Changes in Feeding Behaviour and the Occurrence of Cannibalism in the Early Life History of Walleye (*Stizostedion vitreum vitreum*)

by

D. Bernard McIntyre

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CHANGES IN FEEDING BEHAVIOUR AND THE OCCURRENCE OF CANNIBALISM IN THE EARLY LIFE HISTORY OF WALLEYE (*STIZOSTEDION VITREUM VITREUM*)

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D. BERNARD McINTYRE

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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ABSTRACT

Walleye began feeding on zooplankton and changed to larger prey such as insects and amphipods by midseason in their first summer of growth. The size of prey consumed increased with walleye size. The length and variation in length of minnows consumed in the laboratory increased with walleye length although the ratio of prey length to walleye length decreased. The selection of fathead minnows by walleye shifted to larger than average prey in a pond environment but not in the laboratory.

The diel feeding patterns of walleye may have been influenced by the development of the tapetum lucidum which first appeared at a body length of 27 mm and subsequently increased in size as the fish grew. Small walleye were diurnal feeders whereas larger ones tended to be crepuscular or nocturnal. Median catch per seine haul was not an adequate measure of the relative abundance of walleye in BG2 Pond. Increases in catch were probably the result of changes in habitat or behaviour, possibly related to retinal development, the transition in food type, or both.

Cannibalism was frequent at a prey to cannibal length ratio of 60 % or less. The presence of an abundant supply of fathead minnows inhibited cannibalism, and zooplankton may have reduced the occurrence of cannibalism in walleye up to 100 mm in length. The rate of cannibalism varied from 6 to 33 % per day in laboratory experiments whereas the rate of piscivory varied from 44 to 86 % per day. Cannibalism in mid-summer is an important factor limiting the production of juvenile walleye in rearing ponds but it may be reduced by making the appropriate size of prey available.

ACKNOWLEDGEMENTS

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INTRODUCTION

The study of the early life history of fishes is essential to the understanding of their interactions with the environment. All species develop rapidly in the first few months of life (Balon 1984; Blaxter 1986). During this period they are susceptible to environmental mortality which might not affect them as adults. For example, fluctuations in weather conditions can influence the strength of year classes by increasing or decreasing the mortality of eggs and larvae (Dickson et al. 1974; Pinus 1974; Busch et al. 1975). The potential effect of early mortality on later recruitment has resulted in extensive research on the early life history of economically important species (Alderdice 1985; Blaxter 1986). One such species is the walleye, *Stizostedion vitreum vitreum* (Mitchell).

Decreased commercial catches of walleye (Li and Ayles 1981b) have resulted in attempts to supplement natural populations with pond reared juvenile walleye but there have been problems with variable growth and survival (Miller 1952; Dobie 1969). There have been many attempts to solve these problems by studying the ecology of juvenile walleye in rearing ponds (Smith and Moyle 1945; Cheshire and Steele 1963; Walker and Applegate 1976; Mathias and Li 1982). Data from laboratory studies indicate that an inadequate supply of food can cause starvation and cannibalism during the onset of exogenous feeding at the postlarvae I stage (Cuff 1977; Li and Mathias 1982), a time that is referred to as the early critical period (Li and Ayles 1981a). Data from field studies indicate that late in the first summer of growth, when piscivory becomes the dominant feeding behaviour (Smith and Moyle 1945; Walker and Applegate 1976; Li and Ayles 1981a), there may be additional mortality resulting from starvation and cannibalism (Cheshire and Steele 1963; Laarman and Reynolds 1974). Most mortality occurs at the postlarvae stage during the transition to exogenous feeding (Mathias and Li 1982); therefore any additional mortality during mid-summer when the population is lower would significantly reduce production and therefore recruitment of juvenile walleye. It is difficult, however, to determine those factors influencing the occurrence of cannibalism and its impact on the population because of problems associated with field sampling.

The objectives of this study are to use both laboratory and field experiments to investigate changes in feeding behaviour that occur during the early life history of walleye, to relate these to the development of the tapetum lucidum, and changes in relative abundance and to examine the influence of these factors on the onset and consequences of cannibalism in pond reared juvenile walleye. Field experiments are designed to examine changes in seasonal and diel feeding behaviour, piscivory, the tapetum lucidum and relative abundance. Laboratory experiments are designed to examine piscivory and the effects of food type and walleye length distribution on the occurrence and potential impact of cannibalism.

METHODS AND MATERIALS

FIELD STUDIES

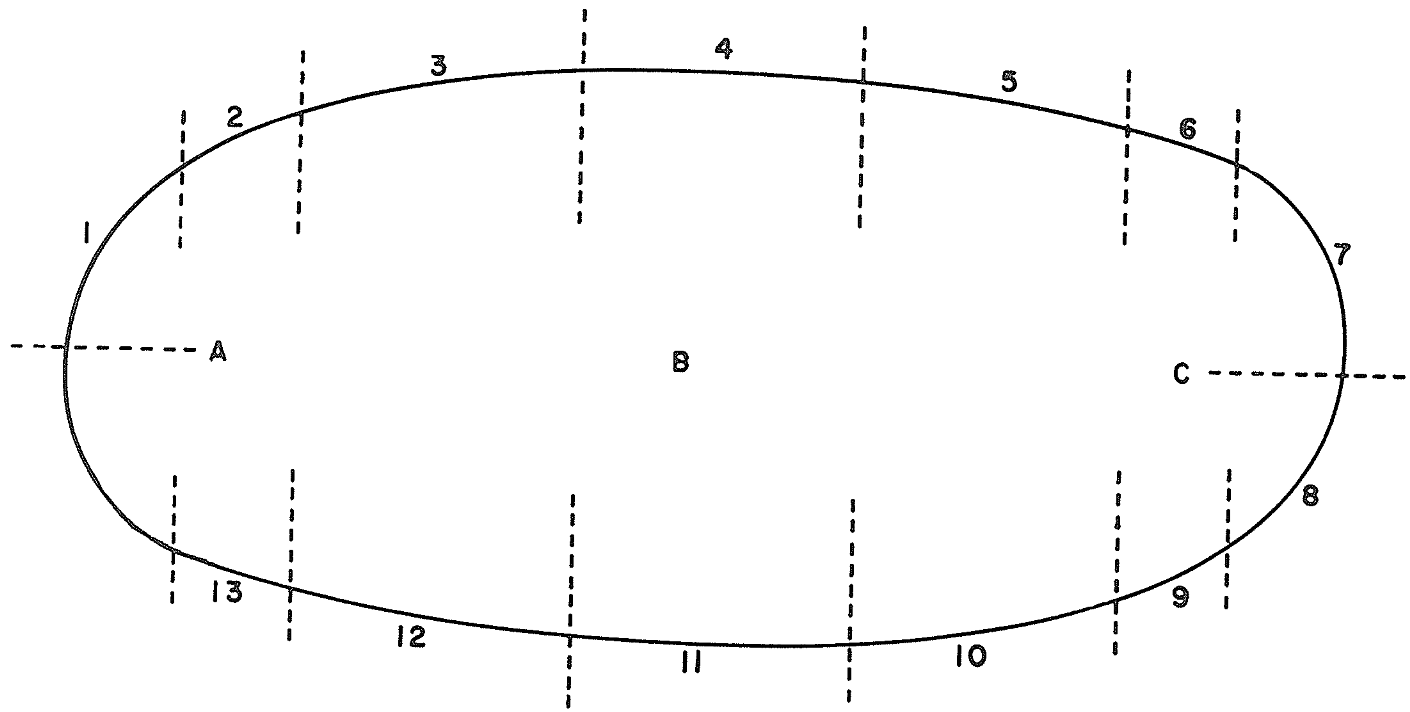
Walleye fry were obtained in 1984 and 1985 from the Province of Manitoba, Fisheries Branch, Whiteshell Fish Hatchery. On May 22, in 1984 and 1985, approximately 30,000 fry were released into each of two stormwater retention ponds controlled by the City of Winnipeg. Bishop Grandin ponds 1 and 2 (BG1 and BG2) are located along Bishop Grandin Boulevard in south Winnipeg (Swanson and Ward 1985). In June 1985 two groups of fingerlings, (one of 1976 and the other of 3396 individuals), were obtained from rearing sites operated by the Manitoba Deptartment of Natural Resources, Fisheries Branch, and introduced into BG1 and BG2 Ponds to supplement fish stocked as fry. BG2 Pond was used for field experiments whereas BG1 was strictly a source of fish for the laboratory experiments. Fry were transported to the ponds in 45 l plastic bags containing water and oxygen and packed in ice. Fingerlings were transported in a 1000 l oxygenated water tank. Juveniles removed from the ponds for experiments were transported to the laboratory in 45 l plastic bags.

In 1984 BG2 Pond was sampled from early June to early September. Weekly samples ranging from 11 to 50 walleye were collected from a total of 12 beach seining stations located around the pond (Fig. 1) and preserved in 10 % formalin. Individual walleye in samples were weighed and measured upon return to the laboratory (wet weight to the nearest 0.1 mg and total length to the nearest mm).

In 1984, 4 to 12 sampling stations were seined each week, between 1000 and 1500 hrs, using a standard haul of 52 m^2 (6.5 x 8 m). Two seine nets were used during the summer to match mesh size with increasing walleye size. To determine if the two nets were equally effective at capturing walleye, both were used during sampling on July 9. The fine mesh net was used on the odd numbered stations and the large mesh net was used on the even numbered ones. A total of twelve stations was sampled (Fig. 1). A Mann-Whitney U test of the catches in each net indicated that there was no significant difference, [T=6; W (alpha = 0.025) =3; W (alpha = 0.475) =22], therefore, data from both nets were combined. Data collected from station 8 (Fig. 1) was deleted because fluctuating water levels prevented consecutive sampling. An anomolous catch of 314 walleye made at station 9 on June 18 was also deleted. The relative abundance of walleye was expressed as the median catch per standard seine haul per day.

Weather data, reported at hourly intervals, was obtained from a weather station at the Winnipeg International Airport

Figure 1. Schematic representation of sampling sites on Bishop Grandin Pond 2. Numbers indicate seining locations and letters show turbidity measuring locations.



1
2
3
4
5
6
7
8
9
10
11
12
13
A
B
C

in 1984 (Environment Canada Monthly Meteorological summary 1984). Air temperature was calculated as an average for the sampling period. Wind speed was estimated as the average for the period between 0400 hrs to the end of each sampling period. Percent cloud cover was estimated at the beginning of each sampling session. Light intensity (in lux) was measured using a Li Cor model Li-185B light meter with a model Li-190SB quantum sensor. Readings were taken at the water surface prior to seining for walleye. The transmittance of light through a sample of pond water taken at mid-depth from each of three stations (Fig. 1), was recorded for wavelengths 400 to 750 nm, in 50 nm increments with a Unicam SP500 Series 2 spectrophotometer. The average transmittance for the stations was then used as a measure of turbidity in the pond.

To study seasonal feeding patterns, 10 walleye were selected randomly from each weekly collection and their stomach contents were analysed. The diel feeding patterns of walleye were studied on July 5 and 6 and on August 7 and 8. During each 24 hour sampling period, 10 walleye were collected at 10 times of the day during each 24 hour period. Sampling times were modified according to seasonal changes in day length. Walleye collected during both diel and seasonal sampling were perserved in 10 % formalin, weighed (mg), total lengths measured (mm) and, later, had their stomach contents analyzed. Organisms in stomachs from walleye collected during seasonal sampling were treated as follows: Copepods were identified to genus and cladocerans to species, amphipods to order, chaoborus larvae and Hexagenia nymphs were listed as incidental items, remains of either zooplankton or insects which could not be classified were listed as either unidentified insect or zooplankton parts, and all other organisms were described to family. In the diel feeding studies items were listed as fish, cladocerans, Diaptomus, Cyclops, unidentified insect or zooplankton parts, Corixidae, or incidental items (Hexagenia, chaoborus, and amphipods). Remaining items were identified to family.

In both diel and seasonal sampling, dry weights for each category of prey were recorded. The total lengths of fathead minnows (FTL) consumed by walleye were estimated from GAP measurements, (McIntyre and Ward 1986), of left pharyngeal arches found in the stomach contents, using the regression equation, FTL= 16.803 (GAP)- 6.162, ($R^2 = 0.969$; $F = 1413$; $df = 47$; $P < 0.0001$). Diaptomid metasome lengths and the total lengths of corixids and amphipods were measured using a dissecting microscope with a measuring eye piece calibrated from a stage micrometer.

In 1985, 6818 and 5474, fathead minnows were stocked into BG2 Pond on July 22 and August 7 respectively. A sample of 30 to 50 minnows was collected from each introduction to determine length distributions. Walleye were collected from the pond within 24 hours of each stocking and preserved in 10% formalin. Numbers of minnows eaten were noted and total lengths estimated from GAP measurements.

In order to document the onset of the tapetum lucidum a number of walleye were collected each week from BG2 Pond and their heads were preserved in 5 % glutaraldehyde in 0.1 M Sorensens phosphate buffer, for 5 hours. For storing, the heads were transfered to, 5 % sucrose in 0.1 M Sorensens buffer. To prepare for infiltration, eyes were first removed and then the lens extracted. Eyes were dehydrated by washing them in a cold ethyl alcohol series (70, 80, 95 %, and absolute). They were then placed in a fresh wash of absolute alcohol and allowed to come to room temperature. Four 30 minute washes with warm absolute alcohol were used to complete dehydration.

Tissue was first cleared in a 1:1 mixture of absolute alcohol and acetone for 15 minutes and then with two 15 minute periods in pure acetone. Infiltration of the tissue with epon-araldite was started in a 1:1 mixture of acetone and plastic and left for 1 hour with a cap on the vial. After one hour the cap was removed and the acetone was allowed to evaporate overnight. Fresh plastic was prepared and poured into molds for embedding. The tissue was then washed in fresh plastic and placed in the molds. The plastic and tissue was incubated at 60 C for several days.

Sections 1-2 microns thick were cut from the embeded tissue in a plane perpendicular to the front of the eye using a Sorel JB4 microtome. Sections were placed on glass slides, stained with toluidene blue and viewed under polarized and nonpolarized light. The tapetum lucidum is composed of crystals of 7, 8-dihydroxanthopterin (Zyznar and Ali 1975) and as a result scatters polarized light. Scattering of polarized light in the pigment epithelium was used as an indication of the presence of these crystals. Since location in the retina may have been a factor governing retinal development, all sections to be photographed were taken from an area adjacent to the insertion of the optic nerve. All photographs taken with polarized light were at the identical light intensity and length of exposure.

LABORATORY STUDIES

Two hundred and forty three small (mean length 40 mm) juvenile walleye were obtained from the Dauphin Lake fisheries rehabilitation project (Fisheries and Oceans, Canada) in July 1985. These fish were held and fed in 200 l aquaria located in the laboratory. They were used along with fish from the retention ponds (BG1 and BG2) to create desired length frequency distributions in laboratory experiments. Fourteen experiments were conducted from early July to early September between 1984 and 1985.

The experimental containers were four 225 L aquaria, arranged as a flow-through system. Flow rates (measured by eye) were low and relatively constant between aquaria and similar among experiments. Water temperatures in experiments ranged from 17 to 26 C, approximating pond temperatures at the time the fish were collected. The duration of each experiment was 24 h, beginning and ending at 1630 hrs with a light regime of 17 h light 7 h dark. Dusk and dawn were simulated using 3 banks of 3 100 watt incandescent bulbs, each set with its own rheostat and timer. Dusk and dawn each lasted one half hour. Early dawn light intensity varied from 2 to 9 lux, dawn 15 to 40 lux and daytime 30 to 70 lux between experimental units.

Before each experiment, groups of walleye were anesthetized with MS 222, measured (total length in mm) and divided into four subgroups with similar length distributions. To avoid cannibalism prior to the experiments, fish in each subgroup were segregated by length while being held for 24 hours without food.

Fish in each experiment were exposed to four food regimes (a) abundant fathead minnows and abundant zooplankton (unit 1); (b) abundant fathead minnows (unit 2); (c) abundant zooplankton (unit 3); and (d) no food (unit 4). The numbers and length range of the minnows used in each experiment were increased as the walleye grew. Distributions varied from 23 minnows at 18 to 35 mm early in the season to 105 minnows at

21 to 54 mm in total length later. Zooplankton numbers were maintained at "visually" abundant levels (approximately 100 individuals per liter) by frequent additions from the rearing ponds. Walleye remaining at the end of each experiment were preserved in 10 % formalin.

The dominant pond zooplankter for the duration of the laboratory experiments in 1984 was *Diaptomus siciloides* (1.0 - 1.3 mm). Late in the season *Daphnia rosea* (1.2 - 1.6 mm) and *Moina affinis* (0.8 - 1.0) were also abundant. During experiments in 1985, dominance varied between *D. siciloides*, *D. rosea* and *Daphnia schodleri* (1.5 - 2.0 mm). The pond plankton was dominated by *Cyclops vernalis* (1.0 - 1.8 mm) late in the season. Figures in parentheses are length measurements of females (Ward and Whipple 1965).

To use fresh total lengths in analyses of units 3 and 4, fresh and preserved lengths of walleye in each were sorted in ascending order and paired. In cases where pairing was difficult , the fresh length closest to (equal to or greater than) the observed preserved length was accepted. Lengths of fresh fish which could not be matched to preserved lengths (missing fish) were believed to have been consumed.

Rates of cannibalism were calculated as the number of walleye missing at the end of an experiment divided by the total number present at the beginning. Rates of piscivory were calculated by the same procedure. Walleye in all experimants were placed in two categories. (a) Potential cannibals were defined as fish which had walleye remains in their stomachs and fish which had available to them, at the end of the experiment, other walleye less than 67 % of their own total length, [the greatest prey to cannibal length ratio found in the literature (McIntyre et al. in press)]. (b) Potential prey were defined as all other walleye in the aquaria at the end of each experiment and all walleye which were consumed. Cannibalized walleye could have been completely digested in 24 h therefore, all cannibals may not have been identified. Consequently mean prey to cannibal length ratios may have been affected.

Lengths of preserved walleye were used in the analyses of units 1 and 2 to facilitate comparisons with the stomach analysis of fish from the field, for which fresh lengths could not be determined. Total lengths of minnows remaining at the end of each experiment were recorded whenever possible. In some cases where the caudal fin had been destroyed, standard length (SL) was measured and the regression, TL = 1.221 (SL) - 0.890 used to estimate total length, (R^2 = 0.984; F = 13667; df = 230; $P < 0.0001$). The total lengths of consumed minnows were estimated from GAP measurements.

Four experiments were conducted in 1984 to determine the upper size limit of fathead minnow that could be consumed by fingerling walleye. The lengths of walleye used were, 47, 57, 71, and 81 mm ± 1 mm. Experiments of 24 hrs duration with 24 hrs starvation time were carried out in 20 litre aquaria. Three walleye were placed in each tank with up to 6 minnows of known length. The minnows used varied in size from 50 to 80 % (TL ± 0.5 mm) of walleye total lengths. At the end of each experiment the number of minnows remaining was recorded.

RESULTS

FIELD STUDIES

Growth and Feeding

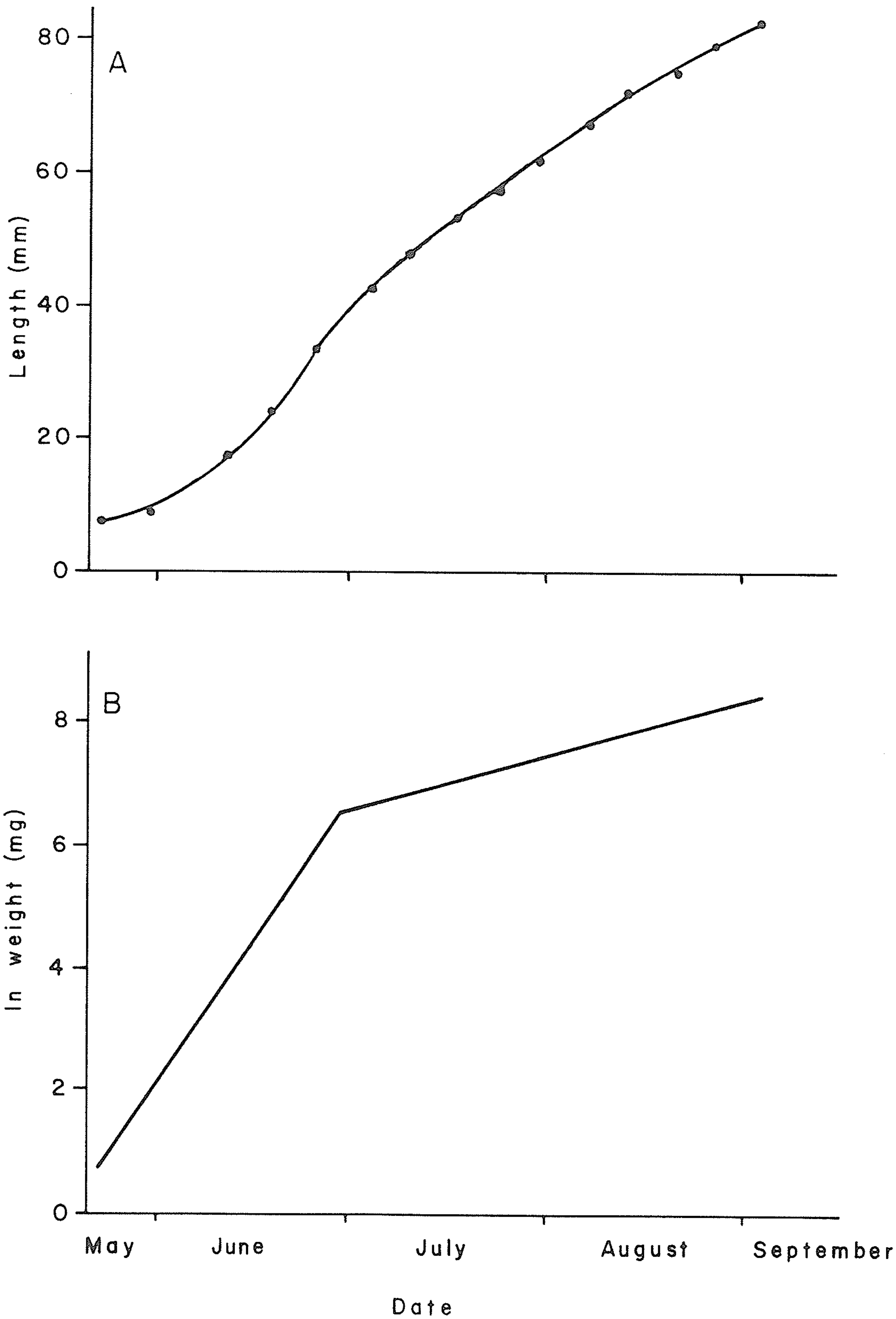
Walleye fry were stocked into BG2 Pond at a mean total length of 8 mm and a mean wet weight of 2.1 mg. Growth in total length was sigmoidal and variation in length increased with time (Fig. 2A). Ninety five percent confidence intervals for daily means did not exceed $\pm$ 2 mm. Walleye attained a mean total length of 82 mm and a mean wet weight of 4533.4 mg by September 3 (104 days old). Two regression lines were fitted to the natural logarithm of wet weight (Fig. 2B). The slope of the initial relationship was 0.1531 but declined to 0.0291 after the fish reached 34 days old.

Median weight of walleye stomach contents was variable during the summer (Fig. 3A). Stomach content weight changed very little from June 25 to July 9 and from July 30 to Aug 21 but increased at all other times (Fig. 3A). The data were divided into three groups, June 11 to July 9 (R1), July 30 to August 21 (R2) and September 3 (R3). The data were

Figure 2. A: Growth in mean total length of walleye from Bishop Grandin Pond 2 in 1984. B: Relationship between the natural logarithm of weight and age of walleye. The equations of the lines are

$$\ln WT = 0.1531AGE + 0.7061$$ before June 25 and

$$\ln WT = 0.0291AGE + 5.4606$$ after.



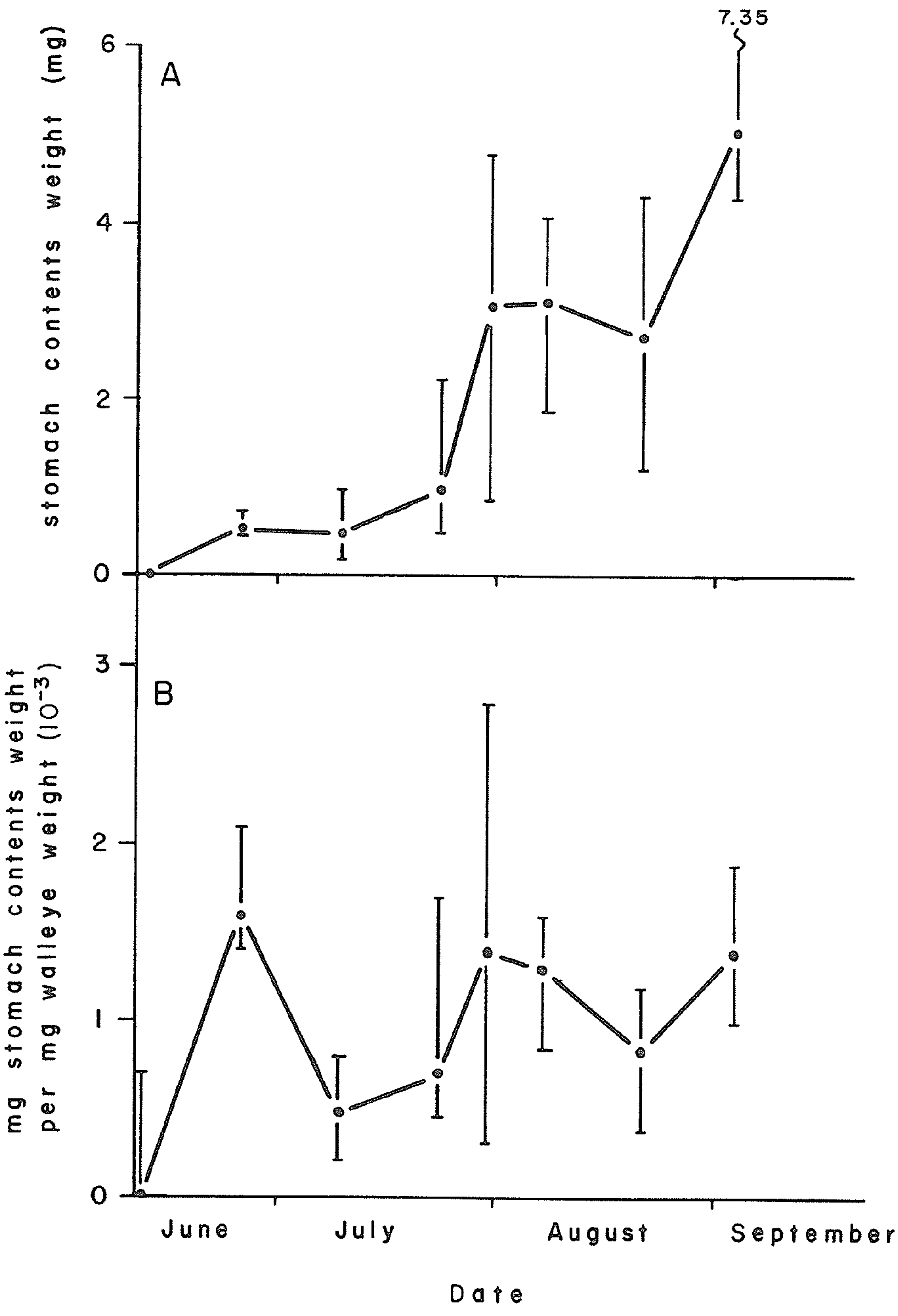
A
Length (mm)
0
20
40
60
80
B
ln weight (mg)
0
2
4
6
8
May
June
July
August
September
Date

not distributed normally, therefore the Kruskal-Wallis multiple comparisons procedure (Daniel 1978) was used to test for significance. Stomach content weights between June 11 and July 9 were significantly smaller than weights found during later periods (R1 - R2 = 28.22; Z = 13.47; R1 - R3 = 44.04; Z = 19.72). Weights from July 30 to August 21 were not significantly different from those on September 3 (R2 - R3 = 15.82; Z = 20.36). The stomach content weight per milligram of body weight was not correlated with increases in stomach capacity which is a function of increasing size (Fig. 3B).

The percentage contribution of food items (by weight) to total daily walleye diet, varied considerably during the season (Figs. Fig4). The percent contribution of Diaptomus to the diet varied between 60 and 85 % until July 9 after which its contribution was near zero (Fig. 4A). The contribution of Cyclops to the daily diet did not rise above 13 % during the summer (Fig. 4A). Daphnia schodleri formed 33 % of the daily diet on June 11 but made up only a small proportion of the diet thereafter (Fig. 4B). The proportion of Daphnia rosea was $\leq$ 17 % (Fig. 4B).

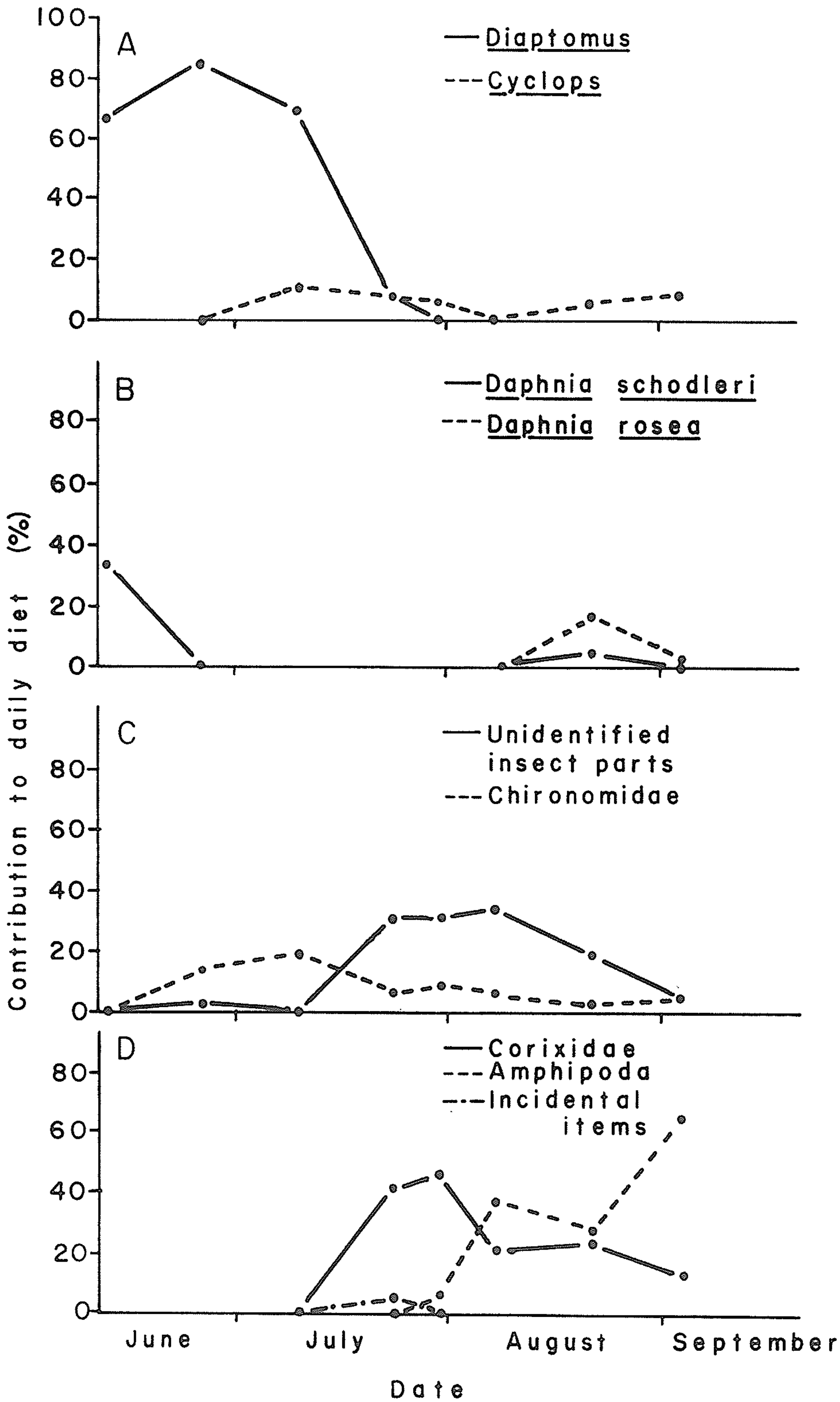
The greatest contribution of chironomid larvae to the diet was from June 25 to July 9 (Fig. 4C). Their contribution was highest on July 9, but had decreased to 10 % by the end of the season. The contribution of insect parts to the diet was highest between July 23 and August 7 but decreased

Figure 3. Median stomach content weight (A) and median stomach content weight per milligram body weight (B) for walleye collected from BG2 Pond in 1984. Upper and lower quartiles are also indicated on each.



7.35
6
4
2
0
A
stomach contents weight (mg)
3
2
1
0
B
mg stomach contents weight per mg walleye weight (10^{-3})
June
July
August
September
Date

Figure 4. Percent contribution of food items to the daily diet (by weight) of walleye from BG2 Pond in 1984.


100
80
60
40
20
0
A
— Diaptomus
--- Cyclops
B
— Daphnia schodleri
--- Daphnia rosea
C
— Unidentified insect parts
--- Chironomidae
D
— Corixidae
--- Amphipoda
-·- Incidental items
Contribution to daily diet (%)
June
July
August
September
Date

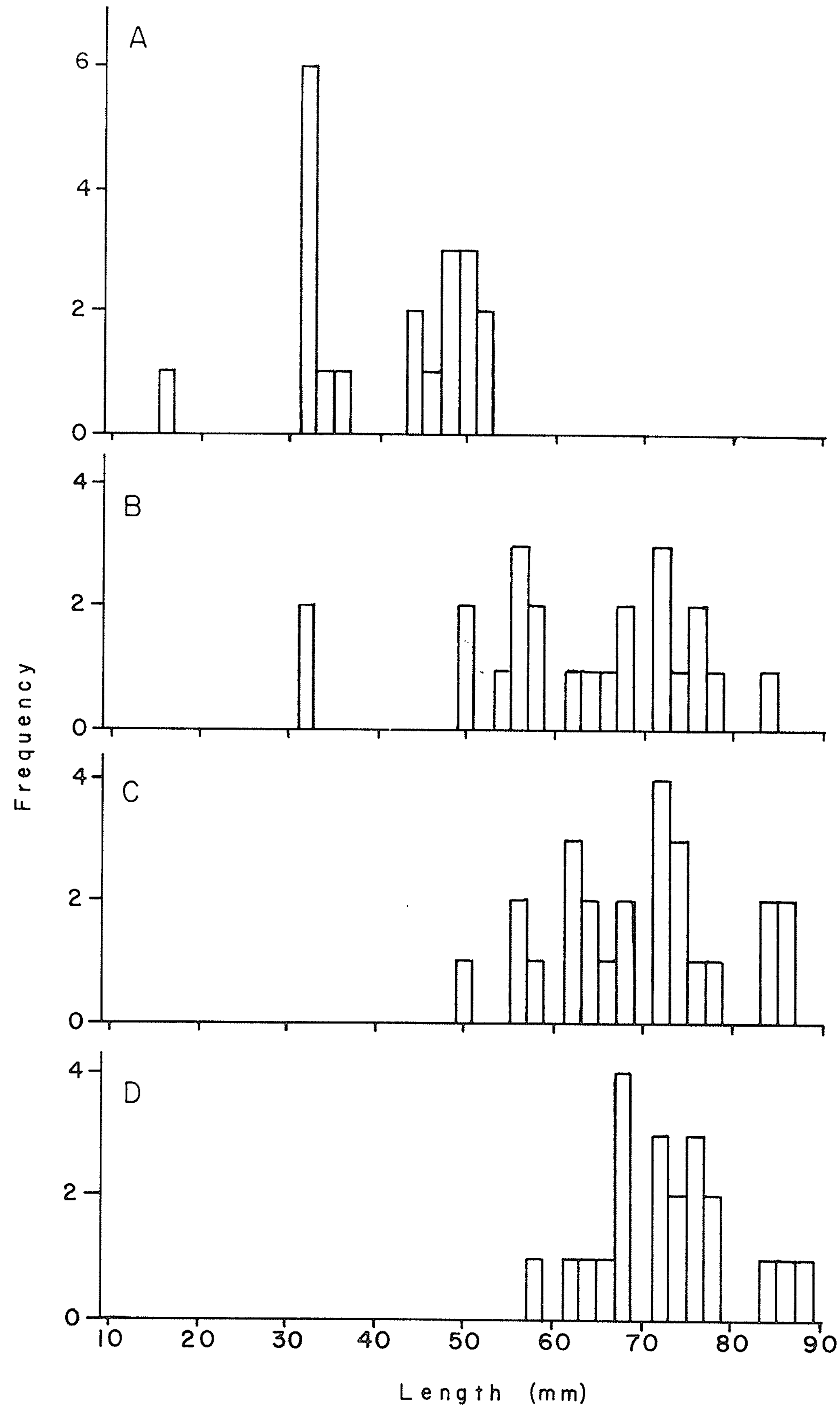
to less than 10 % by September 3 (Fig. 4C). Consumption of corixids occurred after July 23 and was at a maximum of 46 % on July 30. The proportion of the diet formed by amphipods increased steadily after July 30 and reached a maximum of 65 % by the end of the season (Fig. 4D). Incidental items occurred only twice and did not form a large proportion of the diet on either occasion (Fig. 4D).

The transition in food types consumed generally coincided with a progression from small to large prey as the walleye grew. Diaptomus (mean length=0.8 mm) consumed by walleye at an average length of 41 mm dominated the diet until July 9 (Fig. 5). The larger invertebrate categories contributed very little until July 9, after which they dominated the diet. The mean length of walleye which consumed chironomids was 63 mm. Chironomids were not measured because no length would have satisfactorily indicated their shape, however they tended to be intermediate in size between the copepods and the corixids and amphipods. The mean lengths of the larger invertebrates consumed (corixids and amphipods) were 3.8 and 3.7 mm respectively when the walleye were approximately 70 and 73 mm average length (Fig. 5).

Development of the Tapetum Lucidum

Walleye 25 mm or shorter did not possess a tapetum lucidum (Fig. 6A and B). The tapetum lucidum first appeared in walleye in the sample collected on June 25, 1984 (34 days old) (Fig. 6C and D). Tapetal material was first apparent in the distal portions of the epithelial processes near the cone outer segments and spread basaly as the walleye grew (Fig. 7A - D).

Figure 5. Relationship of food type consumed to walleye length in BG2 Pond in 1984. A: diaptomids, B: chironomids C: corixids, D: amphipods.



A
B
C
D
Frequency
0
2
4
6
10
20
30
40
50
60
70
80
90
Length (mm)

Figure 6. Retinas of 25 mm (A,B) and 27 mm (C,D) walleye collected on June 18 and 25, respectively. Bright field (A,C) and polarizing optics (B,D). Tapetum lucidum (t), cones (c), sclera (s). 1200X.

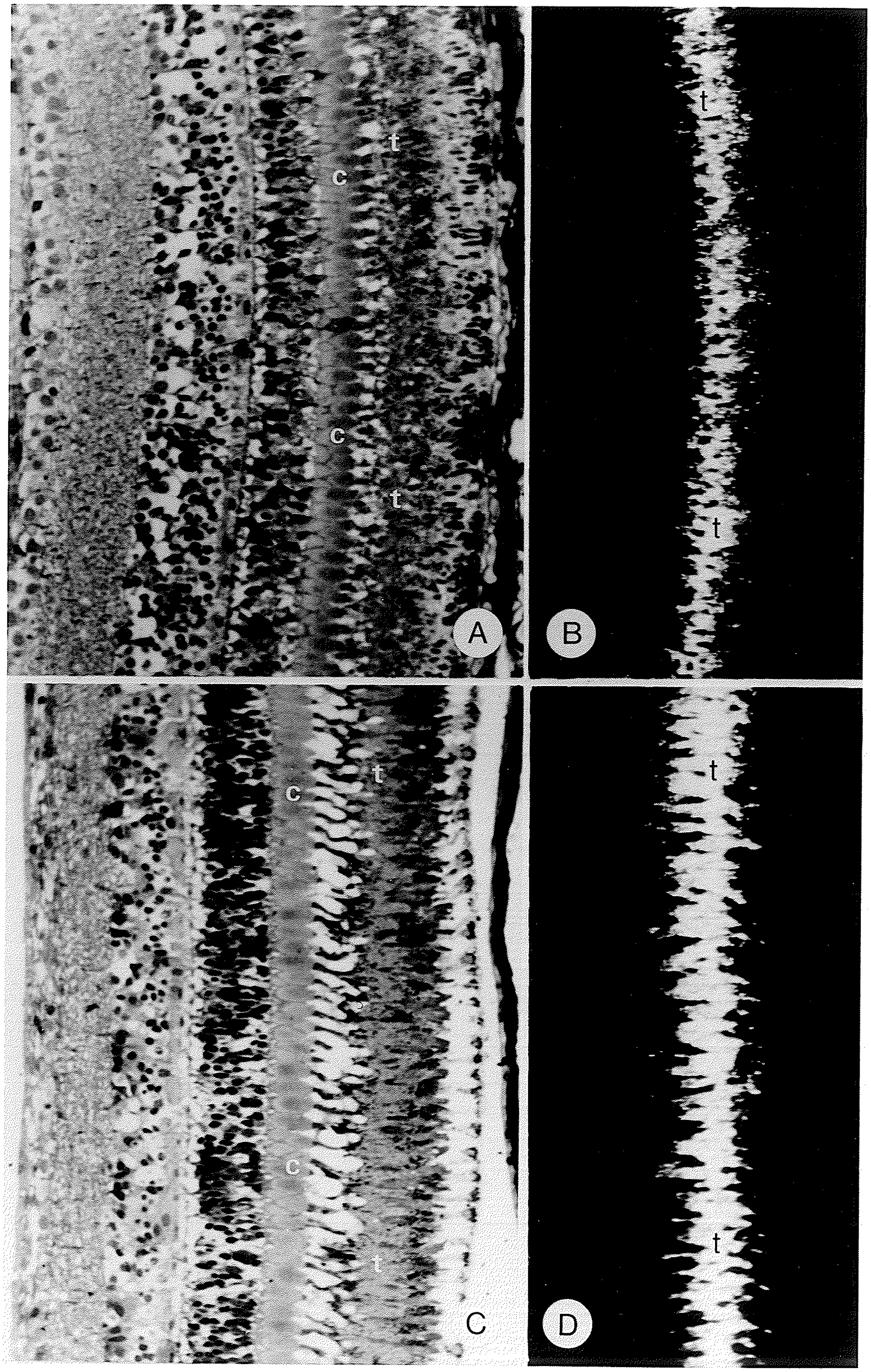
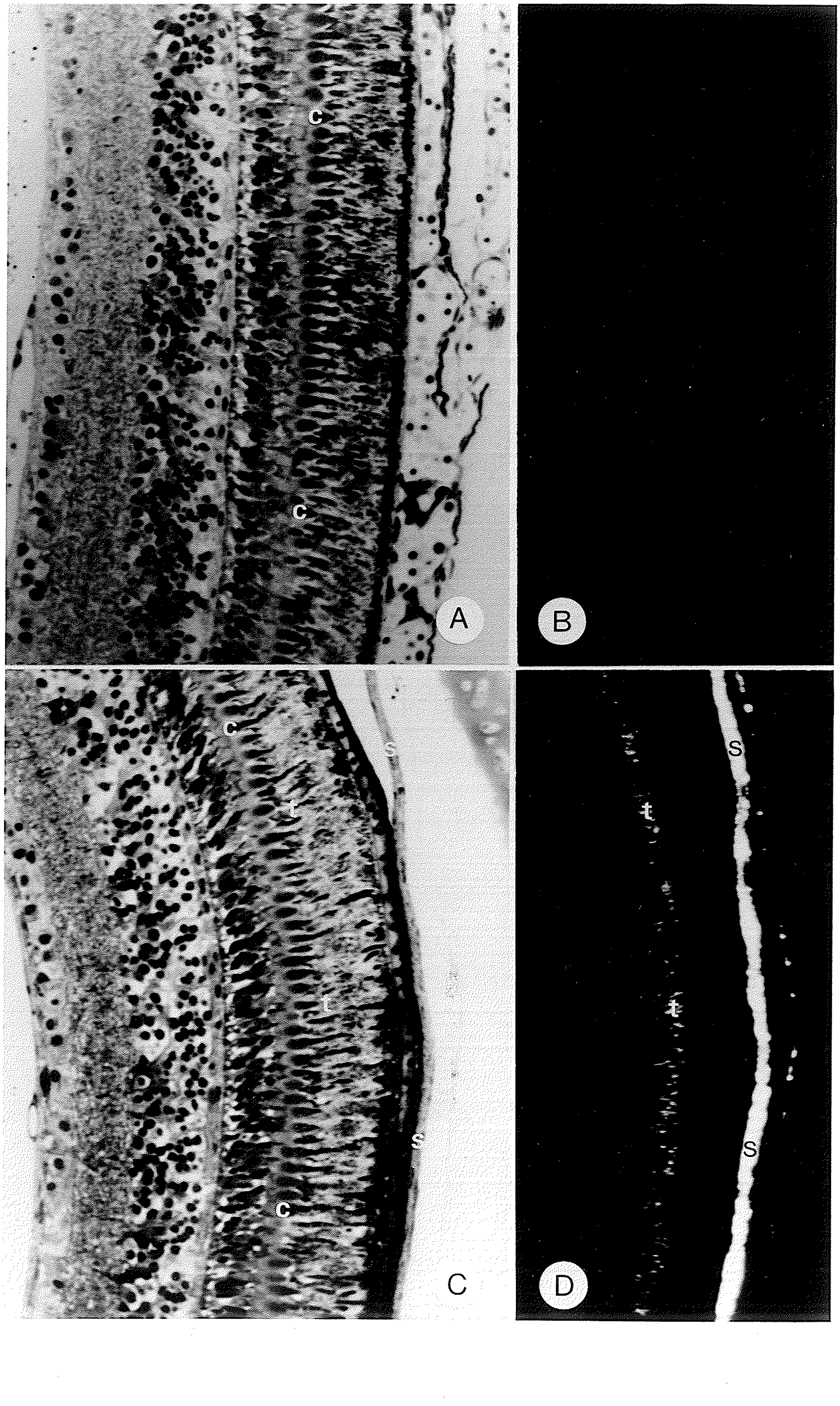

A
B
C
D
c
t

Figure 7. Retinas of 43 mm (A,B) and 65 mm (C,D) walleye collected on July 4 and 23 respectively. Bright field (A,C) and polarizing optics (B,D). Taeptum lucidum (t), cones (c), sclera (s). 1200X.

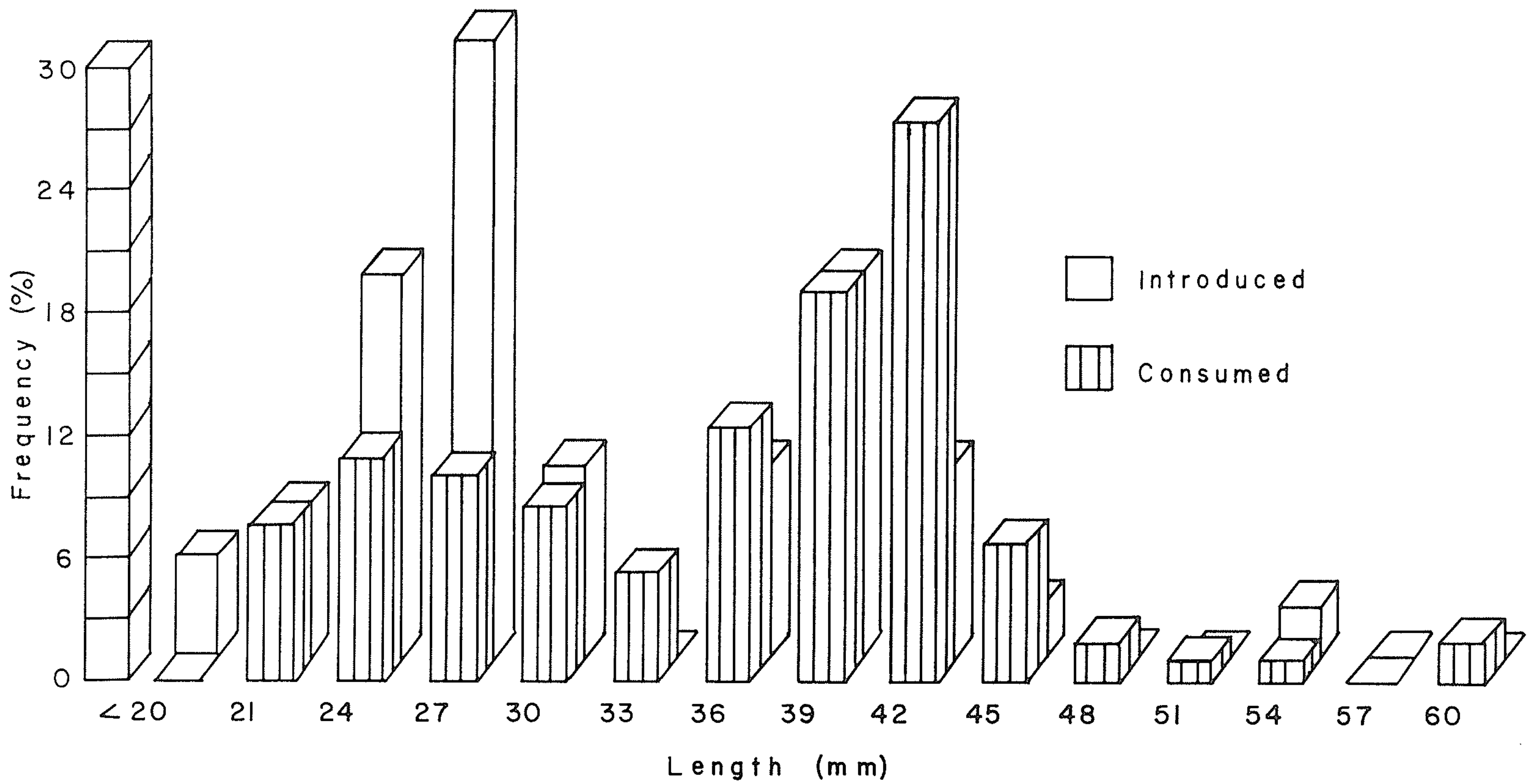


A
B
C
D
c
t
s

Piscivory

The mean length of fathead minnows found in walleye stomachs during diel sampling was significantly larger (T= 2.447; df= 183; $P< 0.05$) than the mean length of minnows introduced into BG2 Pond (Fig. 8). The mean length of minnows selected following the second introduction on August 7 and 8 was not significantly different from the mean length of the introduced fish (Table 1). However, selection of longer than average fish began during the morning of August 8 and continued to the end of the sampling period. Fathead minnows from the July 22 introduction which were consumed by walleye tended to be smaller than the average for the introduced fish although the differences were not significant (T= 1.427; df= 67; $P> 0.05$). The differences in mean lengths consumed from the two introductions may be attributed to the relative scarcity of large minnows in the July 22 introduction (Fig. 9). Consequently, their numbers would have been depleted sooner than those transferred on August 7. There was no linear relationship between the length of minnow selected and walleye length on July 22 and August 7, (R^2 = 0.01; F = 1.3; P = 0.26; and, R^2 = 0.0002; F = 0.01; P = 0.94; respectively), however the variation in lengths of minnows consumed did increase with walleye length.

Figure 8. Length frequency distributions of introduced minnows and those found in walleye stomachs during the 24 hour period between August 7 and 8.



Introduced
Consumed
Frequency (%)
30
24
18
12
6
0
< 20
21
24
27
30
33
36
39
42
45
48
51
54
57
60
Length (mm)

Figure 9. Length frequency distributions of introduced minnows and those found in walleye stomachs on July 22.

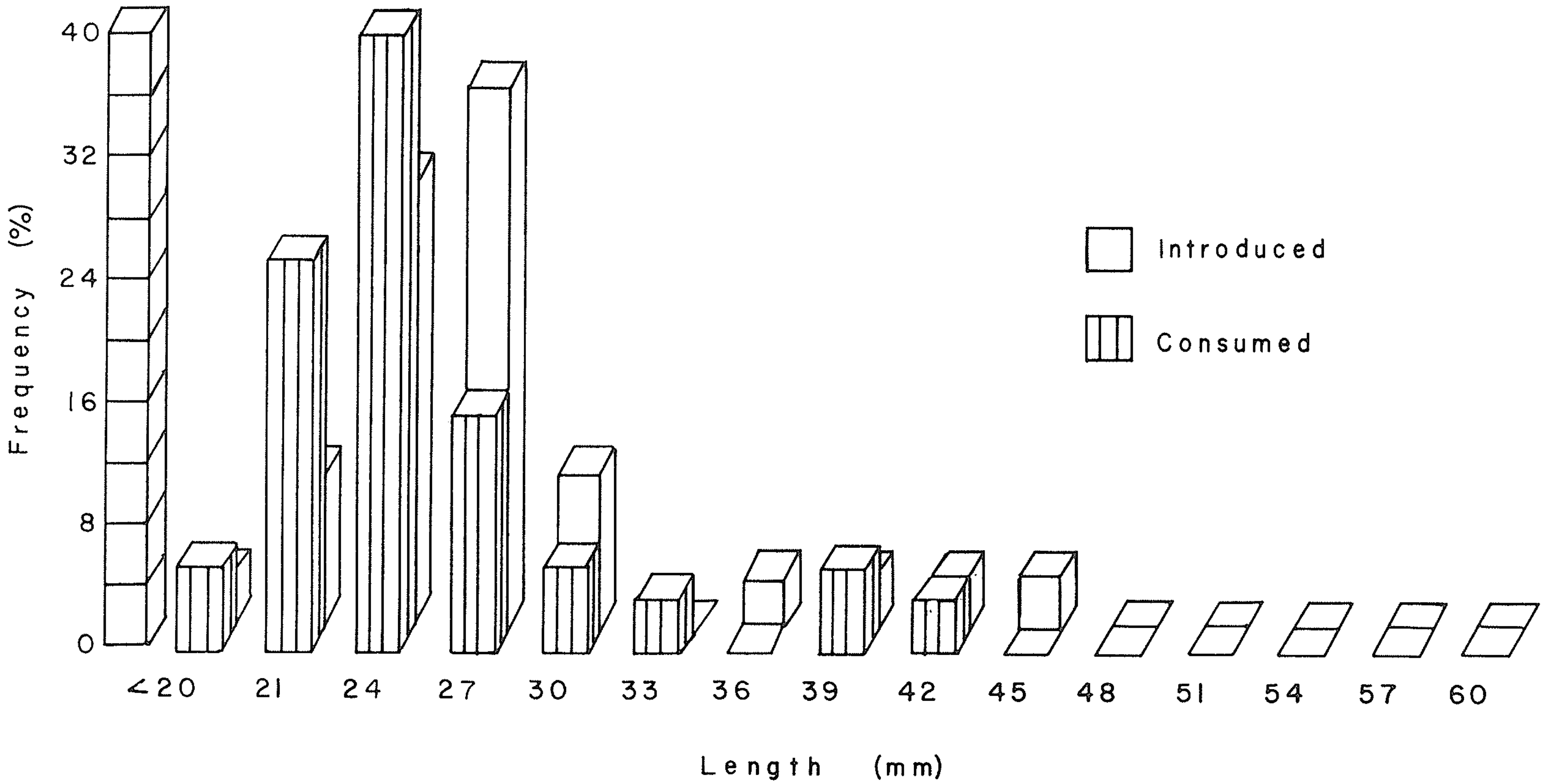

40
32
24
16
8
0
Frequency (%)
Introduced
Consumed
<20
21
24
27
30
33
36
39
42
45
48
51
54
57
60
Length (mm)

Table 1. Comparisons of the mean length of introduced fathead minnows with those found in walleyes stomachs from BG2 Pond during diel feeding studies in August, 1985.

Statistics				
Sample	n	$\bar{x}$	s	t
Introduced	48	30.79	8.3817	-
Evening	38	33.26	9.5427	1.26
Night	11	36.27	8.0261	1.94
Morning	41	37.10	8.0957	3.55*
Afternoon	22	38.14	8.8549	3.29*
Evening	24	35.67	7.3878	2.66*

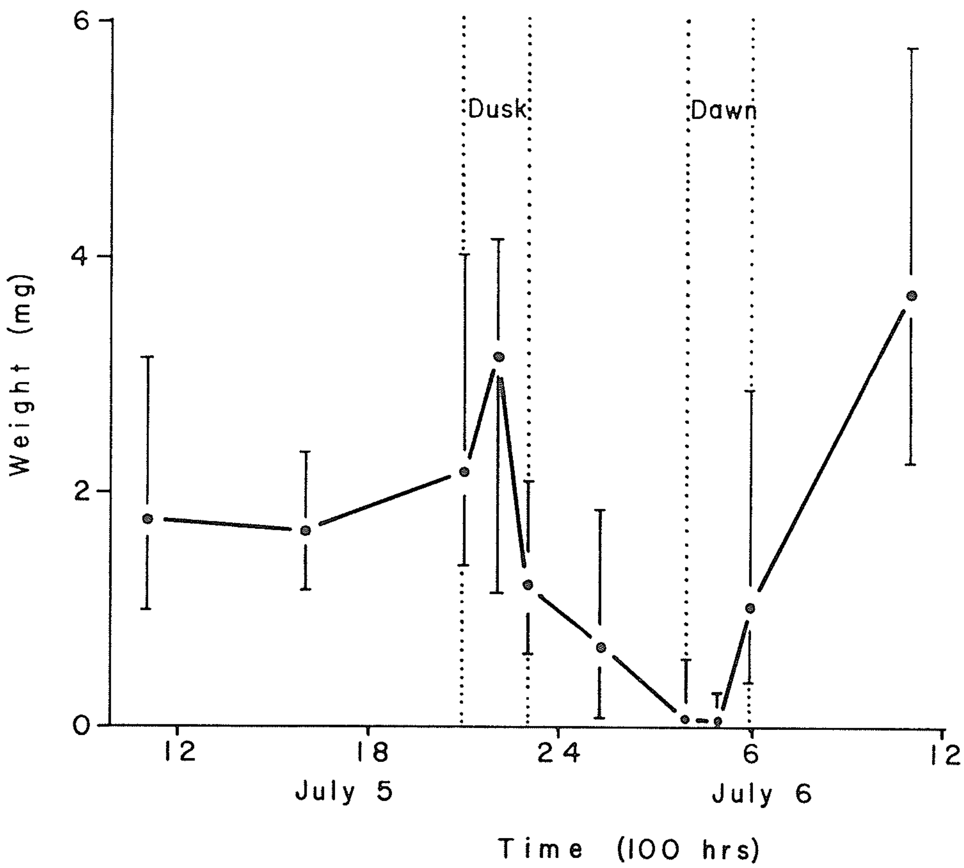
* indicate significance at P= 0.95

Diel Feeding

There were two maxima in the median weight of walleye stomach contents during diel feeding from July 5 to 6, 1985 (Fig. 10). The highest median weights occurred at 2200 and 1100 hrs. Median stomach content weight reached its lowest point between 0400 and 0500 hrs. Walleye ranged in length from 40 to 52 mm. The frequency with which different food items occurred in the stomachs of walleye varied during the sampling period (Fig. 11). Cladocerans and Diaptomus sp. occurred in most stomachs during daylight. Occurrence of both groups was lowest during the low light period (0130 and 0400 hrs) (Fig. 11A and B). Corixids were consumed during the low light period as were unidentified insect parts, reaching maxima from 2300 to 0130 hrs and 0500 hrs respectively (Fig. 11C). Chironomid larvae occurred in a few walleye during most of the sampling period. Fish remains were present only once, during the dawn period (Fig. 11D). Cyclops, unidentified zooplankton parts and incidental items all occurred infrequently during the sampling period. In general, most feeding took place during daylight and consisted mainly of zooplankton. Some feeding did occur at night but was restricted to large items; eg. corixids and other insects.

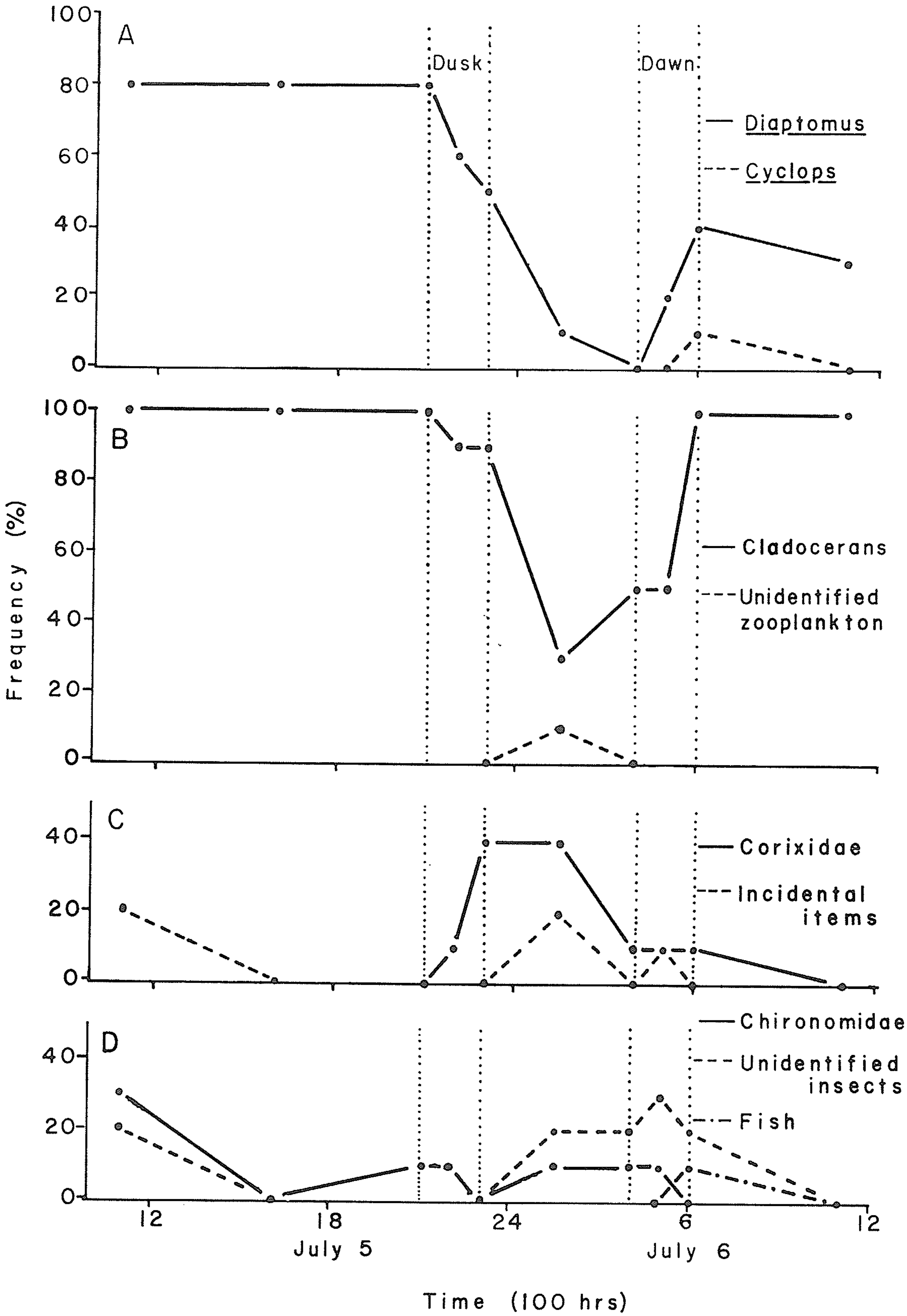
Diel feeding of walleye during the period 2030 hrs on August 7 to 2030 hrs on August 8 was variable but declined with time (Fig. 12). Maxima in the median weight of stomach contents occurred at 2030, 0400, 1130, and again at 2030 hrs. The lowest value was at 1630 hrs. Walleye ranged in length from 81 to 124 mm. Food items in walleye stomachs were restricted to fish, corixids, and incidental items (Fig. 13). The proportion of walleye stomachs containing fathead minnows remained consistently between 80 and 100 % for all sampling times. Corixids reached maxima at 0130 and 0630 hrs. Incidental items occurred several times during the sampling period but only in one walleye on each occasion.

Figure 10. Median weight of stomach contents of walleye from BG2 Pond collected during diel sampling in July, 1985. Upper and lower quartiles are also indicated.



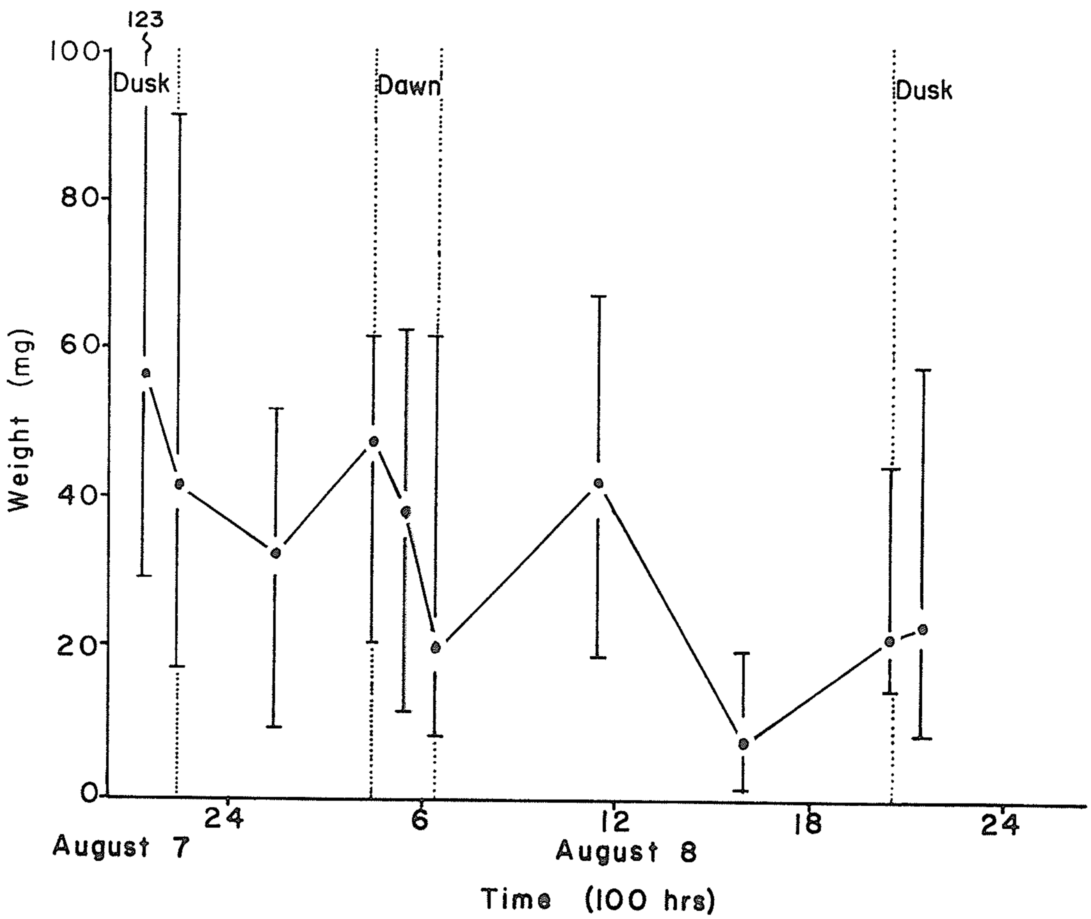
6
4
2
0
Weight (mg)
Dusk
Dawn
12
18
24
6
12
July 5
July 6
Time (100 hrs)

Figure 11. The frequency with which food items occurred in the stomachs of walleye from BG2 Pond sampled during diel feeding in July, 1985.



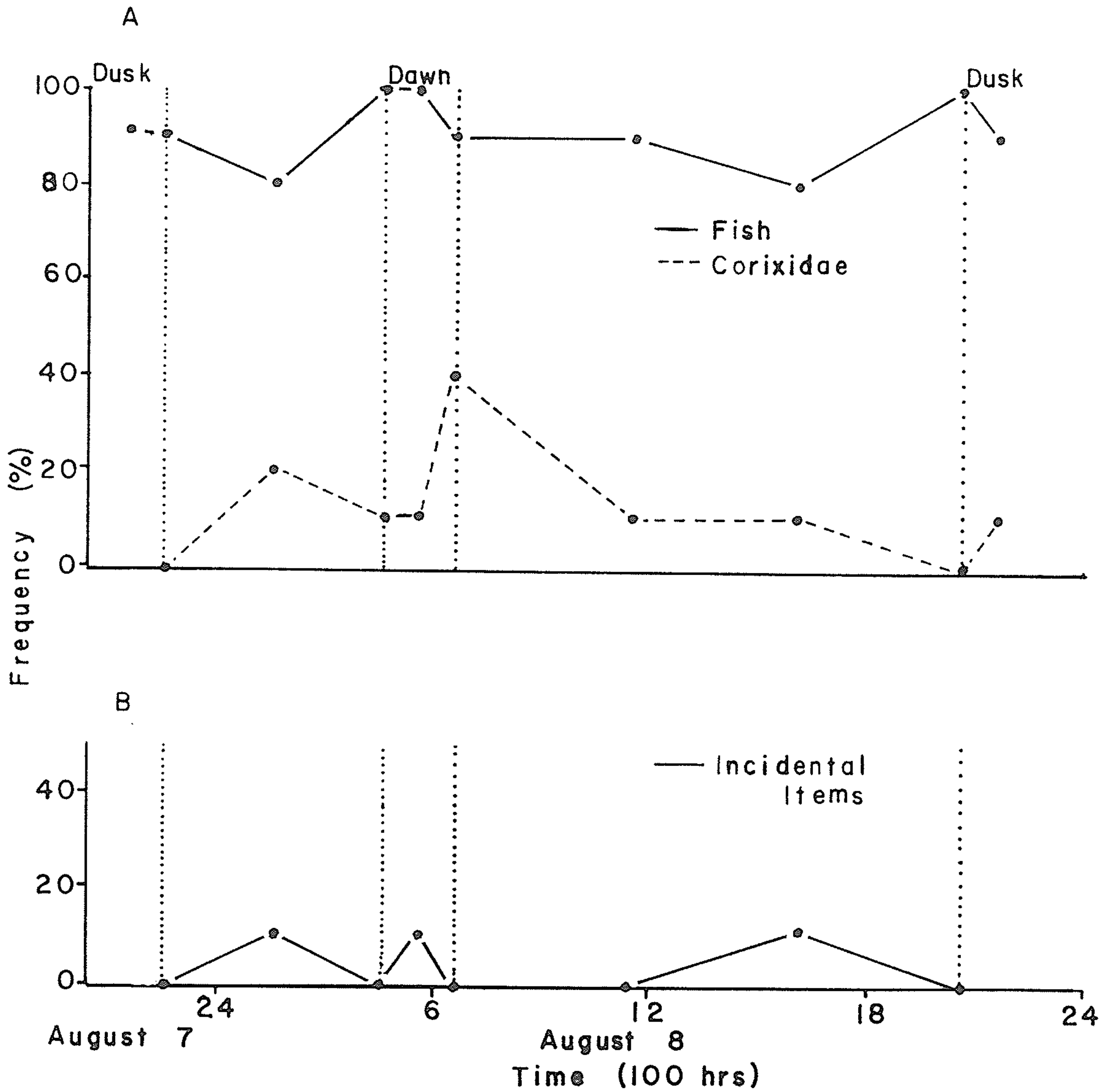
A
Dusk
Dawn
Diaptomus
Cyclops
B
Cladocerans
Unidentified zooplankton
C
Corixidae
Incidental items
D
Chironomidae
Unidentified insects
Fish
Frequency (%)
12
18
24
6
12
July 5
July 6
Time (100 hrs)

Figure 12. Median weight of stomach contents of walleye from BG2 Pond collected during diel sampling in August, 1985. Upper and lower quartiles are also indicated.



123
Dusk
Dawn
Dusk
Weight (mg)
100
80
60
40
20
0
24
6
12
18
24
August 7
August 8
Time (100 hrs)

Figure 13. The frequency with which food items occurred in the stomachs of walleye from BG2 Pond sampled during diel feeding in August, 1985.



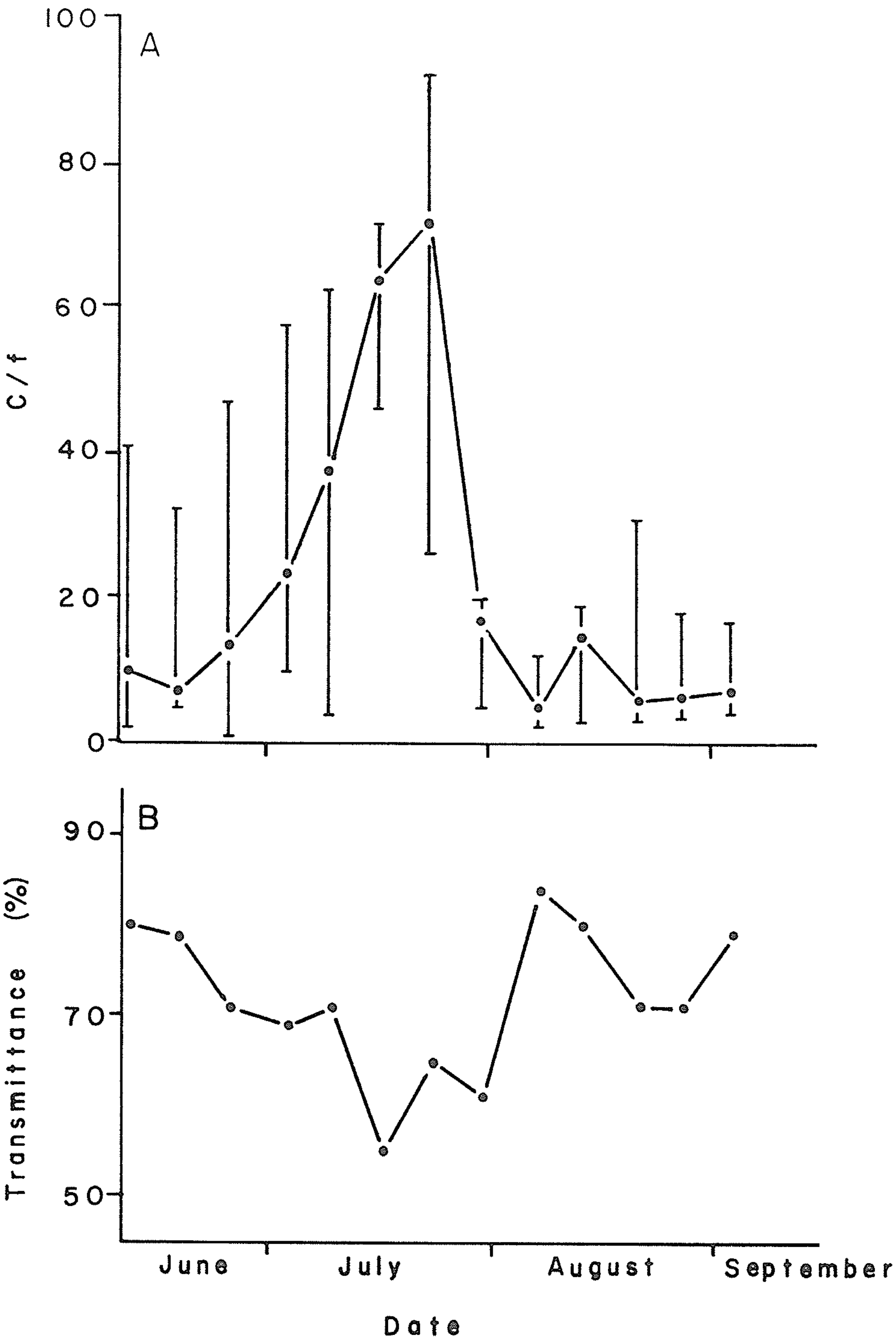
A
Dusk
Dawn
Dusk
100
80
60
40
20
0
Fish
Corixidae
Frequency (%)
B
40
20
0
Incidental Items
24
6
12
18
24
August 7
August 8
Time (100 hrs)

Relative Abundance

Catch per standard seine haul (C/f) was used to estimate the relative abundance of walleye in BG2 Pond (Fig. 14A). The median catch per seine haul was greatest on July 16 and 23 but otherwise was relatively constant. The data was assigned to three periods; June 11 - July 9, (R1); July 16 - 23, R2; and July 30 - Sept. 3, (R3). Since the data were not normally distributed, the Kruskal-Wallis multiple comparisons procedure (Daniel 1978) was used to test for significance. The large catches made between July 16 and 23 were significantly greater than either the earlier or the later catches (R1 - R2 = 38.09; Z = 23.38; and R2 - R3 = 53.08; Z = 21.15). The data from June 11 - July 9 and July 30 - Sept. 3 were not significantly different (R1 - R3 = 14.99; Z = 17.97). The increase in median catch occurred when the walleye were 45 to 60 mm in length.

The environmental variables collected exhibited little or no relationship to the median catch per seine haul. Air temperature at the time of sampling remained relatively stable over the sampling season. Although there was some variability in August and September it did not correspond to changes in catch. The percentage of cloud cover, incident light intensity and wind speed showed no relationship to median catch. The average transmittance of light through a sample of pond water indicated that there may have been a relationship between turbidity and median catch although not a strong one (Fig. 14B).

Figure 14. A: Median catch of walleye per standard seine haul in BG2 Pond. Upper and lower quartiles are included. B: The mean transmittance of light through water samples from BG2 Pond.


100
80
60
40
20
0
A
C/f
90
70
50
B
Transmittance (%)
June
July
August
September
Date

LABORATORY STUDIES

Piscivory

In 1984 and 1985 walleye in experimental Units 1 and 2 showed the same overall pattern of fathead minnow selection. Most small and intermediate minnows and a few large ones were missing after 24 hours. The rate of piscivory varied from 44 to 86 % per day between experiments. The length frequency distributions of minnows in walleye stomachs at the end of the experiments were similar to the length distributions of missing fish, which suggests that selection was consistent for the duration of each experiment. The Kolmogorov-Smirnov two-sample goodness-of-fit procedure (Daniel 1978) was used to test for significance (Table 2). The two distributions differed significantly in only 36 % of experimental units containing fathead minnows. More than half of these occurred in experiments in 1984 where the abundance of minnows may have been limiting. The power of this procedure to detect differences in length frequency distributions was determined through the manipulation of distributions that differed only in location along the horizontal axis. The procedure was found to be sensitive to 3 to 6 mm shifts in location with the power of the test increasing with sample size.

Table 2. Comparisons of the length frequency distribution of fathead minnows found in walleye stomachs with fish missing at the end of 24 hour laboratory feeding experiments.

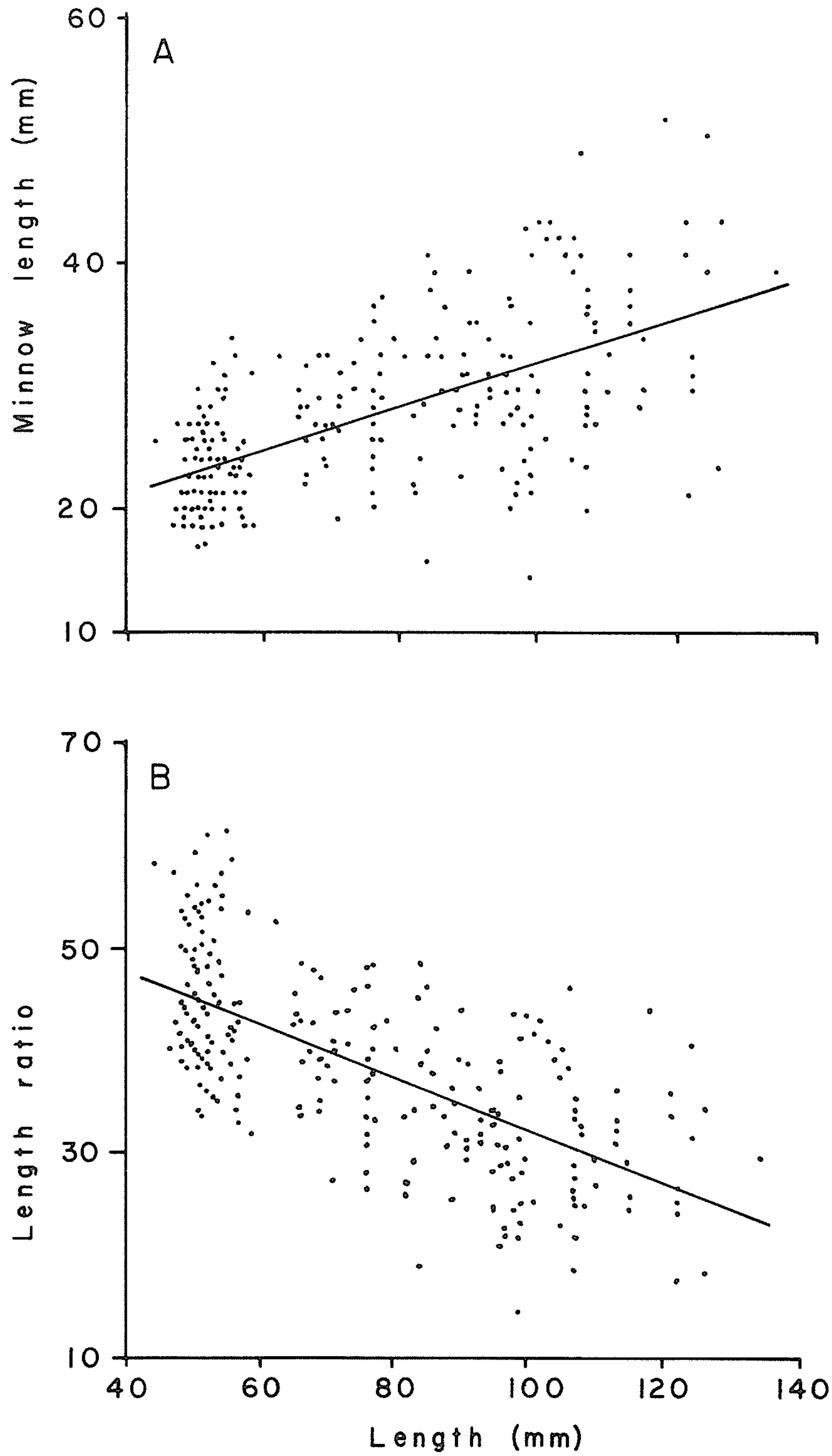
1984			1985		
Number			Number		
Stomachs	Missing	T	Stomachs	Missing	T
7	16	1.00 *	4	28	0.464
4	15	0.750*	5	23	0.478
11	13	0.818*	9	44	0.556*
12	14	0.786*	8	48	0.333
11	10	0.273	18	58	0.157
10	14	0.457	13	69	0.372
4	10	0.500	22	31	0.528*
7	14	0.571	18	34	0.389
14	12	0.571*	17	39	0.370
14	13	0.500	24	33	0.235
			18	20	0.556*
			17	24	0.328
			24	42	0.256
			37	33	0.460*
			16	38	0.273
			20	27	0.350

* indicate significance at P= 0.95

The relationship of estimated fathead minnow total length selected (EFTL) to walleye total length (WTL) for all experiments in 1985 was linear and defined by the equation, EFTL = 14.305 + 0.177 (WTL), (R^2 = 0.40; F = 178.42; df = 274; P < 0.0001),(Fig. 15A). Both the length and variation in length of minnows selected increased with walleye length, although the ratio of prey length to walleye length decreased (ratio = 57.931 - 0.256 (WTL); R^2 = 0.46; F = 232.87; df = 274; P < 0.0001),(Fig. 15B). Data from experiments in 1984 were not included in this analysis because, in some situations, the abundance of minnows may have been limiting.

The upper limit of fathead minnow length that could be consumed varied inversely with walleye length (Table 3). The size of fathead minnows which were consumed decreased as walleye grew and the incidence of dead minnows increased and then decreased as the ratio of minnow length to walleye length increased. The average number of dead minnows in units 1 and 2 at the end of experiments in 1984 was greater than in 1985 (3.5 and 2.1 respectively). Dead fish were generally in the intermediate to large size classes.

Figure 15. The relationship of estimated minnow length selected by walleye to walleye length (A). Relationship of prey:walleye length ratios to walleye length (B). Both figures represent the combined data for all experimental units containing fathead minnows in 1985.



A
Minnow length (mm)
60
40
20
10
B
Length ratio
70
50
30
10
40
60
80
100
120
140
Length (mm)

Table 3. Selection of fathead minnows near the upper size which can be consumed by walleye.

Walleye Length (mm)	Prey to Walleye Length Ratio (%) 50 Percentage			60 Percentage			70 Percentage			80 Percentage		
	Eaten	Dead	Alive	Eaten	Dead	Alive	Eaten	Dead	Alive	Eaten	Dead	Alive
47	100	0	0	67	0	33	0	0	100	0	0	100
57	100	0	0	0	17	83	0	50	50	0	17	83
71	33	50	17	0	17	83	0	0	100	-	-	-
81	17	50	33	0	0	100	0	17	83	-	-	-

Cannibalism

Cannibalism did not occur in any experimental unit which had fathead minnows as a component (Units 1 and 2). Cannibalism was frequent in Unit 3 which had zooplankton as a food source and in Unit 4 which had walleye alone. Cannibalism, when it occurred, always occurred in both Units 3 and 4.

In four of the six experiments in which cannibalism occurred,the number of potential prey eaten was higher in Unit 4 (Table 4). The percentages of potential prey consumed were 28.9 and 41.3 for Units 3 and 4 respectively. The length frequency distributions of walleye used were similar between units in all experiments (Table 4). Rates of cannibalism varied from 6 to 33% per day.

There was a tendency for the number of prey eaten to increase with increasing mean length of potential cannibals in aquaria containing zooplankton, but not in those with walleyes only (Table 4). When data from Unit 3 fish were arranged into length groups it was apparent that zooplankton was an important food for small walleye but, as they grew, cannibalism became frequent and the fraction of fish with empty stomachs increased (Fig. 16).

To determine the effect of walleye length range on the occurrence of cannibalism, the ratio of the mean prey length to mean cannibal length (P:C), expressed as a percentage, was calculated for the six experiments in which cannibalism occurred (Fig. 17). The P:C ratio could not be determined for experiments not exhibiting cannibalism; therefore the ratio of the longest to shortest fish (S:L), also shown as a percentage, was calculated. Cannibalism occurred in 85 % of experimental units in which the S:L and P:C ratios were less than 60 % and in only 7 % of those in which the ratios were equal to or greater than 60 % (Fig. 17).

Table 4. Length distributions and abundance of potential prey and cannibals related to cannibalism during a 24hr period in six pairs of aquaria containing zooplankton or no food.

Zooplankton						No Food					
Mean Length (mm)		Range	Abundance		No.	Mean Length (mm)		Range	Abundance		No.
Prey	Cannibals	(mm)	Prey	Cannibals	Eaten	Prey	Cannibals	(mm)	Prey	Cannibals	Eaten
49	77	40-87	9	9	1	48	78	40-87	8	8	3
51	88	48-107	8	6	1	50	89	44-110	8	6	2
54	99	50-121	8	8	3	53	101	49-124	7	8	5
51	103	45-108	7	5	2	50	103	45-108	8	5	3
55	101	50-123	8	8	3	54	106	47-141	8	8	3
54	102	51-138	6	10	3	59	107	51-138	7	9	3
Totals			46	46	13				46	44	19

Figure 16. The frequency of walleye stomachs containing food items for fish held for 24 hours in aquaria containing zooplankton or no food. Numbers of walleye in each length group are in parentheses.

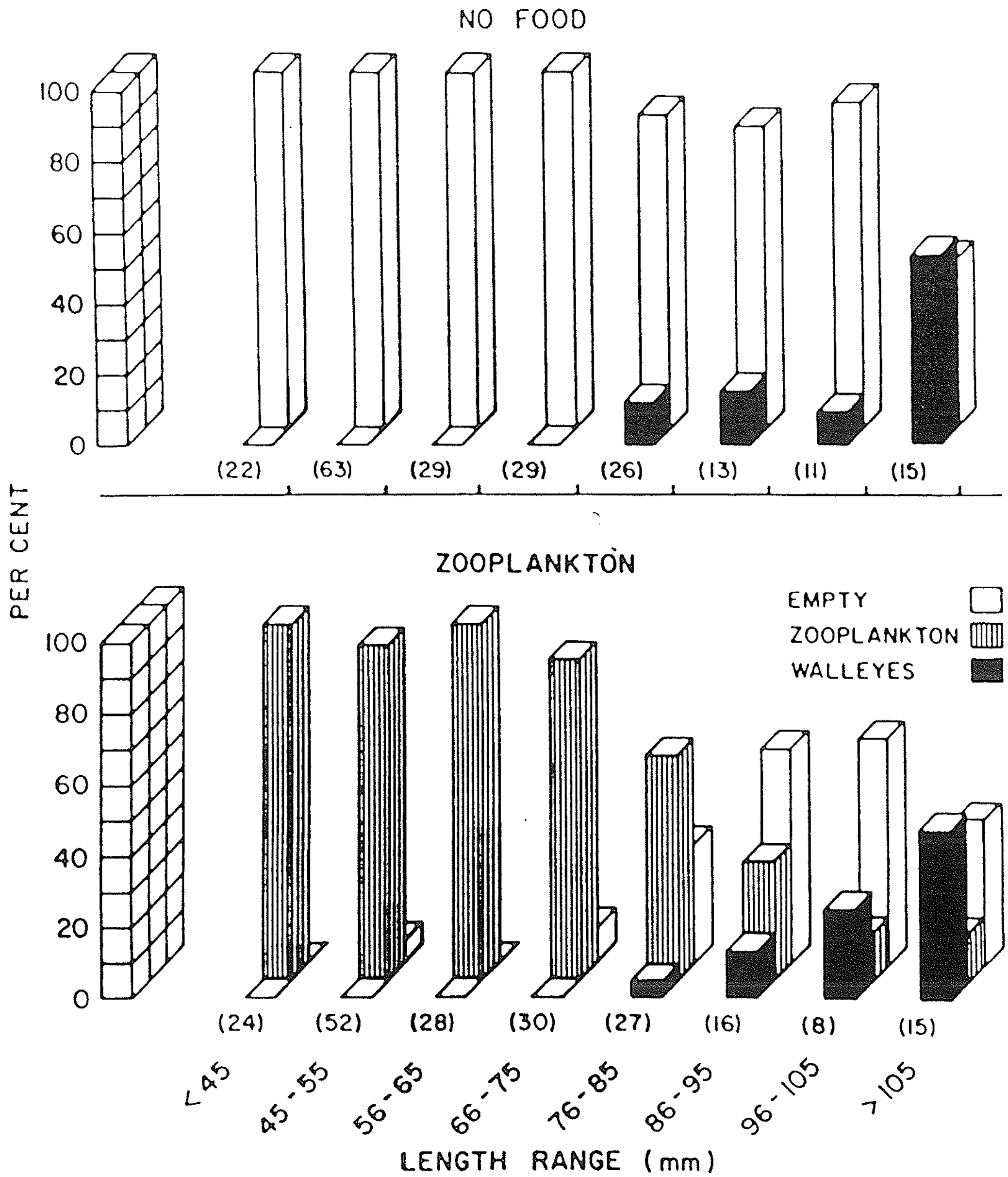
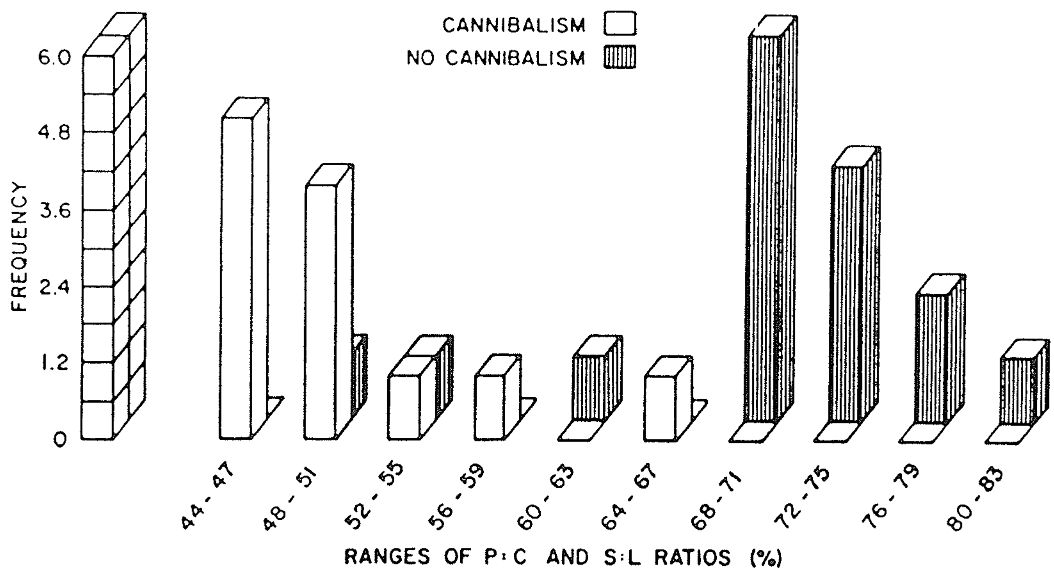

NO FOOD
ZOOPLANKTON
PER CENT
EMPTY
ZOOPLANKTON
WALLEYES
0
20
40
60
80
100
(22)
(63)
(29)
(29)
(26)
(13)
(11)
(15)
(24)
(52)
(28)
(30)
(27)
(16)
(8)
(15)
<45
45-55
56-65
66-75
76-85
86-95
96-105
>105
LENGTH RANGE (mm)

Figure 17. Frequency distribution of the ratios (expressed as percentages) of mean prey to cannibal length (P:C) and shortest to longest fish (S:L) in aquaria with zooplankton or no food.



CANNIBALISM
NO CANNIBALISM
FREQUENCY
6.0
4.8
3.6
2.4
1.2
0
44-47
48-51
52-55
56-59
60-63
64-67
68-71
72-75
76-79
80-83
RANGES OF P:C AND S:L RATIOS (%)

DISCUSSION

Walleye reared in BG2 Pond underwent a major change in their diet in midsummer. Their dominant food changed from Diaptomus (mean length 0.8 mm) to chironomids, corixids and amphipods (mean length 3.7 -3.8 mm). In general, zooplankton formed the bulk of the diet at the beginning of the season, insects such as mayfly nymphs and Chaoborus larvae occurred during the summer and fish were consumed late in the season (Smith and Moyle 1945; Li and Ayles 1981a). At a mean length of 43.5 mm walleye changed directly from zooplankton to fish and began feeding heavily on insects when the introduced forage fish became depleted (Walker and Applegate 1976). Swanson (1986) found that walleye first consumed zooplankton ranging from 0.5 to 2.0 mm in length, then dipteran pupae (2.0 to 4.0 mm) and corixids and amphipods (3.5 to 4.5 mm). The consumption of increasingly larger prey items, as occurred in BG2 Pond, is necessary to maintain growth (Kerr 1971; Mittlebach 1983; Keast 1985). Paloheimo and Dickie (1966) indicate that prey size has an impact on growth efficiency, with the consumption of large 'packages' of energy being more efficient than small ones.

Trends in the sizes of minnows consumed by walleyes in both the field and laboratory portions of this study indicated that walleye were size selective feeders. The positive relationship between walleye size and prey size and the increasing range in the size of prey consumed was similar to that demonstrated by Lake Erie walleye (Parsons 1971; Knight et al. 1984). Swanson and Ward (in press) found that walleye selected larger sized zooplankton than the average size available. Size selection however, may be modified by prey abundance (Knight et al. 1984). When prey species were scarce walleye were less positively size selective. Werner and Hall (1974) indicate that as the abundance of forage decreases diet breadth increases.

The abundance of prey or the size of the walleye may have influenced the transition from zooplankton to insects. Median stomach content weight of juvenile walleye did not increase regularly during the season although the fish progressively gained weight thereby increasing their stomach capacity. The transition from feeding on zooplankton to feeding on insects was associated with a period of rapid increase in the median stomach content weight per gram body weight. This suggested that there was a delay in the transition from one food source to the other. A delay in changing as a result of familiarity with a food type (Hanson and Wahl 1981) might be a factor, however, Mathias and Li (1982) found that in laboratory studies walleye made a rapid transition from <u>Daphnia pulex</u> to the larger <u>Chaoborus</u> sp. when they became available. Perhaps walleye in BG2 Pond reached a maximum in terms of daily intake of zooplankton and were unable to change to a new food source. It may have been neccessary for a new food source to become available or for their own abilities to develop before they could change. Since corixids were visibly abundant at the surface and in the water column in BG2 Pond throughout the season, it is likely that the delay in the transition was the result of walleye ability and not prey density.

Size selection of food by juvenile walleye and the resultant transitions from smaller to larger prey species may have a significant effect on the energy budget and therefore, on growth rate. At high prey densities, consumption of larger items, in theory, provides more net energy gain than the consumption of smaller items because search and handling times are reduced (Werner and Hall 1974; O'Brien et al. 1976; Eggers 1982). Optimal foraging rather than random selection of food by bluegill sunfish (*Lepomis macrochirus*) increased net energy gain from 4 to 10 fold (Mittlebach 1983).

In this study the smallest walleye used in laboratory experiments (40 to 45 mm) were piscivorous. Other researchers have indicated that piscivory is a major feeding behaviour when juvenile walleye reach a length of 60 mm (Dobie 1969; Walker and Applegate 1976; Mathias and Li 1982), although it can occur as early as 17.8 mm (Dobie 1969) or as late as 110 mm (Li and Ayles 1981a). Under laboratory conditions, when there was an abundant supply of minnows of various sizes, walleye may have been piscivorous at a smaller than usual size. In the field where forage fish of the appropriate size may not be as easily accessible, it may take longer before the walleye become piscivorous. In general though, walleye will become piscivorous whenever the size of available forage fish and their own abilities allow it.

The laboratory experiments indicated that prey greater than 60% of walleye length were rarely consumed and that the length of prey relative to walleye length decreased as the walleye grew. The maximum prey to predator ratios for walleye in the literature were, 50 % (Parsons 1971; Mathias and Li 1982) and 40 % (Nielson 1980). Parsons found also that the ratio decreased as the walleye grew. Attacks on minnows larger than the walleye could consume may have resulted in the dead fish found in the middle to larger size classes in some laboratory experiments. On many occasions walleye were observed seizing large minnows but then released them. In these experiments it is probable that walleye attacked larger minnows than they were able to consume because of the limited supply of small fish. Perhaps the upper size limit of forage fish selected by walleye, as determined from field data is too low because larger fish can escape more readily. The upper size limit of prey selected in laboratory experiments may reflect the physical limitations of walleye but may not be comparable to the field situation.

The bias towards selection of large minnows in the BG2 Pond field experiments on August 7 and 8 contrasted with selection on July 22 and that seen in the laboratory. Excluding the minnows that were too large to comsume (see above), selection remained consistent throughout most laboratory experiments. Selection of fathead minnows on July 22 was also in proportion to abundance. On August 7 and 8, after an initial period showing no bias, large minnows were selected more frequently than small ones. However, comparisons of the size of prey in the diet with that in the environment may not properly identify prey selection because of what Werner and Hall (1974) termed effective density, which takes into account reaction distances to different prey. Prey that are more visible have a higher 'effective density' than actual density because of an increased encounter rate. In effect, the occurrence of prey in the diet is a function of both abundance and visibility. Laboratory conditions were necessary to regulate encounter rates so that size selection could be identified.

Transitions from feeding on zooplankton, insects, crustaceans and eventually fish may be related to the development of the retina of walleye. The tapetum lucidum of walleye undergoes major development during their first summer of life. The tapetum lucidum aids in scotopic vision in adult walleye and many other fish (Ali and Anctil 1977). It is composed of highly reflective granules of 7, 8-dihydroxanthopterin and lies in the cells of the pigment epithelium (Zyznar and Ali 1975). The granules fill long processes that extend vitread between the rods and cones. At high light intensities the rods move near the bases of the pigment epithelial cells. Under dark-adaptation the rods occur about midway along the epithelial processes (Zyznar and Ali 1975). The tapetum lucidum may function by causing multiple reflections through the rods. Each time light is reflected more is absorbed thereby increasing the sensitivity of the rods to smaller amounts of light (C. Braekevelt pers comm.).

The first appearence of the tapetum lucidum at a walleye length of 27 mm and its development during the transition in food type from zooplankton to insects and amphipods suggests that it influenced prey choice. Li et al. (1985) indicated that prey choice may be limited by the visual capability of the predator and that visual capability increased with size. Changes in diet breadth in Xenomelanirs venezuelae was the result of growth-related improvements in vision (Unger and Lewis 1983). Narrowing of diet breadth as the fish grew was attributed to increased encounter rates because of increased visual acuity.

Light is the principal abiotic factor controlling activity in walleye (Ryder 1977). Large walleye, with well developed tapeta lucida, tend to feed at low light intensity. The capture of walleye in the shallows of West Blue Lake, a very clear lake, increased after sunset and continued at high levels until sunrise. The decrease in the number of fish with empty stomachs as night progressed, indicated that feeding was occurring (Kelso and Ward 1977).

The temporal feeding pattern exhibited by walleye in BG2 Pond may have resulted from the development of the tapetum lucidum. The 24 hour feeding experiment when walleye were small indicated that most feeding took place during daylight, with some feeding on insects at night. Walleye of the size used in the first 24 hour experiment (40 to 50 mm) would have had a partially developed tapetum lucidum which may have permitted them to feed under low light conditions but did not significantly inhibit them from feeding during the day. Walleye (80 to 124 mm) fed extensively on fathead minnows introduced prior to the 24 hour feeding experiment in August. Most feeding occurred during dusk, night and dawn. Similarly, Mathias and Li (1982) demonstrated that large and small walleye concentrated their feeding in the evening and midmorning. Larger fish also fed at night. The retinas of fish in their investigations were probably at various stages of development, therefore allowing the smaller fish to feed under both bright and dim light conditions while the larger fish fed primarily at night. The appearance of the tapetum lucidum at a length of about 30 mm may be related to the change from positive to negative phototaxis (Bulkowski and Meade 1983). The development of the tapetum lucidum may be related to the change from pelagic to benthic feeding (Houde and Forney 1970; Forney 1976) and the change from diurnal to crepuscular and nocturnal activity (Ryder 1977; Mathias and Li 1982). The relationship of retinal development to feeding behaviour will be better understood when the feeding of walleye lacking a tapetum lucidum has been studied.

The onset and gradual development of the tapetum lucidum may have delayed the change from chironomids to corixids and amphipods. Sufficient development of the tapetum lucidum may be needed in order to change from a pelagic to a demersal foraging behaviour. The effect of the onset of development of the tapetum lucidum on diet may have resulted in the decrease in the instantaneous growth rate. The development of the tapetum lucidum may be very costly energetically (C. Braekevelt pers. comm.). The tapetum lucidum may have also affected the catch per unit effort since its development is associated with sensitivity to light. The transition in diets in BG2 walleye may have influenced the development of the tapetum lucidum (Johns 1981). Laboratory study and a larger number of field samples would be needed to determine if this were the case. The development of such a prominent structure as the tapetum lucidum will have an impact on the feeding ecology of juvenile walleye but to date its effect can only be inferred.

The initial increase in C/f indicated that walleye suddenly became more vulnerable to the sampling gear. The increased catchability may have been caused by changes in the distribution of fish in the pond; ie a change in habitat and a change in behaviour. One result of a habitat change may be an increase in food intake (Mittlebach 1981). The median stomach content weight of walleye in BG2 Pond increased at the time that the food source changed from zooplankton to insects and about the time median catch increased. It is possible that the increased catchability was caused by a change in habitat or foraging behaviour. Perhaps the transition from zooplankton to insects resulted from the sampling of alternate habitats (Werner et al. 1981) and thus, in BG2 Pond, more active use of the inshore regions where there was more chance of being caught in the seine hauls. The subsequent decreases in catch may have been caused by the development of the tapetum lucidum. A well developed tapetum may inhibit the movement of large walleye into the shallow areas of the pond because of high light intensity.

Median catch of walleye in weekly seine hauls was not an adequate measure of their relative abundance in BG2 Pond. Turbidity was the only environmental factor measured that seemed to be related to the changes in catch. Both suspended inorganic material and phytoplankton contribute significantly to the attenuation of light in natural waters (Kirk 1980). Light intensity in the pond may have affected fish movement and thus catch although this relationship is not clear because surface light intensity and cloud cover which could also affect light levels in the pond showed no relationship to catch. It is possible that the nonrandom distribution of fish or other environmental factors not measured may have affected median catch per seine haul.

Diet is a major factor affecting growth rates in fish (Paloheimo and Dickie 1966) although growth rates can also be inherently different (Keast and Eadie 1985). It is differences in growth rates that can lead to variation in length in a population. In many cases increasing variation in growth will result in the development of a bimodal length frequency distribution. The development of bimodality in largemouth bass (Micropterus salmoides) was associated with a transition to piscivory and there were major differences in diet between the two modal classes (Keast and Eadie 1985). Rapid growth in walleye during the first few months of life increased the probability of continued rapid growth because they were able to consume a wider range in lengths of prey (Parsons 1971). Once bimodality is initiated larger fish are able to consume a wider variety of foods, further increasing the size discrepancy (Keast 1985). A modal group of smaller walleye fed on zooplankton and insects whereas a group of larger fish fed exclusively on fish (Swanson and Ward 1985). In a pond population of fingerling walleye, the larger fish caused a temporal shift in the feeding time of the smaller walleye and thus may have limited their food intake (Mathias and Li 1982). Brett (1979) indicated that hierarchies such as this can enhance variation in length. In situations where there is not an adequate supply of food of the right size, increasing variation in length can result in the onset of cannibalism, which is probably one of the most important sources of mortality associated with the pond culture of juvenile walleye (Cheshire and Steele 1972).

The laboratory experiments indicated that the presence of suitably sized forage fish inhibited cannibalism and that an abundant supply of zooplankton reduced cannibalism in walleye up to 100 mm in length. When the range in lengths in a population is sufficient for cannibalism to occur it may not develop if suitable prey are present (Swanson and Ward 1985). Similarly piscivory may be delayed until the walleye are 100 mm long if an abundant supply of larger crustaceans is available (Li and Ayles 1981a). Spiny-rayed fish are less susceptible to predation than are soft-rayed species (Moody et al. 1983) therefore, the presence of a soft-rayed forage species may be a preferred substitute for spiny-rayed fish such as the walleye itself. The availability of forage fish can inhibit cannibalism if they are introduced when the predatory fish are large enough to feed on them (Smith and Moyle 1945; DeAngelis and Coutant 1980; Swanson and Ward 1985).

The walleye length at which cannibalism is first evident can be highly variable but is often associated with the onset of piscivory. Cannibalism first occurred at cannibal lengths of 34 mm (Mathias and Li 1982), 30 to 40 mm Cheshire and Steele 1963) and 46 mm (McIntyre et al. in press). Cannibalism did not take place if the range in lengths in a population was small (Li and Ayles 1981a). The laboratory studies indicated that the critical prey-cannibal length ratio was approximately 60 %, although cannibalism did occur in one case at a ratio of 67 %.

The rates of cannibalism in the laboratory experiments (6 to 33 %) are high relative to the rates found in field experiments. Rates of cannibalism in field experiments varied from, 0.1 % in Lac La Ronge (Rawson 1957), 0.9 to 4.4 % in Oneida lake (Chevalier 1973), 6 to 7 and 5 % in rearing ponds (Mathias and Li 1982; Swanson 1986). However, these mortality rates are instantaneous and operate over long periods of time (Mathias and Li 1982). Consequently, The examination of stomach contents from relatively infrequent collections may underestimate the long term effects of cannibalism in a closed population such as those present in rearing ponds. In contrast, rates of cannibalism in laboratory experiments may be overestimates because of the increased encounter rates between cannibals and their prey in small aquaria. In excess of 5 % of the small walleye in a rearing pond were being cannibalized per day, (Swanson

1986), but this rate of consumption is low relative to the percentage of vulnerable walleye lost per day in laboratory experiments (29 - 41 %). Forney (1976) found that walleye year class strength in Oneida lake was influenced by cannibalism during years where alternate prey were not readily available. Rates of cannibalism similar to those found in the field and those occurring in the laboratory experiments would greatly reduce the production of juvenile walleye in rearing ponds.

Cannibals may initially make up only a small percentage of the total population (Mathias and Li 1982; Swanson 1986); however, once bimodality develops differences in diet between the large and small groups of fish accentuates differences in size making a progressively larger proportion of the smaller mode susceptible to predation (Keast and Eadie 1985). Consequently an increasingly larger proportion of the population is composed of cannibals thus approximating the situation observed in the laboratory experiments.

Walleye consume a variety of types and sizes of prey during their first summer of growth. Although walleye size limits the range of prey they can consume there is generally a wide enough variety in the type and size of prey available that opportunity becomes a factor. The timing of the change from one food type to another is never the same for all walleye and therefore results in differences in diet between fish. Factors such as the development of the tapetum lucidum may also affect diet by influencing prey choice. It is these differences in diet that leads to variation in length. When variation in walleye length is sufficient (S:L $\leq$ 60 %) in the absence of the appropriate size of prey, cannibalism will occur.

The sampling problems associated with field work make laboratory experiments an important part of studies of the feeding ecology of fishes. The use of field and laboratory work here has shown the limitations of field experiments on prey selection. It has also indicated the importance of cannibalism in limiting the production of walleye from rearing ponds and methods for its control. Through the use of intensive culture techniques to provide the appropriate quantity, type and size of prey as the walleye grow, it will be possible to increase the quality and abundance of fingerling walleye available for enhancement programs, provided an adequate artificial food can be developed.

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