C. The reduced abundance observed at elevated temperatures in Lake Columbia may be due to suppression of vertical migration, direct action of lethal temperatures, or thermally induced emigration from the area.

Horizontal patterns of distribution of gizzard shad at the 0.5-m depth were similar to those found by summation of 0.5 and 1.2-m samples during the 24-h periods sampled in May 1977 (Figure 20). The greater relative abundance at the 0.5-m depth after sunset justifies the sampling design starting after sunset. This allows maximum numbers to be captured with minimal effects from clustered distributions (Cassie 1971) and vertical movements induced by light and temperature.

Horizontal patterns of abundance and median lengths of *Lepomis* sp. and gizzard shad indicate intitial downstream drifting by larvae in the cooling lake. Downstream drift of larval fish occurs mainly during the night and is common in a number of fish families, including Catostomidae (Clifford 1972), Percidae, and to a lesser extent in Centrarchidae (Gale and Mohr 1978). Gale and Mohr (1978) suggested an adaptive value in dispersing at night when larvae are less visible to predators. Downstream drift of larval capelin (*Mallotus villosus*) in the St. Lawrence River resulted in the transport of larval fish into the region of maximum primary production in the Gulf of St. Lawrence (Jacquaz et al. 1977). Downstream drift during the night may have evolved as a mechanism to transport larval fish to areas of higher food density. In areas of higher food density travel rates were reduced to anchovy larvae (*Engraulis mordax*) because larvae changed swimming direction

more often (Hunter and Thomas 1974). Continued immigration and reduced exodus in areas of high food abundance would result in aggregation of larvae and, perhaps, enhanced survival. However, in the unique cooling lake environment larvae initially aggregated in the power plant intake, an area of potential entrainment.

Lepomis sp. and gizzard shad responded to water temperature changes while in the pelagic juvenile stages. The greater abundance of gizzard shad near the outfall may be the result of rheotactic behavior, such as has been reported for the aggregation of the alewife (*Alosa pseudobarengus*) in thermal plume areas (Romberg et al. 1974). The importance of thermal preference in aggregation of adult fish in thermal plumes has been reported (Neill and Magnuson 1974, Marcy 1976). Thermal preference and the avoidance of potentially lethal temperatures was important in determining the spatial location of the mode of abundance in the cooling lake environment. Movement of the mode of abundance resulted in fish maintaining a position at water temperatures of 28 to 31 C. Distribution changes that showed the presence of larger fish at warm stations could be partially attributed to the movement of larger and more mobile juveniles into the warmer areas. Petty and Magnuson (1974) found this for juvenile bluegills in a power plant outfall area on Lake Monona, Wisconsin. In the cooling lake however, the effects of increased growth at warm temperatures cannot be discounted.

The ability of pelagic early juveniles to respond to thermal gradients has evolved under ambient thermal regimes and may or may not be of value in the cooling lake environment. Under ambient conditions pelagic early juveniles of spring spawning fishes appear in aquatic systems when thermal gradients are small, but rapid spring warming occurs. Early mobility and thermal responsiveness may enhance aggregation in nursery areas at temperatures where growth and other physiological processes are optimal. Resulting spatial separation of young-of-the-year and adults of lower thermal preference might serve to partition resources and minimize predation (Brandt 1980). The observations that such behavior occurs and that juveniles of other species respond to temperature differentials as small as 0.1 C (Marcy 1976) suggest that it may be important even at ambient temperatures.

In summary, species diversity of larval fish catches was low in 1977 when water temperatures increased rapidly. The median temperature of capture of larval *Lepomis* sp. and gizzard shad was near 30 C. Temperatures > 31 C during thermal stratification reduced the abundance of gizzard shad completing diel vertical movements. After initially drifting with current *Lepomis* sp. and gizzard shad responded to water temperature changes by horizontal shifts in abundance with a mode at 28 to 31 C.

SECTION 6

CONCLUSIONS

Observations suggest that the species diversity of fish in Lake Columbia, Wisconsin declined during the first year of thermal input by the plant. Habitat modification, such as reduced vegetation as a direct result of thermal input, may be the reason for the decrease in abundance of some species. The decline in species diversity was accentuated by fish mortality from temperatures exceeding upper lethal limits, an absence of colonization of warm-water, lake-dwelling species, and limited reproductive success.

Thermal inputs by the power plant modified temporal and spatial characteristics of spawning white bass and black crappie. Resumption of plant operation following a 3-week shutdown resulted in a rapid increase in water temperatures that stimulated spawning, reduced available spawning area, and induced aggregation of sexually mature black crappie at coolest available water temperatures. Water temperatures above expected spawning temperatures induced partial resorption of ovaries, loss of secondary sexual characteristics, and abbreviation of spawning duration. The combined operation of the Columbia I and II generating units induced spawning about 1 month earlier than when only Columbia I was operating.

The rapid increase in water temperatures that induced spawning and subsequent gonadal resorption in 1977 was associated with a lower number of species of larval fishes. If a number of species were stimulated to spawn, as indicated by Figures 8 and 9, then a greater number of ichthyoplankton species would be expected at that time, but this was not observed. Therefore, factors associated with the increase in temperatures must have been responsible for reducing ichthyoplankton species abundance. The number of species of larval fishes was lower during 1977 when water temperatures increased rapidly and reproductive responses were aberrant. This may explain the limited reproductive success observed for some species successful as adults in the cooling lake environment.

Larval and early juvenile stages of bluegill and gizzard shad were responsive to temperature changes within the thermal gradient. Larval forms initially drifted downstream. Pelagic larval and juvenile stages of bluegill and gizzard shad were most abundant at 28 to 31 C and were capable of responding to changes in the thermal gradient induced by changing air temperatures. Larval gizzard shad exhibit reduced diel vertical movements when temperatures are > 31 C. Pelagic larval and early juvenile forms responded to thermal dynamics of the cooling lake by modifying horizontal and vertical distribution patterns.

SECTION 7

RECOMMENDATIONS

1. The disappearance of aquatic vegetation should be expected in cooling lakes with heavy thermal loading. Management to enhance fish populations of species that require vegetation to spawn should not be attempted.

2. Initiation of spawning was approximately 1 month earlier with the thermal input of two 527-MW generating units. If fishery management agencies protect spawning adult fish during spring by closed season, the regulations may not be applicable to cooling lake fisheries. The accelerating of spawning during spring can provide the opportunity to open a fishery while other temperate lake fisheries are closed during normal reproductive season.

3. Power plant shutdowns are often scheduled during spring but rapid temperature increases when plants resume operation can cause aberrant reproductive responses in spring-spawning fish. The operation of more than one generating unit may be beneficial because addition units buffer the effects of rapid changes in temperature of a single unit.

4. Successful reproduction of fish in a cooling lake is spatially limited to water temperatures within the thermal tolerance limits of reproduction. Cooling lake water temperatures and corresponding areas can be estimated during planning. Design should provide adequate area with water temperatures within the thermal tolerance limits of oogenesis, spawning, and incubation during spring.

5. Pelagic larval stages drift downstream in a recirculating cooling lake and will subsequently be entrained by the power plant if cooling lake turnover time is not adequate to permit metamorphosis into the more mobile early juvenile stages. Entrainment should be accepted as a part of the cooling lake environment, however, careful design can minimize entrainment of larval and early juvenile stages. Additional generating units should be augmented by increasing cooling lake area and volume or by providing cooling towers to increase lake turnover time.

6. Early juvenile fish in pelagic stages are mobile and respond to thermal gradients and water currents by congregating in preferred habitats. Cooling lake design can increase juvenile nuersery areas and species diversity by providing heterogeneous habitats with a diversity of water depths, substrates and shoreline configurations. These design modifications would not inhibit the cooling capacity of the lake because cooling is most dependent on surface area.

7. After power plant operation began species diversity declined as a few eurythermal species increased in abundance and other species declined. Sport fish should be stocked early in the operation of the lake so that juveniles can utilize forage species likely to become abundant after the power plant begins operation. Thermally-tolerant nest-guarding Centrarchids and Ictalurids, such as largemouth bass and channel catfish, are likely to be the most successful native species in cooling lakes and should be preferred for initial stocking.

8. After the power plant begins operation water temperatures of the cooling lake may exceed the upper lethal limits of popular cool water sport fish resulting in fish kills. Design can create thermal refugia using water depth and circulation patterns. Fishery managers and the public should anticipate fish kills as a part of starting the long term management of a cooling lake, but recurrent fish kills can be avoided through careful design.

9. Largemouth bass, a species susceptible to over-harvest, was caught at the highest rate by angling near the outfall in winter (0.28 bass/cast) and in cool water near the intake in late spring (0.27 bass/cast: Lozano et al. 1978). Thus, the area near the intake and outfall should be permanently closed to fishing to protect summer and winter aggregations of fish under seasonally extreme thermal conditions.

10. Small reservoirs are often subject to over-exploitation of sport fish populations, particularly when fish are spatially limited by temperature or lake morphometry. Thus, when power plant security is designed, consideration should be given to minimize over-harvest of fish in outfall and intake areas and reduce potential conflicts between power plant security and fisherman.

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