The influence of turbidity upon the piscivorous feeding of juvenile walleye (Stizostedion vitreum vitreum).

by

Lenore J. Vandenbyllaardt

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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

Laboratory experiments in the summers of 1986 and 1987 were conducted to determine relationships between turbidity, piscivory and juvenile walleye (Stizostedion vitreum vitreum) size. The influence of prey species vulnerability was also examined. Walleye ≥ 85 mm in length ate a greater weight and number of fathead minnows (Pimephales promelas) in turbid water than in clear water. Feeding was inhibited in the highest turbidities (100 and 161 NTU) in the 1 h feeding trials, but not in the most turbid condition (121 NTU) of the 4 h trials. In contrast, smaller walleye (≤ 75 mm) fed at similar rates in both clear and turbid conditions, but consumption was inhibited at the highest levels (100 and 161 NTU) of the 1 h trial. Both walleye and fathead minnow activity increased as turbidity increased, increasing the probability of encounters. Consumption of yellow perch (Perca flavescens) was much lower than that of fathead minnows under similar conditions of water clarity. Perch behaviour did not vary with increasing turbidity. The perch remained dispersed and relatively motionless, minimizing the probability of encounters. Increased feeding in turbid water by larger walleye (≥ 85 mm) may be related to the development of functional macroreceptors. The development of scotopic vision early in life permits walleye to occupy a niche unexploited by other predators.

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INTRODUCTION

Subsurface illumination levels in natural waters are affected by a variety of physical factors, such as wave action, ambient surface illumination and turbidity levels (Ryder 1977). Of these factors, turbidity can have the greatest influence in reducing the depth of light penetration. Some of the aquatic animals which inhabit areas of elevated turbidities have overcome the effects of turbidity by enhancing their tactile and olfactory sense organs (Bruton 1985), while others have developed visual adaptations. Most fish, relative to other aquatic animals which feed in the water column, orient by vision; therefore increased turbidity will influence a fish's visual acuity and probably its ability to capture prey. Many fish species, including the walleye, Stizostedion vitreum vitreum (Mitchill), have adapted to these low light conditions.

Walleye are visual predators occurring in clear to moderately turbid waters (Zyznar and Ali 1975). Adult and subadult walleye are primarily crepuscular or nocturnal foragers (Ali et al. 1977), whose feeding forays are inversely proportional to ambient subsurface illumination (Ryder 1977). They are effective visual predators in these dim conditions because they have developed two specializations of the retina which enhance scotopic vision. These are a well developed tapetum lucidum and bundled photoreceptors, both of which develop during the walleyes first year of growth (Braekevelt et al. 1989).

The ability to function effectively in dim or turbid conditions has provided walleye with several competitive advantages. The development of crepuscular foraging by walleye greatly reduces direct competition with their main competitors, yellow perch and northern pike (Ryder and Kerr 1978), as both are strictly diurnal predators (Helfman 1979; Craig and Babaluk 1989).

The switch to crepuscular feeding also allows walleye to take advantage of the "period of confused activity" which occurs at dusk within freshwater fish communities. This is a period of increased activity by diurnal species, as their schools begin to break down at the end of the day (Emery 1973). At this time, walleye visual acuity is approaching optimum, while acuity of the diurnal species is rapidly declining (Ali et al. 1977). The increased activity and reduced avoidance response of the prey species and the optimization of the walleye's visual performance, contribute to the success of walleye as predators in dim conditions. Thereby allowing walleye to exploit a niche unoccupied by other predators.

Experiments were conducted in 1986 and 1987 to investigate relationships between varying turbidity and piscivory in juvenile walleye during their first summer, using fathead minnows and yellow perch as prey. The activity of both predator and prey species were monitored to detect changes in behaviour which might affect the vulnerability of the prey or the efficiency of the predator.

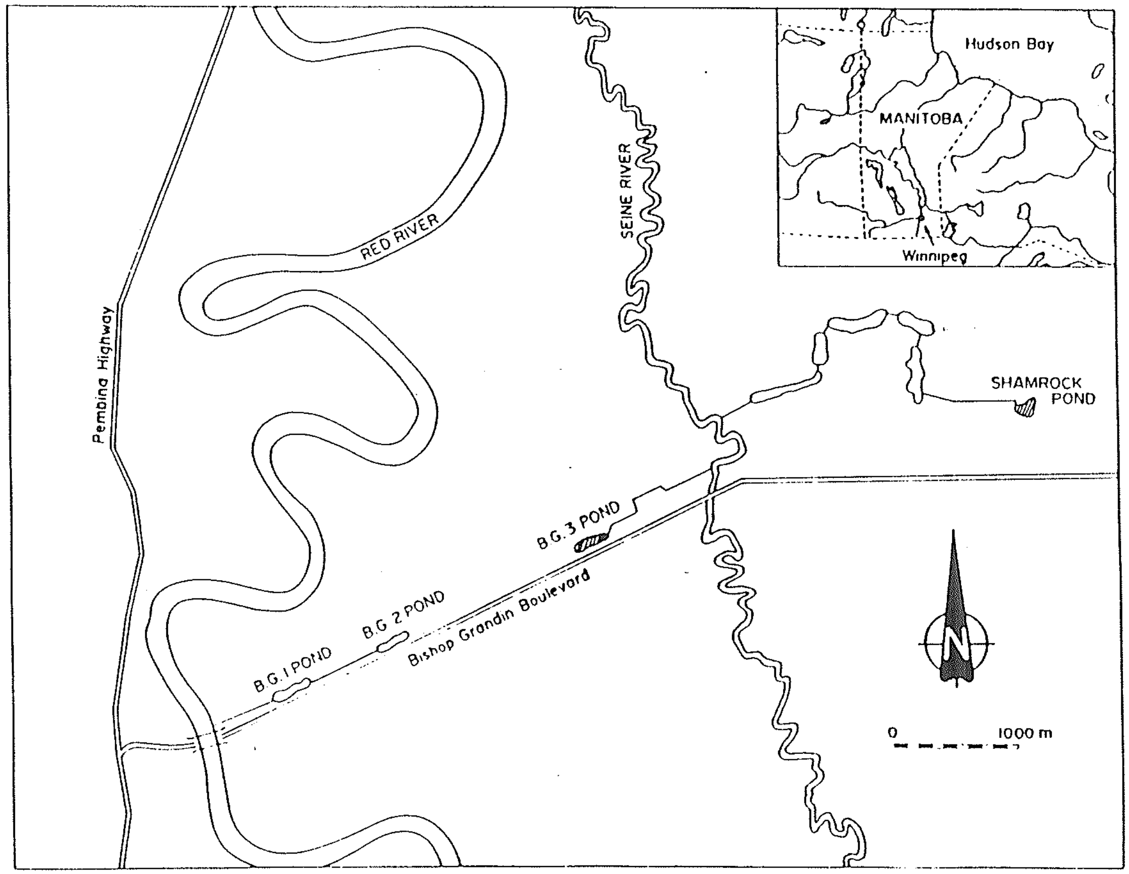
METHODS AND MATERIALS

Walleye used in these experiments were reared in stormwater retention ponds located along Bishop Grandin Boulevard in Winnipeg, Manitoba (Fig. 1). Walleye fry were obtained from the Province of Manitoba, Fisheries Branch, Whiteshell Fish Hatchery. Approximately 30,000 fry were released into the ponds on May 22 and 20, 1986 and 1987 respectively.

Eleven experiments with fathead minnows as prey were conducted from late June to late August in both 1986 and 1987. Six experiments with yellow perch as prey were conducted during the summer of 1987. Experiments were composed of feeding trials under various conditions of water clarity. Five walleye were used in each trial. The average fork lengths of the walleye in the first experiments of 1986 and 1987 were 37 and 40 mm, respectively. Walleye lengths in the final experiments were 101 and 100 mm in 1986 and 1987. Walleye were collected with a seine, measured to the nearest millimetre and transported to the laboratory. They were held in 40 L aquaria (5 per aquaria) for 24 hours without food. Water temperature in the aquaria ranged between 20-22° C, approximating pond temperature at the time the fish were captured. Fathead minnows and perch were collected locally and held in the Animal Holding Facility at the University of Manitoba.

Trials were carried out in 190 L glass aquaria, containing 130 L of water. Illumination for each aquarium was provided by a single 61 cm fluorescent Vita-Lite. A LiCor model Li-185B light meter with a Li-190SB quantum sensor was

Figure 1. Location of the Bishop Grandin stormwater retention ponds.



Hudson Bay
MANITOBA
Winnipeg
SHAMROCK POND
SEINE RIVER
RED RIVER
Pembina Highway
B.G. 3 POND
B.G. 2 POND
B.G. 1 POND
Bishop Grandin Boulevard
N
0
1000 m

used to measure light intensity. Preliminary experiments were conducted with fathead minnows as prey to determine if, in clear water, there was a level of incident illumination which produced a maximal feeding response. Consumption of fathead minnows in clear water was not related to incident light over the range of illumination used in our experiments (Appd. I).

Four experimental treatments of 1, 7, 14 and 121 Nephelometric Turbidity Units (NTU) (McCluney 1975, Kirk 1983) were used in 1986. In 1987 the turbidity range was expanded to five treatments of 1, 23, 42, 100 and 161 NTU for the fathead minnow trials, and 1, 40 and 139 NTU for the perch trials (Table 1, see Appd. II). During the 1986 experiments turbidity was measured with a LKB Ultrospec UV/VIS spectrophotometer by measuring percent transmittance at 350 nm. A calibrated formazin curve (APHA 1985) was employed to calculate turbidity values. A Hach DRT-15B Turbidimeter was used in 1987 to measure turbidity directly.

Turbidity levels were determined experimentally by adding weighed amounts of sediments to 130 L of water in 190 L aquaria, which were aerated for four hours to provide turbulence. Samples were taken to determine turbidity levels during settling. The relationship between turbidity level and time was a negative exponential. The turbidity value when the rate of settling had levelled off was equated to the amount of sediment added. These tests were repeated until a range of turbidity values could be equated to sediment weights and stabilization.

Table 1. Derivation of turbidity values (NTU) used in both four and one hour experiments. Experimental values were the means at the "start" and "finish" of the trial determinations (n). Standard errors of the means are shown.

Target Turbidity Level	Start	Finish	Actual Turbidity Mean	n
<u>Four Hour</u> Fathead Trials				
5	7.6 ± 1.6	5.4 ± 1.5	6.8 ± 1.5	10
15	16.2 ± 2.5	11.3 ± 2.1	14.0 ± 2.2	10
115	127.7 ± 13.4	113.0 ± 13.1	120.7 ± 13.1	9
<u>One Hour</u> Fathead Trials				
25	27.2 ± 0.8	18.8 ± 1.1	23.2 ± 0.8	11
40	51.4 ± 1.6	31.1 ± 1.8	41.4 ± 1.3	16
100	116.1 ± 4.7	83.6 ± 3.9	99.9 ± 3.6	11
150	182.8 ± 5.8	124.3 ± 5.9	153.5 ± 5.3	15
Perch Trials				
40	49.4 ± 3.9	29.6 ± 3.8	39.6 ± 3.0	5
150	178.0 ± 13.7	100.0 ± 6.2	139.0 ± 9.7	5

The required weights of sediments were added to the aquaria four hours prior to the feeding trials, to allow for settling and stabilization to the required turbidities. Circulation, during the stabilization period only, was provided by a single airstone. Air flow was maintained at approximately 2100 mL/min. Water samples were taken at the surface before prey were introduced into the aquaria and at the end of the feeding trial. Turbidity was measured immediately upon the samples being taken. The turbidity value reported for each trial was the average of all values at the "start" and "finish" of the trials (Table 1), rounded to the nearest whole number.

The Red River sediment was collected in the boat launch area at the St. Norbert (49° 45', 97° 09') floodway gates in south Winnipeg, with a 30 cm Ekman dredge. The sediment was air dried, pulverized in a blender and size graded through a No. 30 sieve (U.S. Series alternate sieve designation). The portion which passed through the sieve was autoclaved and stored in a closed container until use. Particle size analysis was done by the Manitoba Provincial Soil Testing Laboratory (Appd II. Table 2).

Experimental Protocol

Walleye were starved for 24 hours prior to the feeding experiments. Groups of five walleye were transferred to each experimental aquarium for acclimation to light and water conditions, for the final 4 hours of the starvation period. The five walleye used in each feeding trial were within a 5 mm length range. In separate 40 L aquaria containing 30 L of water, the prey species were also acclimated to conditions, four hours prior to the feeding trial.

In 1986, the fathead minnows ranged in fork length from 21 to 55 mm. They were divided into seven 5 mm size classes (21-25, 26-30, etc.). Each size class contained 15 individuals, resulting in a total of 105 minnows present per trial. Fathead minnows and perch (Perca flavescens Mitchill) were used as prey in 1987. The minnows ranged from 26 to 40 mm, and were divided into three size classes (26-30, 31-35 and 36-40 mm). Each class contained 20 individuals, resulting in 60 minnows present per trial. Perch ranged in size from 26 to 35 mm and were of two size classes, 26-30 and 31-35 mm. Each class contained 30 fish, for a total of 60 per trial.

Just prior to the start of the feeding trials, air flow into the aquaria was turned off and the airline removed. With the walleye already present, the prey were introduced behind a removable opaque plate. After a short time, during which the prey became reoriented, the plate was removed. Prey were always introduced into the end of the aquaria opposite to where the walleye were located.

The duration of the feeding trials in 1986 was four hours, in 1987 it was reduced to one hour. On completion of the feeding trial, the walleye were removed and placed in a killing solution of MS 222, and preserved in 10% formalin for subsequent stomach analysis. The prey remaining in the aquaria were anaesthetized with MS 222 and their fork lengths were measured to the nearest millimetre.

To calculate the weight of fathead minnows consumed, the stomach contents of all 5 walleye in each trial were analyzed. The fork lengths (FL) of the minnows consumed were estimated from GAP measurements of the left pharyngeal arch, using the regression equation; FL (mm) = 13.481 GAP (mm) + 1.963 ($r^2=0.973$, $P<0.01$, df=88, F=3244) (McIntyre and Ward 1986). These estimated fork lengths were then used to calculate fathead minnow weight in milligrams (FWT), according to the regression equation: Log_{10} FWT = 3.0471 Log_{10} FL - Log_{10} 2.123, ($r^2= 0.88$, df= 172, F= 1285.1, Prob>F= .0001).

The lengths of consumed perch were estimated using opercular bone measurements. Left opercula were removed, dipped in hot water, cleaned and measured using a dissecting microscope with a calibrated eyepiece. The chord length between the opercular hyomandibular articulation and the caudal end of the opercular spine was used to develop the relationship between perch fork length (PL) and operculum length (OP) (LeCren 1947). Perch lengths were estimated by the equation: PL = 15.6114(OP) - 3.2212 ($r^2=.80$, $P<0.0001$, df=33, F=132). The lengths obtained from this equation were in turn, used to estimate perch weight (PWT) in grams, by the following linear equation: PWT = 0.0245(PL) - 0.5321, ($r^2=.81$, $P<0.0001$, df=41, F=173).

Observations were made on the behaviour of both prey species and walleye. The nature of the treatment conditions made it difficult to obtain quantitative data. For example, in the most turbid conditions (100, 121 and 161 NTU), individual fish could only be observed if they were within approximately 5 cm of the aquarium side, therefore behaviourial observations presented are qualitative only. All observations presented on the prey species are those which occurred in the presence of the walleye.

Statistical Analysis

The relationships between the mean length of walleye used in four and one hour trials, the weight of fathead minnows eaten per walleye and water turbidity were investigated using two-way ANOVA. Analyses were applied to the weight consumed per walleye plus one, transformed to natural logarithmic values due to the presence of zero values. Regression analyses were conducted to fit an exponential model to the mean weights of prey consumed by walleye by the addition of one as above, but not transformed. These weights are referred to as adjusted mean weights. The exponential model $1 + WT = e^{(b\,FL - a)}$ was fitted. Consumption of fathead minnows by walleye in clear water and at each turbidity level was examined by one-way ANOVA, using the natural logarithmic transformation. The mean weight and number of fathead minnows eaten per walleye by two length groups of walleye in turbid and clear water were compared by one-way ANOVA. The natural logarithmic transformations was used for both weights and numbers consumed. Analyses of variance were performed using SAS-PC (SAS 1988). Regression analyses of the exponential data were performed using STATGRAPHICS (STSC 1987).

Vanderploeg and Scavia's (1979) electivity index (E^*), was used to calculate prey size selection:

$$E^* = [W - (1/n)] / [W + (1/n)]$$

$$W = (r_i/p_i) / \Sigma(r_i/p_i)$$

where n is the number of prey items available, r is the proportion of item i in the diet and p is the proportion of item i in the environment. A large range of prey length was presented during each trial, so that the size of prey available would not have to be altered during the experimental series, to accommodate the increase in walleye length. As a result, not all prey in a particular trial could be considered in the calculation of selection. Therefore, the selection indices were calculated on the basis that prey greater than 50% (Mathias and Li 1982) of the walleye length were not available for possible consumption. Subsequently, only prey less than 50% of the walleye length were used in the calculations.

RESULTS

Fathead Minnows Trials

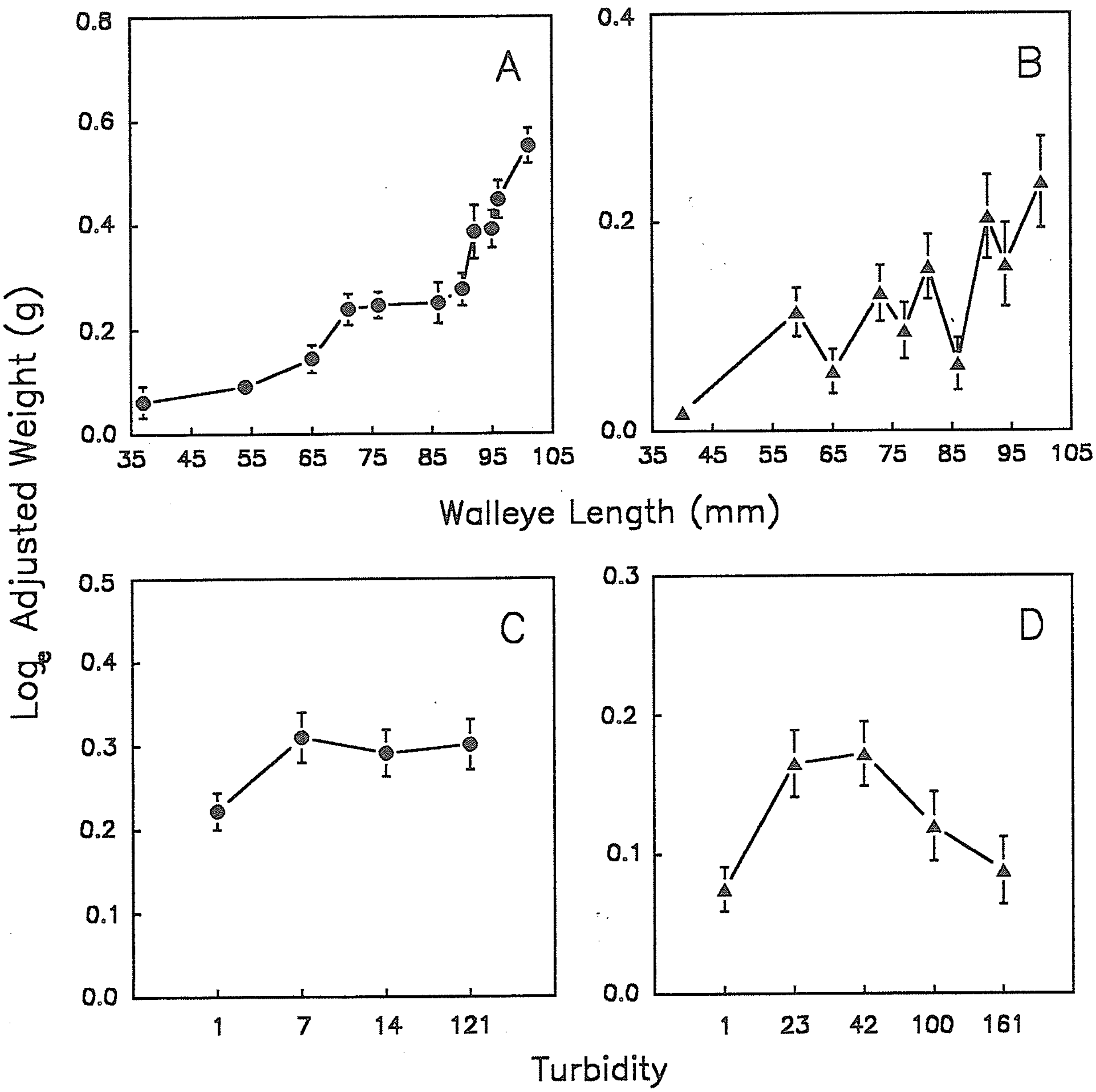
Consumption of fathead minnows by walleye was dependent on walleye length and turbidity, in both four and one hour experiments. Consumption caused by the interaction of walleye length and turbidity was significant during the four hour experiment (Table 2). The weight of fathead minnows consumed increased as walleye grew over the period of the studies (Fig. 2A and B). The relationship between consumption and turbidity was more variable. Consumption was low in clear water during both experiments. While the weight of fathead minnows consumed was high and uniform for all turbidity levels during the four hour trials (Tukey's multiple range-test; $P<.05$). In contrast, during the one hour trials (Fig. 2D) consumption was greatest at the intermediate turbidity levels (23 and 42 NTU), and then declined at the two highest levels (100 and 161 NTU) to a level similar to clear water (Tukey's multiple range-test; $P<.05$).

Relationships between the weight of fathead minnows consumed per walleye per trial and the mean fork lengths of walleye used in each trial were positive exponentials (Fig. 3 and 4), indicating that consumption of fathead minnows increased as walleye grew over the periods of the studies, particularly in the turbid trials. R-square values for consumption increased with increasing turbidity level during the four hour trials from 66.5% (1 NTU) to 90.3 % (121 NTU). Of the significant regressions for the one hour trials, r-square values ranged from 39.4% (100 NTU) to 68.4% (42 NTU). Consumption was generally

Table 2. Results of the two-way ANOVA for differences in the mean consumption per walleye for walleye of increasing length and turbidity level used in four and one hour experiments.

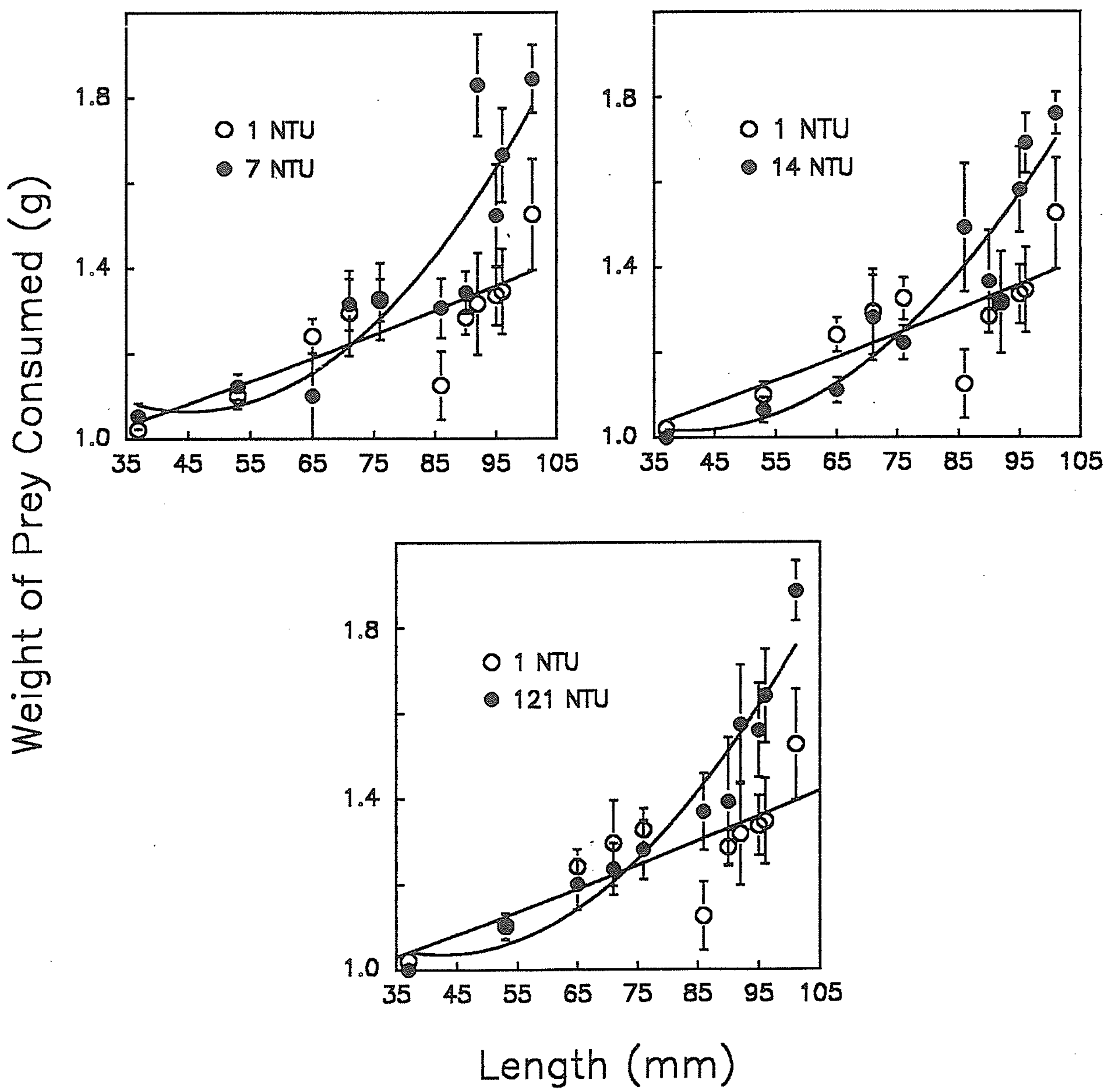
Source	df	F	Prob>F
<u>Four Hour</u>			
Walleye length	10	23.75	<.01**
Turbidity level	3	4.50	<.01**
Walleye length * turbidity level	30	1.54	<.05*
<u>One Hour</u>			
Walleye length	9	5.07	<.01**
Turbidity level	4	4.12	<.01**
Walleye length * turbidity level	36	0.60	ns

Figure 2. The mean weight of prey consumed per walleye with increasing walleye length and at various turbidity levels during the four (A,C) and one hour (B,D) experiments. Standard error bars are shown.



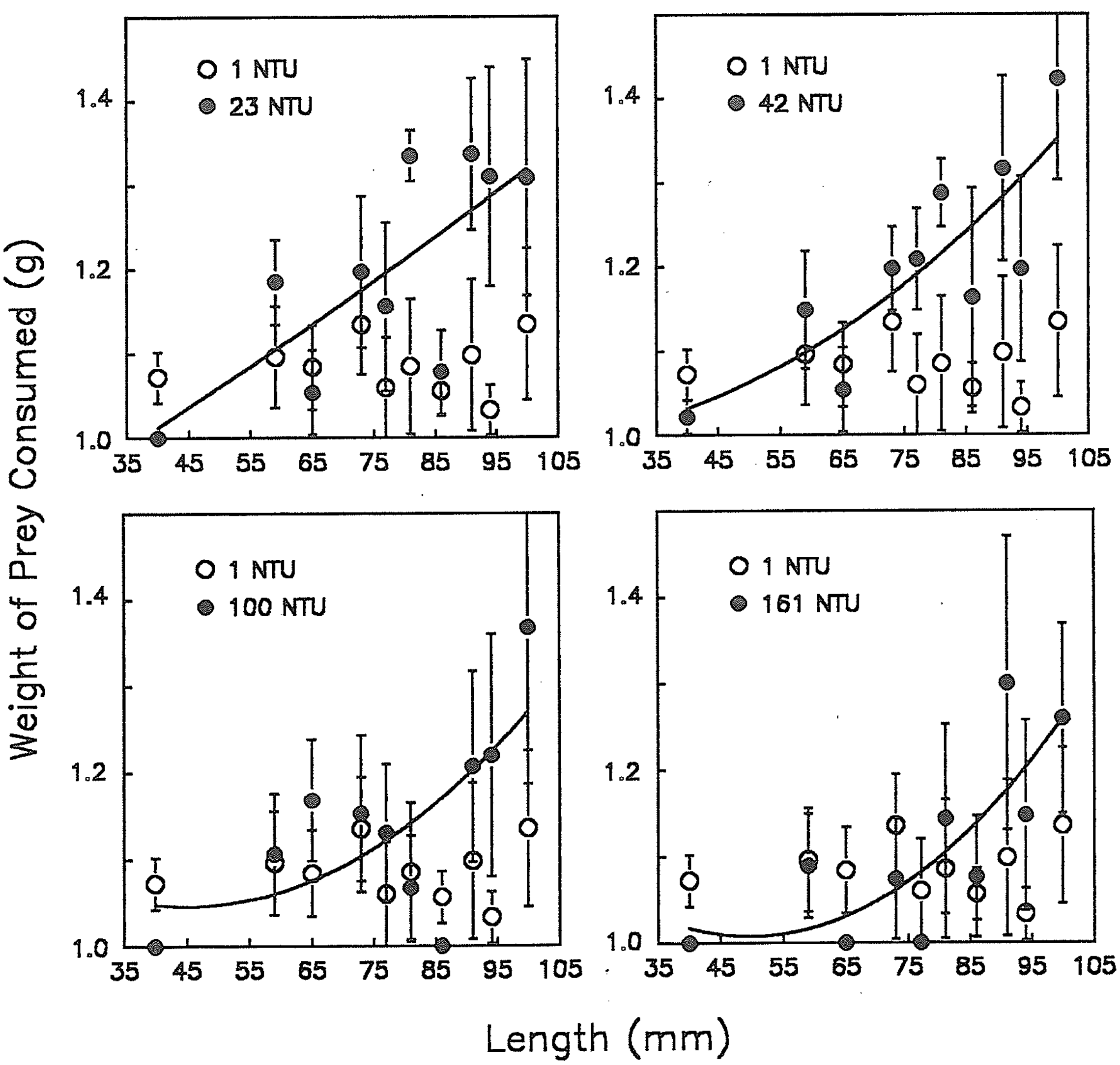
A
B
C
D
0.0
0.2
0.4
0.6
0.8
0.1
0.3
0.5
35
45
55
65
75
85
95
105
1
7
14
121
23
42
100
161
Loge Adjusted Weight (g)
Walleye Length (mm)
Turbidity

Figure 3. Adjusted mean weight of fathead minnows consumed during four hour experiments, with each turbid treatment compared to the clear condition (1 NTU). Regression lines for each turbid treatment are plotted.



Weight of Prey Consumed (g)
1.8
1.4
1.0
35
45
55
65
75
85
95
105
1 NTU
7 NTU
14 NTU
121 NTU
Length (mm)

Figure 4. Adjusted mean weight of fathead minnows consumed during one hour experiments, with each turbid treatment compared to the clear condition (1 NTU). Regression lines for each turbid treatment are plotted.



1 NTU
23 NTU
1 NTU
42 NTU
1 NTU
100 NTU
1 NTU
161 NTU
Weight of Prey Consumed (g)
Length (mm)
1.0
1.2
1.4
35
45
55
65
75
85
95
105

lower and more variable in clear water in both sets of experiments. The only regression which was not significant was the one based on the one hour 1 NTU set of trials (Table 3).

Consumption of fathead minnows by smaller walleye in four hour experiments was relatively low for all turbidity levels (Fig. 3), however as walleye length increased the weight of prey consumed increased more rapidly in all turbid treatments (7, 14 and 121 NTU), than in the clear water (1 NTU) (Fig. 3). A similar consumption pattern was observed in the one hour trials (Fig. 4). Consumption by larger walleye, as in the four hour experiments, increased in turbid water with increasing length. In both four and one hour experiments, there was an increase in rate of consumption when walleye reached a length of about 70 - 85 mm (Fig. 3). The increase in feeding was not as apparent in one hour experiments, but was evident in three of four comparisons (Fig. 4).

Using the 75 - 85 mm length range, the data was separated into two length groups, fish $\leq$ 75 mm and those $\geq$ 85 mm. Result of one-way analyses of variance indicated that there were no significant differences in mean consumption per walleye (Table 4), either by weight or numbers of prey consumed in any of the turbidity levels for fish $\leq$ 75 mm, except in the most turbid condition (161 NTU) of the one hour trials (Tukey's multiple range-test; $P<.05$). Consumption in these trials was significantly less than in the others involving the smaller walleye. Among walleye $\geq$ 85 mm, consumption by weight and number per

Table 3. Results of regression analyses of relationships of the mean adjusted weight (1 + WT) of fathead minnows consumed by walleye of different mean fork lengths (FL). Each trial was conducted at different turbidities (NTU) in 1986 and 1987. The exponential model $1 + WT = \exp^{(b\,FL - a)}$ was fitted.

Turbidity Level	Exponent	df	F	Prob>F
1986				
1	0.005 FL - 0.125	10	17.838	<.01**
7	0.008 FL - 0.344	10	29.087	<.01**
21	0.008 FL - 0.315	10	32.939	<.01**
121	0.009 FL - 0.382	10	84.131	<.01**
1987				
1	0.00001 FL + 1.078	9	0.023	ns
23	0.004 FL - 0.161	9	10.339	.01**
42	0.004 FL - 0.164	9	17.291	<.01**
100	0.003 FL - 0.123	9	5.195	.05*
161	0.004 FL - 0.187	9	9.143	<.05*

Table 4. ANOVA comparisons of the weight and numbers of fathead minnows consumed by walleye of two size ranges at the various turbidity levels of the four and one hour experiments.

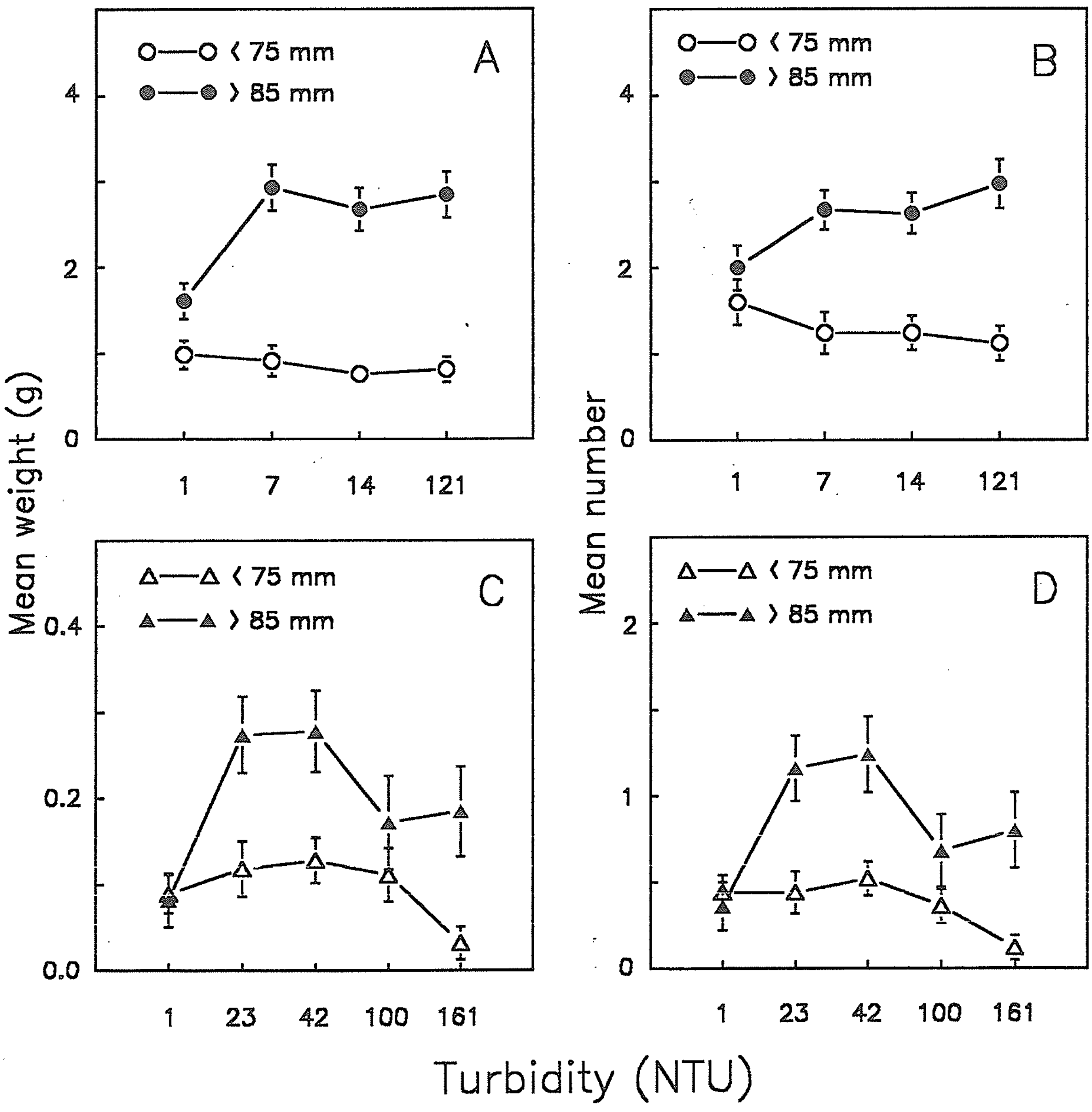
Walleye Size	df	Weight F	Weight Prob>F	Numbers F	Numbers Prob>F
Four Hour					
≤ 75 mm	99	0.368	ns	0.723	ns
≥ 85 mm	119	6.113	<.01**	3.073	<.05*
One Hour					
≤ 75 mm	124	2.565	<.05*	2.500	<.05*
≥ 85 mm	124	3.474	.01**	4.154	<.01**

walleye, in all turbid trials except the one hour 100 and 161 NTU trials was significantly greater than that of the clear water (1 NTU) (Tukey's multiple range-test; $P<.05$).

Consumption by weight and number eaten per walleye among smaller walleye ($\leq$ 75 mm) during four hour experiments was consistently low at all turbidities (Fig. 5A and B). The actual mean weight of fathead minnows consumed varied from 0.20 $\pm$ .03 g ($\pm$ s.e.) (1 NTU) to 0.15 $\pm$ .03 g (14 NTU) per walleye, a difference of only .05 g. The mean number of prey consumed during all turbidity trials was 1.3 $\pm$ .11 minnows per walleye. In contrast, larger walleye ($\geq$ 85 mm), feeding in turbid conditions (7, 14 and 121 NTU), ate a significantly greater weight and number of fathead minnows than they did in clear water (Fig. 5A and B). The mean weight of minnows consumed in 1 NTU trials was 0.32 $\pm$ .04 g, while mean consumption in 7, 14 and 121 NTU trials combined was 0.51 $\pm$ .03 g per walleye, a difference of 0.19 g. The mean number of prey consumed in 1 NTU trials was 2.00 $\pm$ .26, while 2.60 $\pm$ .23, 2.67 $\pm$ .24 and 2.97 $\pm$ .28 minnows per walleye was consumed in 7, 14 and 121 NTU trials respectively.

The weight and number of fathead minnows eaten per fish by the smaller walleye ($\leq$ 75 mm) during one hour trials was low at all turbidity levels, particularly in the most turbid condition (161 NTU), where consumption was one third of that estimated for the remaining turbidities (Fig. 5C and D). The mean weight of minnows consumed during 1, 23, 42 and 100 NTU trials combined was

Figure 5. The mean weight and number of fathead minnows consumed by walleye of two different size ranges in four (A,B) and one hour (C,D) experiments. Standard error bars are shown.



A
B
C
D
○—○ ‹ 75 mm
●—● › 85 mm
△—△ ‹ 75 mm
▲—▲ › 85 mm
Mean weight (g)
Mean number
0
2
4
0.0
0.2
0.4
1
1
2
1
7
14
121
23
42
100
161
Turbidity (NTU)

0.11 ± .01 g, while consumption during 161 NTU trials was 0.03 ± .02 g per walleye. The mean number of prey consumed during the 1, 23, 42 and 100 NTU trials combined was 0.44 ± .05 minnows, while only 0.12 ± .07 minnows were consumed per walleye in the most turbid condition (161 NTU). As in the four hour trials, consumption in weight and numbers of minnows eaten by the larger walleye (≥ 85 mm) was greater within the turbid conditions than in the clear. Consumption was greater at 23 and 42 NTU and intermediate at 100 and 161 NTU. Consumption was lowest at 1 NTU (Fig. 5C and D). The mean weight of minnows eaten in 23 and 42 NTU trials was 0.26 ± .03 g, 0.18 ± .04 g at 100 and 161 NTU and, at 1 NTU 0.08 ± .03 g. The number of minnows eaten per walleye was also greatest in 23 and 42 NTU trials (1.20 ± .14), intermediate at 100 and 161 NTU (0.74 ± .15) and least in clear water (0.36 ± .14).

Analysis of Prey Consumed

Walleye regardless of their length, consistently selected fathead minnows in the smallest size classes (Fig. 6 and 7) in all trials. The mean indices of selection (Vanderploeg and Scavia 1979) for the two smallest size classes of minnows were +0.22 and +0.31 for the four and one hour experiments, respectively (Fig. 6 and 7). Selection for small fathead minnows was especially evident among larger walleye (≥ 85 mm). In contrast, larger walleye showed a strong negative selection for the three largest size classes, -0.49 for the four hour experiments and -0.61 for one hour experiments. Although walleye do consume prey up to 50% of

Figure 6. Size selectivity of walleye consuming fathead minnows in the four hour experiment, at each turbidity level.

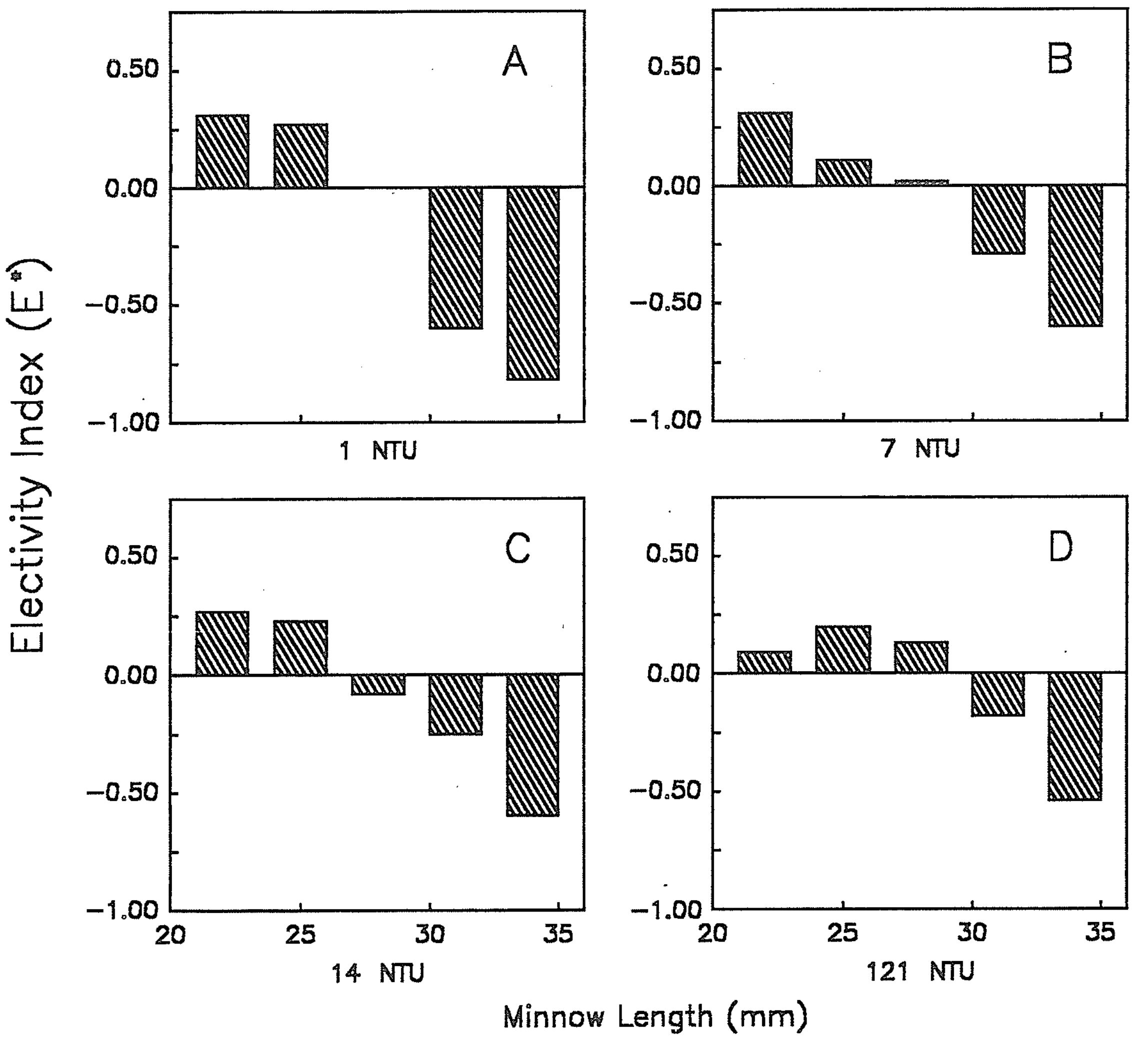
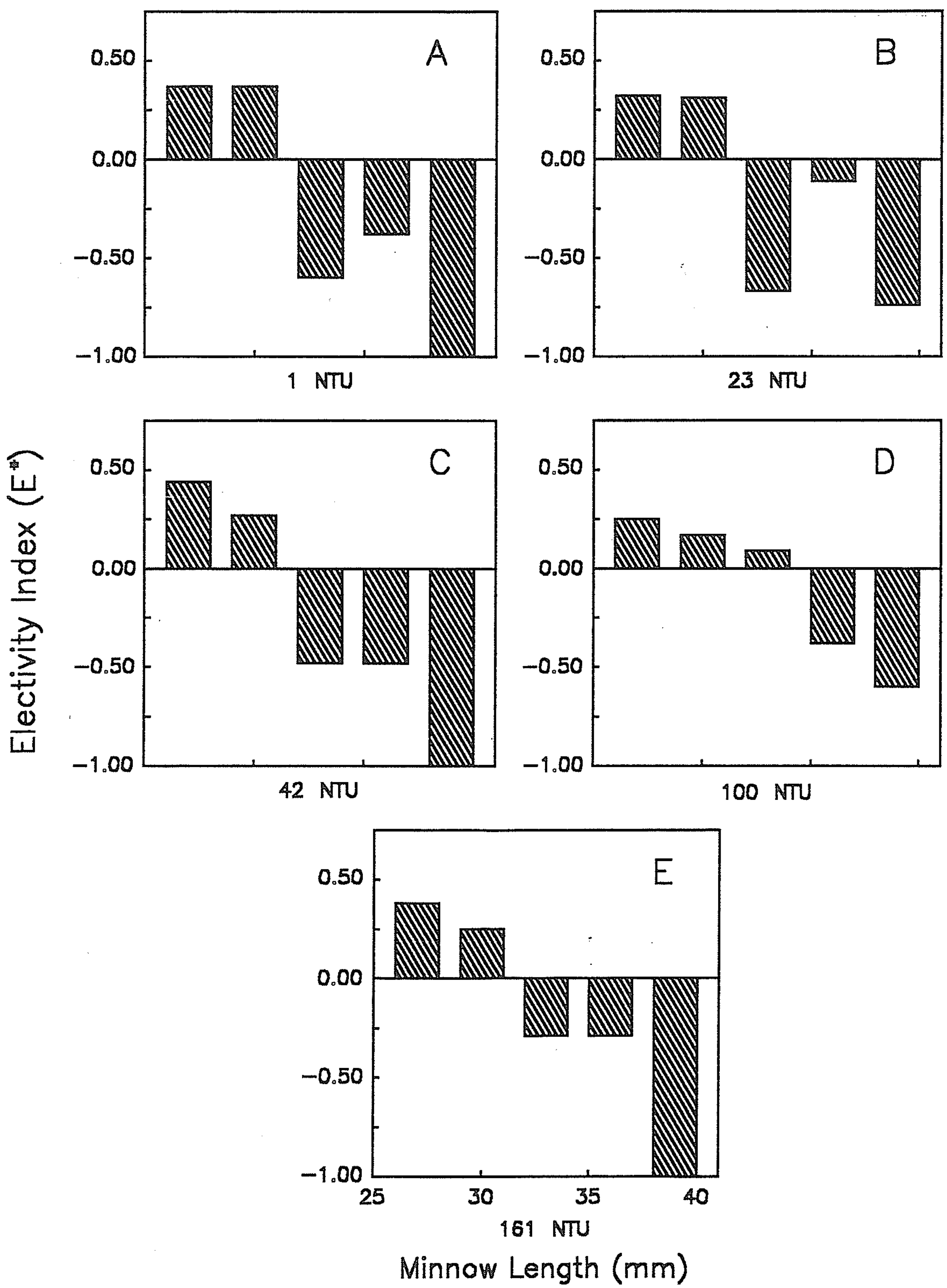

Electivity Index (E*)
0.50
0.00
−0.50
−1.00
A
1 NTU
B
7 NTU
C
14 NTU
D
121 NTU
20
25
30
35
Minnow Length (mm)

Figure 7. Size selectivity of walleye consuming fathead minnows in the one hour experiment, at each turbidity level.


A
B
C
D
E
0.50
0.00
−0.50
−1.00
1 NTU
23 NTU
42 NTU
100 NTU
161 NTU
25
30
35
40
Electivity Index (E*)
Minnow Length (mm)

their body length (Mathias and Li 1982), the size of prey which were taken in our experiments were fish less than 45% of walleye length.

The size of fathead minnows consumed by walleye was independent of turbidity level in both the four and one hour trials, and independent of walleye size during the one hour trial (Table 5). The larger walleye selected larger fathead minnows than the smaller walleye during the one hour trial (Tukey's multiple range-test; $P<.05$). The smallest size class of fathead minnows (21 - 25 mm), was not available in 1987, therefore the mean length of prey consumed was greater, 30 mm in contrast to 26 mm in 1986 (Fig. 8).

Perch Trials

Because there were fewer trials with yellow perch as prey, it was difficult to identify the effects of increasing turbidity on consumption by walleye. Nevertheless, it was possible to make comparisons between consumption of perch and fathead minnow by juvenile walleye (Table 6). Results of a Mann-Whitney test (Daniel 1978) indicated that walleye ate significantly fewer perch than fathead minnows ($T=25.5$, $W_{.05}=43$), at similar turbidity levels. There were however, similar feeding patterns. Consumption of perch in clear water (1 NTU) was lower than in the turbid conditions. Total consumption at 1 NTU was approximately half (0.40 g) that at either the 40 or 139 NTU levels (0.74 and 0.77 g).

Table 5. Results of ANOVA comparing the length of fathead minnows consumed by walleye of two size ranges and turbidity level for the four and one hour experiements.

Comparison	df	F	Prob>F
Four Hour			
Turbidity level	3	2.497	ns
Walleye size	1	23.029	<.01**
Turbidity level * walleye size	3	0.662	ns
One Hour			
Turbidity level	4	2.071	ns
Walleye size	1	2.582	ns
Turbidity level * walleye size	4	0.670	ns

Figure 8. Mean length of fathead minnows consumed by walleye of two size ranges, in the four (A) and one hour (B) experiments. Standard error bars are shown.

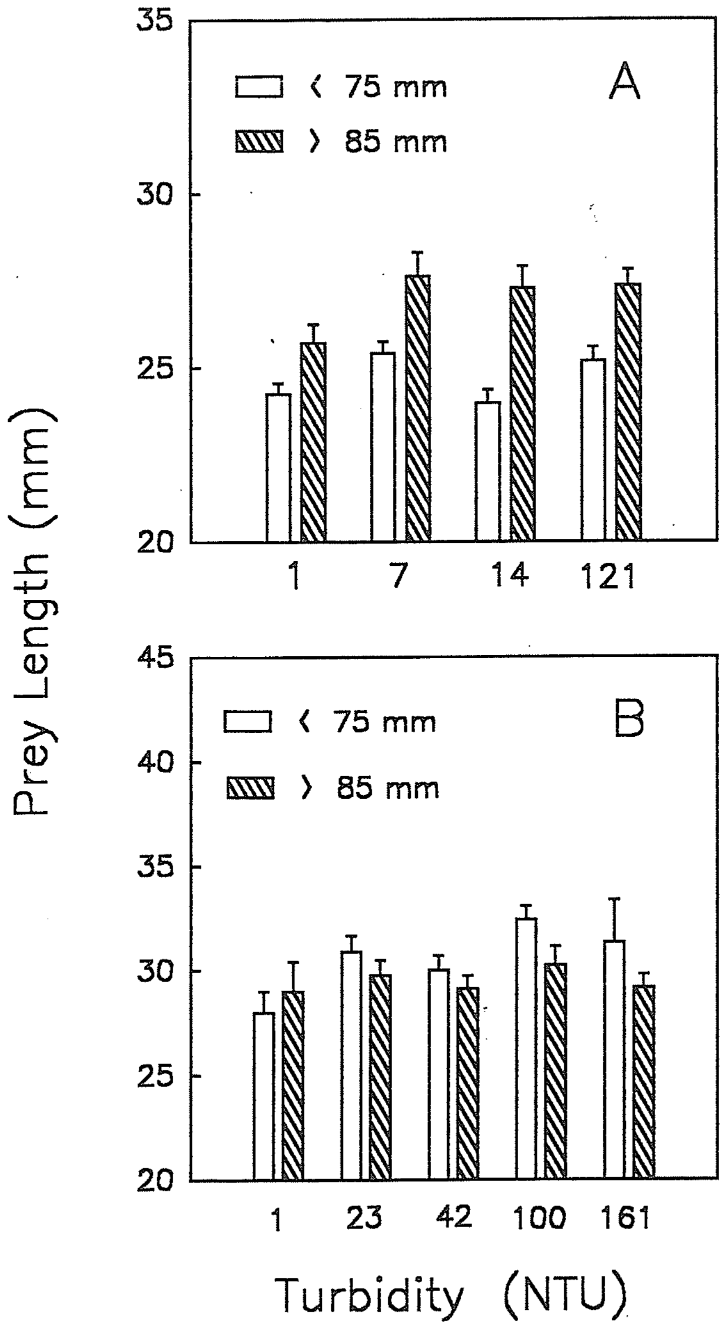

Prey Length (mm)
A
〈 75 mm
〉 85 mm
35
30
25
20
1
7
14
121
B
〈 75 mm
〉 85 mm
45
40
35
30
25
20
1
23
42
100
161
Turbidity (NTU)

Table 6. Comparison of perch and fathead minnow consumption (in grams) by walleye of similar lengths (mm), at various turbidity levels.

Perch				Fathead Minnows			
Turbidity Level (NTU)							
Walleye Length	1	40	139	Walleye Length	1	42	161
63	0.00	0.28	0.20	65	0.42	0.27	0.00
77	0.00	0.17	0.18	77	0.30	1.04	0.00
82	0.41	0.00	0.41	81	0.43	1.44	0.72
86	0.00	0.26	0.00	86	0.28	0.82	0.38

Behaviour

In clear conditions (1 NTU) fathead minnows maintained a tight group near the centre of the aquaria. These groups did not change their position either horizontally or vertically, even though individual fatheads were seen to change their positions within a group. An individual would move slowly through the group until it encountered the group boundary, then it would turn, swim around the edge of the group to a point opposite its initial position, and then begin to move slowly through the group again. In this fashion, group integrity was maintained even though individual fatheads were continually moving.

As turbidity increased, in both sets of experiments, the tightness of the group gradually disintegrated. At intermediate turbidity levels (14, 23 and 42 NTU), the groups began moving horizontally within the aquaria. As well, some minnows were distributed throughout the aquaria. These individuals followed a circular path around the perimeter of the aquaria. The reduced tightness of the central group, its increased horizontal motion and the degree to which individuals moved around the perimeter of the aquaria were a progressive phenomena, which increased as turbidity increased.

Finally, in the most turbid conditions (121 and 161 NTU), the central group was no longer present. Instead, the majority of fatheads could be seen circling the perimeter of the aquaria in a loose school. Certain individuals as well as small groups were seen repeatedly circling the aquaria in the same positions relative to one another. At all turbidity levels, the fathead minnows remained primarily within the upper half of the water column.

Perch behaviour was different from that of fathead minnows. In the clear water (1 NTU), there were no aggregations. Instead perch tended to stay as far as possible from the walleye, remaining relatively motionless and dispersed. As turbidity levels increased, no observable change in perch behaviour occurred.

Unlike yellow perch, walleye behaviour seemed dependant upon turbidity level. Under clear conditions (1 NTU), the walleye spent the majority of their time resting on the bottom of the aquaria. When they were active they seldom left the lower one third of the aquarium. There was no tendency to remain in a tight group or be evenly dispersed.

With increasing turbidity, the walleye began moving about the aquaria, using more of the volume and generally spending less time in contact with the bottom. Finally in the most turbid conditions (121 and 161 NTU), walleye were observed utilizing the entire volume. Behaviour changes, like those of fathead minnows were progressive. Walleye activity increased as turbidity increased. Behaviour changes were similar for all sizes of walleye used in the experiments.

DISCUSSION

Although the weight of fathead minnows consumed increased as walleye length increased, larger walleye ate more in turbid water than they did in clear water. Among walleye $\leq$ 75 mm in length, in both four and one hour experiments, there was no significant difference in the weight or numbers of fathead minnows consumed in clear water and in moderately turbid conditions, indicating that the smaller group of walleye fed on minnows at a constant rate in both clear and moderately turbid water. In the one hour 161 NTU trial, feeding was greatly reduced.

Larger walleye ($\geq$ 85 mm) in both four and one hour experiments were more efficient at capturing prey under turbid conditions than in clear water, as occurs in natural situations (Swenson 1977; Ryder 1977). There was no evidence that differences in prey consumption was related to changes in prey size selection. Similarly, some planktivorous fish do not change the size of prey they select as turbidity increases (Gardner 1981; Brietburg 1984). However, unlike the larger juvenile walleye, consumption by these species is reduced in turbid water. Therefore, increased consumption by walleye and decreased consumption by these planktivores is related to the number of prey consumed: larger walleye consumed more prey of similar sizes in turbid than they did in clear water. Different stomach capacities could account for variations in the weight consumed by small and large walleye, but could not account for differences in the weight or number of prey eaten by walleye in the large group feeding in clear as opposed to moderately turbid conditions (less than 161 NTU).

Walleye are size selective predators, consuming the smallest prey available (Mathias and Li 1982; Parsons 1971; Knight et al 1984). Selectivity is density dependent. As prey density declines, the range of prey sizes consumed increases (Knight et al 1984; Fox 1986). In this study where prey density was high, walleye were strongly size selective, with 75% of prey consumed in the smallest size classes. The fathead minnows eaten were approximately 30% of the walleye length. Parsons (1971) found that similar sized walleye (76 to 99 mm) took prey which were 36% of their own length. The hypothesis that walleye select small prey when density is high (Parsons 1971), was supported by results from my experiments.

The larger group of walleye fed at the same rate in high turbidity (121 NTU) as in moderately turbid water (7 and 14 NTU), during the four hour experiments. In contrast, in one hour experiments, feeding at 100 and 161 NTU was less than at intermediate turbidities (23 and 42 NTU). The longer experimental period could have provided more encounter opportunities or a longer time to adapt to prevailing light conditions. Walleye frequently feed for periods longer than one hour in nature, therefore they would be expected to adapt to altering illumination caused by changing photoperiod or high turbidity. Eventually, some critically high turbidity level would cause feeding to be inhibited.

Ryder (1977) suggested that the rate of change in illumination at dawn and dusk are important in initiating the feeding response in walleye. The high rate of feeding among walleye in the larger length group in low turbidity trials (7 and 14 NTU) may indicate otherwise. Either a behaviourial response to turbidity or a change in visual acuity of either the predator or prey are possible factors initiating feeding in this study.

A change in the feeding rate of juvenile walleye seemed to occur when the fish were between 70 and 85 mm. The most significant feature of this change was their enhanced ability to capture and ingest fathead minnows and perch in turbid conditions. Juvenile walleye grow rapidly in ponds in summer and the time taken to grow from 60 - 80 mm may be about two weeks (estimated from Li and Ayles 1981). Consequently, the ability to feed efficiently on large prey in dim light conditions may develop quickly. The potential to capture large prey is probably important in maintaining a high growth rate (Mittelbach 1983).

Juvenile walleye move from shallow weedy areas to deeper locations offshore during summer (Raney and Lachner 1942). At this time their diet changes from small organisms such as zooplankton to include larger invertebrates and finally small fish (Mathias and Li 1982). The change to piscivory begins when walleye reach a length of about 60 mm and is the dominant feeding mode by a length of 100 mm (Smith and Pycha 1960). Their ability to consume larger food items is a natural consequence of growth; however increased feeding efficiency in turbidity induced low illumination indicates a change in behaviour which may be related only indirectly to increasing size.

Feeding efficiency of a predator may be increased either by changes in its own behaviour and/or by changes in the behaviour of its prey, which make them more vulnerable to attack (Hoyle and Keast 1978). Sullivan and Atchison (1978) found that the degree of schooling maintained by fathead minnows was dependant on predator activity. When largemouth bass pursued and captured minnows, the school increased in tightness. Moody et al (1983) also found that predator activity increased the overall swimming activity of fathead minnow schools. My data indicated that these tight schools became looser in turbid water and that walleye activity increased as turbidity increased. The combination of increased walleye activity and looser aggregations of fathead minnows may have contributed to more frequent encounters between predator and prey and a higher capture rate.

Yellow perch are a primary prey species of juvenile and adult walleye (Doan 1942; Smith and Pycha 1960; Forney 1974). In my experiments walleye were much less successful in capturing perch than fathead minnows. In contrast to fathead minnow behaviour, perch activity did not increase in turbid water, nor did they maintain any aggregations. Nursall (1973) found that perch spent the majority of their time stationary and tended to disperse in response to pursuit, thereby reducing encounters. These differences in prey behaviour between fathead minnows and perch may be a consequence of their different morphologies (Sullivan and Atchison 1976). Anatomically defenceless prey (ie. soft-rayed) rely on social interactions as their anti-predator defense (Wahl and

Stein 1988), while prey with spiny-rayed fins rely on individual defenses (Moody et al 1984). As walleye are visually oriented predators who rely primarily on motion to detect prey (Mathias and Li 1982; Rottiers and Lemm 1985), it is not surprising that they were less able to capture stationary prey (perch) as opposed to moving prey (fathead minnows).

The low capture rate of perch observed in this study may however, not be truly representative of walleye predation on perch in nature. In most North American lakes containing walleye, turbidity levels tend to be lower than the maximum levels used here (121 and 161 NTU). As a result walleye activity is restricted primarily to dawn and dusk periods (Ryder 1977), which coincides with peak perch activity levels (Alabaster and Stott 1978; Helfman 1979).

During twilight periods, when illumination levels decline rapidly, perch experience declining visual acuity, whereas walleye acuity approaches the optimum. Ali et al (1977) suggested that increased perch activity at dawn and dusk together with this reversal in visual acuity's is responsible for successful walleye predation on perch. The experiments conducted in this study were done at constant light levels and at midday, therefore it may be that the conditions required to create the "symbiotic" predator-prey relationship described by Ali et al (1977) were not present, and therefore did not allow walleye to capture perch with the efficiency they would have demonstrated in nature. Another possibility may be that the one hour duration of the feeding trials was insufficient to allow the consumption of perch to proceed normally. It takes northern pike longer to capture spiny-rayed prey than soft-rayed prey (Moody et al 1983). As shown, the rate of fathead minnow consumption also depends on the time available for feeding.

Turbidity is an optical property of a liquid which results in light being scattered and absorbed rather than transmitted in straight lines (Kirk 1983). A major ecological impact of high turbidity is that it reduces the depth of light penetration, thus reducing the visibility of pelagic prey (Bruton 1985).

The majority of freshwater fish are negatively influenced by high turbidity: Most salmonids are intolerant of increased turbidity, even for short exposures (Berg and Northcote 1985; Redding et al 1987), while long exposure at relatively low levels (25 NTU), causes reduced growth (Sigler et al 1984). For juvenile planktivorous fish such as bluegills, increased turbidity does not influence the size of prey consumed even though it significantly reduces the distance at which prey are detected, and subsequently, the number of prey consumed (Vinyard and O'Brien 1976; Gardner 1981).

The influence of turbidity on the feeding of larval fish has received more attention than its influence on juveniles or adults. Generally, for freshwater larvae such as lake herring, shad, freshwater drum and striped bass, turbidity results in an increased concentration of larvae in surface waters (Swenson and Matson 1976; Matthews 1984) and a marked reduction in their ability to capture prey (Matthews 1984; Breitburg 1988). These larvae are visual feeders with small search areas, therefore decreased feeding efficiency in high turbidity may be the result of a reduced visual field (Breitburg 1988).

In contrast, the distribution of some juvenile estuarine and marine inshore fishes are positively correlated with elevated turbidity (Blaber and Blaber 1980; Dadswell et al 1983). Shallow estuarine waters are often turbid but usually produce abundant zooplankton (Dadswell et al 1983). The availability of appropriate prey and reduced predation risk provided by turbid waters often result in these estuaries being important nursery areas for a wide variety of fish. There is also some evidence that high turbidity levels in these waters may enhance the feeding abilities of some larval fish. Turbidity may increase larval feeding by improving the perception of transparent prey in two ways: 1) by increasing the contrast between the prey and the background and 2) by illuminating the prey from all possible directions by the scattered light (Boehlert and Morgan 1985).

Although the feeding efficiency of most piscivorous North American fish is diminished by turbidity (Doan 1942; Gardner 1981; Craig and Babaluk 1989), juvenile and adult walleye are efficient predators at low light intensities caused by turbid conditions (Ryder 1977; Swenson 1977). Walleye possess two retinal adaptations for scotopic vision which develop during their first summer; a tapetum lucidum and bundled photoreceptor forming macroreceptors (Braekevelt et al 1989). Tapetal material begins to appear at a length of 30 - 35 mm (Braekevelt et al 1989), which is coincident with a change from positive to negative phototaxis (Bulkowski and Meade 1983). According to their behaviour in these feeding trials the smallest walleye used were probably negatively phototactic with a developing tapetum.

Tapetal development is a gradual process, and the visual advantages incurred by it should also proceed in a gradual manner. However, walleye feeding efficiency in turbid waters increased significantly in a very short time, between a length of 70 - 85 mm. Evidently these larger walleye have some additional advantage in detecting and capturing prey in dimly illuminated conditions. Odour detection by walleye (Rottiers and Lemm 1983) may be important in locating prey, however the formation of functional macroreceptors in the larger walleye probably was most important in enhancing feeding efficiency within turbid conditions. Bundle formation begins at about 60 - 70 mm of length and is essentially complete by 90 mm (Braekevelt et al 1989).

The development of a functional tapetum lucidum and the subsequent formation of macroreceptors in juvenile walleye during their first summer of life is consistent with the differences in feeding and behaviour which occurred between clear and turbid conditions. The ability to ingest large food organisms such as forage fish early in life (Ward and McCulloch in press), provides the opportunity to maximize energy intake and growth rates (Kerr 1971; Mittelbach 1983). However, to be able to feed efficiently in dimly lit conditions is an additional advantage, one which allows walleye to occupy a niche in which competition from other predators may be reduced (Ryder 1977).

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APPENDIX I

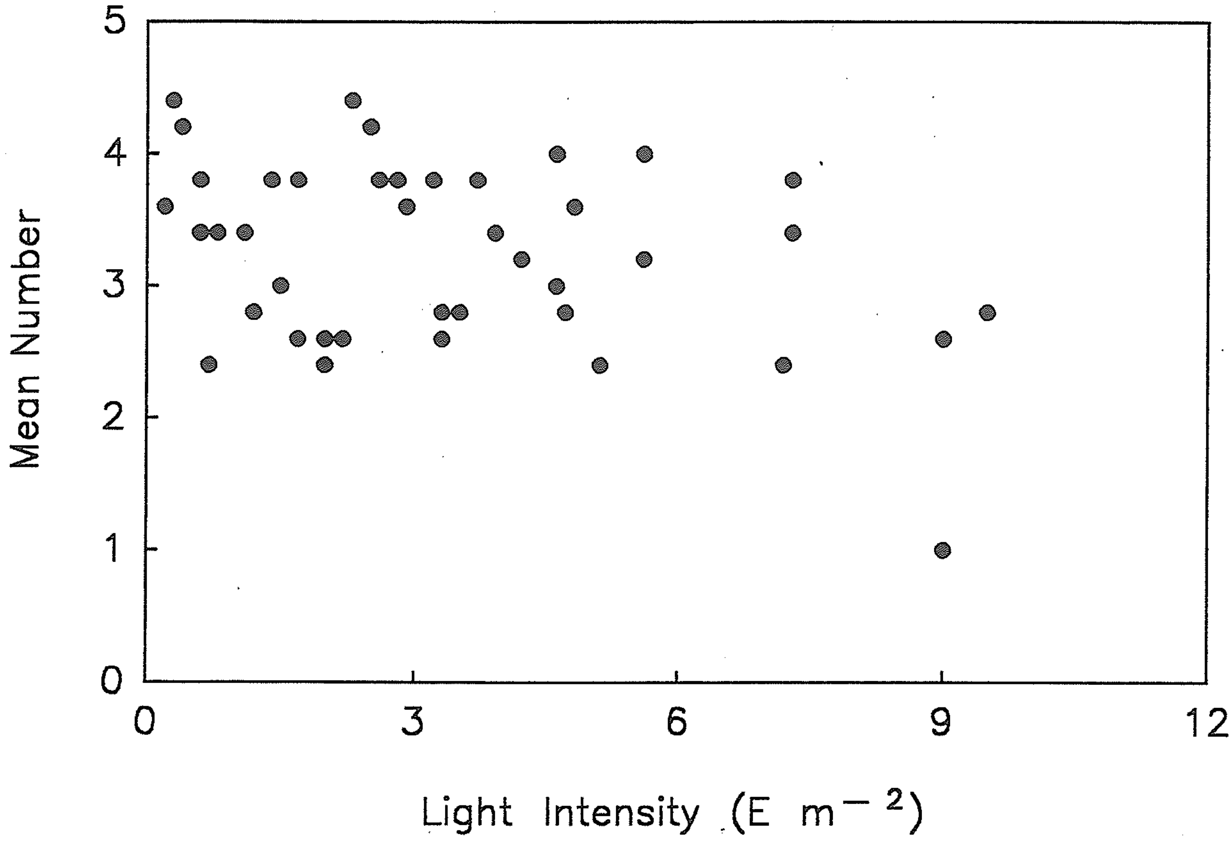
Preliminary experiments to determine the light intensity which provided maximal walleye consumption.

Light intensity experiments were conducted during the winter of 1986. Walleye were seined from the Bishop Grandin ponds in September and transferred to 170 L fibreglass tanks. Walleye were transferred to experimental aquaria 24 hours prior to feeding experiments. No food was provided during this time. Water temperature was maintained at 17° C. Five walleye within a 5 mm size range were placed into each 130 L glass aquarium. Walleye sizes ranged from 96 to 115 mm. Two length ranges of fathead minnows were used as prey, 26 - 30 and 31 - 35 mm (20 per size class). The duration of each trial was 2.5 hours.

Illumination for each aquarium was provided by a single 61 cm fluorescent Vita-Lite. Intensity was varied by changing the height of the lamps above the aquaria. Intensity was measured with a LiCor model Li-185B light meter with a Li-190SB quantum sensor. Intensities tested ranged from 0.2 to 9.5 E m^{-2}. Clear water was used for all trials. The total number of prey consumed by the 5 walleye was recorded.

Results of one-way analyses of variance indicated that there were no significant differences in the mean number of prey consumed per trial between walleye in the ranges 96 - 105 and 106 - 115 mm ($P>.82$, $df=41$, $F=0.049$). Therefore all data were combined in the subsequent analysis. Analyses of variance for the mean number of prey consumed per trial at the various light intensities, indicated that the number of prey consumed was independent of the light intensities tested ($P>.23$, $df=41$, $F=1.586$) (Fig. 1).

Figure 1. Consumption of fathead minnows per walleye in clear water at various light intensities.



5
4
3
2
1
0
Mean Number
0
3
6
9
12
Light Intensity (E m⁻²)

Appendix II

Characteristics of the sediments used to create turbidity and analyses of the observed changes in turbidity levels during feeding trials.

Table 1. The specific weight of sediment required to produce the experimental turbidity levels (NTU) during the four and one hour feeding trials.

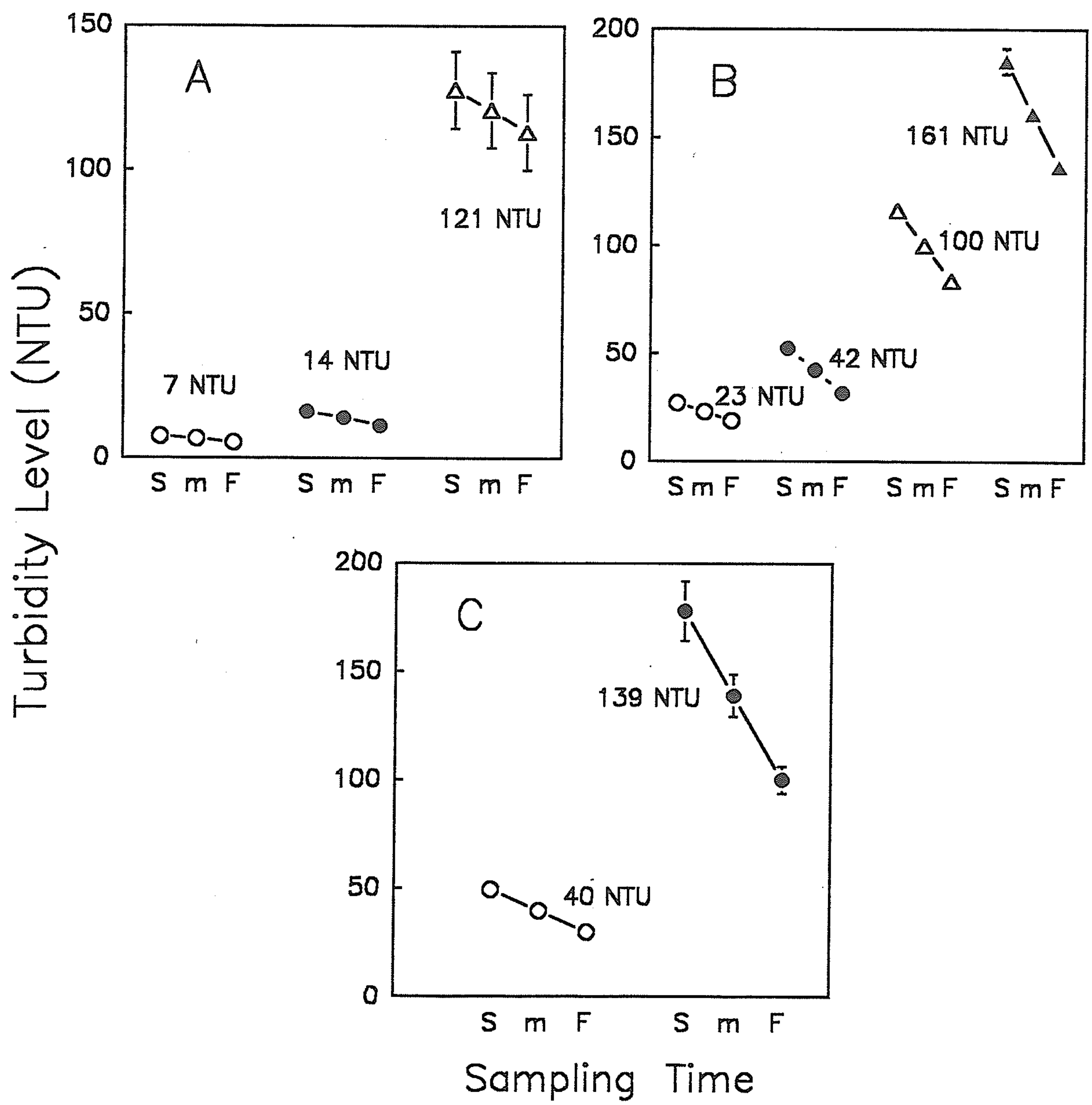
Four Hour Trial		One Hour Trial	
Fathead Minnow Trials		Fathead Minnow Trials	
NTU	Weight (g)	NTU	Weight (g)
1	0.0	1	0.0
7	2.5	23	55.0
14	10.0	42	115.0
121	220.0	100	250.0
		161	390.0
		Perch Trials	
		NTU	Weight (g)
		1	0.0
		40	115.0
		139	390.0

The observed turbidities for all treatment levels of the four hour experiments, did not decline significantly during the feeding trials (ANOVA, $P>.05$) (Fig. 1A). The mean turbidity values for all treatment levels were within approximately one standard error of the target turbidity value : at 5 NTU the mean was 6.8 ± 1.5 (± s.e.), at 15 NTU the mean turbidity was 14.4 ± 2.2 and for the 115 NTU level the observed mean was 120.7 ± 13.1.

Turbidity values during the one hour trials declined significantly during both the fathead minnow and perch trials (ANOVA, $P<.0000$) (Fig. 1B and C), however mean turbidity levels used for each of the fathead minnow and perch trials were similar to the target levels. For the fathead minnow trials the mean for the 25 NTU target was 23.2 ± 0.8 (± s.e.), for the 40 NTU target 42.3 ± 1.3, for the 100 NTU target 99.9 ± 3.6 and for the 150 NTU target the observed mean was 160.8 ± 5.2. For the perch trials, the means were 39.6 ± 3.0 for the 40 NTU target and 139.0 ± 9.7 for the 150 NTU target value. Although turbidity declined during the trials, the main portion of the trial experienced turbidity levels close to target values. Actual changes in turbidity during trials may have been overestimated because the samples were collected from the surface, where settling was first apparent.

Apparently different settling rates between four and one hour experiments may have been caused by differences in the physical properties of the sediments used in the two sets of experiments. Sediments used in one hour experiments had 8% less clay, 7% more silt and 1% more sand (Table 2), than did the sediments

Figure 1. The changes in turbidity for each treatment level during the four (A) and one hour (B) fathead minnow trials and the one hour perch trials (C). Turbidity was determined at the start (S) and finish (F) of each trial, as well as the mean (m) from each paired observation. The solid lines connect the means for each sampling time. Standard error bars are shown.



A
7 NTU
14 NTU
121 NTU
B
23 NTU
42 NTU
100 NTU
161 NTU
C
40 NTU
139 NTU
Turbidity Level (NTU)
S m F
Sampling Time

Table 2. Particle size analyses and textural designation of the sediments used to create turbidity (Manitoba Provincial Soil Testing Laboratory).

	Four Hour Trial	One Hour Trial
	0 % sand	1 % sand
	39 % silt	46 % silt
	61 % clay	53 % clay
Textural designation :	clay	silty clay

used during the four hour experiments. According to Stoke's Law, which describes the settling velocity of a particle, when all other parameters are held constant (ie. density of the particle, density and viscosity of the fluid), the main factor determining settling velocity is the square of the diameter of the particle (Selley 1982). Clay particles are the smallest of all sediments ($\leq$.002 mm), while silt is of moderate size (.05 - .002 mm) and sand consists of the largest particles (2.0 - .05 mm) (Univ. of Manitoba) Therefore, sand settles out first, then silt, while clay particles remain in suspension longest. Medium sized sand particles settle out of suspension almost 1000 times faster than medium sized silt, while silt settles out 1400 times faster than medium sized clay particles. As a result, the increase in silt concentration of 7% produced an 18% increase in the settling velocity of the sediments used in the one hour experiment over that of the four hour experiment. The 8% difference in clay concentration produced a difference in velocity at only the third decimal place, and therefore was not considered to contribute to differences in settling rate between the two sets of experiments. The 1% difference in sand was also not included in the velocity calculations. If we apply the 18% increase to the rate of settling for the one hour experiment, to correct for the differences in sediments, the resultant increase is still insufficient to overcome the effects of variance. Within the one hour experiment, an increase in settling rate of over 200% would be needed to exceed the influence of the variation.

The patterns in the variation of the sum of squares between the four and one hour experiments may give some clue as to the cause of the observed change in settling (Table 3). The "within group" variation in the four hour experiment exceeds the "between group" variation so that the F-ratios produced were not significant. The reverse is true in the one hour experiments. The variation between groups exceeds the variation within groups, producing significant F-ratios (Table 3). The between groups variation is a measure of the deviations of the group means from the overall mean (ie. NTU level at start versus NTU level at finish). The within groups sum of square is a measure of the variation of the data from each group about the mean for that group (Huntsberger and Billingsley 1981), this is also known as the error sum of squares, or the experimental error (Steel and Torrie 1980).

In the four hour trials the variation produced by the experimental error is large enough to mask any changes in turbidity over time. The high experimental error value applying to four hour trials, and the small experimental error associated with one hour trials may be the result of using different methods to measure turbidity between trials. Turbidity during four hour experiments was determined indirectly by measuring percent transmittance of a sample and then using a calibrated formazin curve to calculate turbidity (see Methods). While turbidity in one hour experiments was measured directly with a standardized Hach Turbidimeter. It may be that the indirect method was not as sensitive a measure of turbidity as the direct method, and was therefore unable to detect changes in turbidity similar to those detected using direct measurement.

Table 3. The ANOVA variation partitioned into their sources for the changes in turbidity levels during the four and one hour feeding experiments.

Source of Variation	Sum of Squares	df	F	Prob>F
Four Hour				
7 NTU				
Between groups	24.20	1	1.016	ns
Within groups	428.80	18		
14 NTU				
Between groups	120.05	1	2.252	ns
Within groups	959.70	18		
121 NTU				
Between groups	968.00	1	0.611	ns
Within groups	25330.00	16		
One Hour				
23 NTU				
Between groups	384.73	1	37.123	<.0000
Within groups	207.27	20		
42 NTU				
Between groups	3321.12	1	68.108	<.0000
Within groups	1462.88	30		
100 NTU				
Between groups	5793.14	1	28.208	<.0000
Within groups	4107.45	20		
161 NTU				
Between groups	25696.13	1	49.370	<.0000
Within groups	14573.33	28		