5-1996

Influence of Prey Availability on Walleye (Stizostedion vitreum)

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Porath, Mark T., "Influence of Prey Availability on Walleye (Stizostedion vitreum)" (1996). *Dissertations & Theses in Natural Resources*. 200.
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INFLUENCE OF PREY AVAILABILITY ON WALLEYE *STIZOSTEDION VITREUM*

by

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A THESIS

Presented to the Faculty of
The Graduate College in the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Master of Sciences

Major: Forestry, Fisheries, and Wildlife

Under the Supervision of
Professor Edward J. Peters

Lincoln, Nebraska
May, 1996

INFLUENCE OF PREY AVAILABILITY ON WALLEYE *STIZOSTEDION VITREUM*

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University of Nebraska, 1996

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Management of reservoir walleye stocks is challenged by fluctuating water levels which hinder establishment of the prey fish assemblages found in natural lakes. The success of introductions of schooling pelagic fishes have been evaluated using the body condition of walleye, and their consumption and selection for several levels of prey fish abundance and species. Walleye collected from Lake McConaughy, Nebraska in June to September, 1995, were used in feeding experiments and analysis of stomach contents. Walleye were presented treatments of three prey species, yellow perch, white sucker and either alewife or gizzard shad at three levels of alewife or gizzard shad abundance. Proportions of each prey species in walleye stomachs were compared with the composition of available prey. Alewife was the most abundant prey species in walleye stomachs, and this was not significantly different from their proportion in the prey fish assemblage. In feeding experiments walleye selected for white sucker and yellow perch, and against alewife and gizzard shad. Experiments were influenced by schooling, a predator avoidance tactic of alewife and gizzard shad. Relative weights (W_r) of walleyes were compared from Lake Ogallala and Lake McConaughy by season and length class in relation to the available prey fish composition. Walleye W_r in both lakes changed seasonally depending on walleye length and was influenced by prey size availability. By

October in Lake Ogallala there was no significant difference in W_r by length class and the population could be characterized by a single mean W_r. In Lake McConaughy three levels of walleye condition existed in October, with smaller length walleye exhibiting the lowest W_r. A mean W_r would inaccurately characterize this population.

ACKNOWLEDGMENTS

I would like to thank Dr. Edward J. Peters for his assistance, support and advice throughout the completion of this graduate program. I would also like to thank the members of my graduate program committee, Dr. Gary L. Hergenrader and Dr. Richard S. Holland for their advice and assistance. Assistance in the laboratory and field collections were provided by Eric Laux, Rob Hofpar, Robb Krause, Brett Fessel, Kelly Divis and Shyi-liang Yu. Special thanks go to Darrol Eichner, NGPC Research Biologist, and Monte Madsen, NGPC District IV Supervisor, for their assistance throughout the sampling seasons. Dr. Linda Young of the University of Nebraska-Lincoln, Biometry Department, provided significant statistical support. Cedar Point Biological Station and Dr. Joan Darling provided the use of the mesocosm facilities. Lana Koepke Johnson provided guidance in visual aids and slide preparation.

My wife Kelly, son Zachary, and daughter Allyson provided the inspiration and support needed to undertake and complete this program, and to whom I am eternally grateful.

Funding for this project was provided by the Federal Aid to Fish Restoration Project F-112-R in conjunction with a joint project supported by the Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln and the Nebraska Game and Parks Commission, Lincoln, Nebraska.

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Review of Literature

Walleye, *Stizostedion vitreum,* is a popular gamefish of the family Percidae well suited to coolwater aquatic systems. They sight feed in low-light or nocturnal conditions during dusk and dawn, because their retinal tapetum lucidum affords an advantage over prey fish species (Denton 1971, Ali and Anctil 1977, Collette et al. 1977, Kelso and Ward 1977, Ryder 1977, Ryder and Kerr 1978, Helfman 1981). Percid communities, consisting primarily of walleye and yellow perch, *Perca flavescens*, are the predominant fish assemblage in coolwater lakes, of eastern North American. Percids are physiologically adapted to coolwater mesotrophic conditions, which avoids resource competition with warmwater centrarchid, and coldwater salmonid communities (MacLean and Magnuson 1977, Ryder and Kerr 1978). It is believed that centrarchid species have limited the success of percids in North America to mainly riverine habitats (Collette et al. 1977).

The popularity of the walleye as a gamefish has led to its widespread introduction into impoundments in the southern, central and eastern United States (Hackney and Holbrook 1978), with 48% of walleye introductions being successful (Laarman 1978). From 1986-1991, an average of one billion walleye fry and 32.8 million fingerlings were stocked annually by 32 agencies. These numbers are expected to increase to 50 million fingerlings a year between 1996 and 2000 to meet sport fishing demands (Fenton et al. 1996). Webster et al. (1978), described the extensive stocking of coolwater species as consisting of two main phases, the late 1800's and early 1900's when introductory stocking was viewed as the answer to fisheries management problems, and 1940-1970, in conjunction with the construction of main-stem reservoirs on large river systems.

The decline in new reservoir construction (Kimmel and Groeger 1986) and increased utilization of existing resources by 36 million anglers in the United States (U.S. Department of the Interior 1992) has led fishery managers to introduce prey fish species to support quality stocks of predaceous sport fish (Ney 1981). Pelagic species like threadfin shad, *Dorsoma petenense,* and gizzard shad, *Dorsoma cepedianum,* are the most widely introduced and manipulated populations of prey fish species (DeVries and Stein 1990). Rainbow smelt, *Osmerus mordax,* are usually introduced into cooler northern waters less suitable for warmwater shad species, and have provided a substantial prey base for walleye populations (Jones et al. 1994). Alewife, *Alosa pseudoharengus*, an anadromous schooling fish, is soft-bodied, highly fecund and achieves a maximum total length of approximately 240 mm in landlocked freshwater populations (Carlander 1969). This small adult size is vulnerable to predation by a large proportion of most walleye populations. Use of alewife by salmonids in the Great Lakes, has stimulated interest in them as a food source for other gamefish in reservoirs which lack a native pelagic prey species (Kohler and Ney 1981). However, alewife may compete with larval stages of gamefish species for food or prey upon them (Kohler and Ney 1981, Ney 1981, DeVries and Stein 1990).

Walleye apply heavy predation pressures on prey fish populations, and are believed to be responsible for shaping prey fish communities (Forney 1977, Kelso and Ward 1977, Swenson 1977, Lyons and Magnuson 1987, Tonn et al. 1992, Knight and Vondracek 1993, Rice et al. 1993). Walleye begin opportunistic piscivory shortly after yolk sac absorption, at lengths as small as 30 mm (Mathias and Li 1982). Lyons and Magnuson (1987) found that when age-0 yellow perch were scarce in a northern Wisconsin Lake, walleye predation accounted for almost 100% of adult darter mortality, and 75% of adult minnow mortality. Walleye age-0, 1, 2, like other juvenile predators, are the most abundant and the most gape-limited members of the population (Hambright 1991, Madenjian 1991, Hartman and Margraf 1992).

In the Great Lakes, walleye prey mostly on pelagic prey species like shiners *Notropis spp.*, alewife and gizzard shad in Lake Erie (Parsons 1971, Knight et al. 1984, Hartman and Margraf 1992), rainbow smelt and alewife in Lake Michigan (Wagner 1972), and rainbow smelt in Lake Superior (Swenson 1977). Studies conducted on walleye diets in other parts of the country found gizzard shad (Fitz and Holbrook 1978), threadfin shad (Hepworth and Gloss 1976), white sucker (Beamesderfer and Nigro 1989), channel catfish, *Ictalurus punctatus*, black bullheads, *Ameiurus melas*, and fathead minnows *Pimaphales promelas* (Tyus and Beard 1990, Isaak et al. 1993) were important prey sources for walleye.

The main prey of walleye in their native range, is young of year (YOY) yellow perch (Forney 1974, 1977, Johnson 1977, Kelso and Ward 1977, Nelson and Wahlburg 1977, Swenson and Smith 1976), brook stickleback, *Culaea inconstans* (Kelso 1973), johnny darters, *Etheostoma nigrum*, and white suckers, *Catostomus commersoni* (Stephenson and Momot 1991). Several other minnow species associated with littoral zones and inshore habitats are also important prey for walleye (Johnson 1977, Clady and Nielsen 1978, Lyons and Magnuson 1987).

Studies conducted on walleye populations with alewife as the dominant prey showed that they are highly selected. Kohler and Ney (1981), found alewife to be the primary forage of walleye, white bass, *Morone chrysops*, and striped bass, *Morone saxatilis* in Claytor Lake, Virginia. Wagner (1972) showed that when alewives were abundant in Lake Michigan, they accounted for 71% of the total weight of food consumed by walleye. During the late summer and fall in Lake Erie, alewife dominated the diets of walleye (Parsons 1971, Knight et al. 1984). Walleye, northern pike, *Esox lucius*, smallmouth bass, *Micropterus dolomieu*, burbot, *Lota lota*, and bowfin, *Amia calva*, utilize alewife when they migrate inshore to spawn during May-August in Lake Michigan (Wagner 1972).

Studies suggesting prey selection by walleye rely heavily on stomach content analysis (Parsons 1971, Wagner 1972, Forney 1974, Swenson 1977, Knight et al. 1984, Lyons and Magnuson 1987, Hartman and Margraf 1992, Isaak et al. 1993, Jackson et al. 1993). Analysis of stomach contents can give accurate information on the species, size and nutritional content of the consumed prey (Kelso 1973). However, inferring selective predation from stomachs may be complicated by confounding factors (Larkin 1979), such as habitat overlaps (Swenson and Smith 1976), prey capture rates (Wahl and Stein 1989), preference for soft-rayed prey (Buynak et al. 1982), and competition for limited resources (Wolfert and Bur 1992). Swenson (1977), Stephenson and Momot (1991), and Jackson et al. (1993), stated that abundance of prey, habitat use by prey and availability of different prey to predation, affect actual consumption rates. Differences in evacuation rates for prey species tend to overestimate prey that are slowly digested and underestimate prey that are digested rapidly (Gannon 1976, Bowen 1983). Diel movements and seasonal differences in feeding strategies can also affect what will be found in stomach contents.

Growth rates and survival of walleye are directly related to prey abundance (Parson 1971, Forney 1974, 1977, Swenson and Smith 1976, Kelso and Ward 1977, Knight et al. 1984, Hartman and Margraf 1992). The presence of large year classes of yellow perch or alewife may buffer other species from walleye predation (Wagner 1972, Forney 1974), since walleye prey heavily on age-0 fish in the late summer and early fall (Parsons 1971, Kelso and Ward 1977, Knight et al. 1984, Jackson et al. 1993). Fat content or caloric density is known to change seasonally in fish species in the presence of abundant food resources (Zaret and Rand 1971, Foltz and Norden 1977, Pierce et al. 1980, Rand et al. 1994). Cada et al. (1987), showed that limited food resources influenced rainbow, *Onchorhyncus mykiss,* and brown trout, *Salmo trutta,* body conditions. Bioenergetics models suggest a positive relationship between consumption rates and growth rates (Hewett and Kraft 1993).

Relative weight (W_r) is a condition factor that compares the weight of an individual to a standard weight (W_s) for a fish of the same length, W_r =weight/ W_s x 100 and is highly touted as a management tool for its ability to make comparisons among populations (Wege and Anderson 1978). Brown and Murphy (1991) showed that W_r was correlated with crude fat content in juvenile and hybrid striped bass. Condition factors such as those developed by Fulton (K) and LeCren (K_n), were limited to comparisons between individuals within a population (Anderson and Gutreuter 1983). Murphy et al. (1991) expressed concern about the methods used to develop W_s equations and suggested using the regression-line-percentile (RLP) technique. They also questioned the application of W_r without first clarifying its relationship to other measures of population structure and dynamics. Little correlation has been found between W_r and growth rates of fish populations (Gutreuter and Childress 1990, Liao et al. 1995). Seasonal changes in smallmouth bass, white crappie, *Pomoxis annularis* and black crappie, *Pomoxis nigromaculatus,* W_r are related to food availability (Austen and Orth 1985, Gabelhouse 1991, Neuman and Murphy 1991). Although Stephenson and Momot (1991) showed differences in K factors for walleye by age class, there has been no published documentation of seasonal changes in walleye W_r correlated to differences in prey availability.

Chapter 1: Walleye prey selection in Lake McConaughy, Nebraska: A comparison between stomach content analysis and feeding experiments

Introduction

Lake McConaughy is a 14,000 hectare impoundment of the North Platte River in Western Nebraska. Alewife were introduced from 1986 to 1988 by the Nebraska Game and Parks Commission in an attempt to provide a stable prey base for the declining walleye and white bass populations. The use of alewife as prey by salmonids in the Great Lakes has stimulated interest in them as a food source for pelagic gamefish, especially in reservoirs which lack a native pelagic prey species (Kohler and Ney 1981). The gizzard shad population in Lake McConaughy experiences large fluctuations in recruitment success. An anadromous schooling fish, the alewife is soft-bodied, highly fecund and achieves a maximum length of 240 mm in freshwater (Carlander 1969). Previous introductions of threadfin shad, spottail shiner, *Notropis hudsonius*, and rainbow smelt to establish a pelagic prey base were considered unsuccessful. In natural lakes littoral fishes supply food for piscivores, while the production of littoral prey is greatly decreased and/or highly variable in reservoirs (Wydoski and Bennett 1981).

The purpose of this study is to investigate the predation of walleye on alewife and gizzard shad in Lake McConaughy. Most of the primary literature on walleye prey selection is based on food habit studies. Our objectives were to 1) concurrently examine walleye food habits and estimate prey abundance in Lake McConaughy, 2) conduct feeding experiments to determine prey selection by walleye, at several levels of alewife or gizzard shad abundance in the presence of alternative prey.

Methods

Fish Collections

Walleye and prey fish were simultaneously captured at Martin Bay on the eastern end, and Otter Creek and Sand Point on the western end, of Lake McConaughy from June through September 1995 (Figure 1), using short-duration variable mesh gill net sets and pulsed-DC boat electrofishing (200-250 volts and 8-10 amps). Gill nets were 45.7 meters long, 1.8 meters deep with six 7.6 m panels of (1.9, 2.5, 3.2, 3.8, 5.1 and 7.6 cm) nylon knotted mesh, as used in standard fish surveys by the Nebraska Game and Parks Commission (Zuerlein and Taylor 1985). Nets were set perpendicular to the shoreline in 0.9-10.7 meters of water. Two nets were set at randomly chosen sites within a location for 30 minutes, beginning at approximately 5:00 a.m. (MST). Net contents were sorted for walleye and prey fish species, and reset for another 30 minutes. Walleye collected for food habits analyses, were measured for total length, weighed, scales were taken for aging, and stomachs were preserved in a 10% formalin solution. Walleye to be used in feeding experiments were lightly anesthetized (5 ppm MS-222) and transported in a 5 ppt sodium chloride solution and were not weighed, measured for length, or have scales removed for aging. Prey fish species, yellow perch, white sucker, gizzard shad, and alewife, were captured with electrofishing or frame nets and sorted by species and length. Individuals between 100-170 mm were kept in holding pens for use in the feeding experiments.

From each gill net we recorded the number and species of all prey that were captured to obtain a prey species profile at each sampling site. All prey fish species >300 mm were recorded and released. Prey fish species less than 300 mm were fixed in a 10% formalin solution for further measurements. Preserved prey fish were weighed to the nearest tenth of a gram, and measured for TL. To determine the length of each prey fish species still vulnerable to predation by walleye, the longest (TL) prey of each species found in walleye stomachs was set as the upper length limit of that prey species vulnerability to predation. Prey longer than this length limit were subtracted from the total numbers caught in each net to determine the number of "available" prey. Length frequency distributions were compiled for available prey species by season.

Food Habits

In the laboratory, each walleye stomach was cut length wise, and food items flushed into a petri dish. Contents were examined, and the number, lengths and species of prey fish were recorded. Invertebrates were noted and the approximate number recorded. Prey fish were identified to species when possible. Gizzard shad could be identified by the gizzard at a greater state of digestion than alewife. Partially digested, but still identifiable fish were measured as either standard length (SL), or backbone length (BB), and converted to total length (TL) using regression equations (Knight et al. 1984). Stomach contents were expressed as the proportion of total prey species consumed, and unidentifiable fish were allocated by species at the same proportion as identifiable species. Selection for alewife or gizzard shad, was tested with a chi-square test of homogeneity to compare the composition of prey species in walleye stomachs, and the estimated composition of prey vulnerable to predation (Jelinski 1991).

Feeding Experiments

After walleye were transported to one of three experimental enclosures at Lake Ogallala, Nebraska, they were not handled until their release to minimize stress. Lake Ogallala is a 263 hectare tailwater reservoir located directly below Lake McConaughy. Wind protection for floating net enclosures behind Kingsley Dam, and high turnover rates from daily discharges, prompted the use of this site for the feeding experiments.

Two 28 m^3 (3.1 m on a side), floating net enclosures constructed of 0.6 cm knotless nylon mesh, were suspended in Lake Ogallala and stocked with four walleye (400-640 mm) and 36 prey. Each enclosure was covered with a shade screen to reduce light levels within the enclosure and prevent prey escape or loss to avian predation. Four cylinder shaped nets with a volume of 7.5 m^3 (1.8 m in diameter and 2.4 m tall), were stocked with either one or four walleye (350-400 mm) and six or 12 prey, suspended in Lake Ogallala and covered with a tarp.

Mesocosm tanks (1.8 m x 2.4 m), were filled with water pumped directly from Lake Ogallala, and stocked with a single walleye (300-380 mm) and 12 or 24 prey. A forced airlift system constantly circulated the water within each mesocosm providing a homogeneous environment of temperature and dissolved oxygen. A cylinder shaped net was placed inside each mesocosm tank. Nets were the same volume as the mesocosms, and when placed inside, were used to visually check on walleye and prey at the end of each trial by pulling the sides of the net upwards. Lowering the net returned the tank to its original volume, without inducing stress on the walleye or prey.

Treatments of three prey species at a single density, and in three levels of abundance of alewife or gizzard shad (low, equal, high) were applied to experimental units of a single, or group of four walleye (Table 1). Prey treatments were applied in an incomplete randomized block design in the floating pen enclosures, and a completely randomized design in the mesocosm trials. Each trial contained prey of a single 20-mm length class to avoid biasing prey selection by size, and the maximum length of all prey species were between 25% and 40% of the total length of the smallest walleye.

Trials that resulted in prey consumption were essential, since statistical analysis of "choice type" testing requires that a choice be made, and feeding trials in which no prey were consumed could not be included in this analysis. If the walleye consumed at least 1.5% of their body weight per day, this level of feeding was assumed to be "normal" at our study temperatures (Swenson and Smith 1976, Swenson 1977, Mathias and Li 1982). Trials in which walleye ate at least 1.5% of their body weight per day and displayed consistent feeding, were considered relevant to the study question and analyzed for prey selectivity. Analysis of walleye prey selection was conducted using categorical log-linear modeling (PROC CATMOD), and maximum-likelihood analysis of variance using Statistical Analysis Software (SAS Institute 1988). Preplanned comparisons using orthogonal contrasts were used to delineate prey selection between prey species and treatment levels.

Results

Food Habits

A total of 109 walleye stomachs were examined for food content from fish captured in 45 nets from Lake McConaughy, May-September, 1995. There were 31 empty walleye stomachs and 78 stomachs contained prey items. Of the 78 stomachs, eight contained invertebrates, and 70 contained a total of 97 prey fish. Walleye consumed only alewife and gizzard shad. Two of the 78 walleye stomachs with identifiable prey, contained gizzard shad. Of the 62 out of 97 prey fish identifiable to species, 60 were alewife and two were gizzard shad. Based on our assumption that the unidentifiable fish found in walleye stomachs were distributed the same as the identifiable fish species, we estimated the proportion of alewives consumed to be 92 of 97 fish.

The occurrence of empty stomachs was proportionally higher in smaller walleye length classes (Figure 2). The percentage of empty stomachs in walleye between 250-400 mm was greater than 35% and only 10% or less in walleye between 400-650 mm TL. The average meal size in walleye stomachs containing prey was 1.4 fish. Walleye consumed alewife ranging from 11.5-44% (mean 29%) of their total length. A 196 mm alewife was found in a 475 mm walleye.

Prey fish composition was determined from 16 nets set at Martin Bay, and 23 nets at Otter Creek and Sand Point (Figure 3). Due to their proximity in the reservoir, data collected from Otter Creek and the Sand Point locations could not be considered independent and were combined into a single location. We considered all prey species less than 200 mm to be susceptible to predation by walleye. Length frequencies of prey less than 200 mm was dominated by alewife in all seasons (Figures 4-6). Lengths of most alewife were in the 170 mm size class, with only a few above 200 mm. Age-1 gizzard shad ranged between 140-180 mm in early summer, 170-200 mm in late summer, and by fall most were greater than 190 mm TL.

Alewife were the most abundant prey species at all sampling sites, and within walleye stomachs. There was no significant difference between the proportion of alewife and gizzard shad in the diets of walleye, and their availability at Martin Bay ($p=.106$), and at the combined Otter Creek/Sand Point areas ($p=.079$). This suggests that walleye are feeding randomly on the most abundant prey available, not selectively preying on alewife.

Feeding Experiments

Table 2 summarizes the results of 201 feeding trials conducted in mesocosms, small float pens, and large float pens from May to August 1995. Only 15 of 139 mesocosm trials produced successful feeding, and none met our criteria for normal feeding. This is probably due to high temperatures, high light intensities, and isolating a single walleye in a tank. There were seven successful feedings in 23 small float pen trials, but none met requirements for normal feeding. All successful feeding was completed by groups of four walleye. In large floating enclosures, 38 of 39 trials resulted in consumption of prey and 26 trials met both requirements of normal feeding. A reduced level of feeding was recorded in 12 of the 13 trials which were not considered normal. These trials were all conducted at the end of August, when walleye transported to the float pens had to be tempered by as much as 4 to 6 C°.

Walleye exhibited significant differences in preference of prey by species ($p < .0001$), and by treatment level ($p = .0001$). Maximum-likelihood estimates of the probability of being eaten are highest for white sucker and yellow perch at all treatment levels (Figure 7). The probability of being eaten for either alewife or gizzard shad is not statistically different. At all treatment levels walleye exhibited positive prey selection for white sucker and yellow perch and negative selection for alewife and gizzard shad. Orthogonal contrasts showed differences in preference at all levels between alewife and perch ($p<.0001$), alewife and white sucker ($p<.0001$), shad and perch ($p<.0001$), shad and white sucker ($p<.0001$), yellow perch and white sucker ($p=.0081$), but no difference between alewife and gizzard shad ($p=.218$). This suggests that walleye treated alewife and gizzard shad the same during these feeding experiments.

Discussion

Increasing angler numbers (U.S. Department of Interior 1992, Quinn 1992), and a decline in the construction of new reservoirs (Kimmel and Groeger 1986) has prompted fishery managers to maximize production in existing resources (Ellison and Franzin 1992). High sediment and nutrient loading rates cause reservoirs to mature faster than lakes, and fluctuating water levels inhibit the establishment of littoral vegetation. Introduced species like threadfin shad and gizzard shad (DeVries and Stein 1990), are used to establish a pelagic prey base in these ”littorally challenged” systems because they don't rely on established littoral zones for spawning, or predator avoidance (Ney 1981). Management decisions to stock prey fish species are based on the proposed interaction between predator and prey, and don’t consider the impact on the entire aquatic community (Magnuson 1976, Ney 1981, Wydoski and Bennett 1981, Noble 1986). In recent years, alewife and gizzard shad have segregated in Lake McConaughy, with gizzard shad near the mouth of the North Platte River, and alewife in the deep water along the dam face (Darrol Eichner, pers. comm.). Tisa and Ney (1990), found alewife and gizzard shad to be compatible in Smith Mountain Lake, Virginia, where extensive segregation between adult and larval stages occurred.

Determining selection in a changing prey environment is complicated by variability in sizes and abundance of predator and prey, available habitat, habitat use, predator to prey density, and competition between predators (Swenson and Smith 1976, Buynak et al. 1982, Wahl and Stein 1989,Wolfert and Bur 1992). Previous approaches to investigating prey selection by walleye have been to examine stomach contents and quantify prey abundance through various capture methods. This approach is temporally limited in its ability to make inferences on predator-prey interactions, since the composition of prey will change annually relative to prey reproductive success.

Food Habits

Walleye fed almost exclusively on alewife in Lake McConaughy during 1995. Wagner (1972), and Kohler and Ney (1981), found that the predators in Lake Michigan and Claytor Lake, Virginia, fed primarily on alewife when they dominate the prey base. However, the similar proportion of prey in walleye stomachs and their availability in Lake McConaughy, suggests that selection of prey was random.

Parsons (1971) and Knight et al. (1984) found that walleye fed on abundant YOY alewife or gizzard shad in the late summer and fall. A lack of YOY alewife or gizzard shad in Lake McConaughy during 1995 was consistent with walleye stomach contents. If there had been successful recruitment of alewife and/or gizzard shad, we would have expected to see a shift away from larger alewife to YOY fish in August and September. Without an abundance of YOY prey in Lake McConaughy, adult alewife were the most susceptible to predation by walleye. This is due to the small adult size of alewife and the rapid growth rate of gizzard shad. Considering the deeper body form of gizzard shad, the upper limit of predation length is less for gizzard shad than alewife. Age-1 gizzard shad who survive to fall, are less susceptible to predation mortality than most of the entire alewife population. Walleye greater than 250 mm rarely consume clupeids more than 40% of their total length (Jenkins and Morais 1977, Nielsen 1980, Knight et al. 1984), and this is also true in Lake McConaughy. Walleye less than 350 mm are gape limited to only YOY fish and the portion of the alewife population < 140 mm (Hambright 1991, Maderjian 1991, Rice et al. 1993). Further investigations of the prey base in Lake McConaughy should focus on quantifying YOY abundance and evaluating the conditions necessary for reproductive success of clupeids.

Feeding Experiments

In feeding experiments, walleye selected yellow perch and white suckers over alewife or gizzard shad at all treatment levels. Alewife and gizzard shad were never selected by walleye, even when they comprised 24 out of 36 prey. Walleye may be altering prey selection in these feeding experiments to take advantage of prey accessibility. Prey accessibility is related to the amount of cover available in a particular habitat. Juvenile yellow perch and white suckers utilize available cover as a predator avoidance tactic until they outgrow significant predation risk (Ryder and Kerr 1978). It is believed that alewife and gizzard shad use schooling as their primary predator avoidance tactic. In large floating enclosures both yellow perch and white sucker were more accessible than alewife or gizzard shad, since no cover was available and alewife and gizzard shad were not prevented from schooling. Lyons (1987) observed a similar shift in prey selection by juvenile walleye between field and laboratory experiments. Walleye selected bluntnose minnow, *Pimaphales notatus*, in feeding experiments, while stomach contents showed selection for YOY yellow perch. Increased capture success of bluntnose minnow was believed responsible for the shift in prey selection. Differences in selection of alewife or gizzard shad between field and enclosure studies, suggest that walleye alter their foraging behavior. This concurs with our results that alewife and gizzard shad were treated the same in feeding experiments. Walleye switched prey to take advantage of the more vulnerable or "accessible" prey. This switching of prey has been widely documented (Parsons 1971, Zaret and Rand 1971, Wagner 1972, Forney 1974, Kohler and Ney 1981, Knight et al. 1984, Lyons and Magnuson 1987). In Lake McConaughy, walleye forage on the abundant alewife, since alternate prey is virtually nonexistent. As new prey compositions develop within the reservoir walleye adapt strategies to take best advantage of the "available" forage.

While the feeding experiments may not accurately reflect walleye prey selection in Lake McConaughy they reveal the importance of evaluating prey availability and accessibility. Future experiments should incorporate quantifiable levels of cover and adjust the size and scale of the prey treatment levels. By evaluating the type and amount of cover needed to change the walleye prey selection strategy, valuable information on managing current resources would be obtained. Modeling extremely lopsided proportions of prey abundances, such as those found in Lake McConaughy in 1995, might be better suited for large pond experiments. Our approach of combining food habits analysis with feeding experiments should allow predictive modeling of predator-prey interactions at various levels of prey composition, as long as all variables influencing predation and predator avoidance behavior are considered.

Conclusions

Walleye are adaptable to many prey sources (Knight et al. 1984, Hartman and Margraf 1992), hence their success in being introduced into many nonnative habitats. The impact of introduced species on trophic levels and food webs within the aquatic system should be considered (Wydoski and Bennet 1981, Noble 1986). Alternatives to introductions such as investments in habitat conservation or restoration, are likely to help increase and stabilize prey fish production, along with the predator populations. If we can better define the interaction between a predator and its prey, we will provide an effective tool for basing decisions and implementing management plans aimed at preserving the integrity and productivity of aquatic ecosystems.

Chapter 2: Impact of prey availability on walleye relative weights in Lake McConaughy, Nebraska, 1995

Introduction

Condition factors are used by fisheries managers to assess the relationship between body condition and food availability (Ney 1993). LeCren (1951) developed a relative condition factor (K_n) in which comparisons could be made among individuals within a population. Wege and Anderson (1978) developed the use of relative weight (W_r) where the weight of an individual is compared to a standard weight for that length. Standard weight (W_s) equations are derived from pooled length-weight relationships for each species and allow comparisons between populations. The versatility of W_r make it an attractive management tool. However, evidence of length bias required refinement of the methods used to determine W_s equations (Cone 1989, Murphy et al. 1991, Neuman and Murphy 1991). Using the regression-line-percentile (RLP) technique has produced low variance W_s equations without length bias (Murphy et al. 1990, Liao et al. 1995). The standard length-weight equation for walleye was constructed using the RLP method with data from 114 lakes and reservoirs across North America (Murphy et al. 1990).

Abundance and availability of prey influence the growth and survival of walleye (Forney 1977, Hartman and Margraf 1992, Knight and Vondracek 1993). When prey is abundant, energy stores in the form of visceral or crude fat increase, as seen from organ weight indices (Anderson and Gutreuter 1983). In fishes, weight is more sensitive than length to changes, since growth can be positive or negative, temporary or long lasting (Busacker et al. 1990, Hewett and Kraft 1993). When food is scarce, fat stores are utilized and decrease body condition (Cada et al. 1987, Brown and Murphy 1991). Although W_r has not been correlated to growth rates in fish populations, it has been suggested as a potential indicator of prey availability (Anderson 1990, Gutreuter and Childress 1990, Murphy et al. 1990, Gabelhouse 1991, Liao et al. 1995).

Alewife were introduced by the Nebraska Game and Parks Commission to support the declining walleye and white bass populations in Lake McConaughy, Nebraska from 1986-1988. Alewife were well established by 1989, and began emigrating through the Kingsley Dam hydropower plant into Lake Ogallala in the winter of 1989-1990. By 1992, alewife were competing with the put, grow and take rainbow trout fishery in Lake Ogallala. An investigation of the alewife and rainbow trout community in Lake Ogallala was begun in 1994. Fish collections revealed an abundant alewife population and a small population of large, nearly obese walleye (Peters et al. 1995). In this study we investigated seasonal changes in W_r to determine if there was a relationship to prey availability for walleye in Lakes McConaughy and Ogallala.

Methods

Fish Collections

Walleye were captured in Lake McConaughy from May to October 1995, in Lake Ogallala from May to October 1994, and April to October 1995. Walleye and prey fish were captured with variable mesh gill nets 45.7 meters long and 1.8 meters deep, consisting of six 7.6 m panels of (1.9, 2.5, 3.2, 3.8, 5.1 and 7.6 cm) nylon knotted mesh, as used in the sampling protocols set by the Nebraska Game and Parks Commission for standard fish surveys (Zuerlein and Taylor 1985). Nets were set perpendicular to the shoreline and contents of each net were sorted for walleye and prey fish species. Ten, 30 minute trawls with a three meter otter trawl, were used to assess abundance of YOY prey fishes in Lake McConaughy. Trawling in Lake Ogallala is impractical, so frame nets, beach seines and electrofishing were used as additional sampling methods in Lake Ogallala. Walleye were measured for total length (TL) in mm, weighed (g), and scales were taken for aging. Prey fish were measured for TL (mm). We recorded the number and species of all prey fish captured in gill nets to obtain a prey species profile. Relative abundance of all prey species per 10 mm size class, were compiled by reservoir and season. The length limit of prey vulnerable to walleye predation was determined from the longest prey of each species found in stomachs from a concurrent food habits study. Prey longer than this length limit were not considered available to predation. Data collected from June through September in Lake McConaughy, were combined with fall standard surveys conducted in October 1995, by Nebraska Game and Parks Commission Fisheries Biologists. This was possible due to the use of identical sampling gear, fished in the same manner at the same locations. W_s was calculated using the regression equation, $\log_{10} W_s$ (g)= -5.453 + 3.180 $\log_{10}$ Total length (mm) from Murphy et al. (1990), and W_r was calculated by the equation, W_r=(weight in grams/ W_s) x 100 (Anderson and Wege 1978). Walleye over 150 mm were analyzed by 50 mm length class and season, with May through July representing the early summer, August-September the late summer, and October the fall season. Walleye from Lake Ogallala, were analyzed for differences in W_r by year, season and length class. Lake McConaughy walleye were analyzed by season, location and length class. Comparisons using analysis of variance (PROC GLM), correlation analysis (PROC CORR), and orthogonal contrasts in least squares mean comparisons were conducted with Statistical Analysis Software (SAS Institute 1988).

Results

Fish Collections

A total of 459 walleye were collected from Lake McConaughy and Lake Ogallala. The walleye population in Lake McConaughy is dominated by age-1, 2, 3 fish. In Lake Ogallala the walleye population is not subjected to significant harvest pressure, and has a higher frequency of older individuals within the population. The length limit of prey vulnerable to predation was set at 200 mm for all prey species, as determined from the concurrent food habits study, in which a 475 mm walleye consumed a 196 mm alewife. Prey captured in Lake McConaughy were primarily alewife and gizzard shad, with few yellow perch and white sucker (Figure 3). The most abundant prey were above 160 mm for all seasons (Figure 8). In Lake Ogallala, alewife were more abundant than yellow perch, gizzard shad and white sucker (Figure 9). The most abundant prey were between 140-190 mm in 1994 (Figure 10), and between 150-180 mm in 1995 (Figure 11). Catch per unit effort for alewife was higher in Lake Ogallala (62.2 in 1994, 51.2 in 1995) than in Lake McConaughy (27.5 in 1995).

No YOY alewife, yellow perch, or white sucker, and only 1 YOY gizzard shad were captured from 59 nets in Lake McConaughy, and trawling captured only 5 YOY gizzard shad. Only one walleye stomach in the Lake McConaughy food habits study contained YOY fish. In Lake Ogallala, small prey fish were captured with frame nets, beach seines and electrofishing in addition to variable mesh gill nets in 1994 and 1995 (Figures 12-13).

Statistical Analysis

ANOVA detected no differences in mean W_r between locations in Lake McConaughy (p=.517) or between years in Lake Ogallala (p=.2877). There was a significant difference in mean W_r by season in Lake McConaughy (p=.0004), but not in Lake Ogallala (p=.429). The mean W_r of walleye in Lake McConaughy increased in fall from early and late summer levels (p=.0001), but there was no difference between early and late summer (p=.397). Length class mean W_r was significantly different in both Lake McConaughy (p=.0001) and Lake Ogallala (p=.0007). Individual walleye lengths and W_r were positively correlated (p=.0001). Plots of W_r by length class at capture for walleye in Lake McConaughy (Figure 14), and Lake Ogallala (Figure 15), exhibited a positive relationship between length class and W_r. Length class frequencies are not weighted in ANOVA, and significant differences can be produced from unequal capture proportions such as those observed in Lake McConaughy and Lake Ogallala (Figures 16-17). If W_r changes seasonally, the ANOVA comparisons between classes (locations, lengths and years) will be confounded by seasonal influences because of the positive correlation between length and W_r. Likewise between season, location and year comparisons with ANOVA will be confounded by length influences.

To accurately detect seasonal differences in W_r, comparisons must be made by length class per season within each population. Least square mean comparison in SAS yields a weighted W_r per 50 mm length class in each season and tests for significant differences (α=.05). Using this method we found no differences per length class per season between 1994 and 1995 in Lake Ogallala, and combined the data. When testing within length classes by season in Lake McConaughy we found significant difference among all seasons, which is contrary to the ANOVA result. To determine the influence of season and prey availability on walleye, adjacent length classes of walleye with similar W_r, were grouped and orthogonal contrasts used to test for differences. During the early summer in Lake McConaughy, walleye between 200 to 650 mm were grouped into two W_r classes (Figure 18). Walleye between 200 to 350 mm with a mean W_r of 82.2 and a standard error of ± 1.48, were significantly different (p=.0055) from those between 350 to 650 mm with a mean W_r of 93.3 (± 1.62). In late summer three groups of walleye emerged, and they ranged from 200 to 350 mm, 350 to 500 mm, and 500 to 700 mm, with W_r of 76.1 ± 1.80, 90.2 ± 1.57, and 97.4 ± 4.11 respectively, with differences of p=.0074 and p=.041 (Figure 19). By fall three groups remained although shifted 50 mm longer, 250 to 400 mm, 400 to 550 mm, and 550 to 700 mm, with W_r of 92.0 ± .84, 98.0 ± .93, and 104.0 ± 1.57 with differences of p=.0042 and p=.001 (Figure 20). In Lake Ogallala, early summer walleye were grouped into two ranges of similar W_r, 200 to 600 mm (95.3 ± 1.25), and 600-700 mm (106.6 ± 3.33) with a difference of p=.035 (Figure 21). Two groups were also present in late summer, 200-400 mm (75.8 ± 3.02), and 400-650 mm (96.1 ± 1.19), with a difference of p=.0001 (Figure 22). But by fall there was no significant difference (p=.42) among length classes (Figure 23).

Discussion

Prey Availability

Prey abundance and prey availability are the factors that most impact the growth, condition and survival of walleye populations (Parson 1971, Forney 1974, 1977, Swenson and Smith 1976, Kelso and Ward 1977, Knight et al. 1984, Hartman and Margraf 1992). Partitioning of availability can be influenced by cover, thermal segregation or prey size (MacLean and Magnuson 1977, Swenson 1977, Ryder and Kerr 1978, Adams et al. 1982, Knight et al. 1984, Tisa and Ney 1991, Rice et al. 1993). Segregation by size, impacts the portion of the walleye population unable to consume the most abundant prey (Forney 1974, Madenjian 1991, Phillips et al. 1995). Walleye are gape limited and mouth gape increases as a function of body length (Hambright 1991, Madenjian 1991). The length of prey that walleye can consume averages 28% of body length, with a maximum of 44% (Parsons 1971, Nielsen 1980, Knight et al. 1984). Our results coincide with a range of 11.5-44% and an average of 29%. Walleye that can consume the most abundant size throughout the year are not subjected to seasonal fluctuations of prey availability (Wagner 1972, Swenson 1977, Hartman and Margraf 1992, Wolfert and Bur 1992). Small walleye prey on YOY or juvenile fish whose abundance and size fluctuate seasonally (Parsons 1971, Kelso and Ward 1977, Knight et al. 1984, Lyons 1987, Jackson et al. 1993). As seasons, habitats, and prey abundance change, walleye limited to smaller prey alter their predation strategy (MacLean and Magnuson 1977, Knight et al. 1984, Hartman and Margraf 1992). The presence of large year classes of yellow perch or alewife may buffer other prey species from walleye predation (Wagner 1972, Forney 1974, Lyons and

Magnuson 1987). Gizzard shad rapidly outgrow susceptibility to predation by a majority of the walleye population (Ney 1981), while alewife seldom grow longer than 240 mm in freshwater (Carlander 1969). The netting and trawling results in Lake McConaughy, and the low incidence of YOY fish in walleye stomachs, indicate a low abundance of small prey. In Lake Ogallala we found a much higher relative abundance of small prey.

Seasonal Changes in W_r by Length Class and Prey Availability

Walleye (>500 mm) in Lake McConaughy increased their W_r throughout the seasons because the majority of prey were less than 35% of their total length. With the exception of early summer walleye (600-700 mm) in Lake Ogallala which includes some prespawn captures, W_r increased throughout the seasons for fish more than 400 mm, due to a smaller average prey length (<160 mm) and an overall greater abundance of alewife. The majority of prey were alewife (160-190 mm) in Lake McConaughy and unavailable to predation (>40% of body length) by walleye <350 mm. These walleye were gape limited to smaller less abundant prey, and consequently had a higher incidence of empty stomachs (Figure 2). Walleye (>350 mm) in early summer split into two groups, 350-500 mm and 500+mm. The W_r of 350-500 mm walleye decreased through late summer, in response to the decreasing proportion of available prey.

There were smaller seasonal changes in W_r of walleye in Lake Ogallala due to an abundance of smaller prey. In early summer walleye (200-600 mm) had a similar W_r, but by late summer walleye less than 400 mm decreased, due to a low abundance of prey less than 140 mm. By fall walleye W_r returned to early summer levels for 200-600 mm fish.

Conclusions

It appears that in Lakes McConaughy and Ogallala, there is a gradation by walleye length of the amount of time per year that available size prey is abundant, and is influenced by the rate of length increases per year for each species and the size limit that each walleye can consume. Changes in prey length structure between years or populations will result in differing amounts of time that smaller walleye endure a shortage of suitable sized prey. During these times condition will decrease and the smallest members of the walleye community will experience the poorest body condition or W_r unless alternative prey is found. Large walleye that feed on the most abundant prey throughout the year maintain higher body condition relative to small walleye. This resulted in our positive correlation between length and W_r in Lake McConaughy and Lake Ogallala.

Murphy et al. (1991) suggested that populations with relationships between length and W_r shouldn't be represented by a population mean W_r. Our study supports the assertion that a population mean W_r value will be skewed by length distribution unevenness of a sample and seasonal changes within populations. Using least squares mean comparisons in SAS, is one method that will appropriately weight by season and length class, to detect changes in W_r from biotic factors or as a function of length, and not as a result of the sampling or analysis method (Cone 1990). In reservoirs with an unstable pelagic prey base, we would expect to find variable reproductive success of prey and subsequently a relationship between length and W_r. In Lake Ogallala there was a greater abundance of smaller prey, which reduced seasonal changes in W_r.

Seasonal changes make between population comparisons difficult, unless a standardized time is used based on the ecology of aquatic systems, to determine when to make fish collections (Gabelhouse 1991). The W_r of walleye from fall collections in Lake McConaughy and Lake Ogallala show two different W_r structures. During the summer both reservoirs elicited seasonal changes, but the Lake Ogallala population returned to a single W_r following the successful utilization of available smaller prey fish. A mean W_r for Lake Ogallala could be used to compare between populations and might be indicative of a walleye population with an adequate prey base. Lake McConaughy has three W_r levels in the fall, and suggests that available prey were limited during the growing season. This may mean that a year class failure has occurred for one or several of the prey fish species.

Management Implications

This investigation is an attempt to model the impacts of limited prey availability on walleye populations in reservoirs using standardized survey information. We show that evaluating walleye populations using mean W_r values, may not be appropriate unless there is no relationship between length and W_r , and comparisons are made from collections taken in the same season. The relationship between length and W_r is easily tested using a PROC CORR statement (SAS Institute 1988). If there is no length bias in a population, and collections are made from a similar season, then a mean W_r value is appropriate. I agree with the recommendation of Springer et al. (1990), that the W_s should be used as a benchmark for comparison and not a management goal. If there is a length bias within the population, testing must be confined to similar length classes, and if neccessary by seasons. Grouping adjacent length classes with similar W_r values and testing for differences between groups may result in several levels of W_r. The lowest W_r level represents the length classes of walleye that were prey limited. This is a cost effective method for determining potential problems within the prey assemblage, since traditional methods of estimating pelagic prey is labor intensive. Prior knowledge of potential prey limitations will aid in future management plans.

Further testing of this model for structuring of W_r by prey availability and abundance is needed prior to its implementation as a management tool. Quantification of the differences and structuring of W_r levels related to less severe declines in prey availability need to be investigated. Fine tuning the appropriateness of walleye length class sizes related to yearly growth, increased definition of the seasonal changes in prey fish composition and abundances, and application of bioenergetics modeling of growth related to thermally sub-optimal habitat use, is needed to accurately predict the interactions between walleye and preyfish assemblages in Midwestern reservoirs like Lake McConaughy and Lake Ogallala.

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TABLES

Table 1. Enclosure method, walleye density, prey density, prey treatments and duration of walleye feeding experiments conducted at Lake Ogallala, Nebraska and Cedar Point Biological Station, 1995

Enclosure Method	Walleye Density	Prey density	Prey Treatments Alewife : Yellow Perch : White Sucker	Time (hrs)
Mesocosm Tanks	1	12	High 6:3:3	48
			Equal 4:4:4	
			Low 2:5:5	
		24	High 12:6:6	48
			Equal 8:8:8	
			Low 4:10:10	
Small Floating Net Pens	1	6	Equal 2:2:2	48
		12	Equal 4:4:4	
	4	6	Low 2:5:5	48
			Equal 2:2:2	
Large Floating Net Pens	4	36	High 24:6:6	72
			Equal 12:12:12	
			Low 6:15:15	

Table 2. Enclosure method, number of trials, trials with feeding, and trials considered "normal feeding", in walleye feeding experiments at Lake Ogallala, Nebraska and Cedar Point Biological Station, 1995

Enclosure Method	Total number of trials	Proportion of trials with feeding	Trials considered normal
Mesocosm Tanks	139	15 : 139	0 : 139
Small Float Pens	23	7 : 23	0 : 23
Large Float Pens	39	38 : 39	26 : 39
Total	201	60 : 201	26 : 201

FIGURES

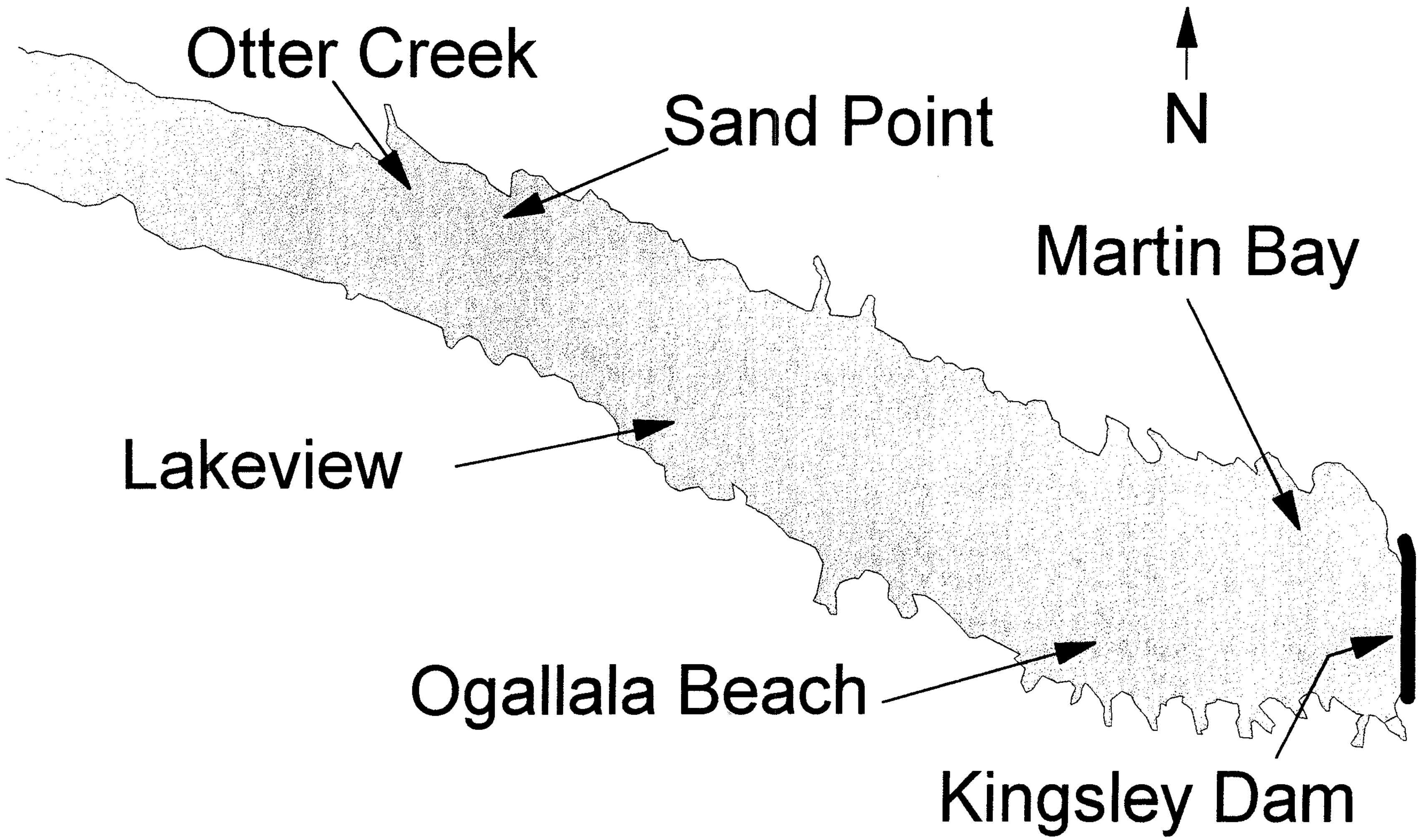

Figure 1. Walleye and prey fish sampling locations in Lake McConaughy, Nebraska, 1995

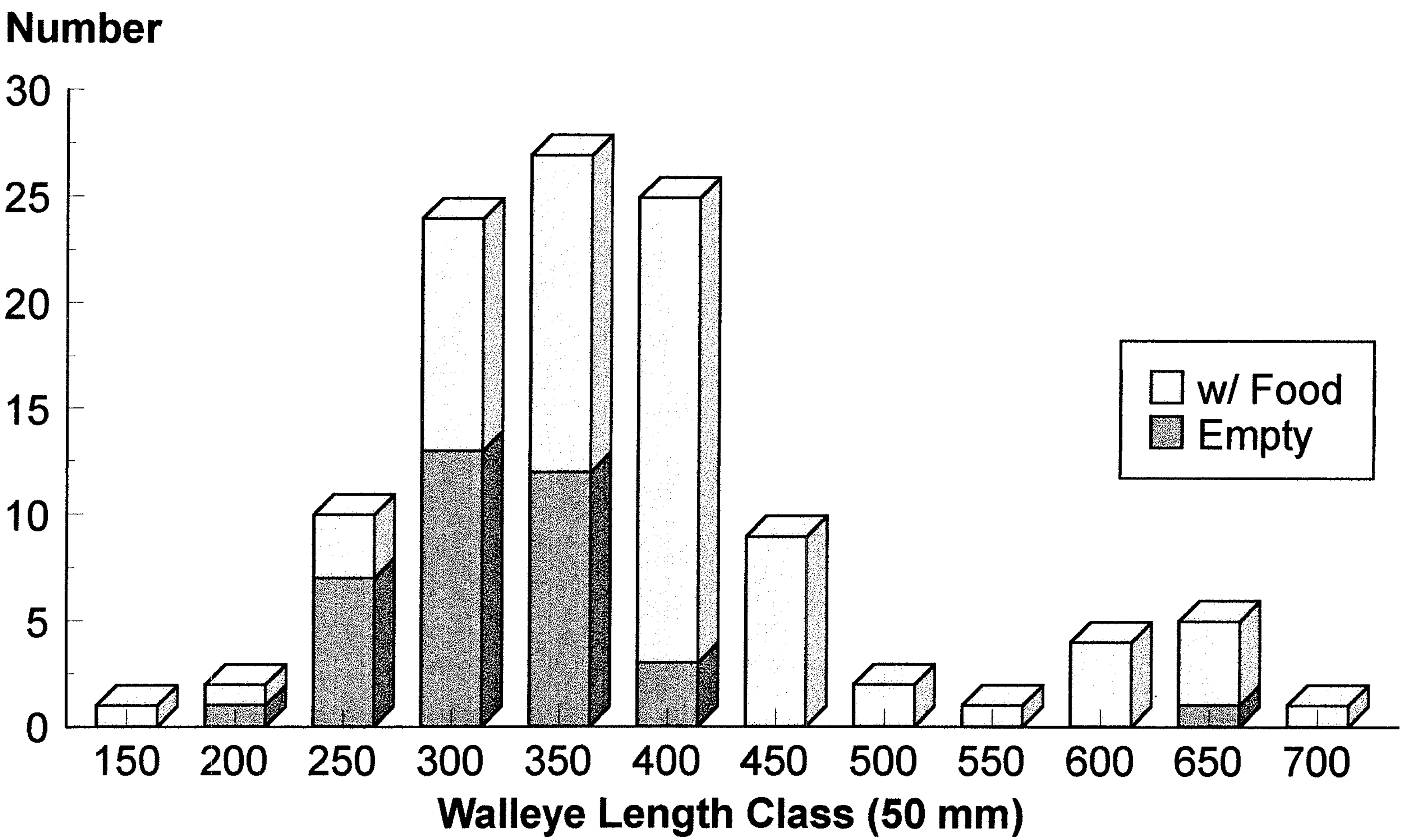

Figure 2. Walleye empty stomach frequency of occurance, from stomach content analysis study in Lake McConaughy, Nebraska, 1995

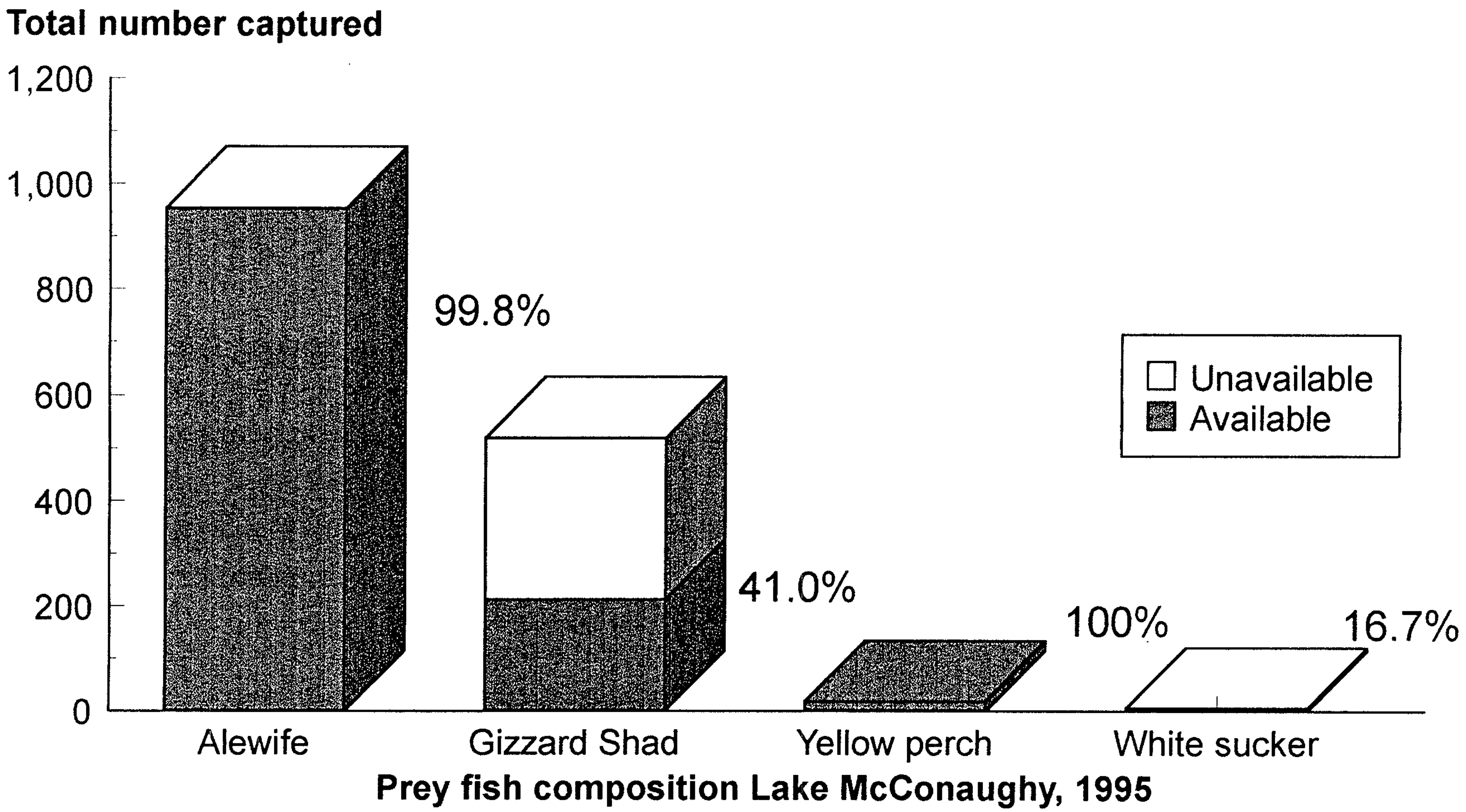

Figure 3. Percent of total number of each prey fish species captured available for predation by walleye in Lake McConaughy, Nebraska, 1995

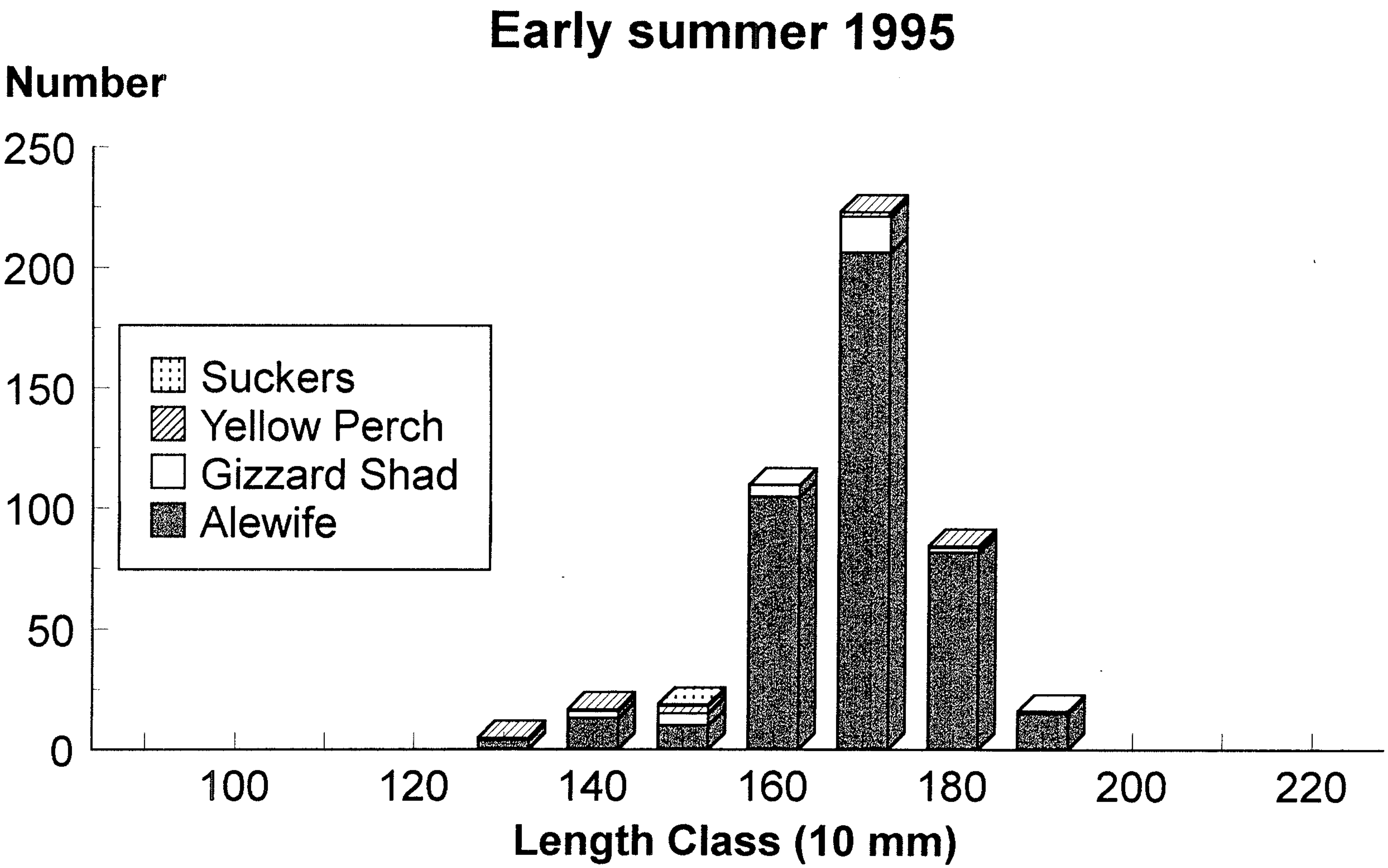

Figure 4. Length frequency by species, of prey fish captured in early summer from Lake McConaughy, Nebraska, 1995

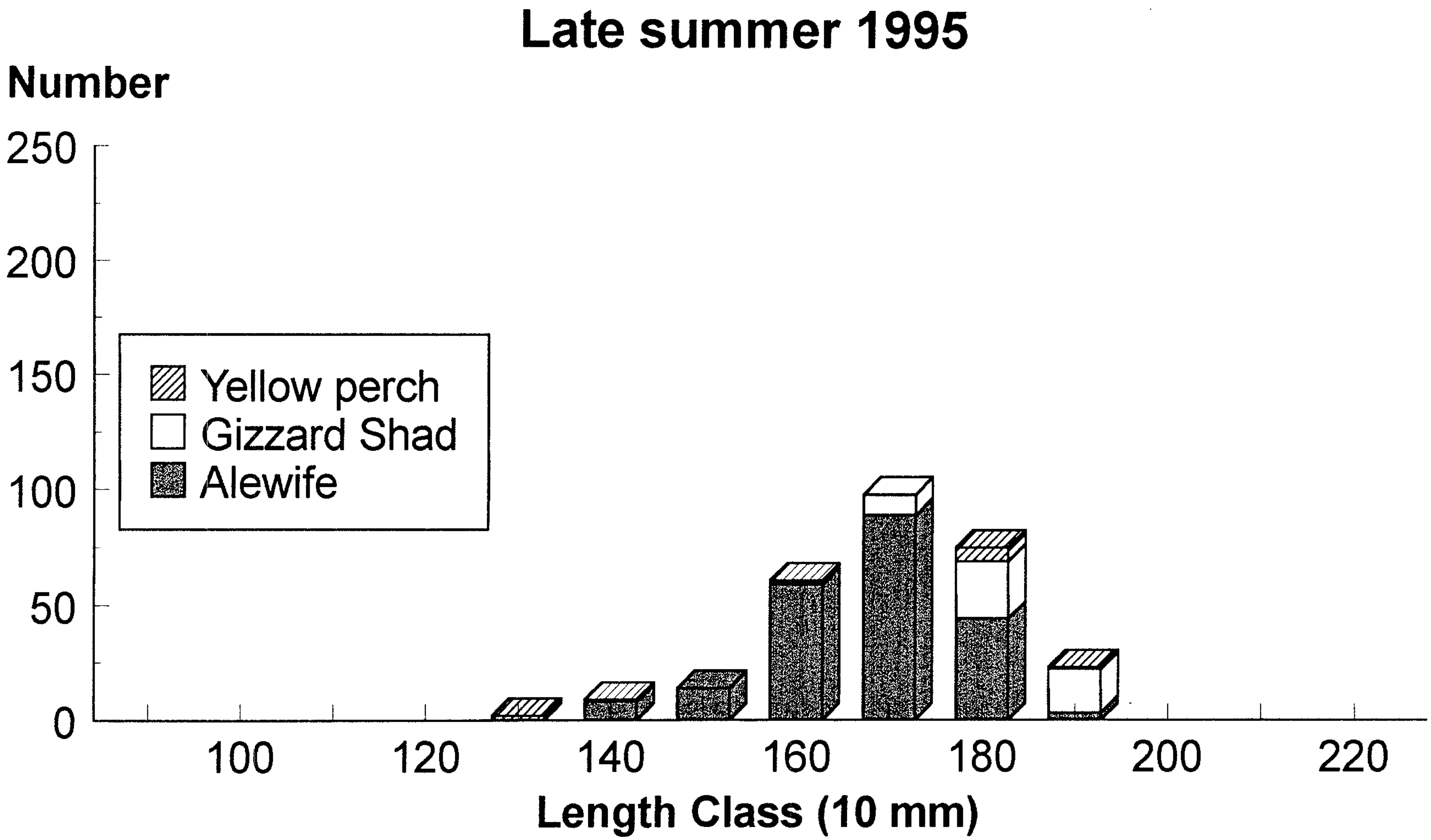

Figure 5. Length frequency by species, of prey fish captured in late summer from Lake McConaughy, Nebraska, 1995

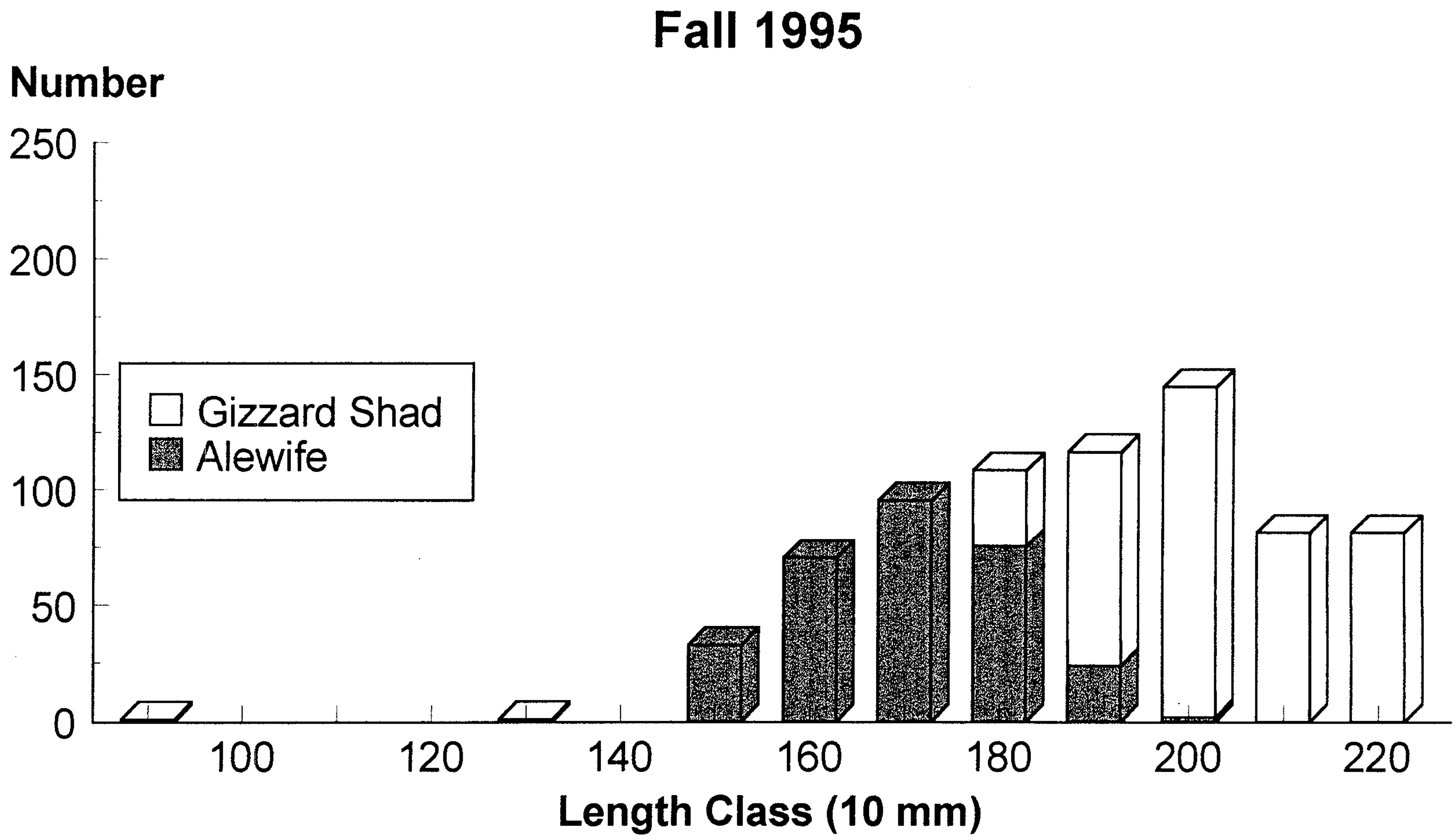

Figure 6. Length frequency by species, of prey fish captured in fall from Lake McConaughy, Nebraska, 1995

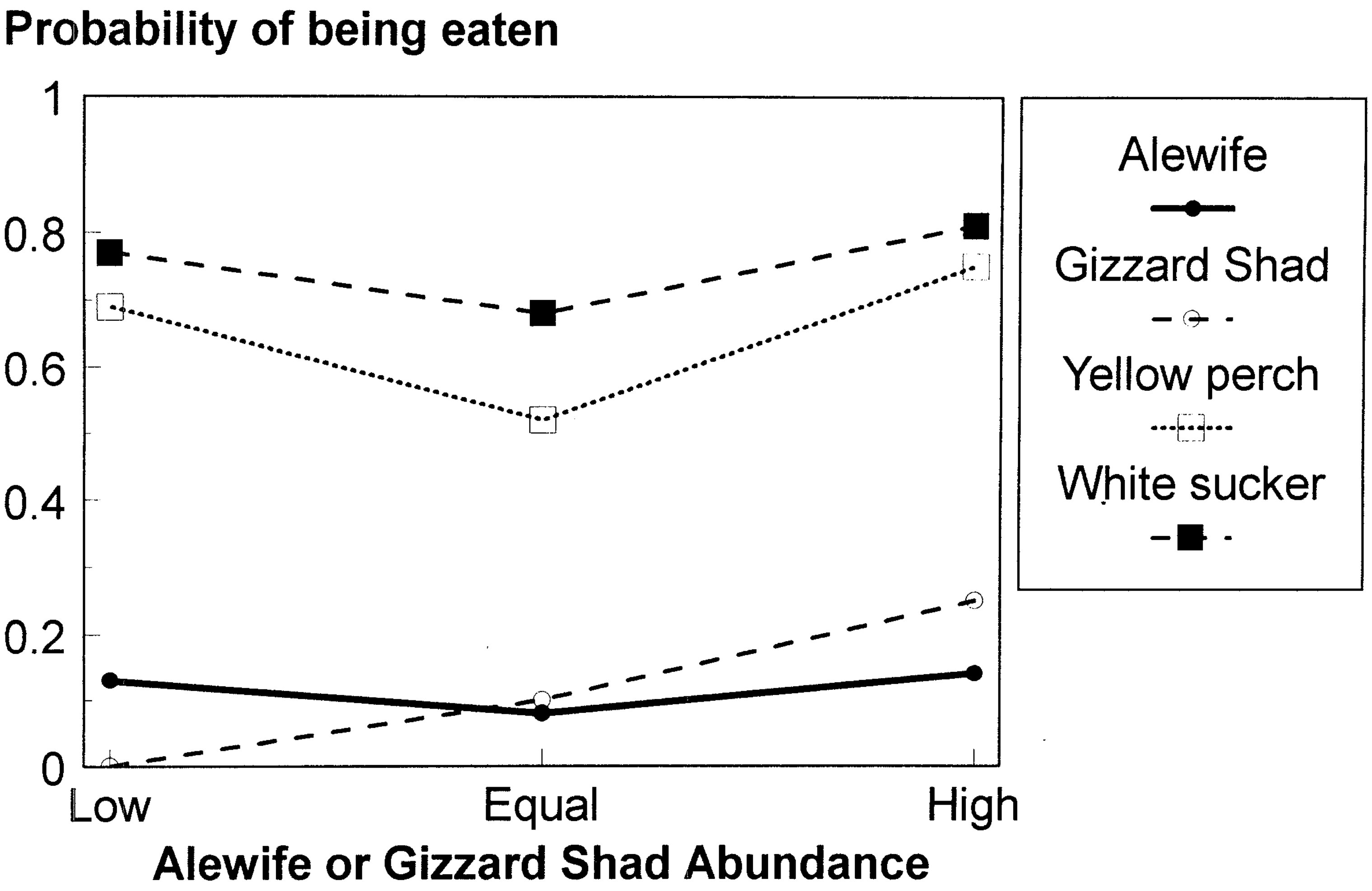

Figure 7. Maximum likelihood estimates of probability of being eaten for each prey species at each treatment level in walleye feeding experiments in Lake Ogallala, Nebraska and at Cedar Point Biological Station, 1995

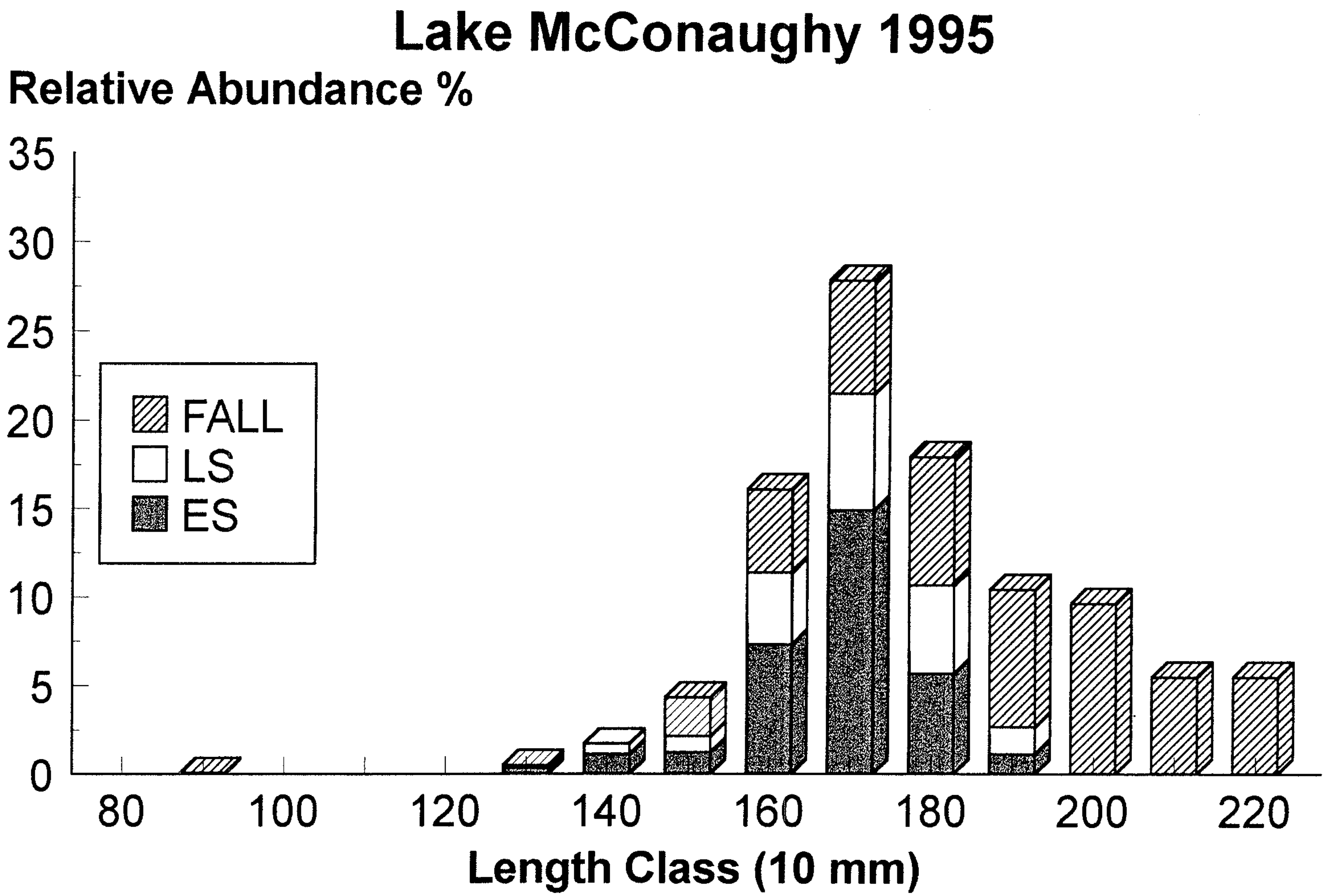

Figure 8. Relative abundance of all prey fish, by length class, captured in early summer (ES), late summer (LS), and fall (FALL) in Lake McConaughy, Nebraska, 1995

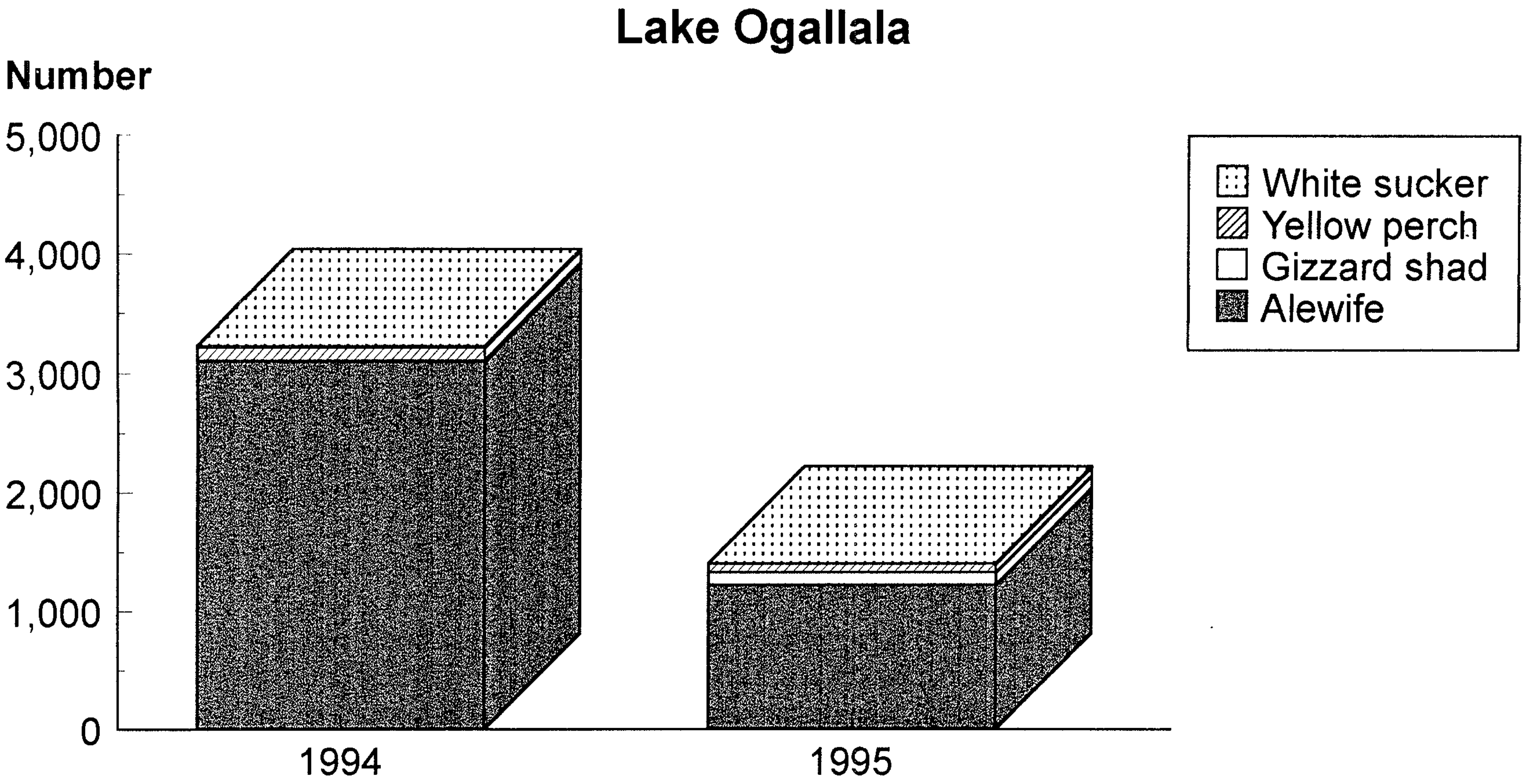

Figure 9. Total number of prey fish captured by species in Lake Ogallala, Nebraska, 1994-1995

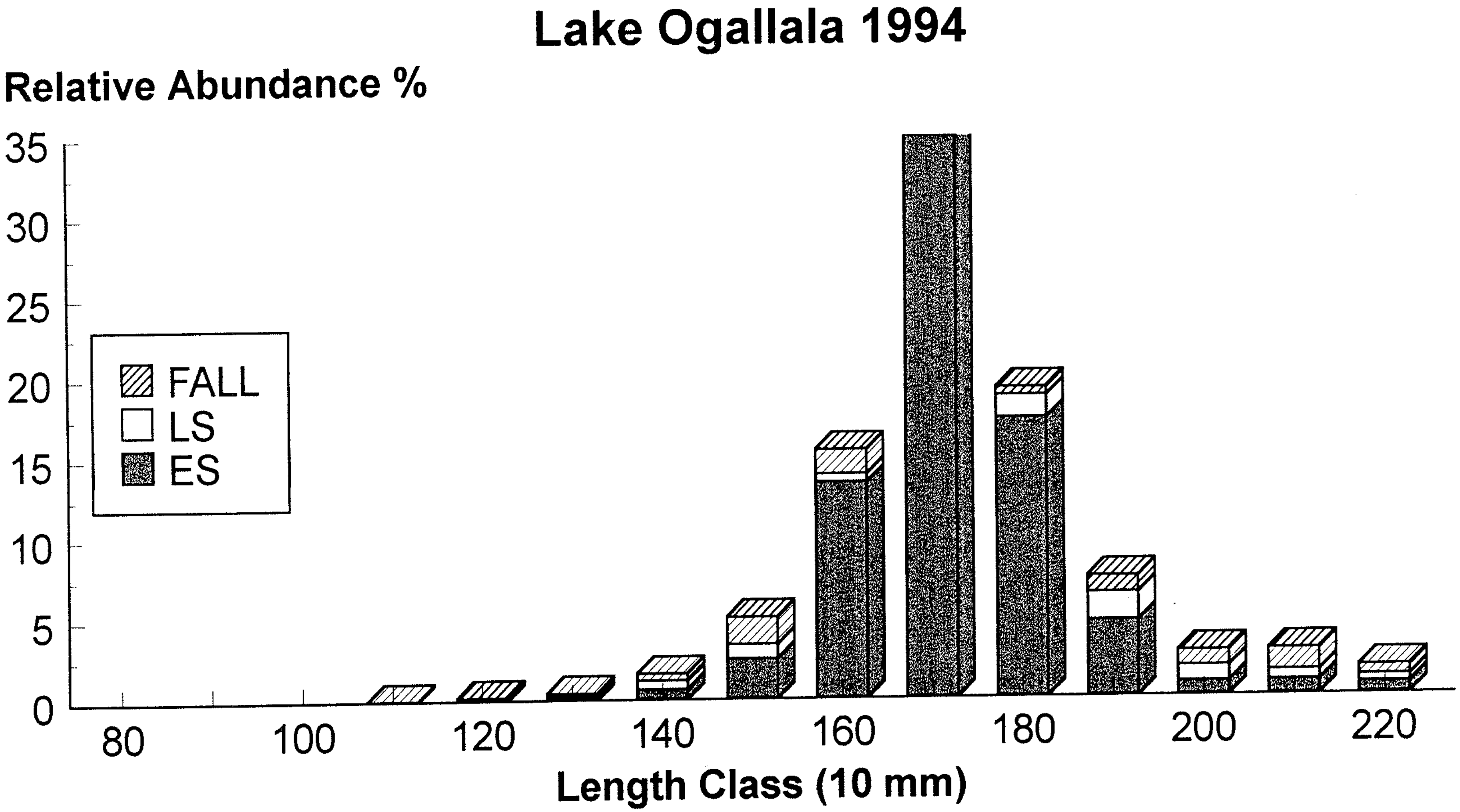

Figure 10. Relative abundance of all prey fish, by length class, captured in early summer (ES), late summer (LS), and fall (FALL) in Lake Ogallala, Nebraska, 1994

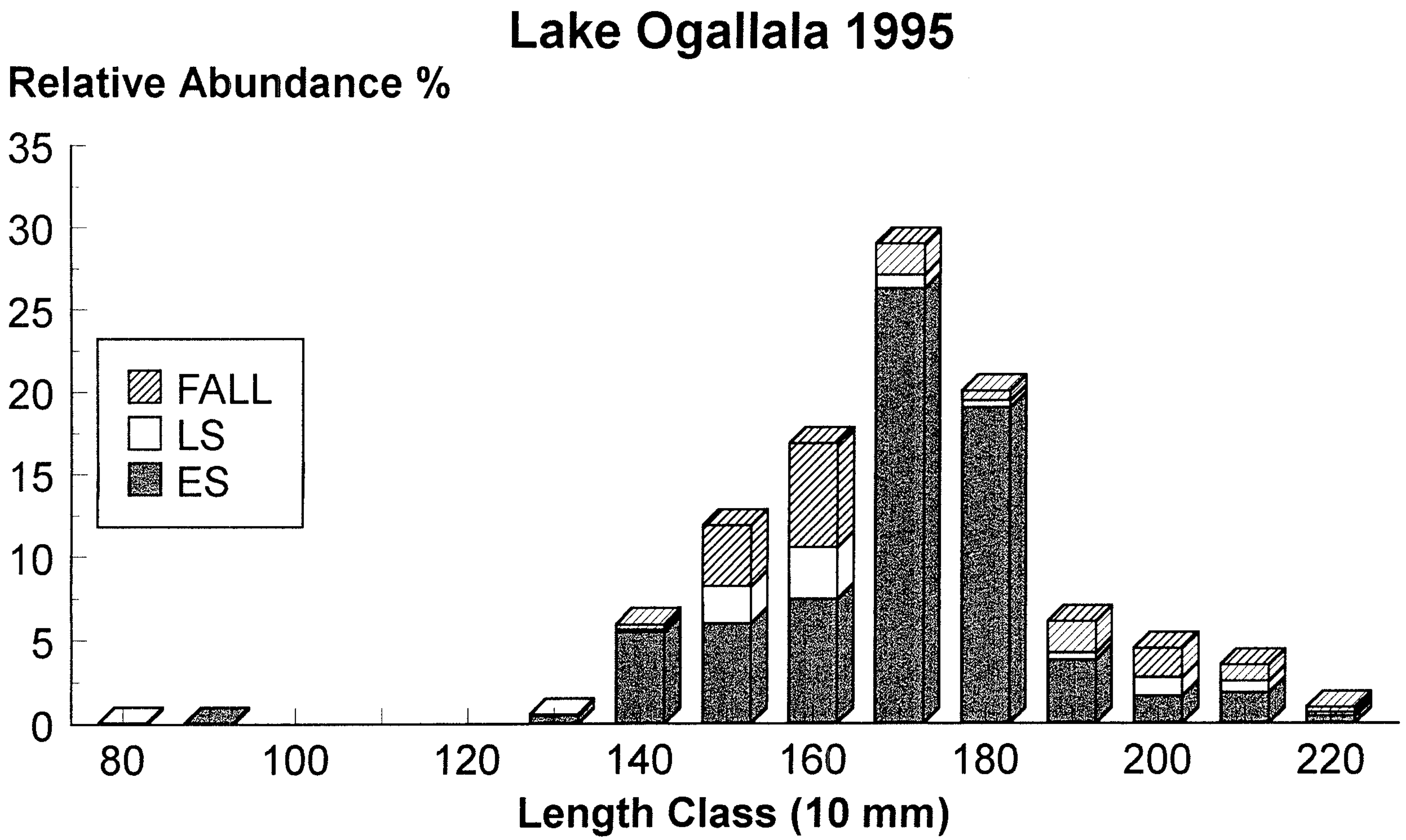

Figure 11. Relative abundance of all prey fish, by length class, captured in early summer (ES), late summer (LS), and fall (FALL) in Lake Ogallala, Nebraska, 1995

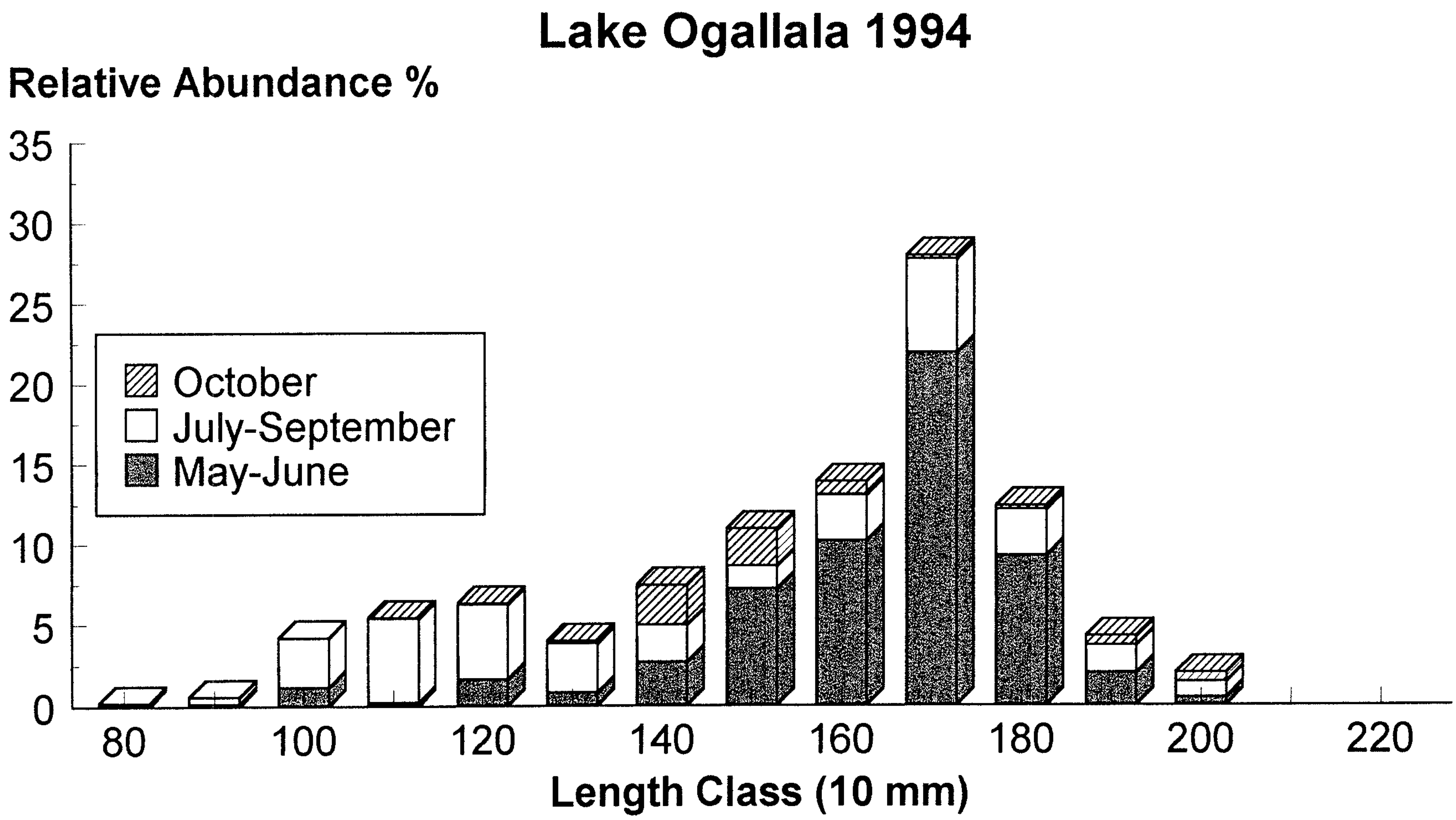

Figure 12. Relative abundance of all prey fish species by length class, captured with gill nets, frame nets, beach seines and electrofishing in May-June, July-September, and October from fish community study on Lake Ogallala, Nebraska, 1994

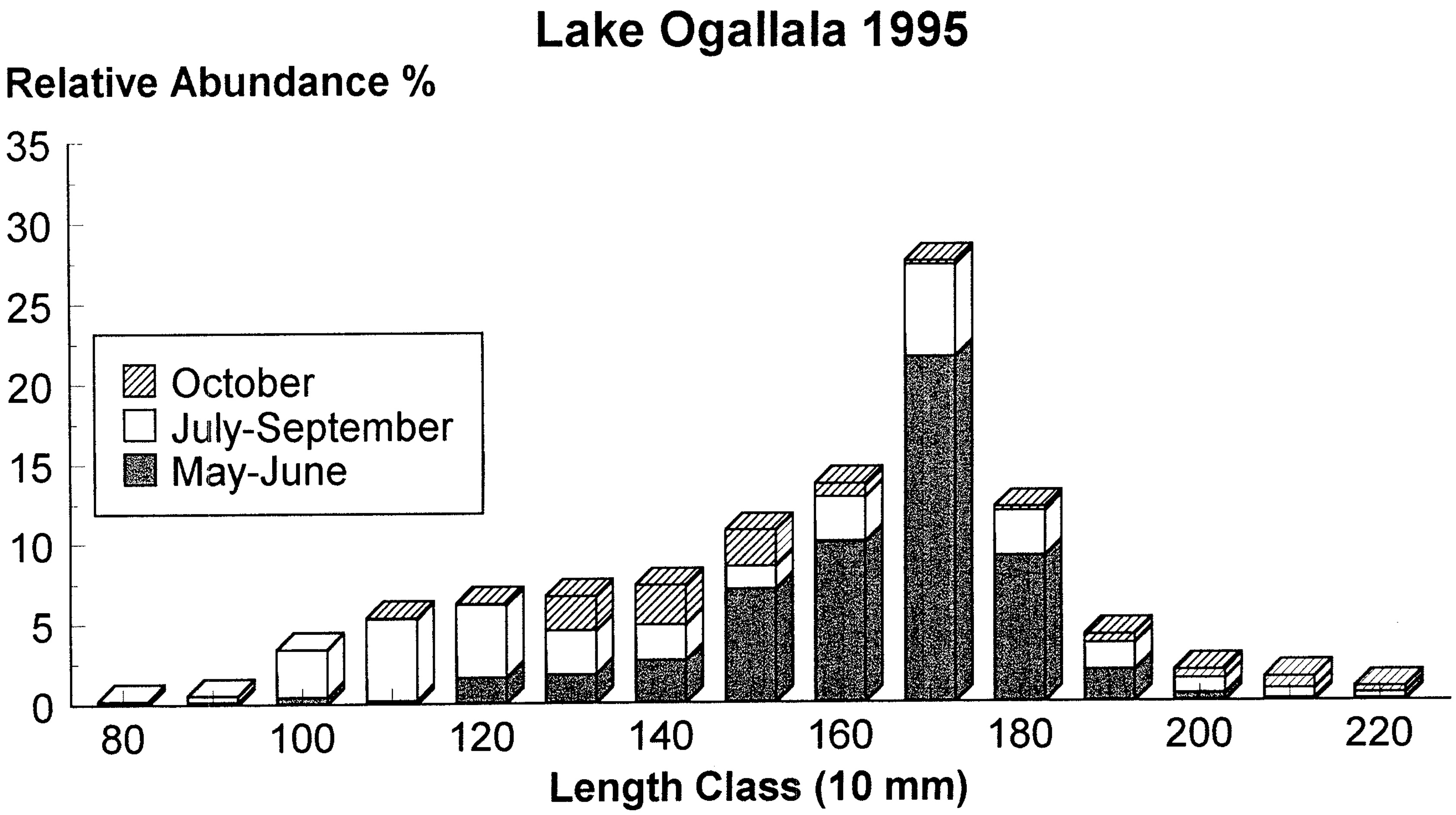

Figure 13. Relative abundance of all prey fish species by length class, captured with gill nets, frame nets, beach seines and electrofishing in May-June, July-September, and October from fish community study on Lake Ogallala, Nebraska, 1995

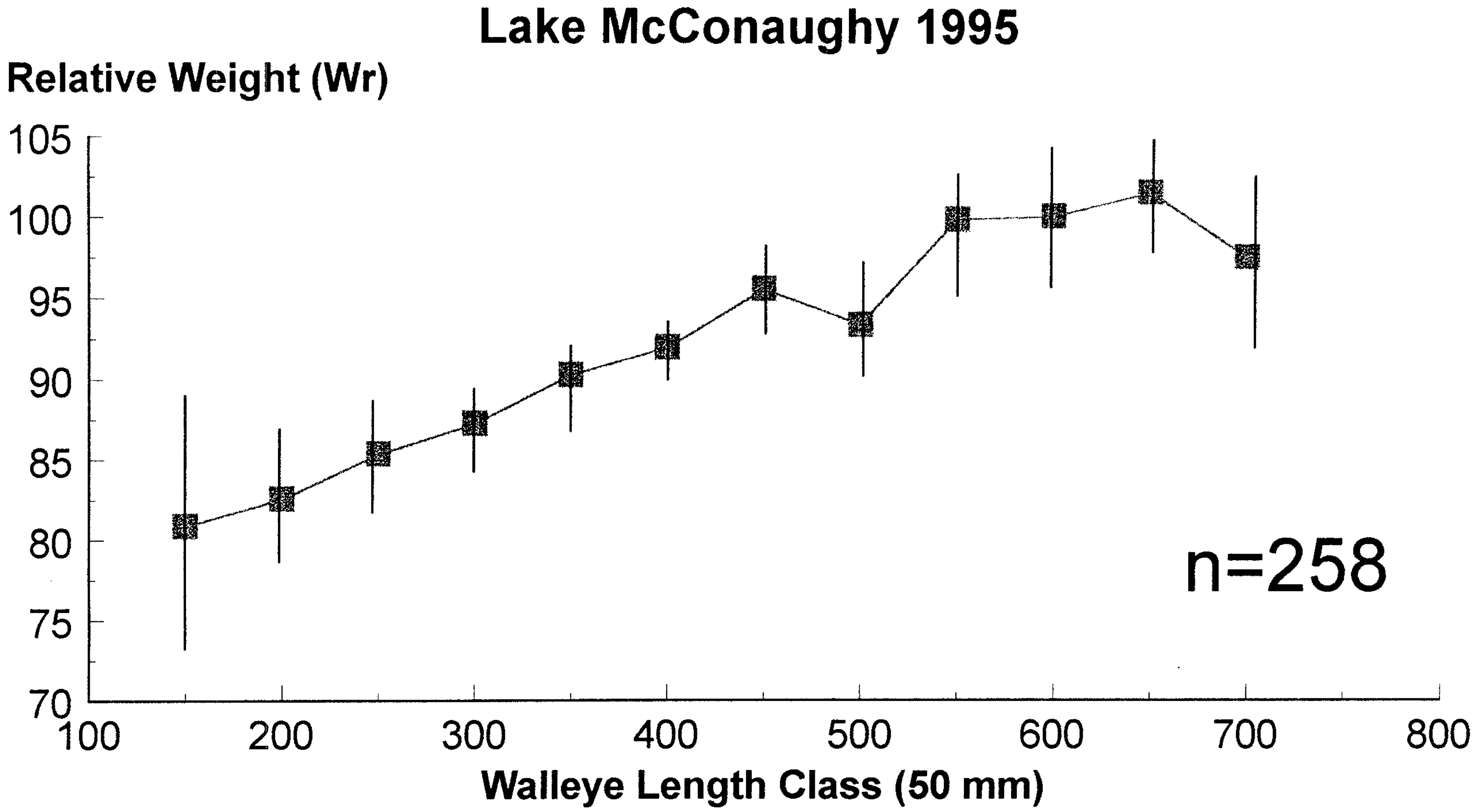

Figure 14. Relative weight (Wr) at capture (±standard error) by length class, of walleye collected in June-October from Lake McConaughy, Nebraska, 1995

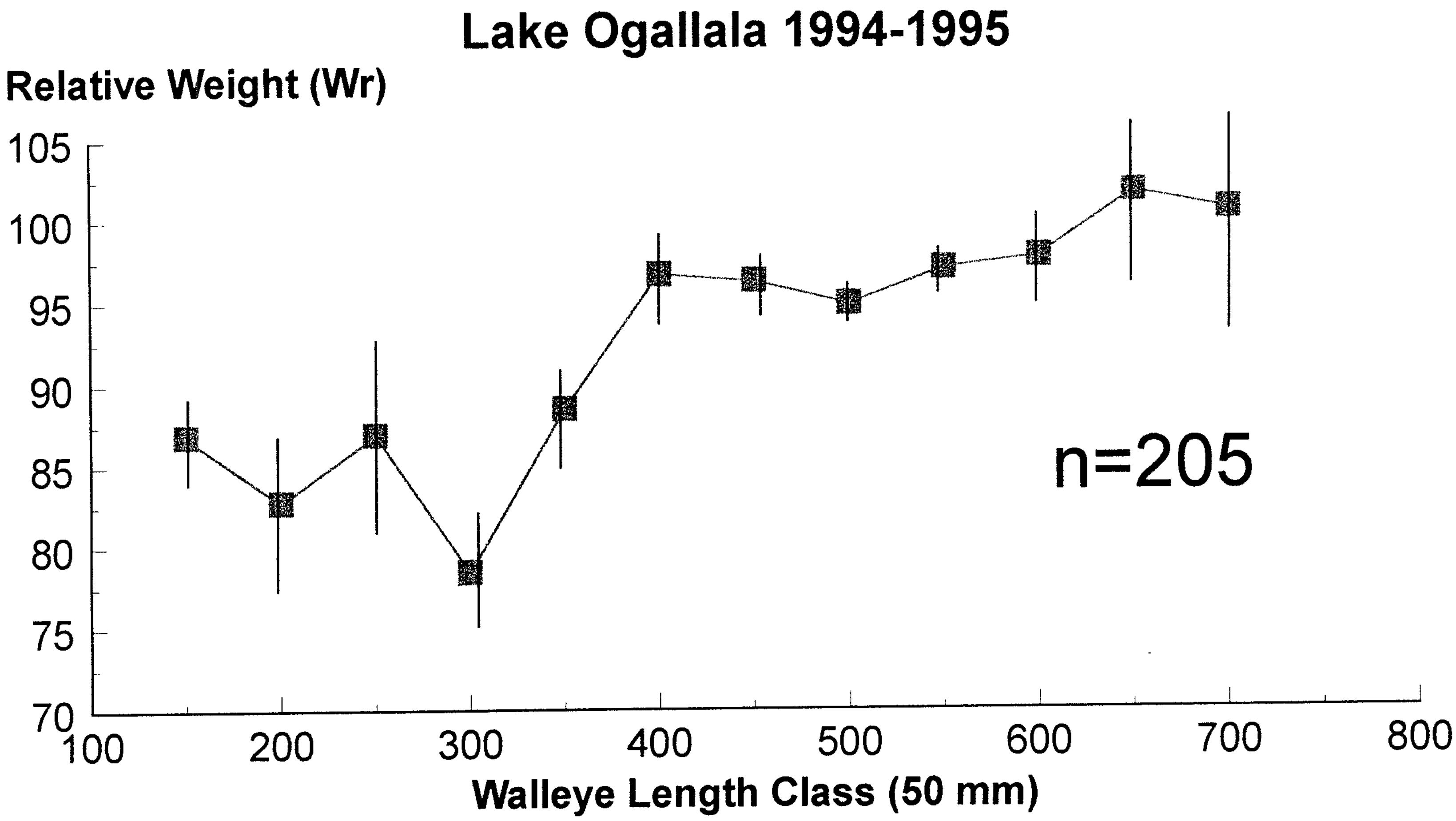

Figure 15. Relative weight (Wr) at capture (±standard error) by length class, of walleye collected in May-October from Lake Ogallala, Nebraska, 1994-1995

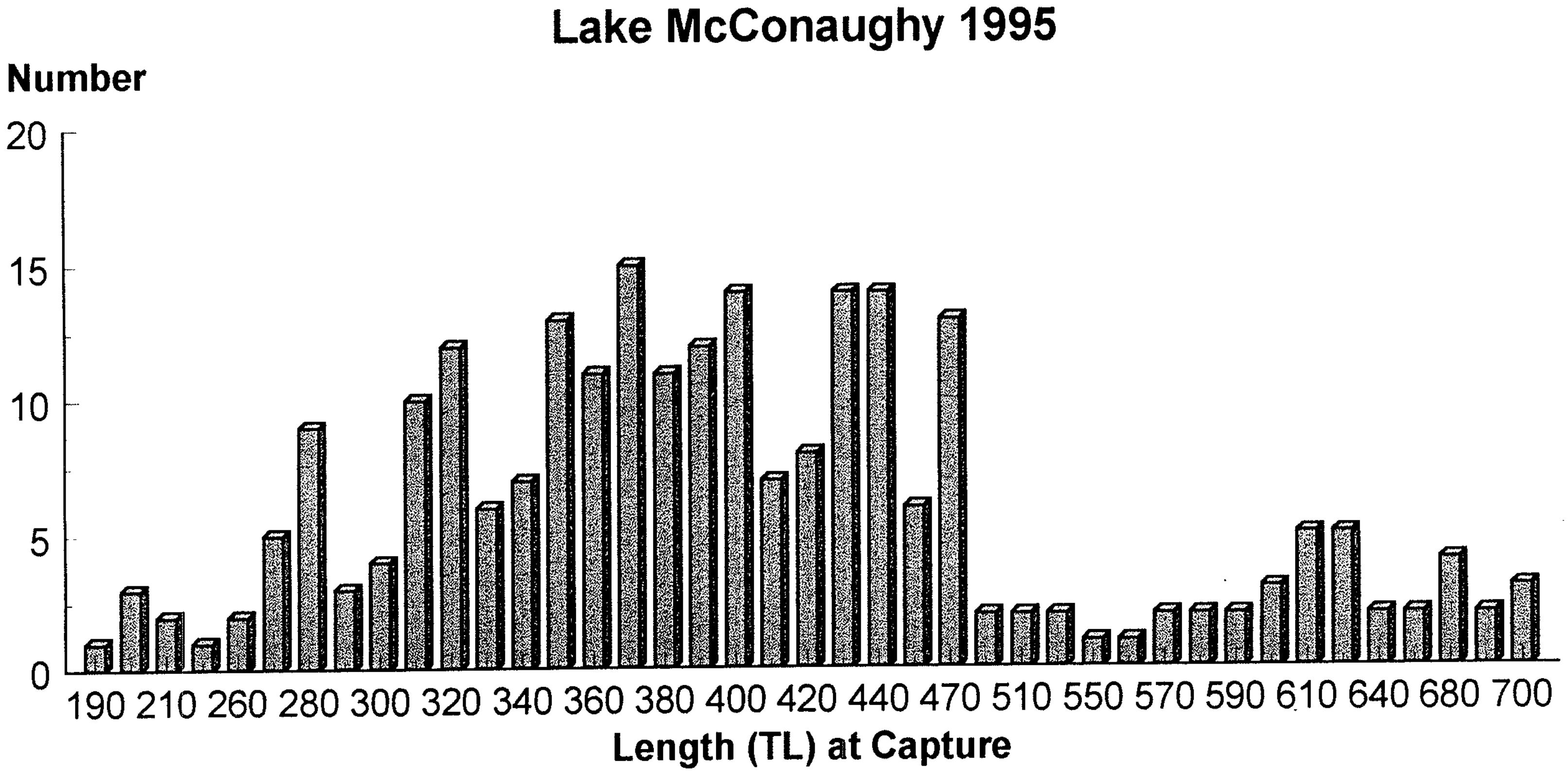

Figure 16. Length at capture of all walleye collected from Lake McConaughy, Nebraska, in 1995

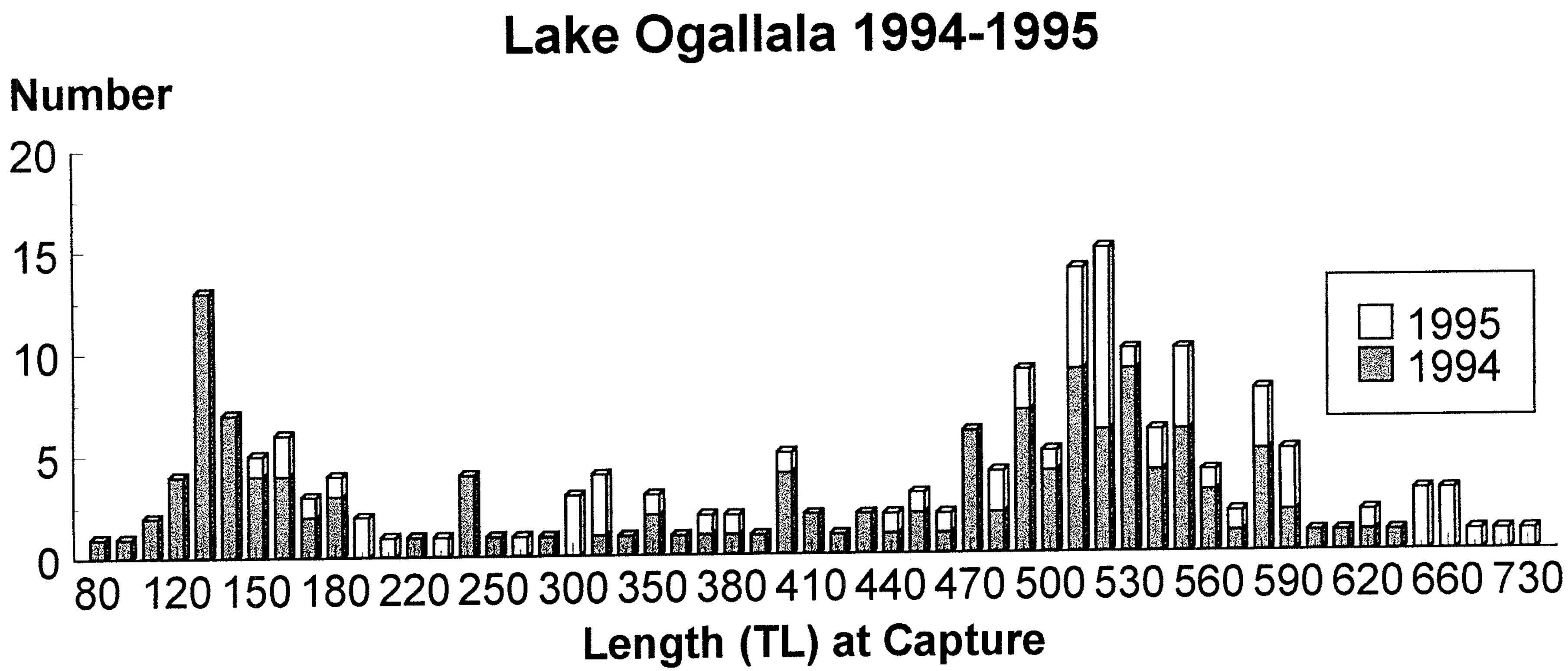
Lake Ogallala 1994-1995

Figure 17. Length at capture of all walleye collected from Lake Ogallala, Nebraska, in 1994-1995

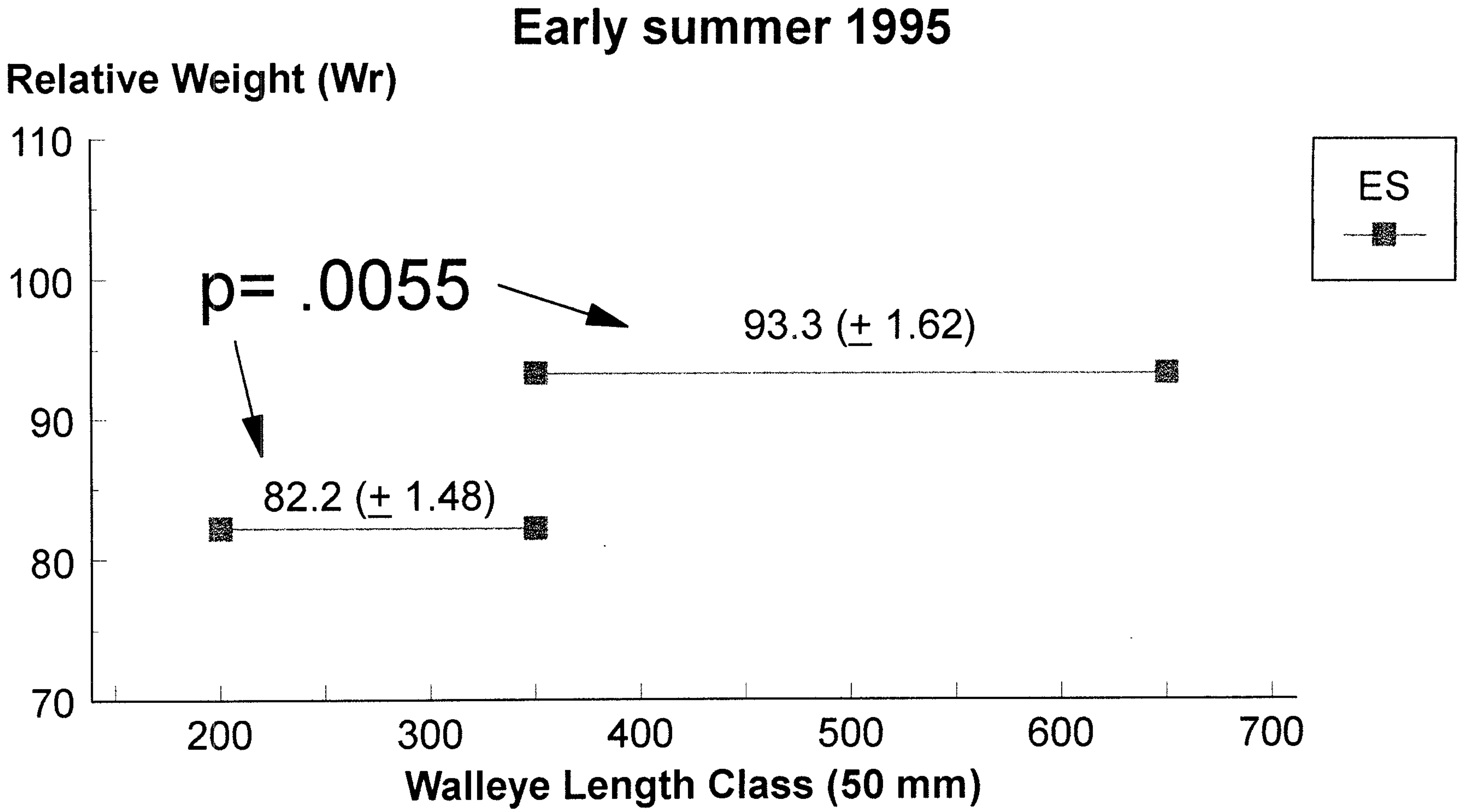

Figure 18. Relative weight (Wr) by length class (±standard error) of walleye in early summer at Lake McConaughy, Nebraska, 1995 (ES= early summer, LS= late summer, F= fall)

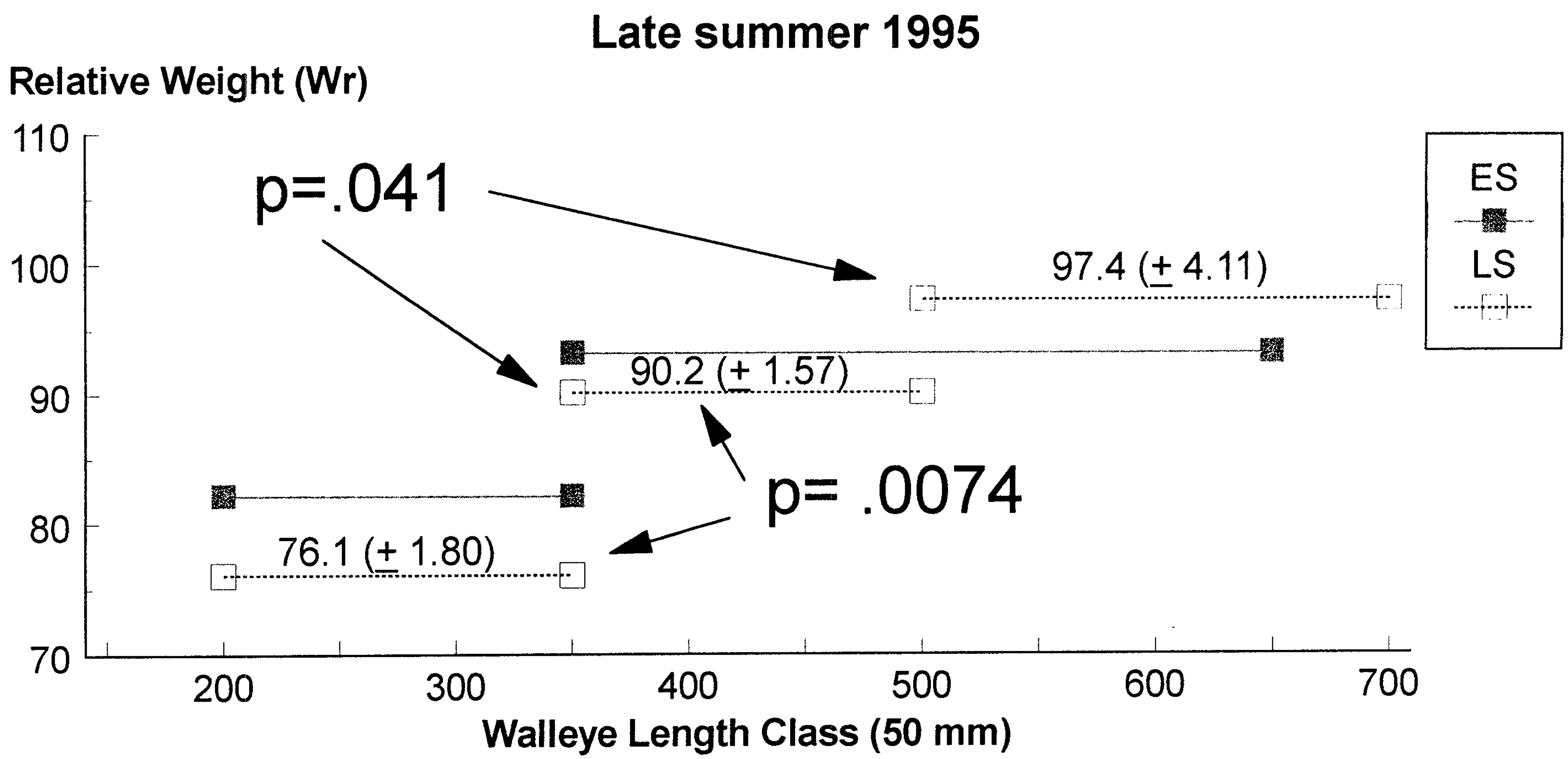

Figure 19. Relative weight (Wr) by length class (±standard error) of walleye in late summer at Lake McConaughy, Nebraska, 1995 (ES= early summer, LS= late summer, F= fall)

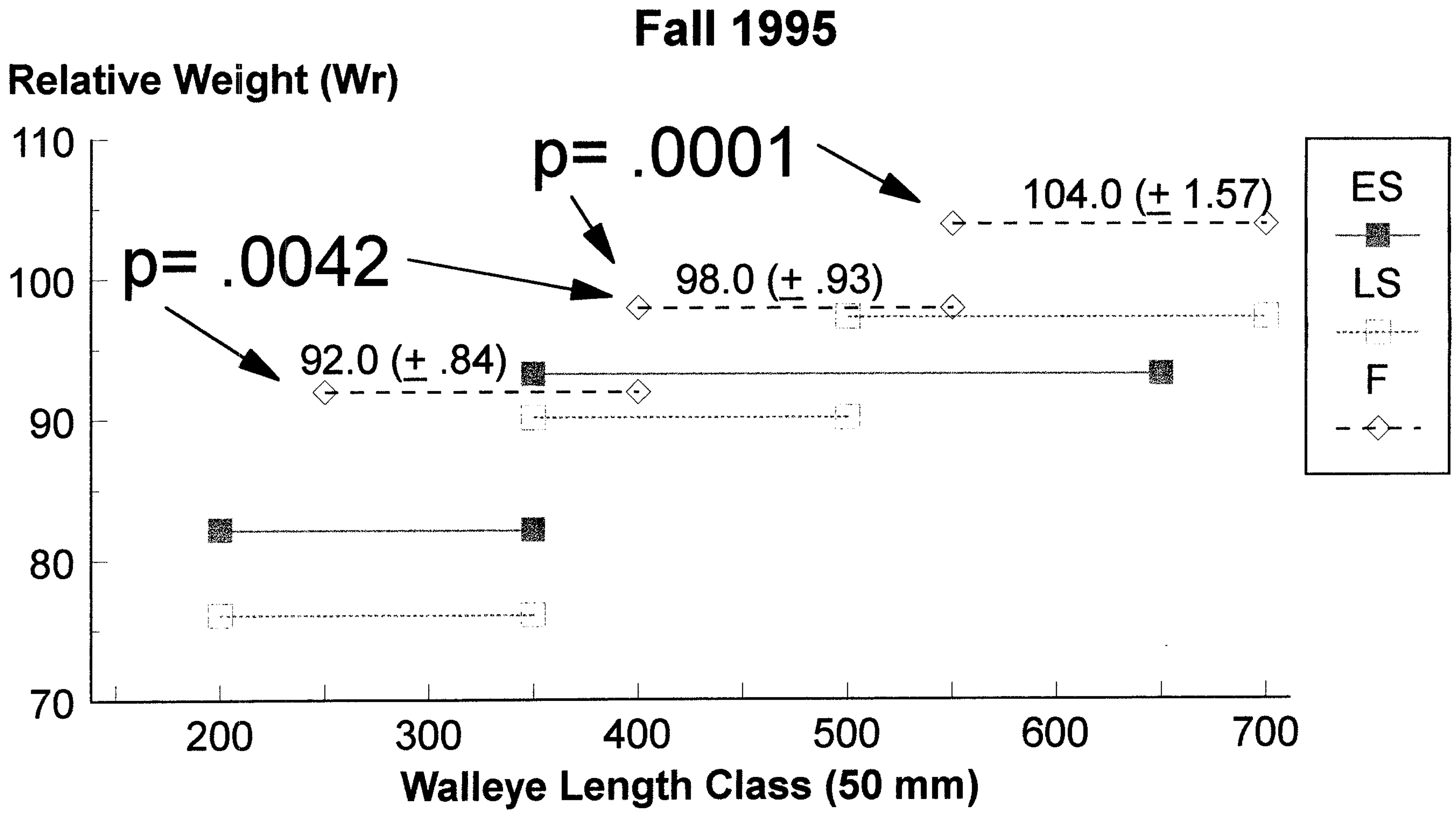

Figure 20. Relative weight (Wr) by length class (±standard error) of walleye in fall season at Lake McConaughy, Nebraska, 1995 (ES= early summer, LS= late summer, F= fall)

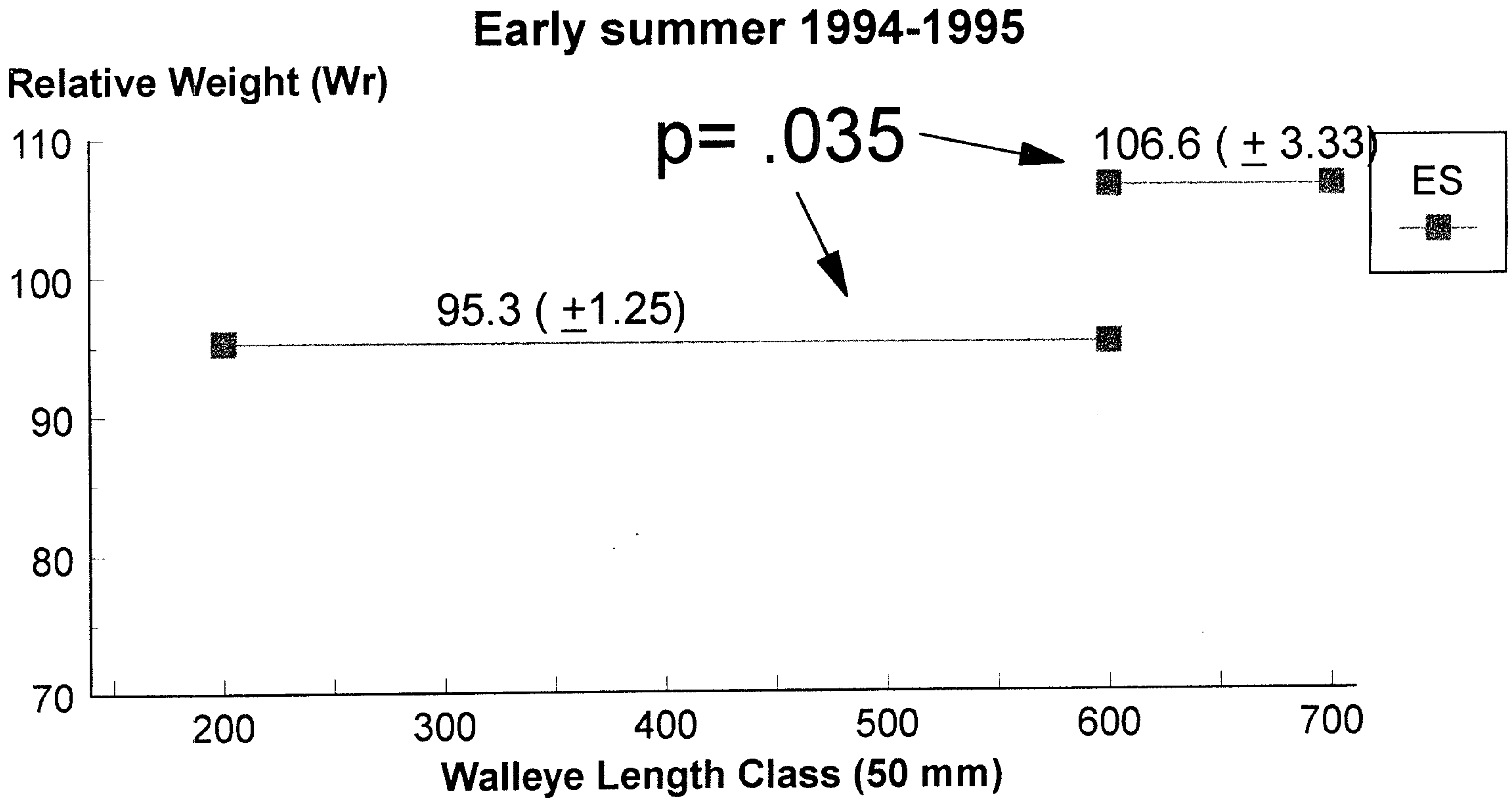

Figure 21. Relative weight (Wr) by length class (±standard error) of walleye in early summer at Lake Ogallala, Nebraska, 1994-1995 (ES= early summer, LS= late summer, F= fall)

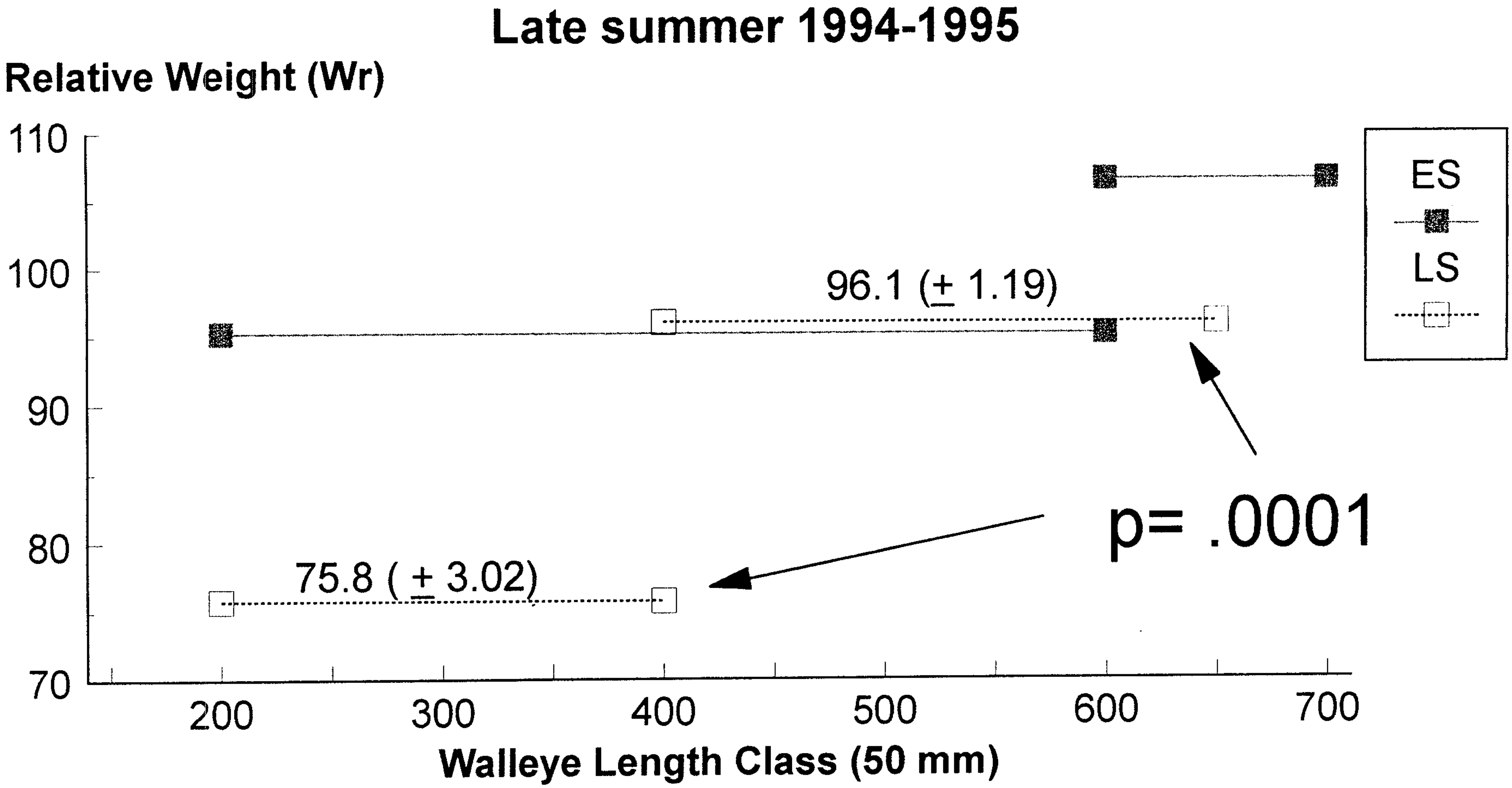

Figure 22. Relative weight (Wr) by length class (±standard error) of walleye in late summer at Lake Ogallala, Nebraska, 1994-1995 (ES= early summer, LS= late summer, F= fall)

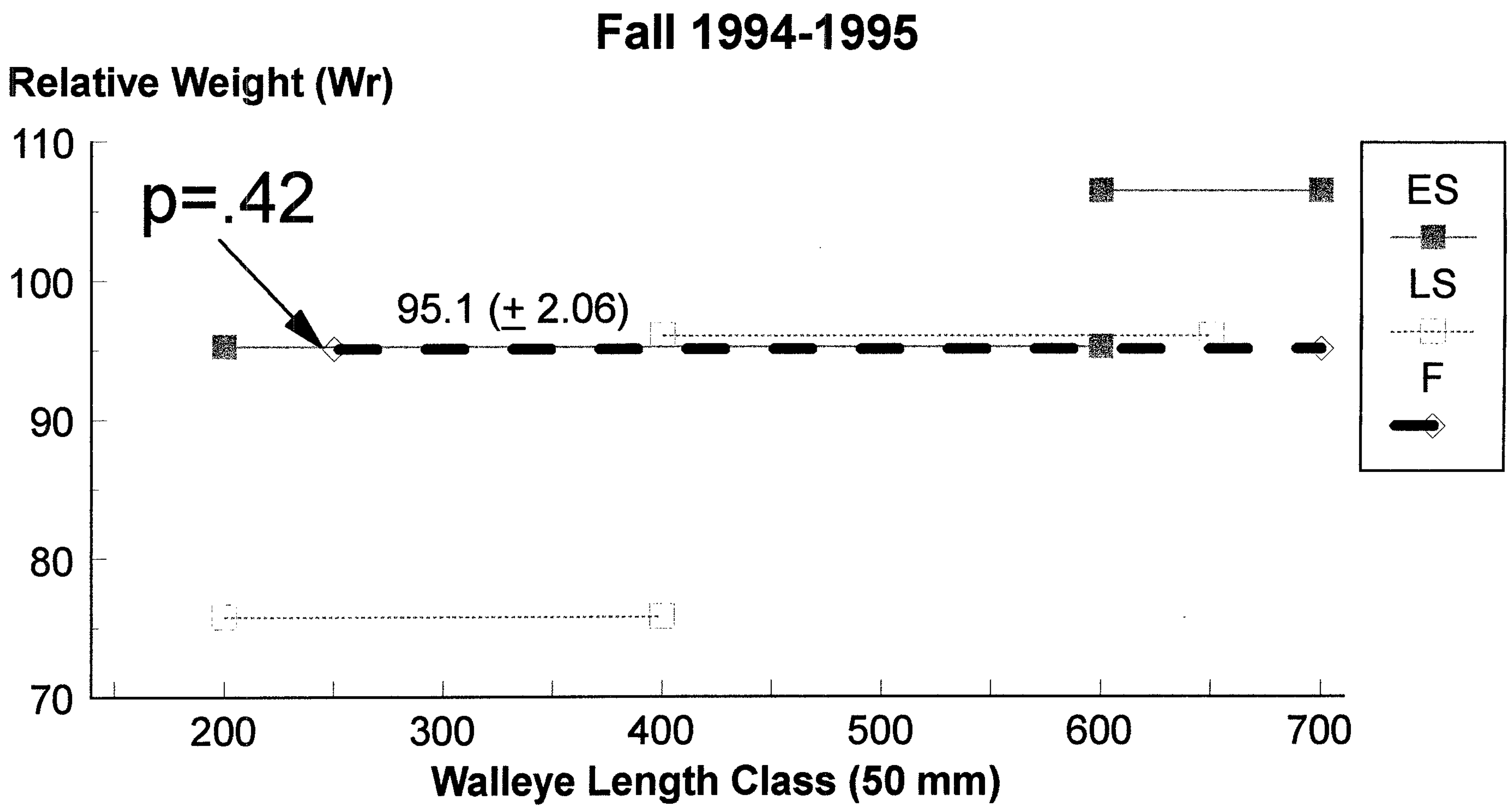

Figure 23. Relative weight (Wr) by length class (±standard error) of walleye in the fall at Lake Ogallala, Nebraska, 1994-1995 (ES= early summer, LS= late summer, F= fall)